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SOME ASPECTS OF THE REPRODUCTIVE BIOLOGY OF TUNDRA PEREGRINE FALCONS

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Some Aspects of the Reproductive Biology of Tundra Peregrine Falcons submitted by Gordon S. Court in partial fulfilment of the requirements for the degree of Master of Science.

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Date Dec 20/95

Abstract

A dense, productive population of tundra peregrine falcons (*Falco peregrinus tundrius*) was studied over five years on a 450 km^2 study area located along the northwest coast of Hudson Bay. The number of territorial pairs varied over the years from 17 to 26. A mean internest distance of 3.3 km represents a nesting density for the population that is among the highest on record for the species.

Morphometric and plumage characteristics of adults in the study population suggest clinal variation between populations of *F.p. tundrius* from further north and *F.p. anatum* to the south.

Pairs of falcons nested on cliffs of less than 30 m in height. Most nest cliffs had a southern exposure, but pairs nesting at north-facing sites did not suffer lower reproductive success.

Falcons arrived on the breeding grounds before most migratory prey species (mid-May) and left the area before October. Mean date of clutch initiation over three years was June 7, but this date was significantly delayed in one year of poor spring weather (relatively lower temperatures and high precipitation).

Nineteen species of birds and three species of mammals were used as prey by the study population; however, in most years the bulk of the diet consisted of six species of birds and one mammal. A dramatic increase in the number of territorial pairs of falcons, coupled with changes in various measures of reproductive performance, in a year of high microtine rodent abundance suggests that the use of mammals by falcons can be significant in some years.

In most years, successful pairs produced about 35 young, or about two young per occupied territory per year. The sex ratio of nestlings was not significantly different from equality. Despite changes in reproductive performance noted in a year of high prey abundance, there were no significant differences among years in clutch size, brood size, or number of young fledged per territorial pair.

Mean clutch size (3.62 ± 0.59) was comparable to that for peregrine populations from both arctic and more temperate latitudes. Mean brood size (2.79 ± 0.78) was most similar to that reported for populations in the central Canadian arctic and Greenland, but was also similar to, and even greater than, that from other populations at more temperate latitudes. Earlier suggestions by some authors that peregrines lay fewer eggs in the arctic part of their

range was not supported by data from the study population.

Twenty-nine separate nesting territories were used in the five years of the study. Territories were held by adult peregrines in all cases. The oldest female on territory was at least five years old, the youngest was three. The oldest male was at least five years old, the youngest was two. Annual turnover of adults was estimated to be 25% (males 16%, females 30%). Maximum annual mortality was estimated to be 23% (males 16%, females 27%). Peregrines showed a high degree of fidelity to previously used nest sites; movement between territories was recorded only once.

Peregrines competed intensively for nesting territories early in the spring, but competition dropped off as breeding commenced. For the most part, territorial interactions were sex specific. Males were more territorial than females in terms of interaction rate and in the distance to which they would pursue intruders. Observations of territorial interactions, and evidence of the existence of non-breeding, non-territorial adults, suggested that the breeding density of the falcon population was limited by a shortage of nesting habitat created through territoriality. Apparent change in territory size in a year of high prey abundance supports the hypothesis that expressions of territoriality and territory size in birds are often mediated by food supply.

Total and partial nesting failures were recorded in the study population. Ten percent of all territorial pairs failed to lay. Failure of territorial pairs to lay accounted for 41% of all failures. Losses of entire clutches accounted for 48% of failures, while losses of complete broods made up only 11% of failures. Seventy-four percent of all territorial pairs were successful in fledging young. Peregrines managed a full hatch with 44% of all clutches. At successful nests, hatching success (% of all eggs to hatch) was 87% and nestling mortality (% of all young hatched that do not fledge) was 14%.

Female peregrines on nesting territories for the first time appeared to lay later, had significantly smaller clutches, but did not show a difference in the number of young fledged when compared to females with greater experience on nesting territories. Falcon pairs nesting in close proximity or in areas of higher intraspecific nesting density did not show lower clutch size, hatch success, or number of young fledged, suggesting that the effect of intraspecific strife on reproductive success was negligible.

Asynchronous hatching was commonly observed in the study population. An investigation of the effects of hatch asynchrony on reproductive success, conducted over two years, showed that 7% of all chicks produced died as a result of brood reduction associated with asynchronous hatching. Most chicks that died were the last-hatched in asynchronous broods of four; about half of the last-hatched members of these broods died within their first five days of life. Mortality occurred through starvation. Surviving last-hatched members of asynchronous broods of four did not show significantly different growth rates compared to other chicks from different hatch positions. Mortality did not appear related to the food available to the parents, but to the inability of last-hatched young to compete with older siblings during feedings. Differential survival of last-hatched chicks in asynchronous broods was linked to differences in the attentiveness of adult females (feeding rate and time spent brooding), prey size, and possibly, nest ledge size. Asynchrony of hatching and brood reduction observed in the study population did not suggest an adaptation in keeping with the brood reduction hypothesis.

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Field studies of the peregrine often involve a considerable number of logistical difficulties and in arctic regions such difficulties are often compounded. Fortunately, I received help from several co-workers and a number of interested volunteers. I gratefully acknowledge the assistance of all employees of the Department of Renewable Resources at Rankin Inlet, particularly the field assistance of M. Bradley, R. Mulders, Dr. C. Gates, and F. Ayaruak. G. Erickson and H. Armbruster capably assisted with the trapping of adult falcons in 1983 and 1985; their help is gratefully acknowledged. Special thanks to H. Armbruster for showing me a few 'cunning trapping tricks' that I would not have imagined.

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I. Introduction

The peregrine falcon (*Falco peregrinus* Tunstall) is probably the most studied of all raptor species, particularly in terms of its reproductive biology. Even before the widespread breeding failures of this species resulting from post-1947 organochlorine pesticide pollution, a variety of observers interested in natural history, egg collecting, game keeping, and falconry, had taken notes on its breeding biology (Hickey 1942, Ratcliffe 1980). Collections of data on annual territory occupancy and breeding success of local peregrine populations often included the contributions of a large number of observers and encompassed many years of observation (Hickey 1942, Bond 1946, Cade 1960, Herbert and Herbert 1965, Ratcliffe 1962, 1969, 1980). Extremely detailed studies of behavior during nesting and post-nesting phases of the breeding cycle have also been undertaken by observers such as Nelson (1970) and Sherrod (1981). Massive population declines in peregrine populations in North America and parts of Europe focused much attention on this species with resulting studies of pesticide accumulation and altered reproductive success dominating the pertinent literature in the late 1960's and 1970's (Enderson and Berger 1968, Hickey 1969, Lincer et al. 1970, Ratcliffe 1970, Cade and Fyfe 1970, Cade et al. 1971, Fyfe et al. 1976). Such studies often contributed indirectly to an improved understanding of the reproductive biology of the peregrine falcon. In the early 1970's efforts were initiated to propagate the peregrine in captivity and such an undertaking required an even greater understanding of the breeding biology of this species. This demand eventually led to a considerable volume of information on the subject (Nelson and Campbell 1973, Cade and Fyfe 1977, Wrege and Cade 1977).

The references cited above represent but a small fraction of the enormous volume of literature that pertains directly to *Falco peregrinus*. The greater portion of this information consists of natural history descriptions of different populations, surveys of population size and productivity, documentation of pesticide accumulation and reproductive failure, and, in more recent years, information pertaining to captive propagation and reintroduction. Although populations have been studied at many locations throughout the world, most of the detailed information comes from investigations of populations in more developed regions where the species is relatively more accessible, or where it has been more likely to have suffered from man-made pollutants. Also, the majority of studies have focused on that part of the breeding season when falcons are easiest to find and observe, namely during incubation and nestling periods. Thus, although the species has been well studied, it remains possible that there is more to be learned from detailed investigations of poorly known populations, or from research conducted during the non-breeding or pre-laying periods.

Another feature that is obvious from even the most cursory review of literature pertaining to this species is that, although well studied, there are aspects of peregrine falcon biology of which surprisingly little is known. Perhaps the best example is the lack of detailed information on population dynamics including: adult and juvenile mortality, recruitment, movement of adult birds between nesting territories, and dispersal of young. Only relatively recently have some of these parameters been measured through mark and recapture of a single population (Mearns and Newton 1984). The lack of this type of information might seem somewhat surprising, particularly in view of level of documentation concerned with pesticide-induced population declines, but can be understood in terms of the considerable logistical difficulties of working with this species and the 'hands off' policies likely to have been prevalent when populations were decreasing. Also, and apparently for the same reasons, it appears that wild peregrines have rarely been considered suitable as vehicles for intensive research on more general questions pertaining to raptor biology, or to ornithology in general. An example of such a question, one which is often the subject of much speculation among students of the peregrine and other raptor species, is whether or not populations are limited, and if so, what role does food supply, nest site availability, and territoriality play in this limitation.

Between 1982 and 1985, I had the opportunity to study a poorly known population of peregrine falcons (*Falco peregrinus tundrius*) nesting along the northwest coast of Hudson Bay. Much of the work involved collection of prey species, addled eggs, and blood plasma samples of adult peregrine falcons as part of an organochlorine pollutant study by the Government of the N.W.T. During the course of this work it was also possible to conduct a detailed investigation regarding certain aspects of the reproductive biology of these birds. In the study, I was limited to five years of data, and, like many previous studies, I was unable or unwilling to experiment with the population to any great degree. As the population had not been described previously, the natural history of the population was documented; however, the primary objective of the research was aimed at describing the more unique aspects of the reproductive biology of the population rather than concentrating on another survey of population size and reproductive performance. Additionally, I attempted to concentrate research efforts on those aspects of peregrine falcon biology that are poorly known or those not previously reported. In the following chapters I discuss some of these findings in terms of their relevance to more general questions pertaining to population ecology of raptorial birds, in particular, the role of food supply and territoriality in limiting population density, and factors that influence the productivity of raptor populations.

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II. Natural History of the Study Population

Introduction

The work of Cade (1960) in Alaska is perhaps the most detailed description of the breeding biology of arctic peregrine falcons (*F. p. tundrius* White). This is not to say that other northern populations have not been studied, however the majority of investigations consist mainly of surveys of population size and breeding success (Cade and Fyfe 1970, Fyfe et al. 1976, Calef and Heard 1979, Kuyt 1980). More detailed studies have, for reasons of logistical difficulty, included only portions of the breeding season and consist mainly of field or blind observations during the late incubation and nestling phases (Burnham 1975, Harris and Clement 1975, Alliston and Patterson 1978, Burnham and Mattox 1984).

In view of the volume of published information, the addition of another natural history description of a peregrine falcon population would seem to require justification: 1) the Rankin Inlet population reported on herein has never been described, 2) its size and density were not fully appreciated until 1981, 3) this population is unique in that it is located on a relatively circumscribed patch of nesting habitat and is comprised of a very high density of pairs breeding in an environment as severe as any in the enormous range of this species, 4) the nesting density is unusually high for arctic populations and, somewhat acharacteristically, is attained apparently without any particular feeding specialization, and 5) observations also suggest that the prey base of this population, both in terms of species composition and chronology of use, is unlike other arctic peregrine populations yet studied.

At Rankin Inlet it was possible to study this falcon over most of the breeding season, from arrival of adults on the breeding grounds to the fledging of young. The size and density of this population and the relative logistical ease of working in this area at certain times of the year made it possible to accurately describe many aspects of the natural history of this population, including: subspecies designation, nesting requirements, nesting density, chronology of the breeding effort, chronology of prey use, and productivity. This introduction will provide an appropriate background to subsequent chapters of this thesis.

Study Area

Research was conducted on a study area near the community of Rankin Inlet, N.W.T., on the western coast of Hudson Bay (62°49'N, 92°05'W). The summers in this region are typically short and cool with July mean high and low temperatures of 13.1°C and 4.5°C, respectively. Spring thaw begins in mid-May, reaching a peak by the first week of June. Ice cover on smaller lakes and ponds begins to melt at this time, however landfast sea ice persists until the second week of July. Average annual precipitation figures include 118.0 cm of snow and 16.0 cm of rain; giving a liquid total of 27.8 cm.

The study area encompassed approximately 450 km^2. The landscape is typical of the barrenlands of Canada with low rolling hills separating a large number of tundra ponds and lakes. Geologically the area is dominated by altered intermediate volcanic rock and derived amphibole schist and gneiss (Wright 1967). Rock outcrops of up to 53 m in height are a prominent feature of the landscape and are particularly well developed as offshore islands in Rankin Inlet. Outcrops with rock faces large enough to be of significance to cliff-nesting raptors occur as much as six km inland and on islands as far out to sea as four km.

Ridge tops, upland areas, and well drained slopes are covered with a formation of lichens, moss, and low shrubs. Labrador tea (*Ledum palustre*), mountain cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are the dominant vascular plants. Bell heather (*Cassiope tetragona*) occurs in moist low lying areas and rock crevices. Vegetation on most slopes and hillsides consists of combinations of heaths with *Dryas interfolia*, *Carex* spp., *Cassiope*, and lichens (Maher 1980). Fifty-three species of birds and ten species of mammals were recorded on the study area. A complete list of these species is given in Appendix I.

Methods

Efforts to document the size of the population of peregrine falcons in the Rankin Inlet area were initiated in 1980 by the Department of Renewable Resources, Government of the N.W.T. Detailed information on nest site distribution, occupancy, and productivity was not obtained until the summer of 1981. Some of the data collected that year (C. Gates, unpublished data) have been included in the following analyses. Research by the author in the study area was conducted from early May to late August in the years 1982, 1983, and 1984. An additional five weeks of field work in the summer of 1985 also contributed productivity data used in the analyses.

Beginning in mid-May the study area was surveyed by snowmobile for arriving falcons. Arrival times and relative abundance of all primary prey species were noted at this time. Precise arrival times for breeding falcons were obtained by more frequent checks at six historically-used peregrine falcon nest sites located in close proximity to the Rankin Inlet townsite. These sites represented the full spectrum of nest cliffs available in the area: island, sea cliff, and inland outcrop sites. By the first week of June breeding peregrines were constantly present at nesting sites. Thereafter the reproductive progress of all pairs was routinely observed.

All terminology related to nesting activity is summarized as follows:

Territory - an area containing one or more nests within the range of a known or inferred 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 the territory of a pair of birds but used in different years.

Occupied territory or occupied nest site - a territory or nest site where one pair of birds is present at some time during the breeding season, although eggs may not be present, and where the presence of birds is made obvious by defense behavior towards conspecifics and potential predators including humans.

Productive territory - a territory occupied by a pair where a minimum of one chick is raised to an advanced stage of development and is assumed to have fledged, or is actually observed to fledge.

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 young per <u>occupied</u> territory.

Density of nesting pairs and the actual size of the study area were calculated using the method described by Ratcliffe (1980). This procedure entailed calculating the average minimum distance between each nest site of occupied territories (mean internest distance). The resultant mean internest distance is a useful index of density for comparative purposes, particularly when comparing peregrine populations that occur along river valleys or coastlines. Nineteen territories, the median number of territories occupied between 1981 and 1985, were used in making this calculation.

Mean internest distance can also be used to compute hypothetical boundaries of study populations, which in turn allows calculation of study area size (Ratcliffe 1980). This method uses mean internest distance as the radius for a circle of territorial influence drawn around the nest site of each pair. The outer portions of circles with this radius, drawn around the outermost nesting pairs provides a boundary to the breeding area. The area within these boundaries represents the study area size. Although originally suggested as a means of measuring density in inland areas where nesting habitat is relatively homogeneous in dispersion, this method serves adequately to establish study area size for the Rankin Inlet population. It also allowed density to be expressed in terms of pairs per unit area, which is also of value for comparative purposes.

The chronology of events during the early nesting period of all pairs was monitored by periodic checks of nest sites throughout the month of June. First egg dates were obtained by backdating from known laying dates and assuming a 48-hour interval (Nethersole-Thompson 1931, in Ratcliffe 1980) between all other eggs in the clutch. Details on nest substratum, exposure, and shelter from overhang were noted during these visits. On these surveys relative abundance of all potential prey species was noted subjectively by placing species into the categories: rare, common, and abundant. Use of these species by peregrines was determined by assessing prey remains at the nest site. In all years but 1981, full surveys of all known and potential nest sites were undertaken in mid-June (early incubation) and again in early July (late incubation) using a helicopter (Bell 206B Jet Ranger). Data on total egg production, nest failures, or egg losses were obtained during these surveys. Clutch size data were available for only nine of 14 laying pairs in 1981.

All nest sites were visited at least three times during each of the field seasons. In 1983 and 1984, nest sites were visited at hatch and at least three times before the young had fledged. Use of prey species by each pair was determined by noting prey remains at the nest and at plucking points on each cliff. Young falcons were banded with a standard U.S. Fish and Wildlife lock-on band; a custom-manufactured blue, anodized band was fitted to the opposite tarsus. The color bands were individually marked with a 3 digit alpha-numeric code and could by read from as far as 40 m using a 45 power spotting scope.

Adult falcons were captured throughout the nesting season as part of a government study of organochlorine pesticide pollutants in these birds. Adults were trapped as they arrived on the breeding area and were also trapped at the nest over small young using standard capture techniques (H. Armbruster, pers. comm.). Captured birds were sampled for blood, banded in the same manner as the nestlings and weighed. A full series of morphometric measurements was also taken.

Results and Discussion

Subspecies of the Study Population

Peregrine falcons are known to nest at latitudes as high a 77°N in North America (White 1968) and 78°N in Eurasia (Dement'ev 1951). The Rankin Inlet population is not as far north (63°N), however the similarity between the timing of events in the breeding cycle of the Rankin Inlet population and that of populations in high arctic locations (Cade 1960, Salmonsen 1950), coupled with the known weather patterns of the Canadian barrenlands, suggests these birds are breeding under climatic conditions as severe as any in the enormous range of this species. Not surprisingly, there has been some degree of ecological divergence in peregrines nesting under arctic conditions, both in terms of morphology and migratory habits. Differences between these birds and conspecifics to the south have stimulated much debate among taxonomists regarding the validity of subspecies designations, particularly in the Old World (White 1968). Peregrines from north of the coniferous forest in North America and from Greenland have only relatively recently been assigned to a separate subspecies, *Falco peregrinus tundrius* White (1968), distinct from the two other North American forms, *F.p. anatum* Bonaparte and *F.p. pealei* Ridgway. It is perhaps most appropriate in discussing the natural history of the study population to relate what is known of the migratory habits and morphology of these birds and establish how well these conform with White's original description of *F.p. tundrius*.

In earlier works on the peregrine falcon, several authors speculated that the large number of peregrines migrating along the eastern seaboard of the United States included many that were of arctic origin (Cade 1960, White 1968). Banding studies have now established that many of these birds originate from arctic breeding grounds as far west as the Yukon River in

Alaska and as far east as Greenland (Mattox 1975, Henny et al. 1982, Burnham and Mattox 1984). White (1968) believed that many of these migrants were members of *F.p. tundrius* and that these birds would winter from as far north as the Florida Keys to as far south as Chile and Argentina. Six of 143 nestlings banded on the Rankin Inlet study area between 1981 and 1984 have been recovered. Four were recovered as fall migrants. All were trapped by wildlife officials along known raptor migration routes including Cedar Grove (Wisconsin), Virginia Beach (Virginia), and two were recovered on Padre Island (Texas). Three adults trapped on the study area had been banded previously as young-of-the-year, fall migrants on Assateague Island (Virginia), Cumberland Island National Seashore (Georgia), and Padre Island (Texas). Both Assateague Island and Padre Island are known as areas of concentration for migrating peregrines, many of which originate in the arctic (Henny et al. 1982).

Only two winter recoveries were obtained for peregrines banded on the study area. Both were young of the year and both were found dead. One was recovered in Simpson County, Kentucky, in December 1983, and the other was reported from Cerro Chato, Uruguay, in February 1982. No mention was made of how long the bird from Kentucky had been dead before the band was submitted, so it is possible that the bird was migrating when it died. The winter record from Uruguay, like the fall migration recoveries, parallels the migratory habit reported for *F.p. tundrius* (White 1968).

White (1968) based much of his subspecific description of *tundrius* on the contention that arctic birds were of smaller body size than other peregrines in North America. He provided measurements of wing chord, tail length, and body weight for both sexes of *tundrius* drawn from a sample of museum specimens. Unfortunately he did not provide his raw data, thus precluding a statistical comparison with birds from this study. White also made no statistical comparisons between his sample and samples of either *F.p. pealei* or *F.p. anatum*. Only the latter subspecies could overlap with the population at Rankin Inlet. A statistical comparison of wing chord and tail length measurements from birds from the study population and a captive population of *F.p. anatum* (Canadian Wildlife Service, Wainwright, Alberta) did relate significant differences in the morphology of these two groups of birds (Table 2.1). As the sample population of *anatum* was captive, any differences in body weight between the samples were ignored.

Table 2.1 Morphometric comparison of peregrine falcons from Rankin Inlet study population, original sample used by White (1968) to define *Falco peregrinus tundrius*, and a sample population of *Falco peregrinus anatum*

			Males			Females		
			Wing Chord (mm)	Tail Length (mm)	Weight (g)	Wing Chord (mm)	Tail Length (mm)	Weight (g)
F.p.tundrius	White (1968)	n	64	64	12	62	62	19
		x	308.3	140.5	610.9	351.8	167.8	952.0
F.p.tundrius	Rankin Inlet	n	14	15	15	32	32	31
		x	318.0[1]	139.4[2]	607.0	361.3[3]	164.4[4]	920.0
F.p.anatum	C.W.S. Wainwright	n	14	14	14	16	16	16
		x	320.7[1]	147.7[2]	600.0	365.8[3]	175.6[4]	899.4

Statistical comparison between Rankin Inlet sample and C.W.S. Wainwright sample

[1] **Student t-test df = 27 t = 0.88 $P = 0.39$**
[2] **Student t-test df = 27 t = 5.33 $P < 0.01$**
[3] **Student t-test df = 46 t = 2.13 $P = 0.02$**
[4] **Student t-test df = 46 t = 7.08 $P < 0.01$**

The Rankin Inlet sample and that of White (1968) were similar in terms of body weight and tail length. However, the mean wing length of the Rankin Inlet sample was closer to that for the sample of *anatum*, as illustrated by the lack of a significant difference in wing length for the males of the two samples. This lack of conformity of the Rankin Inlet sample to that used to define the tundra peregrine might be explained in terms of subspecies intergradation. Rankin Inlet, in terms of latitude, approaches the southern limit of the range reported for *F.p. tundrius* (White 1968). Indeed, White reported intergrading characteristics of *tundrius* and *anatum* from specimens collected as far north as the south end of Southampton Island, N.W.T.

Similarity between peregrines breeding at Rankin Inlet and the sample analysed by White was also less distinct in terms of plumage characteristics. White (1968) based much of his subspecific description on plumage characteristics that he believed were unique to *tundrius*. In brief, adult *tundrius* were deemed distinct from *anatum* and *pealei* in that the overall plumage was "lighter", particularly the head and ventral surface. He described typical specimens as having a large white auricular area on the head with the malar bar below the eye, columnar in shape. The breast was generally less extensively marked than in other subspecies and the wash or ground color of the ventral plumage was noted as fai[illegible] to lacking.

Appraisal of all but the most obvious plumage characteristics is subjective at best, however only one half to two thirds of the falcons in the study population showed plumages similar to that described by White (1968). As predicted in the original paper, males more often than females represented the 'classic' tundra peregrine in plumage. Head and face characteristics varied from exceptionally light individuals, with the supercilliary stripe and large white auricular areas, described by White, to very dark birds with no auricular space at all and the malar stripe developed as a black cap over the entire head. There was also considerable variation in breast markings, particularly in the females. Some individuals showed very heavy barring on the breast and, similar to *anatum*, the wash of the whitish parts of the plumage was often rufous.

These differences can be expected as White (1968) speculated that intergrading plumage characteristics are likely to be observed at latitudes similar to that of Rankin Inlet. In referring to a bird from Hudson Bay which had been suggested as a type specimen in an earlier subspecies proposal, White was incapable of assigning it to either *tundrius* or *anatum*. Overall, plumage and morphometric assessment of the study population tends to support the idea of a cline of variation between populations of *F. p. tundrius* from further north and *F. p. anatum* to the south.

Nest Site Characteristics

The number of occupied territories on the study area varied from 17 in 1981 to 26 in 1985. The smaller number is probably the least accurate as observers were new to the study area in that year, no helicopter surveys were undertaken, and some territorial pairs were probably overlooked. It is extremely unlikely that any territorial pairs were overlooked on the study area from 1982 to 1985. The 26 pairs in 1985 represent an exceptional year when the population apparently responded to the periodic abundance of one or more prey species; thus, the figure of 19 to 20 occupied territories most accurately represents the yearly breeding population of peregrine falcons on the study area. The nesting activities in these five years involved use of 29 separate cliffs.

Traditional use of certain nest cliffs within the nesting territory of a pair of peregrines is well documented (Ratcliffe 1980). In the study area the traditional use of such cliffs by peregrine falcons is marked by the profuse growth of the lichen *Xanthoria elegans* which grows well in association with the high nitrogen content of the heavy fecal deposition below the nest ledges of raptors and in the immediate vicinity of raptor nest sites. Occasional use of these cliffs by rough-legged hawks (*Buteo lagopus*) and gyrfalcons (*Falco rusticolus*) also contributes to this diagnostic marking.

Nest sites were all on cliffs located relatively close to water bodies. Of 29 separate cliffs known to have been used since 1981, 21 bordered on the ocean or were within 150 m of the shoreline. Three other cliffs were located in the centre of islands or peninsulas and five were located on the mainland; all were within 300 m of substantial water bodies.

The cliff faces used for nesting varied between 7 m and 30 m in height. The lowest nest was 4 m from the base of a 12 m face and the highest was 26 m from the base of a 30 m face. The security of nest sites, at least in terms of human access, was poor. Of 68 clutches laid between 1981 and 1984, all but seven were accessible without a climbing rope. The high degree of accessibility of peregrine nests in arctic regions compared to southern populations was also noted by Cade (1960). However, ease of access may only reflect the type of cliffs that the birds are 'forced' to nest on rather than a poor choice made by each nesting pair. Alliston and

Patterson (1978), in their study of peregrines in the northern Keewatin and southern Franklin districts, found only four of 35 nest sites to be accessible without climbing equipment.

Of the 29 separate cliff faces used between 1981 and 1984, 17 faced southwest, 5 faced northeast, 3 faced north, 3 faced south, and 1 faced west. Cade (1960) suggested that peregrine falcons selected nest sites that provided protection from wind and storms. Considering the severe nature of arctic environments one might expect these birds to select preferentially those cliffs with a southern exposure, and thus take advantage of any beneficial microclimatic characteristics offered by such positions. Burnham (1975), working in Greenland, noted that exposure of nests averaged due south and he concluded that the choice of a nest site was ultimately determined by a combination of warmth and the presence of overhanging rock.

Although 20 of 29 nest cliffs in the study area did have a southern component to their exposure, this may simply indicate a greater abundance of this type of cliff rather than a preference on behalf of the birds. Rock outcrops in the study area are oriented along a northwest-southeast axis, consequently cliff faces most often faced either southwest or northeast. Many of the more precipitous cliffs in the area had a southwestern exposure. These cliff faces were created by the plucking action of glaciers that at one time advanced from the northeast. In these cases the plucking or cliff-creating action occurred on the leeward or southwest side of rock obstacles, therefore leaving a greater number of cliffs with this type of exposure in the area. Unlike the nesting cliffs described by Burnham and Mattox (1984), nest ledges under overhanging rock were very rare in the study area. Of 68 breeding attempts between 1981 and 1984, only three nests were located on ledges under overhanging rock.

Overall, it appears that cliff faces of any exposure could be used for nesting. Birds that nested on cliffs with northern exposures suffered no disadvantage in terms of reproductive success. Pairs nesting on north-facing sites showed no significant difference in the number of young fledged compared to a sample which nested on cliffs with a southern exposure (from a sub-sample of pairs selected at random and independent of one another, 10 pairs nesting on cliffs of each type of exposure Mann-Whitney U Test $U=49.0$ $P=0.94$). It is probable that territorial behavior and availability of nest sites were the major factors determining nest site selection. Interestingly, exposure of nests used by a dense population of rough-legged hawks nesting in 1980 did not differ significantly from that of sites used by peregrines in 1981 (Chi-square$=0.01$ df$=1$ $P>.90$)(Gates, unpublished data). This suggests that exposure of nest sites may not be critically important to the hawks as well.

Actual nest locations, in the form of natural rock ledges or abandoned rough-legged hawk nests, were superabundant in the study area. This was illustrated by the fact that of 68 breeding attempts recorded between 1981 and 1984, precisely the same ledge or nest was reused on only three occasions, never in successive years. Eggs were laid on broad, open ledges of up to 2 m wide and 4 m long and in as small an area as the flattened remains of a stick nest, less than a metre square.

Peregrine falcons lay their eggs in a shallow bowl-like structure or scrape, which is scratched into the substratum of the nest ledge (Burnham 1975, Cade 1982). Three different types of substrata underlay the scrapes made by falcons in this study population. Loose soil, often including small rock chips and dead ground vegetation made up the substratum of 17(27%) scrapes. Scrapes made on ledges of thick turf encompassed 18(29%) nests. The use of abandoned rough-legged hawk nests was recorded in 27(44%) nest attempts since 1981. Such nests were in various states of repair and often consisted of nothing more than a decaying mass of sticks and humus. In all cases there was enough of a soil base to form an adequate scrape.

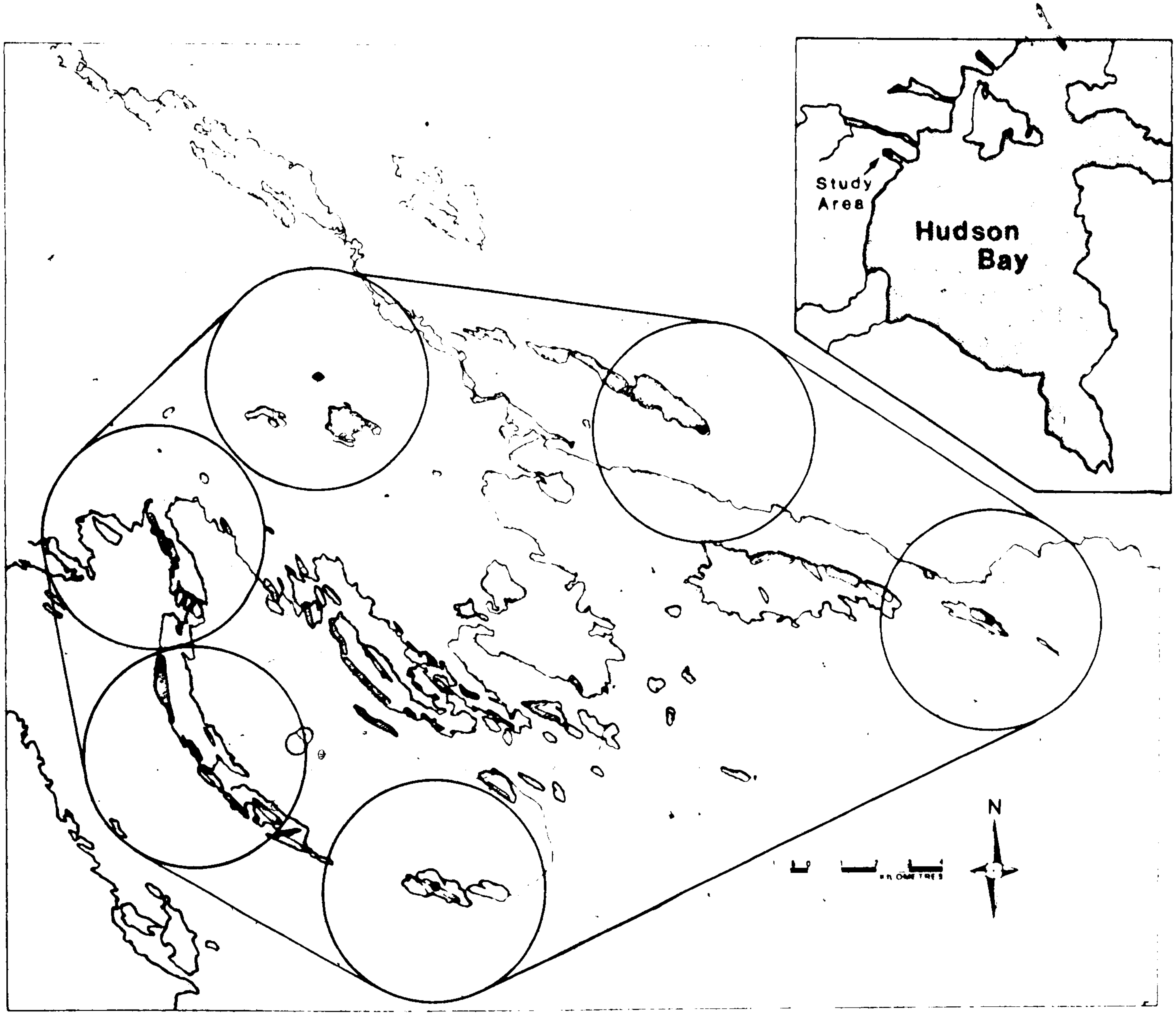
The use of stick nests of ravens (*Corvus corax*) and raptor species, particularly the rough-legged hawk, is not unusual for arctic peregrines. Calef and Heard (1979) reported that 30% of peregrine falcon nest sites at Wager Bay and on the Melville Peninsula, N.W.T., were on old stick nests. In many areas nest building species provide a platform on ledges that otherwise would be too small for peregrines to use; and these nests are often located in areas completely inaccessible to mammalian predators. Such structures also provide loose substrata for scrapes on rock ledges that would otherwise lack them. Indeed, much of the soil on cliff ledges, including heavily vegetated examples, may have its origin in ancient stick nests of species like the rough-legged hawk. Around Rankin Inlet at least, the use of the area by breeding rough-legged hawks greatly increases the number and variety of nest ledges available to peregrines.

Density of Nesting Pairs

Using the method described by Ratcliffe (1980), a mean internest distance of 3.3 ± 2.0 km was calculated for the study area. Internest distances ranged from 700 m to 9850 m. The mean internest distance was used to define a study area size of 450 km^2 (Figure 2.1). Thus a

Figure 2.1 Rankin Inlet study area as defined by a mean internest distance for the population of 3.3 km.

● - outermost nesting territories in population
—— - boundary of study area


Study Area
Hudson Bay
N
KILOMETRES

density of occupied nest sites per unit area computes to approximately one pair of peregrines for every 24 km^2 (19/450).

In terms of mean internest distance, the density of peregrines in the study area is one of the highest recorded in North America, second only to that for populations of *F.p.pealei* on the Queen Charlotte Islands. There a mean internest distance of 1.6 km was calculated (Beebe 1960). The mean internest distance at Rankin Inlet is higher than at all other arctic locations yet recorded and approaches the highest known densities for the peregrine in Great Britain; those recorded for populations nesting in association with seabird colonies on the sea cliffs of southeast England and some Scottish islands (Ratcliffe 1969) (Table 2.2).

Comparison of the mean internest distance to other populations must be done with some caution, as they are often based on study areas much larger than that at Rankin Inlet. Nesting habitat for peregrines, particularly in the arctic, can be quite patchy. As a result, larger study areas are likely to have larger mean internest distances. This was shown by Alliston and Patterson (1978) who recorded a mean internest distance of 15.9 km for their entire study area but discovered escarpments of "optimal" habitat that harbored much higher densities of birds, one with a mean internest distance of 5.4 km.

Similar reservations can be made regarding comparisons of density in terms of pairs per unit area. Such a comparison also assumes that the size of study areas in different studies are calculated in similar ways. Even if this method is constant, differences in the physiography of different study areas and consequent heterogeneity of usable habitat, or lack of uniformity in the distribution of nesting habitat, can contribute a great deal to variation in density figures. The Rankin Inlet study area shows neither uniformity nor randomness in the distribution of nest cliffs, moreover, more than one half of the area used to compute the density figure consists of ocean surface. Despite the inherent problems in comparisons of density, a figure of one pair per 24 km^2 does illustrate the unusually high density of peregrines in the Rankin Inlet area. Fyfe (1969), for example, estimated a density of one pair per 50 km^2 for "optimum" habitat on the N.W.T. mainland and the arctic islands, Burnham (1975) estimated one pair per 200 km^2 on his study area in Greenland, and Hickey (1942) estimated a density of one pair per 1364 km^2 for the eastern United States.

In conclusion, there can be little doubt that Rankin Inlet represents an exceptional breeding area for peregrine falcons. However, it is most unlikely that this extraordinary density

Table 2.2 Mean internest distances for peregrine falcon populations from different locations

Author	Location	Habitat Type	Subspecies	Mean Internest Distance (km)
White and Cade (1971)	Alaska	A	*tundrius*	6.0
Burnham (1975)	Greenland	B	*tundrius*	6.3
Calef and Heard (1979)	Northern Keewatin, N.W.T.	B and C	*tundrius*	8.0
Alliston and Patterson (1978)	Franklin and Keewatin, N.W.T.	B	*tundrius*	15.9
Beebe (1960)	Queen Charlotte Islands	C	*pealei*	1.6
Ratcliffe (1969)	Great Britain	C	*peregrinus*	2.6
Ratcliffe (1972)	Great Britain	B and C	*peregrinus*	5.5 6.4
This Study	Rankin Inlet	B and C	*tundrius*	3.3

A = riverbanks and escarpments bordering rivers
B = rock escarpments surrounded by open land, tundra or highland areas
C = cliffs bordering the ocean

can be extrapolated to any other section of the Keewatin mainland or coastline. The study area at Rankin Inlet is relatively small and, as Ratcliffe (1980) pointed out, local concentrations of cliffs in an area where they are otherwise sparsely distributed sometimes produce unusually close clustering of pairs. This could be the case at Rankin Inlet only on a larger scale where the local cliffs have attracted a high density of pairs which, unlike other dense populations, show no strict feeding specialization on colonial birds.

Chronology of the Breeding Season

i) Arrival of Adults

Peregrine falcons were recorded on the study area as early in the year as May 10. However, pairs of birds were rarely recorded at nest sites earlier than May 20. Of six cliffs routinely checked each spring from 1982 to 1984, pairs were recorded at nest sites before May 20 on only three occasions, but by May 28 of each year all six nest sites had pairs in attendance.

Alliston and Patterson (1978) summarized spring migration and arrival information for peregrine populations north and west of Hudson Bay. Although this information is limited, it tends to agree with my observations. The authors commented that the spring arrival of peregrines in the Keewatin was on average two to three weeks later than in interior Alaska (Cade 1960, White 1969). They concluded that the difference reflected the more severe climate in northwestern Hudson Bay even though the two areas are at similar latitudes. Observations at Rankin Inlet also support their conclusion that the migration of adult peregrines into the areas north and west of Hudson Bay closely parallels that of populations in Greenland (Salmonsen 1950) and the Eurasian tundra (Dement'ev 1951).

Observations at Rankin Inlet suggest that arrival of peregrines onto the breeding grounds is related to spring weather patterns. An unusually heavy snowfall was recorded in this area in the spring of 1983. Blizzard conditions during the second half of May contributed to snowfall records that were nearly thrice those for the same period in 1982 and slightly over 50 times those for the same period in 1984 (Ministry of Transport Records, Rankin Inlet)(Table 2.3). In 1983 peregrines were seen as early as May 10, but disappeared with the onset of poor weather on May 16 and were not seen again until May 25. Of the six sites monitored for returning peregrines in 1982, all had pairs in attendance by May 25, and in 1984 five of six were attended by pairs on the same date. On this date in 1983 only two of six sites had pairs in

Table 2.3 Mean temperature and total precipitation for late May and early June in Rankin Inlet, N.W.T., 1982 to 1984.

	May 16-31		June 1-15	
Year	Mean Temperature (°C)	Total Precipitation (mm)	Mean Temperature (°C)	Total Precipitation (mm)
1982	-3.2	7.3	-1.1	5.4
1983	-6.6	20.2	0.9	96.8
1984	-2.5	0.4	2.5	5.2
Mean (1981 to 1985)	-3.4	10.24	1.21	22.78

attendance; the remaining four showed no sign of falcons.

Arriving peregrines in all three years were first encountered at the two highest cliffs on the study area, both of which faced southwest. Low, north-facing, inland outcrop sites were usually the last to show adult falcons in attendance. Large cliffs often had more than a pair of falcons in attendance; as many as five adult birds were encountered at one cliff. Aggressive interactions between falcons in such situations were frequent. This suggests that those falcons arriving first tend to claim the larger, and perhaps higher quality nest cliffs. Hickey (1942) discussed the "magnetism" of large "first class" cliffs to peregrines and noted that such cliffs were often the highest in the area, provided superior security, and were always occupied even after years of nest failure caused by human persecution. It is possible that such cliffs exist in the suite of nest sites available at Rankin Inlet, however an alternative explanation may be that these tall cliffs provide better security and protection from the prevailing northwest wind during the first few days birds are on the breeding ground when weather conditions can be severe. Such protection is not provided by low, north-facing sites. Thus, pairs that subsequently settle at these low cliffs may seek shelter elsewhere initially. Incidental observations of color marked adults in the study population suggest this to be the case. For example, a marked pair of birds which regularly occupied a low, north-facing cliff from 1981 to 1984, was seldom recorded at the cliff before the last few days in May. Observations showed that the birds were often present much earlier, but chose to perch on the south faces of nearby hills and on an esker located 1.5 km north of the nest cliff.

Cade (1960) stated that peregrines in Alaska occupied cliffs immediately upon arrival. As mentioned, arriving peregrines at Rankin Inlet perch at cliffs upon arrival but do not show a strong attachment to these sites until about the last week in May. Before this date it is difficult to guarantee their presence at any nest cliff when using conventional survey techniques. Birds that have recently returned to the breeding grounds will frequently fly silently from the nest cliff and leave the area if approached by an observer. Agonism between peregrines perched at the same cliff often began immediately upon arrival, but defense of the nest site against human intruders through protest vocalizations was rarely recorded until late in the last week of May or the first week of June.

Some authors (Dement'ev 1951, Cade 1960) believe that in arctic populations of the peregrine, the sexes arrive on the breeding ground simultaneously. Observations at Rankin Inlet also suggest that arrival time is independent of sex. However, there is no evidence to suggest that previously mated pairs arrive at the same time. This also suggests that members of pairs do not winter or migrate together. Color marking showed that individual adults that had bred successfully at a cliff the previous season may return some days before their mate. In one case, a marked male was present at a nest cliff for eight days before the marked female from the previous season arrived. She was successful in driving away another unmarked female that had occupied the cliff in the interim.

ii) Laying to Fledging

The earliest record of laying the first egg in a clutch for the Rankin Inlet population was June 1; the latest was June 19. It is established that peregrines usually lay eggs at 48 hour intervals (Nethersole-Thompson 1931, in Ratcliffe 1980), so dates of clutch completion (four eggs) for these records would be June 6 or 7 for the early case and June 24 or 25 for the late case. The mean date of clutch initiation for three consecutive seasons was June 7, 1982 (n = 5), June 13, 1983 (n = 14), and June 8, 1984 (n = 14), making the mean date of clutch initiation significantly different between years (Kruskal-Wallis Test H = 14.84 $P<0.01$). Multiple comparison tests (Conover 1980) showed that dates of clutch initiation in 1983 were significantly later than in both 1982 and 1984.

Cade (1960) summarized published data on clutch initiation in arctic peregrines. The data are generalized with the most detailed information coming from studies over the entire breeding season, in which laying date was estimated by backdating from date of clutch completion. However, in other studies clutch initiation dates have been estimated by backdating from hatch dates and by using parameters as dubious as the 'known age' of young in the nest or fledging interval. More recent studies of the tundra peregrine have incorporated these methods (Harris and Clement 1975, Allison and Patterson 1978).

Cade (1960) found that most pairs of *F.p. tundrius* on the Colville River in Alaska initiate laying in the first week of June but some started as early as the third week in May. He also reported that peregrines breeding between 64°N and 66°N in the Yukon basin, a latitude comparable with the Rankin Inlet study area, initiated clutches three to four weeks earlier than those on the Colville. Clutch initiation dates for the study population, however, fit the range of June 2 to June 17 previously estimated for peregrines in the districts of Franklin and Keewatin

(Alliston and Patterson 1978). These data again suggest a great deal of similarity between the timing of breeding events for peregrines on coastal Hudson Bay and those from high arctic locations.

The data from Rankin Inlet also show that there exists considerable variation in the mean date of clutch initiation from year to year. As with the arrival times, there was a significant delay to the start of the local breeding effort in 1983. It is possible that the late arrival of adults onto the breeding grounds may have prompted this delay. Also, precipitation figures for early June of this year were much higher than for the same period in 1982 and 1984 (Table 2.3). It is conceivable that the slow melt of snow from desirable nest ledges delayed laying in 1983. At nest cliffs where melt was extremely delayed, evidence suggests that some females may have been forced to use less preferred nest ledges as the more preferred ledges remained covered with snow well into June. At one cliff where two stick nests were known to have been used alternately from year to year since 1980, a normal clutch was laid by a marked female on a very exposed, accessible grassy ledge while the stick nests retained snow on them. This clutch was subsequently lost under unknown circumstances, whereas the same marked female had successfully produced young at this cliff in 1981 and 1982.

The nesting chronology of the peregrine falcon is sufficiently well known to be able to establish from the date of laying, the timing of subsequent events in the breeding cycle. Incubation lasts about 32 days (Nelson 1972), most young fledge between 40 and 45 days of age (Cade 1960), and the young make their first kills 25 to 30 days after first flying (Sherrod 1981). Sherrod found that age of first kill, or age of potential independence, varied with individual and sex. In his sample, males killed at an average of 27.7 days after first flying, and females killed at an average of 30.9 days after their fledging date. In the study population, a clutch initiated June 7 would be completed about June 13. Incubation, if initiated in earnest with the first or second egg, would provide an asynchronous hatch spanning July 9 to 15. Young from such a brood would fledge as early as August 19 to as late as August 30. Independence would occur, based on Sherrod (1981), as early as the beginning of the third week in September and as late as the first week in October. Using a similar chronological sequence, and any of the laying dates listed earlier, one can demonstrate that the majority of broods will fledge during the last third of August. However there exist some cases where young may fledge as late as the end of the first week in September, giving a date of independence well into October.

The period of post-fledging dependence is often difficult to establish in southern populations of the peregrine and has received little documentation in the arctic. In the south, young peregrines may frequent the nest cliff for some time after they are proficient hunters (Ratcliffe 1980), however at Rankin Inlet young peregrines are rarely seen after the end of September (C. Gates, M. Bradley pers. comm.) suggesting that many begin migration very shortly after, or perhaps even before, they have gained this independence. Cade (1960:182) summarized nesting records for northern peregrines and concluded that, "in arctic latitudes peregrines must lay their eggs not later than the beginning of the third week of June to ensure successful rearing of young, because by mid September the bulk of their food is gone". Generally, this is true for the study population and casts doubt on the survivorship of young fledged very late in August or early September. It is possible that young that are not fully independent of their parents when migration begins are fed as they move south or that they kleptoparasitize or scavenge the kills of parents, siblings, other peregrines, or perhaps other raptors during this period. Examples of such behavior have ~~been~~ reported for migrating peregrines (Dekker 1980).

To conclude, the length of the breeding season for peregrines in the study area is not substantially different from that of other populations at high latitudes. There is nothing to suggest any difference in the length of most parameters of breeding chronology in this population and those previously reported for the species. The only periods that are noticeably shortened are the pre-laying courtship period, the total time with eggs, as incubation is initiated before clutch completion, and perhaps the total time of post-fledging dependence. Cade (1960) speculated that courtship may be completely eclipsed in northern populations or that courtship might be initiated on the wintering grounds or on migration. Evidence against the latter comes from the asynchronicity of arrival times of marked pairs alluded to in the previous section.

Chronology of Prey Use

Peregrine falcons, in terms of their use of avian prey, are recognized as being euryphagous. Even in areas where the avifauna is impoverished, such as the boreal or tundra zones, peregrines may prey on a large percentage of all species represented (Cade 1960, Burnham 1975). Cade (1960) warns that this feeding classification must be qualified as some pairs and even some populations of peregrines may develop a high degree of specialization on a particular prey species. This invariably occurs when one species, for example a colonial alcid, greatly outnumbers other potential prey species in the area. As previously mentioned, such specialization on a specific prey species can lead to unusually high densities of nesting peregrine falcons (Beebe 1960).

Nineteen species of birds and three species of mammal were recorded as prey items of peregrine falcons at Rankin Inlet (Table 2.4). Eliminating bird species that peregrines are incapable of killing for reason of size, these falcons use about 50% of the species available to them in this area. This figure does over-estimate the importance of some prey species as many of the birds considered available when making this calculation were in fact comparatively rare or accidental in the study area. Cade (1960) also found that arctic peregrines take a wide variety of prey species, concluding that no one species constituted a major portion of the diet. This was also true for the study population with certain qualifications. First, subjective appraisal of prey remains at the nest cliff suggests that, although a wide range of species are taken, the bulk of the diet is comprised of six species of birds and one species of mammal. Second, an individual prey species can be critically important to the entire falcon population at certain times of the year. Third, individual pairs may use a single species intensively while raising their young. Fourth, certain mammal species are used more frequently in years when they are super-abundant, and this abundance is apparently reflected by the number of peregrines attempting to breed, and to some degree, the reproductive success of individual pairs.

Rock ptarmigan and snow buntings are present on the study area when peregrines arrive in the spring. Both are very important as prey at this time, as is shown by their remains at all nest cliffs. The use of these birds contrasts with other studies which stress the spring arrival of northern peregrines being closely synchronized with the arrival of waterfowl (Dement'ev 1951, Cade 1960, White 1969). With the possible exception of the large geese, waterfowl arrive on the study area some weeks after peregrines, a point which again highlights the severe nature of the climate on the study area relative to most other studies of the peregrine in the north. Ptarmigan were rarely seen on the study area after the first week of June and either leave the area or disperse onto the tundra at a very low density. No evidence of breeding was recorded for ptarmigan in the area and remains of these birds were never recorded at cliffs.

Table 2.4 List of prey species used by peregrine falcons nesting on the Rankin Inlet study area, 1981 to 1985.

Birds		Relative Frequency
Northern Pintail	*Anas acuta*	3
Oldsquaw	*Clangula hyemalis*	3
Common eider	*Somateria mollissima*	2^2
Rock ptarmigan	*Lagopus mutus*	4
Semipalmated plover	*Charadrius semipalmatus*	3
Lesser golden plover	*Pluvialis dominica*	2
White-rumped sandpiper	*Calidris fuscicollis*	2
Baird's sandpiper	*Calidris bairdii*	2
Dunlin	*Calidris alpina*	2
Semipalmated sandpiper	*Calidris pusilla*	3
Red phalarope	*Phalaropus fulicaria*	1
Arctic tern	*Sterna paradisaea*	1
Long-tailed jaeger	*Stercorarius longicaudus*	1
Black guillemot	*Cepphus grylle*	2
Horned lark	*Eremophila alpestris*	4
Water pipit	*Anthus spinoletta*	4
Palm warbler	*Dendroica palmarum*	1^1
Lapland longspur	*Calcarius lapponicus*	4
Snow bunting	*Plectrophenax nivalis*	4
Mammals		
Arctic ground squirrel	*Spermophilus parryii*	2^2
Collared lemming	*Dicrostonyx groenlandicus*	2
Brown lemming	*Lemmus sibricus*	2

Codes:

1 - recorded at up to 25% of nest sites in study area
2 - recorded at between 25% and 50% of nest sites in study
3 - recorded at between 50% and 75% of nest sites in study
4 - recorded at between 75% and 100% of nest sites in study area
[1] - recorded on only one occasion
[2] - juveniles only

after early June. Snow buntings did breed locally and were recorded as prey items throughout the breeding season.

Three other species of passerine birds, horned lark, Lapland longspur, and water pipit were also important prey species for the study population (Table 2.4). All three arrived before waterfowl or shorebirds and were used extensively early in the season. Horned larks and Lapland longspurs were the most numerous bird species in the area as reflected by a density of horned larks as high as 1.6 pairs per hectare, recorded on the tundra north of the Rankin Inlet townsite by Maher (1980). Both larks and longspurs, and to a lesser degree snow buntings and water pipits, were taken by all pairs of falcons in the study area. Adults were used throughout the season and, at some falcon nests, fledglings of these species provided the bulk of the food used to raise young peregrines. Young passerines are often just out of the nest as young peregrines are hatching. These birds, with their poorly developed powers of flight, are easily caught by adult peregrines and at most nest sites are used intensively. Harris and Clement (1975) also noted that the hatch of peregrine eggs coincided with the fledging of passerines and also believed that adult passerines were more vulnerable as they began the molt at this time.

Eight species of shorebirds were recorded as prey items for the study population (Table 2.4). Of these, five breed locally and are probably taken throughout the entire breeding season. No one shorebird species approaches the abundance of any of the passerine species discussed earlier and the relative greater frequency of passerine remains at falcon nests reflects this difference. Of all species, the semipalmated plover and the semipalmated sandpiper are the most numerous on the study area. Both are frequently recovered at peregrine nest sites, mainly adults in early to mid-June and juveniles in late July and early August.

Waterfowl remains were rarely encountered at nest cliffs before the first week in August. It was about this time that female peregrines began taking a more active role in hunting and their larger size was reflected in a greater proportion of large prey species brought to the nest. Adult and juvenile pintails and oldsquaw were recorded as prey items while only juvenile common eiders were represented (Table 2.4).

Black guillemots congregate at sea ice cracks and open leads in the study area as early as June 19. They probably begin to occupy colonies during the first week of July, shortly before breakup. Most colonies are situated at the bases of sea cliffs where the birds lay eggs amongst rock rubble. Their pattern of dispersion during all parts of the summer months is therefore very clumped. Not surprisingly, peregrines nesting above or near these colonies prey upon guillemots to a large extent. Three pairs of peregrines in the study area annually specialized on adult guillemots during the period when falcons were raising their young, although passerines supplemented these diets. There was no evidence of predation on juvenile guillemots

One of the more unique aspects of prey use by peregrines in the study area was the presence of small mammals in the diet (Table 2.4). Arctic ground squirrels and two species of lemming were recorded as prey items. Arctic ground squirrels (juveniles) were recorded at eight nest sites within the study area, and evidence of use of this species was obtained in all years of the study. Three nesting pairs incorporated juvenile ground squirrels as a major portion of their diet while raising young. Whether the use of these mammals reflects a unique specialization of a few individual birds or simply the close proximity of the nests to a squirrel colony is a matter of speculation, but the tendency of pairs to make heavy use of the most numerous prey species in the area suggests the latter. Interestingly, all pairs that used ground squirrels to any degree nested on sea cliffs that bordered the mainland; at inland sites ground squirrel remains were rarely recorded.

Northern peregrines have been recorded to take arctic ground squirrels, but Cade (1960), in Alaska, found that this species made an insignificant contribution to the diet of peregrines, both in terms of total numbers and biomass. In contrast, prey remains at certain falcon nests at Rankin Inlet suggest that ground squirrels could be important in both capacities, particularly while adults are raising young. Peregrines are normally recognized to be bird predators (Ratcliffe 1980, Cade 1982) and observations such as those by Cade (1960) support the widespread contention that the contribution of mammals to the diet is insignificant (Hickey and Anderson 1969). The extensive use of ground squirrels and lemmings by pairs of falcons in the Rankin Inlet population seems unique in this regard. It is, however, easy to see how the use of these mammals might evolve, as there are no trees in the area and a great proportion of the prey taken by all pairs consists of fledgling passerines which are taken on or near the ground.

Lemmings were recorded at nest sites in 1985 only; it is possible, however, that these mammals may have been taken in small numbers in previous years but were overlooked in nest debris. Although falcons attempted to pluck lemming carcasses, little remained of these mammals after each feeding. In 1985 lemmings appeared abundant, and remains including whole carcasses were found at a significant proportion of nests in the study area (Table 2.4).

Again, in view of the lack of identifiable remains after feedings at the nest, lemmings may have been underrepresented in the assessment of prey use by falcon pairs in the study population in this year.

Although only the two lemming species were recorded at nests, other species of microtines in the area included the meadow vole, *Microtus pennsylvanicus*, and the red-backed vole, *Clethrionomys gapperi*. Studies at Eskimo Point, N.W.T., 240 km south of Rankin Inlet, established that the populations of all four of these mammals peaked in 1985. Not only were the populations substantially greater than in the previous four years, but individuals in 1985 were of larger body size than those of previous summers. Researchers responsible for these findings suggest that it is not unreasonable to assume that this peak in microtine numbers was synchronized over an area large enough to include Rankin Inlet (F. Mallory pers. comm.). The dramatic increase in the population of nesting rough-legged hawks in the Rankin Inlet study area in 1985 supports this assumption (Figure 2.2).

Apparently, the peregrine population in the study area also responded to the peak in microtine numbers and increased by six territorial pairs (30%)(Figure 2.2). The percentage of pairs to lay showed a measurable increase, and the mean brood size for the population was greater in this year than in all other years of the study. The total number of young peregrines produced on the study area was nearly double that in any of the previous four years (Tables 2.5, 2.7, and 2.8). Bertram et al. (1934) reported similar findings for peregrine populations in northern Norway, and Cade (1960) related personal correspondence which suggested a similar response of peregrine populations to microtine abundance on the Melville Peninsula, N.W.T.

Although he considered both of these records, Cade (1960) concluded that there was little evidence from any arctic locale to suggest that peregrines should be considered a "lemming predator" in the same sense as the snowy owl (*Nyctea scandiaca*), jaegers (*Stercorarius spp.*), or the rough-legged hawk. He based this conclusion on the fact that peregrines, unlike "lemming predators", appeared to show no increase in population density and no increase in reproductive yield when faced with an abundance of these prey species. Cade also believed that any response shown by falcon populations under these circumstances was probably indirect; for example, peregrines might prey on the "lemming predators" and would consequently benefit from their abundance. Cade also mentioned the possibility that ptarmigan cycles might be in phase with those of microtine species and that the abundance of these birds might account for

Figure 2.2 Number of rough-legged hawks and peregrine falcons to initiate breeding each year on the Rankin Inlet study area, 1981-1985.

● - peregrine falcon
○ - rough-legged hawk

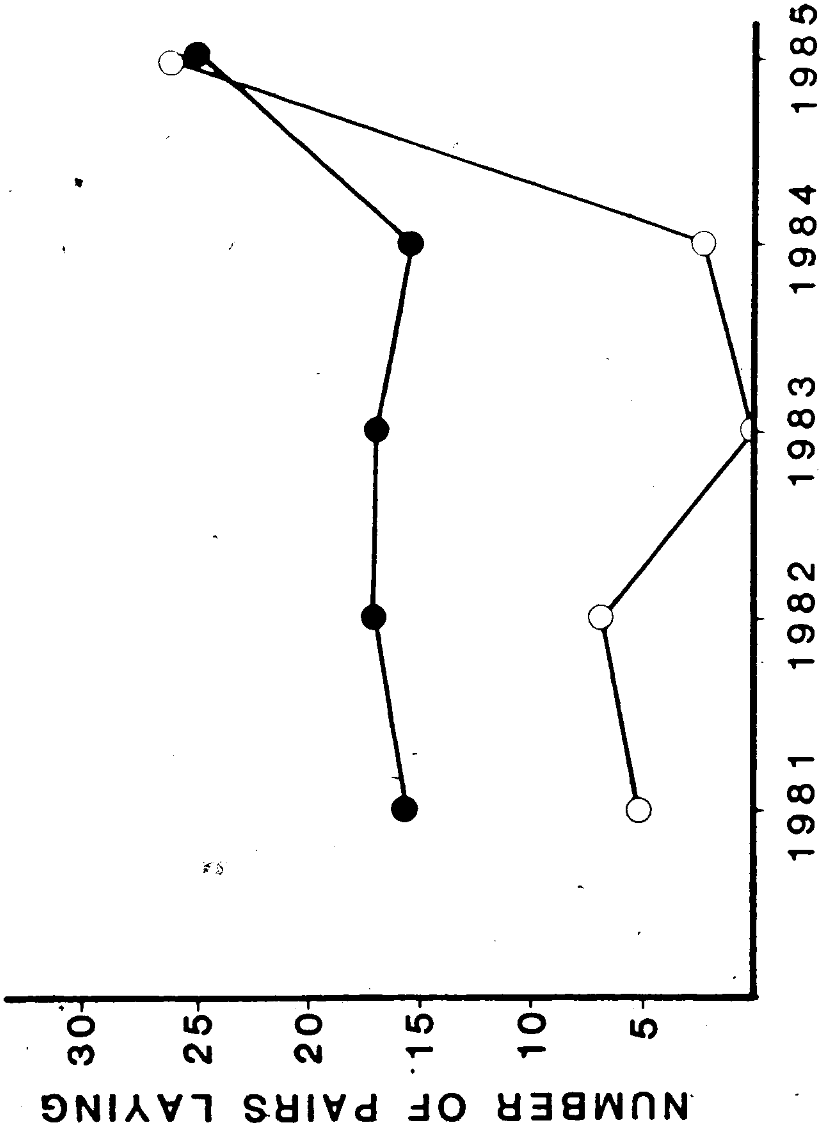

NUMBER OF PAIRS LAYING
30
25
20
15
10
5
1981
1982
1983
1984
1985

Table 2.5 Breeding success of peregrine falcons on the Rankin Inlet study area, 1981 to 1985.

	1981	1982	1983	1984	1985
Number of occupied territories	17	19	19	20	26
Number of pairs laying eggs	16	17	17	16	25
Number of eggs produced	unknown	63	60	58	92
Number of pairs producing young	15	14	14	14	20
Number of pairs fledging young	15	14	13	12	20
Number of young hatched	unknown	39	42	43	unknown
Production	36	35	36	37	61

Table 2.6 Number of clutches of different sizes for peregrine falcons on the Rankin Inlet study area, 1981 to 1985.

Year	Number of clutches of following sizes				Total	Mean ± S.D
	1	2	3	4		
1981	0	1	3	5	9	3.44 ± 0.73
1982	1	0	2	14	17	3.71 ± 0.77
1983	0	0	8	9	17	3.53 ± 0.51
1984	0	1	4	11	16	3.63 ± 0.62
1985	0	0	8	17	25	3.68 ± 0.47
All years	1	2	25	56	84	3.62 ± 0.59

Table 2.7 Number of broods of different sizes for peregrine falcons on the Rankin Inlet study area, 1981 to 1985.

Year	Number of broods of following sizes				Total	Mean ± S.D.
	1	2	3	4		
1981	2	6	6	1	15	2.40 ± 0.83
1982	0	5	7	2	14	2.79 ± 0.70
1983	0	6	6	2	14	2.71 ± 0.73
1984	0	5	5	4	14	2.93 ± 0.83
1985	1	2	12	5	20	3.05 ± 0.76
All years	3	24	36	14	77	2.79 ± 0.78

Table 2.8 Clutch size, brood size, and productivity (mean±S.D.) of peregrine falcons on the Rankin Inlet study area, 1981-1985.

	1981	1982	1983	1984	1985	*P*	All
clutch size	3.44±0.73	3.71±0.77	3.53±0.51	3.63±0.62	3.68±0.47	0.50[1]	3.62±0.59
n =	9	17	17	16	25		84
brood size	2.40±0.83	2.79±0.70	2.71±0.73	2.93±0.83	3.05±0.76	0.16[2]	2.79±0.78
n =	15	14	14	14	20		77
productivity	2.40±1.11[4]	1.84±1.30	1.89±1.45	1.85±1.66	2.35±1.47	0.20[3]	2.03±1.41
n =	17	19	19	20	26		101

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[1] Kruskal Wallis 1-way ANOVA H = 3.33

[2] 1-way ANOVA F = 1.68 df = 4,72

[3] 1-way ANOVA F = 0.54 df = 4,96

[4] potentially biased in that at least two territorial pairs may have been overlooked

any change in falcon population density or productivity

From the data (Tables 2.5 to 2.8, Figure 2.2), the population of peregrines at Rankin Inlet showed a response to increased prey abundance in 1985 both in terms of increased population density and by a slight rise in the mean reproductive output of falcon pairs. Besides the snowy owl and the rough-legged hawk, no dramatic increase in the presence of "lemming predators" was noted in this year, thus indirect effects noted by Cade (1960) are an unlikely explanation of these phenomena. Also, ptarmigan were present on the study area only in the early spring, and were never encountered during the summer. No dramatic increase in ptarmigan numbers was noted in the spring of 1985. Thus, it is difficult to implicate an increase in ptarmigan abundance as a cause for the changes in the falcon population observed in 1985.

The changes observed in the density and reproductive success of the study population in 1985, and their relevance to peregrine population dynamics, will be discussed in subsequent portions of this thesis. However, it should be noted that the most parsimonious explanation of these increases relates directly to microtine abundance. In keeping with the conjecture of Cade (1960) regarding the potential importance of avian prey density (ptarmigan), it may be that the changes in the peregrine population were related to an increase in the abundance of avian prey (in this case passerines), which in turn occurred coincidentally with that of the microtines. However, subjective appraisal of prey abundance on the study area did not suggest a dramatic increase in the numbers of any avian prey species in 1985. Additionally, I can find no records which conclusively demonstrate that passerine abundance varies in phase with that of microtines.

It might also be suggested that the increase in the peregrine population in 1985 represented some form of recovery from a pesticide-induced population decline. As discussed in detail later in this thesis, preliminary results of pesticide residue analyses of eggs from this population collected in 1981 and 1982, did not suggest a chemical problem. The high reproductive success of this population relative to others also supports this contention.

In conclusion, the use of mammalian prey by peregrines at Rankin Inlet represents a significant departure from patterns of prey use previously reported for the species. Evidence obtained in 1985 strongly suggests that periodic fluctuations in the populations of small mammals can affect the breeding density and reproductive output of this population. However, only continued study involving detailed documentation of prey use conducted over a series of microtine peaks will clearly determine the relative importance of these mammals as prey for the peregrines nesting at Rankin Inlet

Productivity

i) Yearly Productivity of the Study Population

As 1985 represents an exceptional year for the study population in terms of total production, it is best discussed separately in certain comparisons. This is also necessary as it was not possible to obtain detailed information on brood reduction in this year, thus making comparisons with other years somewhat awkward.

On average, 74% of pairs on territory were successful in producing young (Table 2.5). In most years of the study, successful pairs produced about 35 young or about two young per occupied territory per year (Tables 2.5 and 2.8). Annual production added about the same number of males as females to the population. Of the 108 young produced between 1982 and 1984, 56 were males and 52 females. Sex ratios varied from 16 males to 20 females in 1983, to 23 males to 14 females in 1984, none of which was significantly different from an equal sex ratio (Chi-square analysis $P>0.05$). This agrees with nestling sex ratios previously reported for the peregrine (Hickey 1942, Ratcliffe 1980) and for other species of raptorial birds (Newton 1979).

Between 1981 and 1984, yearly constancy in terms of the number of pairs that produce eggs, the number that produce young, and the total number of young fledged is particularly obvious (Table 2.5). The increase in the size of the breeding population in 1985 alters the impression of constancy to some extent, but it is interesting to note that, although brood size was greater in 1985 compared to other years, there were no significant differences among all years in clutch size, brood size, or number of young fledged per occupied nest site (Table 2.8). An increase in density of a peregrine population of the proportion seen at Rankin Inlet in 1985 is highly irregular, and will be discussed in detail in subsequent portions of this thesis. However, such fluctuations are common in many other raptor species, particularly those utilizing prey species which also fluctuate in abundance (Galushin 1974). As noted in the section on chronology of prey use, the increase in peregrine density on the study area in 1985 was also linked to an increase in prey abundance. In terms of reproductive performance, this conclusion is supported by increases in mean brood size and number of young produced per territorial pair in this year. Although these measures of reproductive performance were not significantly different from those in other years, the changes observed in 1985 were in the direction one might predict if food supply was greater in this year. Also, in 1985 the proportion of all territorial pairs to lay eggs was greater than in previous years of the study (note that at least two territorial pairs were probably overlooked in 1981)(Table 2.5). This increase could also be related to more abundant food in this year. This conjecture is supported by the experimental work of Newton and Marquiss (1981) who virtually eliminated 'non-laying' in a population of European sparrowhawks (*Accipiter nisus*) through the provision of supplemental food to pairs in the pre-laying phase of the breeding cycle. Abundant food, in the form of microtines, would have been available to the peregrines nesting at Rankin Inlet during the pre-laying phase in 1985.

Consistently high reproductive output of pairs in this population is noteworthy as there existed speculation that climatic vagaries and associated changes in food availability might result in sharp fluctuations in the reproductive success of northern peregrines (Cade 1960). This possibility was a potential criticism of suggestions that pesticide-induced reproductive failure had caused measurable population declines in arctic peregrines over the last two decades (Cade and Fyfe 1970, Fyfe et al. 1976, White, in press). The surveys that documented the decline were performed only once every five years. Detractors of these methods, and their conclusions, have suggested that, at least in arctic situations, poor reproduction, or a reduced number of productive pairs, may simply represent the type of normal fluctuation mentioned above and is not indicative of a population decline.

A five-year run of data from one population is probably too brief to say that large reductions in reproductive success could not occur in some years for any or all arctic populations. However, conditions that might have produced such perturbations were recorded during the years of study at Rankin Inlet. For example, severe spring weather in 1983 forced a significant delay in the mean laying date of the peregrine population in the study area. It is conceivable that such conditions could have contributed to reduced reproductive success outright, or perhaps forced a change in food availability during that breeding season. Reduction in the nesting success of local passerines could have been a possibility. Despite these possibilities, no dramatic alteration in any reproductive parameter (at least to fledging) of the peregrine population was noted in 1983.

It is also interesting to note that the population of rough-legged hawks nesting sympatrically with the peregrines suffered almost complete reproductive failure in the study area during some years when peregrines were consistently productive. Although these birds initiated breeding in most years (Figure 2.2), fewer than 15 young were produced in 1981 and 1984. No young were produced in 1982 and 1983. Although not measured precisely, total production for the population of rough-legged hawks in the study area in 1985 was at least 60 young. Presumably most of the variance in rough-legged hawk productivity was related to microtine rodent fluctuations, however any other factors that may have contributed to complete reproductive failure in some seasons were not reflected in the success of the peregrine population over the years.

ii) Productivity of the Study Population Compared to Other Populations

The mean clutch size of 3.62±0.59 for the study population is similar to that of various populations from both arctic and mid-temperate latitudes and is only noticeably greater than clutch sizes reported from Alaska (Cade 1960, Haugh 1976)(Table 2.9). Similarly, the brood size figure reported for peregrines in Alaska (Cade 1960) is the lowest of the arctic samples reported here (Table 2.10). The mean brood size of the Rankin Inlet population, calculated using data from all years of the study, is most similar to that reported by Kuyt (1980) for peregrines nesting along the banks of the Thelon River, in the Keewatin District of the N.W.T., and that reported for a population in Greenland (Burnham and Mattox 1984). Overall, mean brood sizes for most of these arctic samples are similar to, or even greater than, those of populations at more temperate latitudes. However these values still fall below the average brood size figure recorded for a pre-pesticide population of *F.p. anatum* in the eastern United States (Hickey 1942).

These comparisons are important because Hickey (1942) suggested that northern peregrines laid smaller clutches than populations at more southerly latitudes. This suggestion opposes trends seen in a great many other species and is contrary to general hypotheses which directly relate latitude and clutch size (Ashmole 1961, Ricklefs 1980). Indeed, a report on the reproductive success of peregrines in Eurasia concluded that the most northern of the subspecies in that region, *F.p. leucogenys*, has the largest clutch size (Dement'ev 1951). Some authors (Bond 1946) have questioned the validity of Hickey's sample as most of the clutches

Table 2.9 Clutch sizes (mean±S.D.) for peregrine falcon populations from different studies

Subspecies	Number of clutches	Clutch Size	Region	Author
F.p.anatum	282	3.72±0.72	Eastern U.S.A.	Hickey (1942)
F.p.peregrinus	479	3.66	Great Britain	Ratcliffe (1980)
F.p.tundrius	24	2.87±1.18	Alaska	Cade (1960)
F.p.tundrius	77	2.67	Alaska	Haugh (1976)
F.p.tundrius	24	3.33±0.82	NW Hudson Bay	Alliston and Patterson (1978)
F.p.tundrius	13	3.31±0.75	Thelon River N.W.T.	Kuyt (1980)
F.p.tundrius	84	3.62±0.59	Rankin Inlet	This study

Table 2.10 Brood sizes (mean±S.D.) for peregrine falcon populations from different studies

Subspecies	Number of broods	Brood Size	Region	Author
F.p.tundrius	58	2.41±1.03	Alaska	Cade (1960)
F.p.peregrinus	93	2.57	Great Britain	Ratcliffe (1980)
F.p.anatum	124	3.05±0.80	Eastern U.S.A (pre 1945)	Hickey (1942)
F.p. pealei	34	2.70	Queen Charlotte Islands, B C	Beebe (1960)
F.p.tundrius	73	2.80	Greenland	Burnham and Mattox (1984)
F.p.tundrius	19	2.53±0.84	NW Hudson Bay	Alliston and Patterson (1978)
F.p.tundrius	16	2.88±0.72	Thelon River N W T	Kuyt (1980)
F.p.tundrius	57	2.70±0.78[1]	Rankin Inlet 1981-1984	This Study
	28	3.04±0.88[2]	Rankin Inlet 1983-1984	This Study
	20	3.05±0.76[1]	Rankin Inlet 1985	This Study
	77	2.79±0.78[1]	Rankin Inlet 1981-1985	This Study

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[1] Excluding young that died as a result of asynchronous hatch and using chicks at least two weeks of age
[2] Including young that died as a result of asynchronous hatch

reported were from egg collectors, who often tend to collect the unusual clutches of greater than four eggs, for example. However, the small mean clutch size reported by Cade (1960) in Alaska seemed to support Hickey's view and Cade's statistical comparison of his sample and that from the eastern United States verified a significant difference in clutch size between the two areas. Thus, Cade (1960) also supported the idea that clutch size in the peregrine declined with increasing latitude. Yet I found no significant difference between the mean clutch size of the Rankin Inlet population (N = 84) and that reported by Hickey (1942) from the eastern United States (n = 282)(Mann Whitney U Test U = 11185.5 $P = 0.36$)(Table 2.9) This was true even though a significant portion of Hickey's sample contained unusually large clutches of five eggs or more, clutch sizes never recorded at Rankin Inlet.

Cade (1960) concluded, from his observations of clutch size in Alaska that egg production in arctic peregrines might be reduced for reasons of climatic severity or that such peripheral populations had a high percentage of young females. His data, however, represent by far the lowest clutch size among arctic samples, and more recent data from the same region (Haugh 1976) report clutch and brood sizes that are also lower than for other populations of *F.p. tundrius* reported here. This suggests that peregrines nesting along the Colville river may not be as productive as those nesting in other parts of arctic North America.

The contention of both Cade and Hickey that northern peregrines lay fewer eggs was also supported by their data on hatching success. Cade (1960) recorded a mean brood size of 2.41 ± 1.03 whereas Hickey recorded 3.05 ± 0.80 young per successful nest. The mean brood size at Rankin Inlet population (2.81 ± 0.85 n = 57), calculated using data from 1982 to 1984, was greater than that reported by Cade for Alaska. It is also greater than that reported as a mean for peregrine populations in Great Britain and populations of *F.p. pealei* on the Queen Charlotte Islands, British Columbia. However, the mean brood size for the Rankin Inlet population was significantly smaller than that of Hickey's sample from the eastern United States (n = 124)(Mann Whitney U Test U = 2715.0 $P < .05$)(Table 2.10)

This comparison seems to support the contention that northern peregrines produce fewer eggs and consequently fewer young than populations to the south. However, it is important to realize that this comparison was made using brood size figures obtained from the study population two weeks after all eggs had hatched. This procedure was followed as most authors report brood sizes for young at banding age, or older. At Rankin Inlet it was also possible to count all broods shortly after hatch before most nestling mortality had occurred. As northern peregrines frequently hatch eggs asynchronously (Dement'ev 1951, Burnham and Mattox 1984, R. Fyfe pers. comm.), there is potential for nestling mortality and brood reduction. Chick death resulting from an asynchronous hatch was a significant factor in reduction of broods in the study population, and this reduction usually occurred within the first week after hatch. If the young that died for this reason are included in the sample and compared with that from the eastern United States (Hickey 1942), no significant difference in mean brood size is evident (Mann Whitney U Test U=1728 *P*=0.97)(Table 2.10). Indeed, if a similar comparison is made between the sample from the eastern United States (n=124)(Hickey 1942) and broods from Rankin Inlet in 1985 (n=20), a year when brood size was greater than in previous years, again no significant difference is evident (Mann Whitney U Test U=1214.0 *P*=0.87)(Table 2.10). Therefore, it is possible that both Cade and Hickey may have underestimated the importance of brood reduction when they assumed that data on brood size supported their idea that peregrine falcons nesting at high latitudes produce fewer eggs.

Although the number of young fledged per occupied territory ranged from 1.84 ± 1.30 to 2.40 ± 1.11, 1.9 young fledged per occupied territory probably best represents a normal year for the Rankin Inlet population (Table 2.8). The figure of 1.9 young per occupied territory is high compared to figures from Alaska where Cade (1960) reported a range of 0.7 to 1.5 young fledged per occupied territory. Hickey and Anderson (1969) reported a figure of 1.5 young per occupied territory for populations in both the United States and Britain. Burnham and Mattox (1984) recorded a high figure of 2.6 young per occupied site, but warn that their figure, like many of those of other studies, was obtained when young were still at the nest, just prior to fledging. The authors believe that there exists considerable mortality of young birds during this period, so the number of young that actually fledge may be lower. Ratcliffe (1980) reported productivity of 1.31 fledglings per occupied site for the British population for years 1976 to 1979, and also mentioned an undisturbed population that may have produced as many as 2.0 young per occupied territory. He believed that productivity in the latter case was probably not only enough to sustain that population but served to supply breeding birds to nest sites over a much wider area. Ratcliffe also believed that productivity of below 1.0 fledgling per occupied site was not enough to sustain most peregrine populations.

Such high fledging success for birds in the study population indicates that, discounting the effects of asynchronous hatching, they have little problem raising most young to fledging age. Such ability reflects an abundant prey base, and few decimating factors such as parasites or predators. *Protocalliphora* (Hickey 1942) and argasid tick infestations (Oliphant et al. 1976) have occasionally been implicated in nestling mortality of falcons. No evidence of these parasites was obtained over the five years of this study. This is not unexpected, at least for the ticks, as birds in this population rarely use the same nest ledge in consecutive years. Potential nest predators such as the arctic fox (*Alopex lagopus*) were very rarely seen on the study area during the five field seasons, and snowy owls were seen regularly only in 1985. However, the fact that individual falcons in this population will not hesitate to strike snowy owl decoys and will occasionally strike humans as they approach the nest suggests that the importance of mammals and other raptors as potential nest predators cannot be overlooked.

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III. Observations on Territory Use and Territoriality of the Study Population

Introduction

The peregrine falcon (*Falco peregrinus*) has the largest natural distribution of any bird, rivalled only by the raven (*Corvus corax*) and the osprey (*Pandion haliaetus*) (Cade 1982). Its presence is determined by the availability of prey and access to suitable nesting habitat. Like any raptor, the number of pairs breeding in an area will be set by one of these two critical resources, whichever is in shorter supply (Newton 1979). An intriguing aspect of peregrine populations is how both food supply and nest site availability, in addition to the territorial nature of the birds themselves, appear to combine and ultimately affect the number and distribution of falcon pairs over the landscape.

The importance of these factors in determining population density and the distribution of nesting pairs appears to vary between regions. In areas where nesting habitat is extremely dispersed, for example, small isolated escarpments of rock separated by many kilometres of flat land, the number of falcon pairs is limited by the availability of nest sites, and population density will be set at low levels. Such a population might be expected in inland portions of the barrenlands region in arctic Canada where it is difficult to imagine territoriality determining breeding density as it is unlikely that 'neighboring' pairs would overlap even in their use of hunting ranges. It is possible, however, that in such situations strong competition for each nest site could exist.

In areas where nesting habitat is not limiting, variation in peregrine population density is often correlated with local food supply (Ratcliffe 1962, 1969). This is particularly obvious when potential nesting habitat is evenly dispersed. Ratcliffe (1969) showed that peregrine densities in Great Britain showed a rough correlation with productivity of the local landscape. He documented a decline in the number of pairs in an area over a large number of years, presumably as a result of declining prey populations which in turn were associated with the encroachment of agriculture. It is in this type of habitat that pairs are often evenly spaced, a pattern that suggests the strong influence of territorial behavior (Newton 1976, 1979, Ratcliffe 1980).

If food is super-abundant and nesting habitat is not limiting, peregrine population density responds commensurately. It is in this situation that peregrines appear to reduce their space requirements to a minimum and populations attain their highest known densities. The highest densities in Great Britain, for example, occur along cliff faces located close to seabird colonies (Ratcliffe 1962, 1980). The dense populations of island nesting peregrines off the northwestern coast of North America feed on colonial alcids whose populations have been described as "astronomical" (Beebe 1960). Peregrine density there is the highest on record, as illustrated by the population on Langara Island, British Columbia, that at one time may have included between 11 and 23 nesting pairs on a land mass only 18 km² in size (Nelson 1977).

Even the earliest observers of the peregrine noted spacing patterns of occupied territories and many assumed that territoriality was instrumental in limiting the number of pairs breeding in any area (Ratcliffe 1980). The relationship seen between food supply and nesting density has also contributed to speculation about the influence of variation in prey abundance on this density limiting mechanism. Nelson (1977) addressed this question in relation to the various hypotheses on population limitation in birds, and concluded that only those of Lack (1954, 1966) and Wynne-Edwards (1960, 1962) were appropriate to a discussion of population limitation in the peregrine falcon. In brief, Lack (1954, 1966) proposed that the breeding rate of any species was maximal relative to its food supply and that mortality outside of the breeding season, presumably through starvation, was instrumental in limiting population size. In this way the size of subsequent breeding populations would be set in accordance with available food supply. Lack believed that territorial behavior did not directly limit the size of the breeding populations but simply served to space out the surviving individuals.

Wynne-Edwards (1960, 1962), in direct opposition to Lack, proposed that populations are limited through competition either for position in a dominance hierarchy or possession of territory. He believed that the result of such competition would be a stable population that was limited in size below the carrying capacity for the given area. Like Lack (1954, 1966), he conceded that food supply was the ultimate limiting factor for any population but believed that the limits of such a resource would rarely be approached as density of the breeding population was limited through mechanisms such as territoriality.

As Nelson (1977) pointed out, Wynne-Edward's ideas about an organism's ability to avoid overharvesting its food supply are particularly relevant to discussions of the role of territoriality in raptor populations. Wynne-Edwards suggested that birds may be capable of "quantitative habitat appraisal" whereby territory sizes are adjusted in relation to available food supply. Evidence for this comes from the work of Holmes (1970), who found that the size of the territories of dunlin (*Calidris alpina*) varied with the food availability of the habitat. territories were largest in areas where food was less abundant and less dependable, whereas territories were considerably smaller in areas of higher food abundance. A similar relationship provides a theoretical explanation for variation in the densities of the peregrine populations alluded to earlier. A direct link between territory size and food abundance also allows for the possibility that the densities of such populations may change through time with corresponding changes in food availability. There is evidence that some species, mainly lemming predators, may change territory size on an annual basis as they track the fluctuating abundance of their food (Pitelka et al. 1955). There is even evidence that nectivorous birds may do this on a daily basis as they defend territories that vary in size relative to the number of open flowers (Gass 1979).

With raptors, it has been proposed that many populations are limited by a shortage of nesting sites created by the territorial nature of the birds themselves. Again, the degree of territoriality seen, and consequently territory size, is believed to be directly related to food availability (Newton 1979, Village 1983). In regard to the peregrine, a similar link between food supply and territoriality has been assumed and this combination is believed to be the main factor responsible for setting population density (Ratcliffe 1962, 1969, 1980, Nelson 1977). As mentioned earlier, habitat availability can occasionally contribute to this limitation, but is more often thought to affect the distribution of nesting pairs (Ratcliffe 1980).

Although these conclusions are accepted, it is perhaps instructive to consider the evidence upon which they are based. Newton (1976, 1979) summarized a considerable body of circumstantial evidence suggesting that densities of most breeding raptors are limited. Much of this information was drawn from studies of the peregrine falcon, and consists of four main observations: 1) the long-term stability of many raptor populations would be unexpected unless numbers were limited in some way; 2) the presence of surplus, reproductively capable adults in the population suggests that some mechanism prohibits them from breeding; 3) in populations of raptors that have recovered in areas where they were extirpated, new birds have returned to the same nest sites and in the same numbers, which suggests an upper limit in numbers or a given carrying capacity for the species in a given area; and 4) in continuously suitable habitat there is remarkable constancy in the spacing of territorial pairs which is also consistent with the idea that territorial behavior may be limiting the density of nesting pairs.

Direct observational evidence linking territoriality to population limitation in the peregrine appears to have been rarely recorded. Records of territorial interactions among these birds are rare and anecdotal and for the most part entail reactions of territorial holders to intruding falcons in the immediate vicinity of the nest cliff (Cade 1960, Nelson 1977, Ratcliffe 1962, 1980). Most authors concede that these observations are not evidence that territorial behavior is responsible for the pattern of pair spacing or that such behavior may ultimately determine the number of pairs present in any one area (Ratcliffe 1969, Nelson 1977). Only Nelson (1977), working with the highest recorded density of peregrines in the world, could tentatively identify territorial boundaries between pairs, some of which were separated by less than one km. Cade (1960) found that the territorial aggressiveness of peregrines in Alaska was highly variable among individuals. His model of territoriality in this species could explain the most minimal internest distances but does not implicate territorial defense as the mechanism that spaced most of the pairs in his study area (Nelson 1977). Other authors have faced similar problems, prompting speculation that territorial advertisement through visual signals such as flight displays, in addition to aggressive encounters, may serve to space pairs or to inhibit other falcons from setting up territories between traditionally used nesting cliffs (Ratcliffe 1962, 1969, 1980, Nelson 1977).

The interpretation of agonistic interactions between peregrines is complicated by the fact that, for the most part, intraspecific territoriality is often highly variable among individuals and is most often recorded only in the immediate vicinity of the nest cliff. There is little to suggest defense of foraging areas which can be very large. This is particularly obvious at higher population densities where closely spaced pairs nest at some minimum internest distance but may overlap a great deal in their use of hunting ranges (Cade 1960, Nelson 1977). For this reason Ratcliffe (1980) has suggested that the term 'home range' for peregrines should not necessarily be considered in the context of defended space. In this way peregrines are different from other raptors, short-eared owls (*Asio flammeus*) for example, that defend territories which include both the nesting territory and hunting range (Lockie 1955, Pitelka et al. 1955). Such a difference may reflect the much larger space requirements of the peregrine or the fact that these birds require cliffs for nesting. As cliffs are often clumped in their dispersion, nesting peregrines may be 'forced' into concentrations which entail defense of a nesting territory yet necessitate much overlap in the use of foraging space. This does not rule out the possibility that territoriality may limit the number of pairs using a large area as peregrines may simply partition the available nesting habitat rather than combined nesting and foraging areas. This type of limitation was seen in the work of Village (1983) on the European kestrel (*Falco tinnunculus*), where breeding pairs appeared to exclude potential breeders from usable nests, but did not prevent them from using suitable foraging habitat.

From previous studies (Cade 1960, Ratcliffe 1962, Nelson 1977) it is clear that observations of territorial aggression in the peregrine cannot be used to explain any pattern of pair spacing except possibly in the densest populations. Therefore it is difficult to identify positively territorial aggression as the mechanism through which populations are limited. This however might only reflect the difficulties involved in observing territorial encounters. Nelson (1977) believed we lack these data because observations were often restricted to the immediate vicinity of nests and thus were unlikely to pick up 'border' disputes or even any territorial advertisement that might indicate the importance of territoriality in pair spacing.

In Rankin Inlet, N.W.T., I had the opportunity to observe patterns of territory use and territorial behavior of a population of peregrine falcons over a number of nesting seasons. The population is located on a relatively circumscribed patch of nesting habitat and territorial pairs exist at a density higher than anywhere yet recorded for the arctic; a mean internest distance of 3.3 km was calculated for 19 pairs nesting in the 450 km^2 study area. As in areas occupied by other populations, there seemed to be, to the human eye, an abundance of nesting habitat in addition to the traditionally used cliffs. This suggested the possibility that the density of the breeding population is limited, and raises questions about the role of territoriality in such limitation.

Yearly surveys of territorial pairs and observations of marked individuals allowed an accurate description of the annual use of territories for the population. To gain some understanding of the permanence of peregrine falcon territories in the study population, yearly turnover and fidelity to nest sites were investigated through mark and recapture of adult birds. The nature of the nesting habitat, a high population density, color marked individuals, and the relatively high frequency of territorial interactions made it possible to evaluate both circumstantial and direct observational evidence for population limitation in these birds. At Rankin Inlet it was logistically feasible to study the behavior of falcons as they arrived on territory and throughout the early nesting period. As these birds often had as little as two weeks between arrival on the study area and laying, the period of territorial establishment relative to many other peregrine populations was extremely reduced. For this reason agonistic interactions were relatively frequent and behavioral observations at this time made it possible to evaluate whether or not there existed strong competition for nest sites in the area, a prerequisite of population limitation. Such observations were also used to assess territorial behavior as a possible mechanism through which [illegible] of birds in this population were spaced and through which density was ultimately limited. The response of the study population, in terms of territory use, to the increased abundance of one or more prey species also allowed speculation on the relationship between territoriality and food abundance.

Methods

Territory use by the study population was recorded during five summers, 1981 to 1985. Early spring surveys by snowmobile were normally successful in finding most territorial pairs, but intensive helicopter surveys of the all nesting habitat in the study area were conducted after breeding had commenced to ensure that no pairs were overlooked. Falcon territories were considered as either 'regulars' or 'irregulars' depending on their history of use (after Mearns and Newton 1984). Territories used at least twice in the five years of the study were considered 'regulars', those used only once were deemed 'irregular'.

During nesting surveys, all adults on territory were observed at close range with binoculars or spotting scope to ascertain whether or not they were banded. Intensive color banding of adults in the population, to aid in investigations of territorial interactions, territory dynamics, and population studies, began in 1982. Adults were captured each year as they arrived in the spring using pigeons as bait, and were also snared at the nest over eggs or small young using standard capture techniques (H. Armbruster pers. comm.). Adults were banded with a standard U.S. Fish and Wildlife lock-on band; a custom-manufactured blue-anodized aluminum band was fitted to the opposite tarsus. The color bands were individually marked with a three digit alpha-numeric code and could be read from as far away as 40 m using a 45 power spotting scope. Adult birds were either identified by reading the band or by retrapping each year. An effort was made to identify the occupants of the same territories each year. This was not always possible because some territories were not occupied in successive years, or because some pairs did not lay or failed before trapping was attempted. The trapping had no noticeable effect on nesting pairs; there were no nest failures or desertions after trapping and there was no mortality of young or adults related to these activities. Trapping and color marking yielded information on alternate nest site use, recruitment, site fidelity, and population turnover. Trapping and observations of color marked birds also made it possible to gain evidence of non-breeding adults. Turnover and mortality data were analysed following the methods of Mearns and Newton (1984).

To evaluate whether there existed strong competition for traditionally used nest sites, a series of behavioral observations was made in the spring months of 1983 and 1984. In each year observations were made at four different nesting cliffs. Two were in close proximity (2 km or less) to other territories, considered 'clustered', and two were 'isolated' (6 km or more) from other nesting pairs of falcons. Observations were made when logistics and spring weather permitted, and consisted of 2.0 hours of observation at each type of cliff each day, alternating between pairs of sites every second day. All observations were made between 1200 and 1700 hours.

Observations were made by spotting scope 250 to 350 m from the base of the nest cliffs. Every attempt was made to keep track of both members of the pair during these short observation periods. This precluded detailed focal animal samples for each bird, however on most occasions it was possible to note behaviors pertaining to territorial interactions or advertisement such as vocalizations, aggressive posturing (Cade 1960, Nelson 1977), or movement for both birds during exchanges with other falcons. In the event of an aggressive encounter between an 'intruder' and the pair of birds 'resident' at the cliff as observations commenced, the sex of the combatants was noted and every effort was made to keep track of the identity of the individuals involved during the encounter; color banding often aided in this regard. The majority of territorial interactions resulted in chases away from the nest cliff. As the study area has relatively little relief, no trees, and is snow or ice covered during the early part of the breeding season, most chases were clearly visible and could be followed from beginning to end. Only chases between adult peregrines that were viewed in their entirety were included in the analyses. The pattern and distance of each pursuit were plotted on a contour map. In view of the rarity of these interactions, and in consideration of the brevity of the observation periods, results were pooled for the two years of observation.

Results

Patterns of Territory Occupancy

The number of territorial pairs was relatively constant from 1981 to 1984 (Table 2.5). It is possible that at least two territorial pairs were overlooked in 1981. In the first four years, the population was relatively stable at 19 or 20 territorial pairs, but increased to 26 pairs in 1985. The distribution of territorial pairs in the study area over five years is illustrated in Figure 3.1.

Throughout all years, 29 separate nesting territories were identified. Twenty-three of these were considered 'regulars' and six were 'irregular' territories. At its peak in 1985, the population consisted of pairs at 22 'regular' territories and 4 'irregular' territories. Alternative nest cliffs were used by many of the pairs occupying 'regular' territories. Positive evidence for use of alternative cliffs was available through banding studies but circumstantial evidence, such as pair spacing or use of perch points, was used to tentatively identify alternates used by other pairs (Figure 3.1). In the sample of known alternates, based on the movement of both members of a pair, the distance between cliffs used by the same pair in different years ranged from 550 m to 2025 m, with a median of 950 m (n=8). The new pairs that appeared in 1985 occupied completely new 'irregular' territories and also used alternate nest cliffs of 'regular' territories.

Age Characteristics of Territory Holders

Between 1981 and 1985, a total of 89 adult peregrines (58 females and 31 males) were caught and banded, recaptured, or identified by reading numbered leg bands with a spotting scope (Table 3.1). As females were more likely to attack bait pigeons and were easier to catch at the nest, they were marked in larger numbers than were males. All birds captured or identified, with the exception of two females, were resident on territories at the time. The two females not on territory were captured in early spring but were unsuccessful in entering the study population as territory holders.

The oldest known female breeding on the study area was at least five years old, the youngest to attempt breeding was known to be three. Of the 19 marked females breeding in 1985, four were at least five years old, three were at least four years old, seven were at least

Figure 3.1 Peregrine falcon territories in the Rankin Inlet study area, 1981-1985.

▨ - potential nesting habitat
○ - years occupied
○—○ - alternative nest sites
○- -○ - possible alternative nest sites of one territory

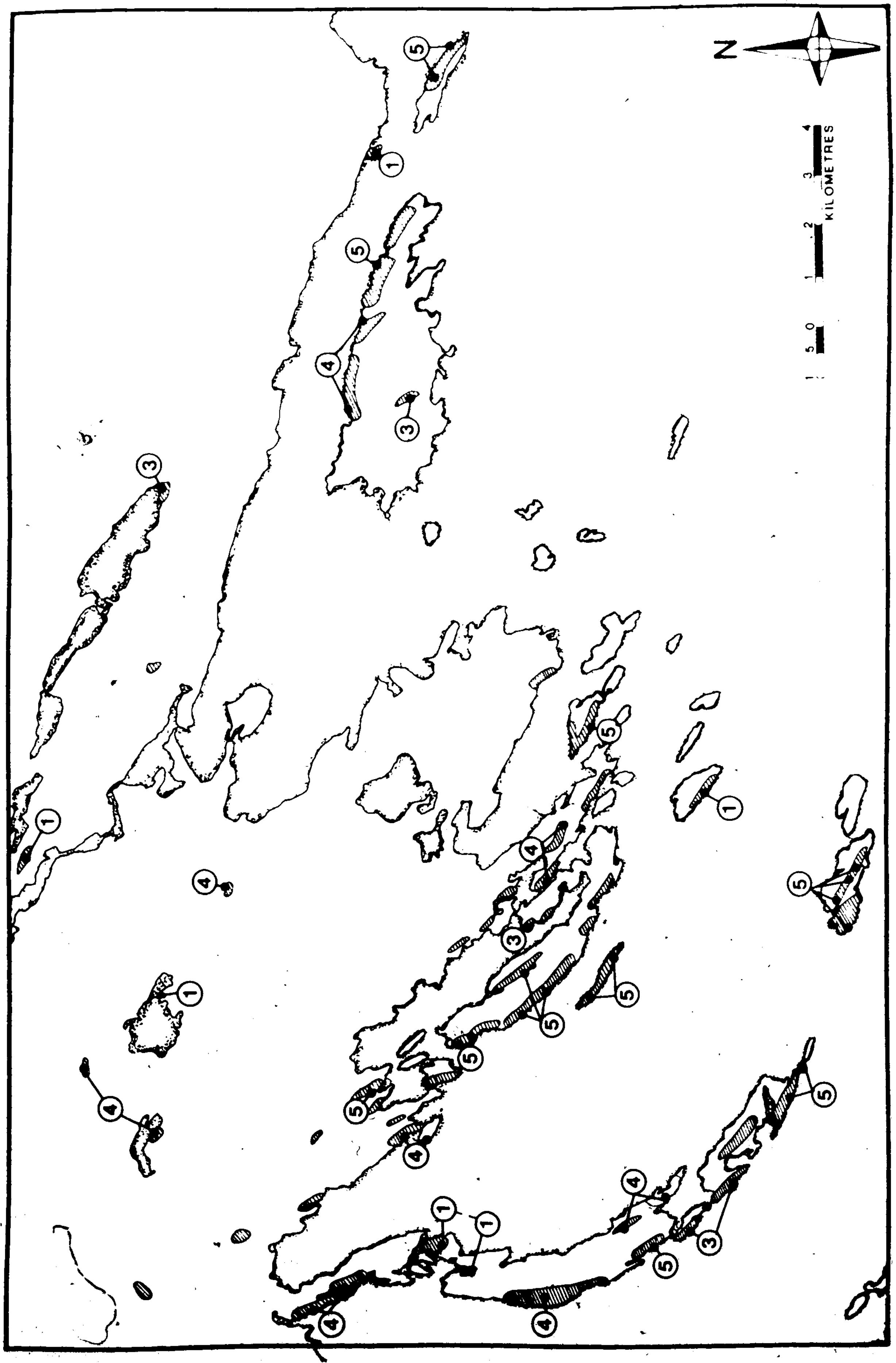
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Table 3.1 Number of peregrine falcons handled in different years.

	1981	1982	1983	1984	1985	Total
Adult Males	0	5	7	9	10	31
Adult Females	1	9	15	14	19	58
Nestlings	36	33	36	36	61	202

With reference to adults, 'handling' included birds that were trapped or retrapped, as well as those identified at nesting territories by reading band numbers three years old and the remaining five, banded in 1985, were at least two years of age. The oldest known male in the population was at least five years old and the youngest to attempt breeding was two years old. Of the ten marked males present in 1985, three were at least five years old, one was at least four years old, and the remainder, all banded in 1985, were at least two years of age. Since these are minimum ages, relative to the year in which the bird was banded, it is very likely that many of the birds were much older.

Between 1981 and 1985, 205 young were produced on the study area, all but three were banded (Table 3.1). If two years of age is used as the minimum age of recruitment for the study population, then by 1985, 105 of these marked young were old enough to enter the breeding population, yet only three had actually obtained territories on the study area by 1985. A male and a female obtained 'regular' territories at three years of age in 1984. A male established a new territory ('irregular') as a two year old in 1985. The female obtained a territory 20.5 km from her natal cliff while the males obtained territories 6.8 and 6.2 km from their natal cliffs. Although the banding status of two adult males was not ascertained, all other birds forming the six new pairs of the population increase of 1985, with exception of the two year old male mentioned above, were unbanded and hence were of unknown age.

Evidence of Non-breeding Birds

Evidence for non-breeding birds was obtained primarily through observations made in 1983 and 1984. This evidence consisted mainly of birds known to have been excluded from territories early in spring, or adults, apparently without territories, encountered late in the summer. Early spring surveys of potential nesting habitat gave the impression that the number of adult peregrines present was in excess of that comprising the breeding population. The excess was very difficult to quantify however, as the birds did not react strongly to territorial intrusion by humans and would often fly away from cliffs when approached. Thus, it was difficult to conclude with certainty that the same bird was not encountered more than once on a single survey.

It was not unusual to encounter more than two adult peregrines at nest cliffs early in the spring and territorial interactions frequently involved as many as four adults. As many as five adults, one male and four females, were seen perched at one cliff at one time. Similar observations gave the impression that males were either less numerous than females on the study area, or were less tolerant of conspecifics of the same sex than were females. The latter impression was later confirmed (see below).

Spring trapping showed that some adult peregrines that arrived on territories first were often replaced by others before breeding commenced. Of eight females trapped at territories early in the spring, two were unsuccessful in either maintaining residency there or on other territories within the study area in the same year or subsequent years. One of these birds was known to be seven years old at the time. On one other occasion an unbanded female was present at a nest site with a banded male eight days before the banded female, the mate from the previous nesting season, arrived and eventually replaced the unbanded female on the territory. A similar replacement involving an unbanded adult male was also observed.

Adult peregrines, apparently without territories, were encountered late in the nesting season. On two occasions adult males of banded pairs were encountered at their nest cliffs with unbanded adult females. This was only recorded in August, a time when adult females were away from cliffs for extended periods, presumably on hunting forays. These adults were readily identifiable as strangers because they did not engage in active nest defense when observers approached the nest. Extended visits at these nest sites by observers attracted the attention of the resident territorial female on both occasions. Both times fighting ensued with the intruder being driven from the area.

On visits to nest sites of 15 minutes or greater, the defense of the territory by the adult pairs often attracted other peregrines. Occasionally these were yearling birds but most often they were adults. Such birds usually arrived from a high altitude and their presence was announced by a change in vocalizations of the adults defending the territory. The "cacking" call, usually given in interspecific defense, changed to the "eechip" call, which is given in intraspecific interactions (terminology of Nelson 1977). In most cases, at least one adult from the territory attacked the intruding falcon. On some occasions the intruding peregrine initiated the aggression. Interactions were at least as serious as those observed in the spring, and bodily contact was not uncommon.

Fidelity to Nest Sites, Population Turnover, and Mortality

Considering the logistical difficulties involved in marking populations of raptors, it is not unexpected to find a paucity of information regarding the population dynamics of these birds. The best published information on the peregrine comes from a six year study in Scotland by Mearns and Newton (1984). For comparative purposes, I have analyzed population turnover and mortality data for the population at Rankin Inlet using the same techniques. With these methods, one examines whether the bird identified at any territory in a second year was the same bird identified the year before, or a different one. A territory was included more than once if its occupant was identified in more than two years, the unit of observation being one territory per year.

At Rankin Inlet, of 19 territories where males were identified in successive years, on 16 it was the same individual in the second year and on three it was a different one (Table 3.2). Of 37 territories where females were identified in successive years, on 26 it was the same individual in the second year and on 11 it was a different one (Table 3.3). Annual turnover for each sex was therefore 3/19(16%) for males and 11/37(30%) for females. For both sexes combined it was 14/56(25%).

Mearns and Newton (1984) found that a significant portion of the population turnover, at least with females, was due to movements between territories. At Rankin Inlet, of 16 males that were identified at territories in a later year, all were at the same territory. Of 27 females identified at territories in a later year, all but one were on the the same territory. Since the study area was relatively small, 450 km^2, and the marked status of all pairs on the area was sufficiently well known, it is possible to say that none of the missing birds had relocated to other territories on the study area. After considering the effect of movements between territories (within the boundaries of the study area), the maximum possible annual mortality rate would be: females 27%(10/37), males 16%(3/19), and for both sexes combined 23%(13/56).

At least within the confines of the study area, these results suggest a high degree of fidelity to the nest site. The one female that changed territory moved only 3.5 km. In the period between 1981 and 1985, four females had been present at the same territory for at least four years, four others for at least three years, and seven had been at the same territory for at least two years. For male peregrines, three had been present at the same territory for at least four years, three for at least three years and one was known to be at the same cliff for at least two years. The longest period recorded that a pair remained intact was four years.

Table 3.2 Maximum losses of male peregrine falcons from the study population in different years (after Mearns and Newton 1984)

	1982	1983	1984
Identified on territories where identification was also possible in the next year	5	7	7
Identified on the same territories in the next year	5	7	4
Identified on different territories in the next or later year	0	0	0
Total identified in a later year	5	7	4
Maximum loss	0(0%)	0(0%)	3/7(43%)

Table 3.3 Maximum losses of female peregrine falcons from the study population in different years (after Mearns and Newton 1984).

	1982	1983	1984
Identified on territories where identification was also possible in the next year	9	12	16
Identified on the same territories in the next year	6	9	11
Identified on different territories in the next or later year	0	0	1
Total identified in a later year	6	9	12
Maximum loss	3/9(33%)	3/12(25%)	4/16(25%)

Territorial Behavior

As predicted from the findings of other students of the peregrine (Cade 1960, Ratcliffe 1962, 1969, 1980, Nelson 1977), territorial interactions were not frequently witnessed, even under the optimal conditions presented at Rankin Inlet. However, I believe that on this study area, particularly in the early spring, the frequency of such interactions was much higher than most peregrine populations yet studied. The data obtained are limited, but were sufficient to address the question as to whether or not there existed strong competition for traditionally used nest cliffs. Details of actual aggressive encounters between falcons over nesting territories also allowed an evaluation of the importance of territorial behavior as a mechanism for pair spacing.

Aerial combat and chases were always accompanied by 'eechip' vocalizations (Nelson 1977) and frequently involved bodily contact. Grappling in flight as described by Nelson (1977) was occasionally observed but serious fighting on the ground was not witnessed. On one occasion such a contest is believed to have resulted in the death of an adult male peregrine. The bird was found at the base of a nest cliff and had been decapitated, plucked slightly in the area of the neck, but was not eaten. Similar remains have been recorded following prolonged aerial combat for both peregrine falcons (Hall 1955) and prairie falcons (*Falco mexicanus*)(R. Fyfe pers. comm.)

Observations encompassed a total of 195 hours. Sixty-one separate territorial interactions were recorded in which a resident flew from the cliff towards an intruder and engaged in a chase. Interactions involving sub-adult birds were comparatively rare and were never recorded before breeding had commenced; these were excluded from all analyses. Of all chases, 57(93%) were sex specific interactions. Two chases involved females pursuing males and two involved aggressive flights of males towards females. Of the sex specific chases, 35 involved a chase between a resident male and a male intruder. In only one case was the original resident known to have been driven from the cliff. Female to female chases were recorded on 22 separate occasions. Both males and females that were categorized as residents at the cliffs observed were, in some situations, replaced as territory holders before breeding commenced. With the exception of the male mentioned above, the behavioral interactions associated with these replacements were not witnessed.

Interaction rates were calculated using only data on aggressive chases between adults. Vocalizations, aggressive posturing, and display flights related to territorial interactions were not considered in the analysis. To illustrate the trend in the frequency of territorial interactions throughout early spring, interaction rates were calculated for four separate periods of approximately 10 days each (Table 3.4). A Stuart-Cox Test for Trend (Conover 1980) established that there was a significant drop in the interaction rate as spring progressed ($P<.05$). Low sample sizes precluded any comparison of interaction rates between 'clustered' and 'isolated' classes of nest cliffs, the raw data do not suggest any difference between classes.

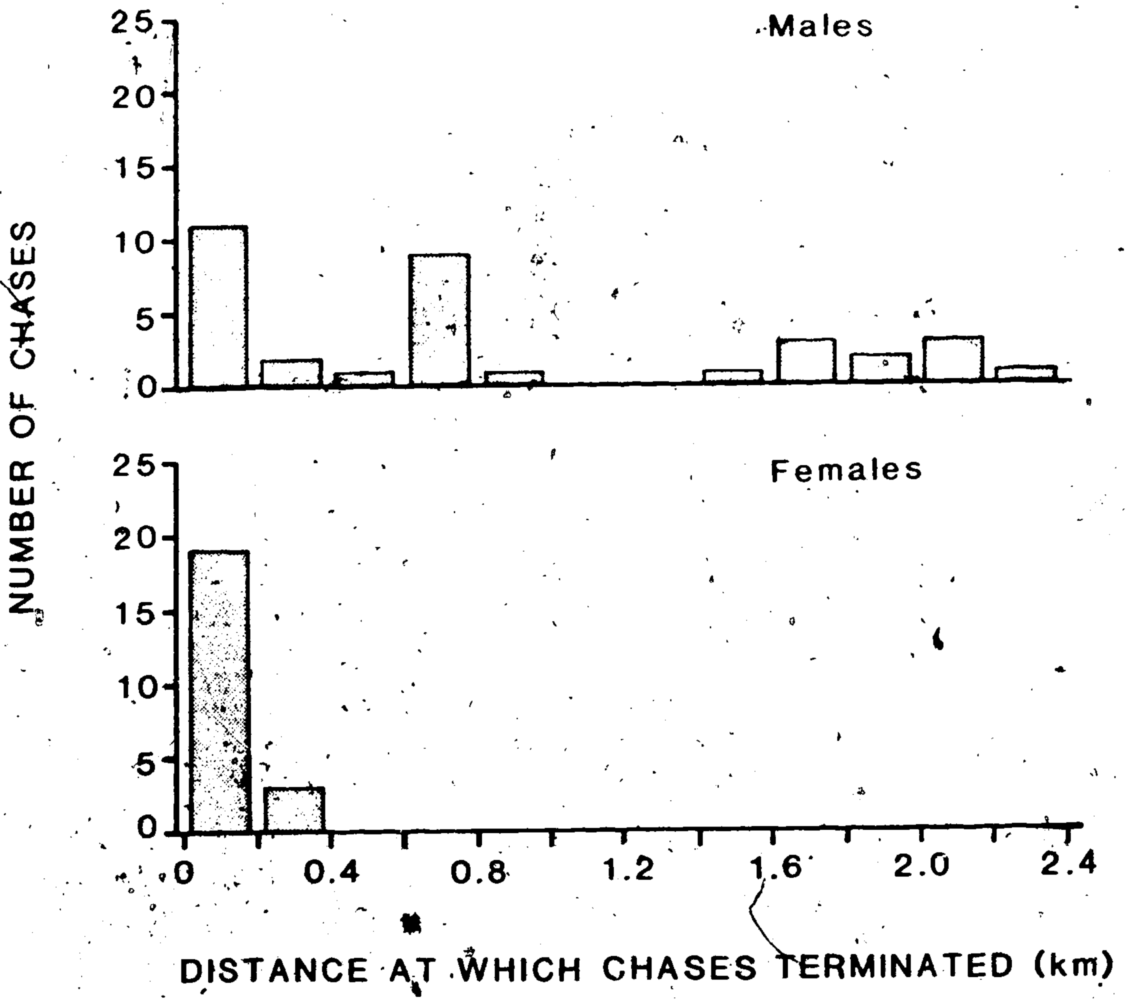
Map plots of actual chases provided some information on possible limits of defended space for pairs in the population. There was considerable variation in the distance that individuals, or the same individual, would initiate or terminate territorial interactions. Contiguous boundaries could not be identified between neighboring territories and there was little to suggest that any or all interactions between a resident pair and an intruder involved members of neighboring pairs.

Serious aerial combat in the immediate vicinity of nest cliffs could last several minutes but usually degenerated to a chase away from the cliff. Male peregrines terminated these chases at significantly greater distances (n = 34, median = 800 m, range = 50-2250 m) than did females (n = 22, median = 140 m, range = 40-350 m) (Mann Whitney U Test U = 125.0 $P<0.01$) (Figure 3.2). Males defending isolated nest sites chased intruders over significantly longer distances (n = 22, median = 900 m, range 50-2250 m) than did males at clustered sites (n = 12, median = 250 m, range = 50-1000 m) (Mann Whitney U Test U = 70.5 $P=0.02$). There was no significant difference in the pursuit distances of female peregrines at the two different types of nest sites (Isolated Sites - n = 9, median = 60 m, range = 40-350 m, Clustered Sites - n = 13, median = 150 m, range = 50-220 m Mann Whitney U Test U = 51.0 $P=0.65$). In many cases chases between males were followed by high altitude display flights back to the nest cliff by the resident male.

Table 3.4 Territorial behavior of adult peregrine falcons in the Rankin Inlet study population during spring months

Observation Period	Total Hours of Observation	Total Chases Observed (Interaction Rate (No./hr))	
		Males	Females
May 20-31	73	28 (0.38)	16 (0.22)
June 1-10	50	2 (0.04)	4 (0.08)
June 10-20	28	4 (0.14)	2 (0.07)
June 20-30	44	0 (0.00)	0 (0.00)

Figure 3.2 Distribution of pursuit distances for spring territorial interactions of male and female peregrine falcons nesting at Rankin Inlet, N.W.T.


NUMBER OF CHASES
Males
25
20
15
10
5
0
Females
25
20
15
10
5
0
0
0.4
0.8
1.2
1.6
2.0
2.4
DISTANCE AT WHICH CHASES TERMINATED (km)

Discussion

Territories and Turnover of Territorial Pairs

From Figure 3.1 it is clear that Falcon pairs occupied some territories every year, others in most years, and some territories only once in five years. Of the 29 nesting territories used between 1981 and 1985, only ten were occupied in all five years. Banding studies have shown that this pattern is not explainable in terms of alternate nest site use or movements of adults between territories. Some pairs that occupied territories for as long as three years simply disappeared and territories were left vacant. At other territories pairs of birds appeared, often bred successfully, but were absent the following year. These territories were often occupied by completely new pairs in later years. Hickey (1942) suggested that there exist different 'grades' of nest cliffs, identified by their dimensions and history of use. He noted that "first class" cliffs were often very high and were always occupied, even if pairs using them were continually persecuted and suffered poor productivity. The occupancy pattern described for Rankin Inlet suggests a similar situation and it is possible that cliffs with the highest vacancy rate are somehow less suitable for nesting.

At territories used only once in the five years ('irregulars'), there was nothing to suggest that members of these pairs had previously nested in the area. Such birds were particularly evident in 1985 when 'new' pairs established territories at alternative nest sites of pairs at 'regular' territories or on available nesting habitat between such territories. Ratcliffe (1980) also noted that such 'new' pairs could occupy alternative nest sites and occasionally contributed to an increase in population density. He concluded, however, that such pairs were usually unsuccessful and sooner or later disappeared. At Rankin Inlet, however, a comparison between the mean number of young fledged at nest sites occupied in only one year (n=6) and that from sites occupied in all five years (using 1985 production only, n=10), did not indicate a significant difference (Mann Whitney U Test U=16.0 P=0.14). The peculiar aspect of these 'new' pairs in Rankin Inlet was that, although often successful, they failed to return to the cliff the next year. Some members of these pairs were color banded, yet these were never recorded in the breeding population in subsequent years. These results suggest that a certain percentage of the breeding population in any one year will occupy territories the location of which cannot be predicted from one year to the next.

The population turnover analysis, based on the presence or absence of territory holders in consecutive years, showed a high degree of fidelity to nest sites by both sexes at regularly occupied nest sites. This is particularly apparent when one considers the small contribution (2%) that between-territory movements made to turnover figures (25%). Mearns and Newton (1984) noted that 8% of an annual adult turnover of 19% was attributable to movement. Adults that changed territories moved from 3 to 33 kilometres. A movement of the latter distance would take birds well beyond boundaries of the study area, and hence would not be detected. The dearth of nesting habitat outside of the study area also suggests that if such movements occur, they would be even greater in size than those reported by Mearns and Newton (1984).

As movements between territories apparently contributed little to turnover rates in this population, most of the annual turnover observed can be linked to mortality. The maximum annual mortality rate of 23% (sexes combined) was high relative to that recorded for the only other study based on mark and recapture of adult peregrines. Mearns and Newton (1984) recorded a maximum annual mortality of 11%. This difference may indicate population differences; certainly the severe arctic climate at Rankin Inlet and the much more extensive migration of the tundra peregrine are considerations in this regard. Mearns and Newton (1984) were working with a population at a more temperate latitude comprised of birds which apparently do not move far, if at all, from the breeding area in winter months (Ratcliffe 1980). The climate at Rankin Inlet is probably as severe as at any location in the range of the peregrine falcon and birds from this population are known to winter as far south as Uruguay.

Some evidence that this mortality estimate is valid comes from ~~other~~ studies based on band recovery data which placed annual adult mortality for peregrines at 28% in Finland (Mebs 1971, in Mearns and Newton 1984) and as high as 32% in Swedish populations (Lindberg 1977). Enderson (1969) estimated adult mortality of North American populations at 25%, similar to the estimate obtained here. Mearns and Newton (1984), however, pointed out that band recovery data for raptors (Newton 1979) and other species of birds (Perrins 1971) usually provide an over-estimate of adult mortality. The authors also note that many of the higher estimates were calculated for populations showing the effects of pesticide pollution. Indeed, Enderson (1969) concluded that a mortality rate of 25%, considering reproductive parameters for most peregrine populations, is indicative of a declining population.

The reproductive performance of the study population at Rankin Inlet does not indicate a pesticide problem at present, and a 23% annual adult mortality is not unreasonable in view of this high productivity. This is clearly illustrated by simulating the population's growth or maintenance, varying annual adult mortality, using a 66% mortality of juveniles in their first year (approximately mid-range between previous estimates 56% (Hickey and Anderson 1969) and 70% (Enderson 1969)), and reproductive statistics for the population, namely a 74% nesting success and an average brood size of 2.7 young (1981-1984). At an annual adult mortality of 25% the population would remain stable. Dropping adult mortality to as low as 20% produced an adult cohort that, in less than 20 years, doubled that of the present breeding population. As a 23% annual mortality of adults lies between these extremes, it is not indicative of a declining population.

Although a 23% annual adult mortality is conceivable, it should be noted that this estimate was obtained using a small sample and that there are several factors which could contribute to possible error. As noted, the most significant cause of overestimating mortality would be movement between nesting territories. Such movement might be prompted by the strong competition for nest sites that exists at Rankin Inlet. It is possible that some individuals, banded in previous nesting seasons, are forced to nest elsewhere, or do not breed at all. This would inflate the mortality estimate. The observation that some adult peregrines on the study area are on territories for only one year before replacement tends to add support to this idea. It is probably also noteworthy that the low adult mortality estimate obtained by Mearns and Newton (1984) was for a population recovering from a population crash. Such birds would have access to an abundance of nesting habitat, perhaps making the effects of competition for nest sites negligible.

Population Limitation

Of the phenomena summarized by Newton (1979) and interpreted as supporting density limitation in breeding raptors, only constancy in the size of the breeding population and the existence of non-breeding adults would apply to the study population. Relative constancy in the number of breeding pairs is well established for many peregrine populations (Cade 1960, Ratcliffe 1962, Hagar 1969). Such constancy was observed in the study population for years 1981 to 1984, even though some of the pairs making up the yearly totals were not always at the same territories from year to year. In any case 19 or 20 territorial pairs appeared to represent a maximum density for the peregrine population on the study area. The appearance of six new pairs in 1985 seriously challenged that conclusion.

As discussed in Chapter 2, there is strong evidence that this population increase was related to increased abundance of at least one prey species. Newton (1976, 1979) predicted constancy of raptor populations only in stable environments; this includes stability of a food source. Peregrine populations have been known to decrease in response to declining prey abundance (Ratcliffe 1962, Nelson 1978), thus an increase in response to abundance is not difficult to accept. It should be noted, however, that these population declines occurred over substantial time periods, much greater than one year. In any case, the increase seen in 1985 does challenge the assumption that density of the study population was limited to 19 or 20 pairs. A possible explanation for this increase, in support of population limitation, comes from observations of variable territory sizes in other raptor species wh[illegible] utilize prey which is periodically super-abundant (see below).

Another major source of evidence for population limitation is the existence of a non-breeding cohort in the population. The presence of such birds, which are themselves capable of breeding, is basic to any argument refuting Lack's (1954, 1966) claim that territoriality serves simply to spread out surviving individuals rather than actually limit the density of breeding pairs. Evidence for a non-breeding component in peregrine populations comes from records of single-season mate replacements and rapid recovery of heavily persecuted populations (Ratcliffe 1962, 1980, Newton 1976, 1979). The observations of non-breeding birds at Rankin Inlet also provide evidence that these birds exist.

There are a number of arguments, however, that could, if true, invalidate these observations as evidence for population limitation. Possibly the birds replaced at territories in the spring were forced to move off and simply bred elsewhere, perhaps at nest sites that were of lower 'quality'. For the most part this seems unlikely, as many of these birds were involved in agonistic interactions with pairs up until, and frequently after, laying had been initiated. These birds would then have had a very short period of time in which to find a mate and breed. At the very least, such birds might show a significant delay in their nesting chronology. Many of the peregrines nesting outside the study area do use nesting habitat which, at least to the human eye, looks extremely poor relative to most nest cliffs used by the study population. Some cliffs are no more than 3 m high with virtually no protection from ground predators. Nevertheless, birds using these sites did not show a delay in their breeding chronology.

The possibility exists that the intruding adult peregrines encountered at nest cliffs later in the breeding season were simply members of neighboring pairs. This could have been true for the two unbanded females recorded with territorial males of banded pairs, as well as those falcons drawn in by defense behavior of territorial pairs. The banded status of females at neighboring nest sites eliminated the possibility of the former. The fact that peregrines were drawn to the defense behaviors of pairs at both 'clustered' and 'isolated' sites suggests that these birds were not always members of neighboring pairs. Also, if one considers the severity of the fighting that resulted in such situations, it is difficult to understand why such aggression would occur between birds already in possession of territories. Anecdotal observations such as these, suggest the existence of a non-breeding component in the population, but provide no impression of the size of such a component. Nelson (1977) speculated that these birds may number from 50% to 100% of the breeding population.

Recorded recruitment into the study population also suggested a large number of non-breeders. Peregrines successfully obtained territories in the study population at two and three years of age. As of 1985, 105 young banded within the study area between 1981 and 1983 were at least two years old. Assuming the maximum annual mortality of juveniles to be 66% (from the population simulation mentioned earlier) and a maximum annual adult mortality of 23%, at least 21 (20%) of the young produced between 1981 and 1983 would have been available as recruits for the study population. Only three of these (15%) had obtained territories by 1985. The absence of the remaining 18 birds suggests that either juvenile mortality is much greater than estimated for this population, there is great dispersal of young from the breeding area, and/or there exists a substantial reservoir of unrecorded non-breeding birds within the study area.

As with the adult birds, high mortality of juveniles relative to other populations is a possibility, particularly considering the severe nature of the arctic climate during the post-fledging period and the fact that these birds have a very short time in which to gain independence before migration. The extraordinary length of the migration of arctic peregrines relative to other populations may also induce higher mortality. Dispersal between birthplace and subsequent breeding site could also explain the absence of marked recruits in the Rankin

Inlet population. Mearns and Newton (1984) recorded median dispersal distances for male and female peregrines of 20 and 68 km, respectively, values that are biased by not finding distant dispersers. Birds dispersing greater than 30 km would not have been detected in the study population. Again, the dearth of nesting habitat beyond the study area suggests that any such movements would have to exceed 30 km by a considerable margin.

Although the effects of emigration have been considered in the interpretation of results, it should be noted that peregrines immigrating onto the study area could also contribute to the number of non-breeding adults. Also, the potential excess discussed thus far, in terms of local recruits, has included only locally produced birds under four years of age. Peregrines are known to live up to 18 years in the wild (Hall 1955). Therefore it is entirely possible that there could exist a substantial number of locally produced, unbanded birds, over four years of age, that are not breeding. Some support for this possibility comes from the fact that, of the 12 adult peregrines making up the six new pairs in 1985, only one was known to be a banded bird.

Newton (1979) noted one curious feature of raptor populations that seems to question the existence of non-breeding birds. Although there is evidence for a surplus of breeders, not all territories are occupied in all years. Some are deserted, while others are occupied by single adults. The same pattern was noted on the Rankin Inlet study area. Ratcliffe (1962) discussed this and noted that with the desertion of one territory there is often a new one established somewhere else, thus population constancy is maintained. Even in very dense populations it was not unusual to observe unused territories in some years. For example, at Rankin Inlet one territory used before 1985 was unused in that year of very high population density. Ratcliffe (1962) attributed this phenomenon to a "resistance to overcrowding" which apparently varies from time to time and occasionally allows 'new' pairs to be established. In this way, Ratcliffe (1962) hints at variability in territorial influence, a key assumption in the explanation of the population increase in Rankin Inlet discussed below.

Territoriality

Evidence presented in the previous section suggests that the density of the population under study is limited. Is territoriality involved in this limitation? Does strong competition exist for nest sites in this population? Does territorial behavior of the birds themselves account for the pattern of pair spacing? Does territoriality create a non-breeding surplus in the population by preventing some birds from breeding between traditionally occupied territories?

Unlike many other populations of the peregrine located at more temperate latitudes, the falcons at Rankin Inlet occupy the nesting area for a very well defined period of time each year. The birds occupy the nest cliffs immediately upon arrival in spring when intraspecific territoriality is manifested. The intensity of agonistic interactions among peregrines at nesting territories is clearly evident to the observer. That mortality occasionally results from such competition is testament to this appraisal. The frequency of territorial interactions dropped sharply as spring progressed (Table 3.4). This suggests that the birds compete vigorously for territories when they arrive in May, and that competition drops off as pairs are established and breeding begins.

Territorial interactions observed between birds in the study population did not appear different to those reported in previous studies (Cade 1960, Nelson 1977), with a few notable exceptions. Cade (1960) described encounters where both members of a pair attacked intruding birds and that such attacks were preceded by the "cacking" call. Birds in the study population never gave this call intraspecifically, and most interactions were accompanied by the "eechip" vocalization, an observation consistent with that of Nelson (1977). Although both adults often took to the air during encounters, most chases included only two birds and were most often sex specific. The only time that both members of a pair regularly combined efforts in attacks was well after incubation was underway. Such attacks were frequently directed at birds in sub-adult plumage that appeared late in the summer. These interactions were excluded from the analysis.

Although it is apparent that adult peregrines compete for territories each year, the influence of territorial behavior on population limitation seems less clear. From the data male peregrines appeared more territorial, both in terms of the frequency of interactions and in the distance to which they would pursue an intruder of the same sex. Pursuit distances of females suggested that they defended only the immediate vicinity of the nest. This explained the apparent tolerance of other females in the vicinity of the nest cliff early in the spring. Taken together, these observations suggest that the critical resource for any female might only be a male in possession of a nest cliff. Thus, the actual density of the population would be set by interactions among the males.

The median pursuit distance for male-male interactions in early spring was 800 m. If this is taken as a radius of repulsion for falcon territories, then territorial aggression can explain internest distances of up to 1.6 km. As can be seen in Figure 3.1, many pairs were separated by greater than 1.6 km, often with much suitable nesting habitat between them. Also, many pairs in the study area were separated by substantially less that 1.6 km, however, these were never in view of one another. Males at these 'clustered' sites showed a median pursuit distance of only 250 m, possibly indicating that their defense distances were shortened in deference to the nearby pairs. Interestingly, an internest distance based on this median of 250 m is 0.5 km, the approximate absolute minimum internest distance reported for at least six different peregrine populations from Britain, Alaska, and the Queen Charlotte Islands (summary in Nelson 1977).

These observations, considered in relation to the distribution of nest sites and the availability of nesting habitat at Rankin Inlet, do not suggest that falcon territories are contiguous, or even that they represent areas of a discreet size with defended borders. The pattern seen here more closely approximates the model of spatial occupancy for northern peregrines proposed by Cade (1960). Here the nest cliff is viewed as the centre of a large home range and territory is considered as a series of threshold perimeters around the nest cliff itself; the tendency to defend the territory decreases as the distance away from the nest increases. Cade (1960) considered that there is some minimum perimeter around the nest, perhaps 110 m, that is defended at all times, but believed that attacks initiated at greater distances occur unpredictably. Outer perimeters included areas where intruders are sometimes attacked and a more distant zone where attacks occurred only over items of food or favorite perch points.

To borrow from this model, perhaps the male peregrines at Rankin Inlet also defend territories with the nest cliff at the centre and exercise dominance over a plot of terrain, but the ability to maintain that dominance status decreases as they move out from the nest site. Perhaps some males, being more dominant, will defend larger areas than others, thus explaining some of the variability in internest distance seen in the study population. Certainly, some of the more distant chases observed at Rankin Inlet (up to 2.2 km) demonstrate that agonistic interactions between adult peregrines can occur a considerable distance from the nest cliff.

It is possible that in some situations much of the nesting habitat defended by any male is poor relative to other areas. Thus, the pressure from other birds to establish at nest cliffs nearby could be quite low, tending to exaggerate the size of the apparent territorial influence of any pair. Conversely, in areas where nesting habitat is of higher quality, pressure from other falcons for use of space, manifested in the form of higher rates of territorial interaction, might force pairs, or males, on the basis of energetics, to increase their threshold of territorial defense and thus allow other pairs to establish nearby. In support of this, Village (1983) explained variation in the size of territories of the European kestrel by proposing that such variability reflects greater pressure on nesting pairs from intruders in areas where the density of usable nests was greatest. A similar situation could exist in the study population where low internest distances in some areas may reflect greater pressure from potential breeders for nest cliffs that are somehow more 'desirable'. This seems possible, particularly if such nest cliffs are not in view of one another. Nests in the areas of highest nesting density at Rankin Inlet were never in view of one another.

If the variation in both pursuit distance of males and internest distance observed at Rankin Inlet can be explained by greater pressure on nesting pairs from intruders in some areas than in others, then one would expect higher rates of territorial interaction at these cliffs. Observations designed to test this would have to separate interactions resulting from closer nesting neighbors and those resulting from contact with intruders; color marking could aid in this regard. Although the limited information obtained here did not suggest a difference in interaction rates between the two types of sites, more data, facilitating a more comprehensive comparison of interaction rates between 'isolated' and 'clustered' types of nest cliff, are needed to adequately address this question.

Territory and Food Supply

Village (1983:644), in his investigation of the role of nest site availability and territorial behavior in limiting the breeding density of European kestrels concluded: "...although food supply may have ultimately been limiting breeding numbers, its effect was mediated through the behavior of breeding pairs reducing the availability of nests." If we assume that territoriality plays a similar role in determining the density of breeding peregrine falcons at Rankin Inlet, then the population increase observed in 1985 is particularly instructive in terms of territory dynamics. Nelson (1977, 1978) concluded that territory size of peregrines was related to prey abundance and was adjusted, albeit slowly, to ensure adequate food supply. He suggested that territory size would not vary appreciably from one year to the next as the food supply of peregrines tends to be stable, a fact that is reflected in the synchronous hatching of their eggs. Asynchronous hatching in raptors is normally recognized as an adaptation to a variable food supply (Lack 1954).

In 1985 the peregrine population in Rankin Inlet increased by about 30% and the productivity of nesting pairs was greater than in any of the previous four nesting seasons. There is evidence that this increase was related to an increase in prey abundance (a lemming high). New pairs set up territories at alternative nest sites of other more regularly producing pairs, established 'new' territories between traditionally used nest sites, and the less regularly occupied territories were, with one exception, all occupied in this year. This correlation suggests that territory size was reduced in response to increased prey abundance. Assuming that this is a valid explanation, then the resident birds must have reduced the radius of territorial influence over a very short period of time to allow new pairs into what was in other years defended space. The similarity between the response of this population of peregrines and that of certain lemming predators, such as the parasitic jaeger and short-eared owl (Lockie 1955, Pitelka et al. 1955), is striking. A similar response was also documented for the European kestrel, where territory sizes were smaller and nesting densities were higher in a year of high prey abundance (Village 1983).

Such a dramatic and sudden shift in territory size directly contravenes Nelson's (1977) model of peregrine territoriality which requires long-term stability of territory size. Indeed, the long-term stability in the size of peregrine populations (Cade 1960, Ratcliffe 1962, Hagar 1969) suggests that an increase of this magnitude is highly irregular. Interestingly, Nelson indirectly made allowances for such an increase in attempting to explain asynchronous hatch in northern populations of peregrines, a phenomenon widely reported for the arctic subspecies (Dementiev 1951, Enderson et al. 1972, Burnham and Mattox 1984, R. Fyfe pers. comm.). Nelson (1977:315) suggested:

> "...apparently this allows later-hatched young to be 'sacrificed' so that a few strong young rather than a number of weak young are reared in those years when occasional harsh weather occurs in the breeding season and significantly reduces prey abundance. Under northern conditions one could expect territory size to contain an extra buffer against sporadic weather while still being established in relation to the long-term carrying capacity of the area."

If one accepts this conjecture and considers what may happen when prey is periodically superabundant, it is possible that a reduction in the defense of this "buffer" zone could allow additional pairs into the habitat, providing an explanation for the population increase of 1985.

It is interesting to speculate on the possible mechanism through which this change could have occurred. During this year of increased abundance of lemmings, falcons arriving in spring woul[illegible]d a plentiful and easily caught food source. Indeed, it has been suggested that lemmings may be particularly vulnerable around the time that peregrines arrive (late May), as spring thaw is underway and many of these animals may be flooded out of their burrows (F. Mallory pers. comm.). The falcons might be able to achieve rapid increase in body condition resulting through a combination of abundant food and reduced foraging time. As the amount of time spent away from the nest cliff on hunting forays decreased, so would the frequency of contact with other falcons. Agonistic interactions with other birds frequenting alternative nest sites or perch points would be less common. Despite the extreme mobility of the peregrine and the density of the population at Rankin Inlet, this conjecture remains possible because a reduction in the frequency of agonistic interactions, over what in previous years was defended space, could result in new pairs becoming established at either alternate nest sites of traditionally used territories, or on suitable habitat between such territories.

It is also possible that potential incoming pairs might be in better physical condition in years of high prey abundance and could provide more vigorous competition for nesting space. Some of this speculation is supported by Village (1983), who found that, in good vole years, European kestrels defended smaller areas around their nests. This apparently permitted more pairs to use nests that were normally unavailable in years of low rodent abundance. Village (1983) could not determine whether the reduction in territory size was a result of decreased aggression of original occupants or increased persistence of incoming pairs. However, the greater intensity and duration of territorial interactions (fighting) in the year of high prey abundance suggested the latter.

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IV. Factors Affecting Reproductive Success of Pairs of Peregrine Falcons at Rankin Inlet, N.W.T.

Introduction

Numerous detailed studies of breeding raptors, particularly those conducted over a number of consecutive seasons, have contributed to a considerable body of information on factors which affect breeding rates of these birds (review in Newton 1979, Chapter 8). The more detailed of these studies have documented a reduction in reproductive output during each phase of the breeding cycle, including failure of pairs to lay, complete nest failures over eggs or young (Craighead and Craighead 1956, Newton 1976, Craighead and Mindell 1981), and in some cases losses of individual eggs or young from successful nests (Mebs 1964, Newton 1976). Newton (1979) summarized a wide variety of factors, both biotic and abiotic, which directly relate to these losses, and to reduction of breeding success among raptors in general. The aim of this chapter is to document annual reduction in breeding success in a population of peregrine falcons nesting at Rankin Inlet, N.W.T., and to investigate a number of factors which may directly cause this reduction. I examine the effects of age of adults, experience of adults on nesting territory, and intraspecific nesting distance and density on reproductive success in this population. Additionally, I assess the relative contribution of brood reduction, resulting from asynchronous hatching, to annual reduction in reproductive output.

In many species of birds, individuals breeding for their first time are characterized by later laying dates, smaller clutch size (Kluijver 1951, Newton 1976, Finney and Cooke 1978), and occasionally, lower probability of breeding success (Ravelling 1981). At Rankin Inlet it was possible to investigate the effects of age on breeding success on a very limited scale. Color marking of the adult population also made it possible to compare breeding success of individuals with varying experience (one year versus more than one year) on a nesting territory. The strong fidelity of local peregrines to nesting sites (Chapter 3) suggested that falcons on a territory for the first time may also have been breeding for their first time. This possibility was also considered in the interpretation of results.

In dense populations of raptorial birds, social interactions involving both interspecific and intraspecific strife have been associated with reduced breeding success (Schmutz 1977, Schmutz et al. 1980, and Gargett 1971, 1975, in Newton 1979). Schmutz et al. (1980), in a study of ferruginous (*Buteo regalis*) and Swainson's hawks (*Buteo swainsoni*), found that the chance of nesting failure increased with increasing proximity of nests. The authors attributed this to elevated levels of interspecific aggression between close nesting pairs. Gargett (1971, 1975, in Newton 1979) found that black eagles (*Aquila verreauxi*) used a variety of nests within each of their territories, but tended to avoid using nests close to those of pairs from neighboring territories, particularly when such nests were directly in view of one another. He noted that pairs nesting close to one another were more likely to fail, and showed significantly poorer nesting success, than those more widely spaced in the population.

From Chapter 2, it is clear the density of peregrine falcons nesting at Rankin Inlet is among the highest on record, an observation supported by the fact that some of the nests in this population are less than 1000 m apart (Figure 3.1). From Chapter 3, it is apparent that there exists a considerable level of intraspecific competition for nest sites in this population, and that aggressive encounters between territorial pairs and other peregrines throughout the breeding season are not uncommon. In consideration of the high population density and the level of intraspecific strife observed, it is not unreasonable to suggest that pairs nesting in close proximity might be prone to higher levels of intraspecific conflict, possibly reflected by lowered reproductive success. This possibility was tested with the data from Rankin Inlet.

Asynchronous hatching has been reported for a wide range of bird species (review in Clark and Wilson 1981). The competitive disadvantage faced by later-hatched members of such broods often results in brood reduction. In many raptor species, this reduction is often enhanced through fratricide and cannibalism by older brood members (Ingram 1959, Bechard 1981). Lack (1954) proposed that asynchronous hatching and associated brood reduction represent an adaptation of birds having a long nestling period, and utilizing an unstable food supply. He suggested that with this mechanism, birds could fledge large broods in years when food was abundant, but in times of scarcity, broods would be reduced to a size which adults could successfully feed.

Asynchronous hatching is not frequently recorded for the peregrine falcon, an observation that suggests a high degree of stability in its food supply (Ratcliffe 1980). Most records of asynchronous broods in this species come from populations nesting at arctic latitudes (Dement'ev 1951, Enderson et al. 1972, Burnham and Mattox 1984). Brood reduction associated with such asynchrony has been reported (Enderson et al. 1972), but the effect of this mortality in terms of the annual productivity of an entire population has not been addressed.

Asynchronous hatching and associated brood reduction were commonly observed in the population of peregrines at Rankin Inlet, and the relative access of nest sites in this area provided an opportunity to measure accurately the frequency of this phenomenon. The relative impact of mortality associated with asynchronous hatching on the reproductive success of the population was determined. This intensive study also made it possible to investigate the causes of brood reduction and to assess whether this phenomenon occurs in this population for the same apparent reasons it does in other raptor species. The patterns observed permitted speculation on the adaptive significance of asynchronous hatching in arctic peregrines.

Methods

Data on reproductive success used in the analyses were collected over five consecutive nesting seasons, 1981 to 1985. Detailed information on hatching success and mortality of newly-hatched chicks was available only in 1983 and 1984. Details of nest losses and desertions were obtained on helicopter surveys conducted during incubation, and through periodic visits to nests throughout the entire nesting season.

The relationship between previous experience on nesting territory and reproductive success was evaluated through trapping and banding of adult peregrines (Methods, Chapters 2 and 3). Trapping was initiated in 1982, thus, information on the success of peregrines with varying experience on territories in the study area was available from 1983 to 1985. Only female peregrines were used in the comparison because the number of males for which experience on a territory was known (9) was too low for meaningful comparisons. Although reproductive success of individuals with as many as four years experience on the same territory was known, statistical comparisons were limited to between samples of females breeding at a territory for their first time (at least within the study area) versus those occupying the same territory for two years or more. The effects of any potential differences in territory 'quality' were assumed to be negligible.

The effect of intraspecific nesting proximity on reproductive success was evaluated each year, 1983 to 1985. The analysis involved determining the relationships between clutch size, percent of eggs hatched within each clutch (hatching success), number of young fledged and distance to nearest neighbor. As Schmutz (1977) pointed out, this analysis takes into account the impact of only one nesting pair on the reproductive success of another. Therefore, to strengthen the analysis, the cumulative impact of all pairs nesting within a radius of 3.3 km (the mean internest distance for the population) of each nest site was considered. Here, the density of pairs in the area defined by this circle was again compared to clutch size, percent of eggs hatched, and number of young fledged. Data on hatch success were not available for 1985.

The effects of hatching asynchrony on the survivorship of nestlings, and on the productivity of the population in general, were evaluated in 1983 and 1984. In these years, all nests within the study area were routinely visited during the time of hatch. On these visits, hatch order was determined and each chick was marked for future identification. The ages of chicks were determined on these visits by observing hatch progress and, in some cases, predicting time of hatch; chicks still moist from the egg were assumed to be less than 24 hours old. In most cases, time of hatch was obvious, but occasionally age had to be estimated from parameters such as the day at which eggs pipped (assuming hatch to follow approximately two days following pipping (H. Armbruster, pers. comm.)), or from body weight comparisons with chicks from the same hatch position and of known age. The margin of error in estimates is believed to have been no greater than one day.

After these initial assessments of hatch order, degree of asynchrony, and age of chicks, nests were visited at least three times before the young were 30 days of age. The body weight of chicks from each hatch position was recorded on each visit. Chicks under seven days of age were weighed with a 0-200 g Pesola scale; older chicks were weighed using a 0-2000 g Pesola scale. In the event that young had been recently fed, weight of crop contents was estimated and substracted from the total weight. Visits to nests were as brief as possible and had no noticeable effect on the nesting success of pairs; there were no nest failures or desertions recorded immediately following these visits.

The growth of chicks from all four hatch positions was compared using data from broods in which the fourth hatched chick survived to fledging. Growth curves were compared graphically, and an analysis of covariance was used to compare the slope of weight gain over time for chicks from all four hatch positions. Only data from the straight line portion of growth curves were used. Because they are dimorphic, male and female nestlings were analysed separately.

To evaluate conditions of early nestling life which may have contributed to the mortality of last hatched nestlings, falcon nests were monitored using time-lapse super-8 cameras (Temple 1972). Cameras provided a continuous record of events at three nests where pairs were successful in hatching all four eggs, at two sites the last-hatched chick died and at one it lived. The cameras recorded nest events every three minutes and the segment of film analysed included the five days after the hatch of the youngest brood member. All nestling mortality associated with asynchronous hatching occurred within this period. Analysis of films was designed to elucidate any differences in feeding rate, parental attendance (brooding or shading young), and in the sizes of prey items fed at each nest site. Inattentive periods were measured by calculating the percentage of frames in any day in which the female was not either feeding, brooding, or shading young.

Results and Discussion

Total and Partial Nesting Failure, Losses of Eggs and Young

Failures may occur at any point during the nesting season and may involve either failure of territorial pairs to lay, losses of entire clutches or broods, or reduction in clutch or brood size during incubation or nestling phases. For the most part, complete nest failures occur most frequently during the earlier stages of the nesting cycle (Newton 1979) The failure of territorial pairs to lay has been cited as making a significant contribution to the total nesting failures seen in populations of raptorial birds (Newton 1976, Craighead and Mindell 1981). Newton (1976), in his detailed study of the European sparrowhawk (*Accipiter nisus*), found that birds failed to lay in 12% of all nesting attempts. Craighead and Craighead (1956), studying a wide variety of raptor species in the United States, found that 7.5% of all territorial pairs of raptors did not lay. At Rankin Inlet, 10% (10/101) of peregrine pairs occupying nesting territories between 1981 and 1985 failed to lay. The proportion of pairs failing to lay in any year varied from as high as 20% in 1984 to 4% in 1985.

Although failure to lay was a significant contribution to the total of all nesting failures, losses of entire nests of clutches and broods of young were significant. Of the 91 pairs that successfully laid a clutch, 77 produced young and 74 pairs eventually fledged young. Thus, about 74% of all pairs to initiate a breeding attempt were successful in fledging young. This compares to the figure of 65% obtained by Newton (1976) for the sparrowhawk. Losses of clutches, 13 (48% of all failures), were more than four times as common as losses of nests containing young (3, 11% of all failures). Of those nests lost that contained eggs, seven involved desertion of entire clutches, while six pairs lost the eggs either through breakage or some unknown circumstance. Similar to the trend noted by Newton (1976) for the sparrowhawk, desertion of clutches most often occurred early in incubation.

Of the six pairs which eventually lost all their eggs, details of loss were known in only three cases; all three involved breakage and loss of individual eggs as incubation progressed. One female laid an egg outside the nest scrape, two more in the scrape, but broke both of these during incubation. Another female, incubating a clutch of four eggs on June 27, was discovered perched beside the remains of a single cracked and addled egg on July 20. A third female broke two eggs of a clutch of four mid-way through incubation. The remains of two embryos which had died at the time of pipping were discovered in the nest debris some weeks later. At three other nests where eggs were lost, no remains of eggs were found. Nest predation was unrecorded in this population of peregrines and seemed to be rare or nonexistent. Indeed, abandoned clutches were often left unattended for some weeks, yet were untouched by scavengers or potential nest predators such as arctic ground squirrels, as noted by Cade (1960), herring gulls (*Larus argentatus*), and jaegers (*Stercorarius spp.*).

The patterns of egg breakage described above have been reported for pre-pesticide (pre-1947) populations of peregrine falcons (Hickey 1942), but may also represent the effects of pesticide pollution (Ratcliffe 1970, 1980). Ratcliffe (1970) found that failures related to pesticide pollution involved breakage of thin-shelled eggs during incubation and that breakage was often followed by consumption of the contents by the adult female. Partially eaten remains of eggs were found at two nest sites at Rankin Inlet.

Reproductive failure associated with organochlorine pollutants such as D.D.T. occurs when egg shells are reduced by 20-25% of their normal thickness (Ratcliffe 1980). Ratcliffe (1980) reports that thinning in this range has been correlated with D.D.E. (the primary metabolite of D.D.T.) residues in eggs of 13 ppm. Enderson et al. (1982) reported a mean 23.3 ppm D.D.E. in a sample of peregrine falcon eggs from the western United States. They concluded that most of the eggs in the sample contained enough D.D.E. to correlate with egg shells 20-25% thinner than normal.

Preliminary analysis of a small sample of addled eggs (n=5) collected at successful nests at Rankin Inlet revealed D.D.E. levels of no greater than 6 ppm (Canadian Wildlife Service, unpublished data). These results, coupled with the relatively productive nature of the Rankin Inlet population, do not suggest any widespread effect of chemical pollutants. However, it is important to caution, that pesticide residues have yet to be measured in samples (eggs or blood plasma of adults) taken from the majority of the birds in this population. Therefore, it remains possible that some members of this population may be carrying heavy pesticide loads so that failures recorded that involved egg breakage may be attributable to pesticides.

Besides losses of entire clutches, another significant factor contributing to reduced reproductive output was partial nest failures or infertility of eggs. Newton (1976) showed that the percentage of females in a population of sparrowhawks to obtain a complete hatch ranged from 21% to 44%, depending upon habitat. Peregrine falcons at Rankin Inlet managed a full hatch for 44% of all clutches laid in years 1983 and 1984. These data indicate that some eggs are lost, through either breakage or infertility, in about one-half of all clutches that eventually hatch.

Hickey (1942) addressed the importance of loss of peregrine eggs during incubation by calculating the difference between the mean number of young fledged and the mean brood size using a sample of productivity from North American peregrine populations; he noted a "drop" of 23.3% from clutch size to fledging number. A ratio of mean number of young fledged to mean clutch size, using Hickey's data, would be about 0.77. From his analysis, Hickey (1942:188) concluded that: "about one egg in every set fails to hatch". Similar conclusions have been drawn for peregrines nesting in arctic Eurasia, where it is believed that "generally one egg is unfertilized" (Dement'ev 1951:90). Hickey (1942) cautioned that his conclusion was open to question, however, as he quoted data from egg collectors reporting fertility of peregrine eggs as high as 95%. Likewise, Bond (1946), studying peregrines in the western United States, estimated egg loss from his data and found that it failed to approach 25%.

Comparison of average number of young fledged per successful pair and mean clutch size using data from Rankin Inlet produced a ratio of 2.79/3.62 or 0.77, similar to that obtained using data from Hickey (1942). However, detailed investigation of hatch success conducted in 1983 and 1984, supports the idea that fertility in peregrine clutches is much higher than that indicated by a comparison of clutch size and fledging success. As might be predicted, the source of the underestimate comes from unrecorded mortality of very young chicks. A ratio of total eggs hatched to total eggs produced in these years was 85/98, giving a hatching success of about 87%.

Pairs that totally failed with young accounted for 11% (3/27) of all failures. In all cases these losses occurred before the young were one week old. At one nest the entire brood disappeared; dead, emaciated young were found at two other abandoned nests. Some young were also lost from successful nests, although these losses could only be quantified in 1983 and 1984. In these years, 85 young were hatched, only 73 fledged, giving a nestling mortality of 14%. Hagar (1969), studying a population of peregrines in Massachusetts, found that nestling mortality varied from as low as 14% at "superior" nest sites to as high as 26% at "poorer" sites. Ogden and Hornocher (1977), in their study of prairie falcons, found that 17% of all young that hatch do not fledge. At Rankin Inlet, six of the 12 peregrine chicks that died were lost in complete nest failures described above. The remaining six died, presumably of starvation, as they were the last-hatched young in six asynchronous broods. The conditions contributing to this mortality are discussed in detail below.

Experience on Nesting Territory and Breeding Success

Peregrines attain adult or breeding plumage at two years of age (Ratcliffe 1980), but some have been reported as breeding birds at one year of age (Hickey and Anderson 1969, Mearns and Newton 1984, Canadian Wildlife Service, unpublished data). For the most part these young birds are usually unsuccessful or fledge few young (Hickey and Anderson 1969, Canadian Wildlife Service, unpublished data). Little has been reported on the breeding success of peregrines in adult plumage that are apparently breeding for their first time. At Rankin Inlet, the success of peregrines breeding for their first time (at least within the confines of the study area) was known in only four instances. A male, aged three years, paired with a female of unknown age; no eggs were laid. A two-year-old male paired with a female of unknown age; four eggs were laid, one young was produced, but it died after three days of life. A three year old female, paired with a male of unknown age, laid three eggs, but abandoned the clutch early in incubation. Another female, aged three years, paired with a male of unknown age, laid a clutch of four eggs, and successfully raised a brood of three young.

In terms of relative experience on nesting territories, female peregrines known to be nesting on a territory for the first time (at least within the confines of the study area) showed a failure rate of 18% (4/22), whereas females nesting at the same territory for two or more years failed 11% (2/19) of the time. This unusually low failure rate in both cases reflects the fact that the failures reported here do not include pairs that failed to lay. The lack of a large difference in failure rate may initially suggest that birds in the two groups were of similar age and that birds on territory for the first time were actually experienced breeders from other territories. However, Hammerstrom (1969), studying a population of American harriers (*Circus cyaneus*), where age was known, found no difference in the percent of pairs successful in classes of sub-adult and adult birds. Therefore, it is still possible that peregrines in the study population breeding at a territory for the first time may have actually been breeding for their first time.

The mean clutch size and number of young fledged appeared to be greater for females with more experience on territories (Tables 4.1 and 4.2). A statistical comparison of reproductive success of females on territory for their first time versus that for females on territory for two or more years did show a significant difference in clutch size (3.45 ± 0.51 (n = 22) versus 3.78 ± 0.53 (n = 19)) (Mann Whitney U Test U = 134 *P* = 0.02), but not in number of young successfully fledged (2.23 ± 1.27 (n = 22) versus 2.79 ± 1.13 (n = 19)) (Mann Whitney U Test U = 145.5 *P* = 0.08). Some similarity exists between these findings and those from known age sparrowhawks studied by Newton (1976). Newton (1976) found that birds breeding in their first year had significantly smaller clutch sizes, but suffered no difference in subsequent measures of breeding success. Likewise, at Rankin Inlet, females nesting on a territory for the first time had smaller clutch sizes than birds with greater experience on nesting territories, but had similar fledging success. Initially this suggests that the birds less experienced on territories were proportionately better as parents, however, it is more likely that this pattern reflects the losses of last-hatched young from broods of four. The loss of chicks from this hatch position will be discussed in detail below.

Newton (1976) also noted, as have students working on non-raptorial birds (Kluijver 1951, Finney and Cooke 1978), that birds breeding for their first time tended to lay later than other birds in the population. Data from Rankin Inlet on this point are very limited, but subjective appraisal of the relative age of young produced by the population each year also suggests females on a territory for their first time were among the latest to lay. The last clutch to be initiated each year, 1983 to 1985, was laid by a female on territory for the first time.

Although some of the evidence is subjective, these overall results bear similarity to those involving birds of known age and suggest that many of the birds breeding at territories in the study population for the first time are indeed breeding for the first time. Unfortunately, sample sizes were too small to permit pairwise comparisons of reproductive performance of the same female for her first and second years on a territory. Thus, the relative effects of age on the results could not be ascertained. It remains entirely possible, however, that the effects of nesting at a new territory, particularly in view of the high degree of territoriality seen in this population, could also be responsible for the differences seen here. It is also possible, that the differences recorded reflected the relative experience of the males at different territories or were related to differences in the 'quality' of the nesting territories themselves. It is interesting to

Table 4.1 Clutch sizes of female peregrines with varying experience on nesting territories - Rankin Inlet, 1983 to 1985.

Year on territory	Number of clutches of following sizes			Total	Mean ± S.D.
	2	3	4		
1	0	12	10	22	3.45 ± 0.51
2	1	2	8	11	3.64 ± 0.67
3	0	0	5	5	4.00 ± 0.00
4	0	0	3	3	4.00 ± 0.00

Table 4.2 Number of young fledged by female peregrines with varying experience on nesting territories - Rankin Inlet, 1983 to 1985.

Year on territory	Number of young fledged				Total	Mean ± S.D.
	0	2	3	4		
1	4	8	7	3	22	2.23 ± 1.27
2	2	2	7	0	11	2.27 ± 1.19
3	0	0	3	2	5	3.40 ± 0.55
4	0	0	1	2	3	3.67 ± 0.58

note that the only successful bird, in the small sample of first known (known age birds) breeding attempts, was on a territory that was among the most productive over the five years of the study. The others were on territories that were either irregular in their pattern of use or in the success of pairs using them. It is possible that in the unsuccessful pairs, both members were inexperienced, and that the one successful female was simply a replacement at a territory owned by an experienced adult male. It is also possible, as mentioned in Chapter 3, that these more regularly occupied territories are somehow more suitable for nesting. Thus, the assumption that territories are of equal 'quality' may also be open to question. Only further study involving large samples of marked birds of known age will conclusively separate the effects of age, experience, and territory on overall breeding success.

Intraspecific Harassment and Breeding Success

Schmutz (1977), working with Swainson's and ferruginous hawks, found a significant positive correlation between hatching success of any pair and the distance to nearest neighbor. This finding was supported by a significant negative correlation between the same reproductive parameter and nesting density using data from the same year. Schmutz (1977) concluded that when hawks nested in close proximity to same or other *Buteo* species, their hatch success was lower. He was not successful in documenting a similar relationship between distance to nearest neighbor (or density of pairs) and number of eggs laid or number of young fledged, but maintained that the reduced hatching success was caused by some form of behavioral conflict between close nesting pairs.

As mentioned in the introduction, observations of territorial interactions of peregrine falcons within the study area suggested that behavioral conflict between pairs nesting in close proximity is a definite possibility. Analyses similar to those of Schmutz (1977), using productivity data from Rankin Inlet for the years 1983 to 1985, showed no significant relationships between either nearest neighbor distance or nesting density and clutch size or number of young fledged (Tables 4.3 and 4.4). There was a significant relationship obtained between hatching success and nearest neighbor in 1983 (Table 4.3), but this relationship was not borne out in a comparison of hatching success and nesting density for the same year or in similar comparisons using data from 1984 and 1985. Furthermore, the correlation obtained was negative, suggesting that closer nesting pairs were more successful in hatching eggs than those

Table 4.3 The relationship between reproductive performance of peregrine falcons and distance to nearest neighbor at Rankin Inlet, 1983 to 1985.

Year	Parameter	Number of pairs	Correlation coefficient	*P*
1983	Clutch size	17	-0.09	0.36
	Percent hatched	17	-0.42	0.04
	Number fledged	17	-0.39	0.06
1984	Clutch size	16	0.07	0.40
	Percent hatched	16	0.06	0.41
	Number fledged	16	0.01	0.48
1985	Clutch size	25	-0.20	0.17
	Number fledged	25	0.19	0.18

Table 4.4 The relationship between reproductive performance of peregrine falcons and density of nesting pairs at Rankin Inlet, 1983 to 1985.

Year	Parameter	Number of pairs	Correlation coefficient	*P*
1983	Clutch size	17	0.18	0.24
	Percent hatched	17	0.32	0.09
	Number fledged	17	0.22	0.19
1984	Clutch size	16	-0.19	0.23
	Percent hatched	16	0.03	0.45
	Number fledged	16	0.07	0.39
1985	Clutch size	25	0.25	0.11
	Number fledged	25	-0.14	0.25

nesting at greater distances, precisely the opposite of what might be expected if intraspecific harassment affected productivity. These results suggest that, although the possibility remains that close nesting pairs in the study population may face higher levels of intraspecific aggression, this disturbance is not reflected in decreased reproductive success of these pairs.

Asynchronous Hatching and Brood Reduction

As seen from the discussion of failure to nest and nest losses, a significant number of young are lost each year even from successful nests. In many species of birds this reduction in brood size is a direct result of competition for food among siblings of asynchronously hatched broods (Lack 1954). The adaptive significance of brood reduction in species faced with an unstable food supply is well accepted as a possible explanation of asynchronous hatching (Newton 1979). The peregrine falcon, over much of its very large range, shows a synchronous hatch (Ratcliffe 1980). Thus, based on the brood reduction hypothesis, this suggests a reliable food supply is available for this species over most of its range. However, asynchronous broods have been reported for this species coming from investigations of populations breeding at high latitudes: Greenland (Burnham and Mattox 1984), arctic Eurasia (Dement'ev 1951), Alaska (Enderson et al. 1972) and northern Canada (R.Fyfe, pers. comm.).

Enderson et al. (1972) provide the most accurate documentation of asynchronous hatching in their time-lapse film study of four peregrine nest sites in Alaska. There, three broods hatched with relative synchrony, but a fourth clutch of four eggs showed hatch intervals after the first egg of 10, 60-72, and 110 hours. The latter pattern can be explained by the female beginning incubation shortly after laying the first egg. As female peregrines are believed to lay at 48-hour intervals (Nethersole-Thompson 1931, in Ratcliffe 1980), initiation of incubation with the first egg of a clutch of four, could result in an age spread between the first and last-hatched young of up to six days.

Asynchronous hatching of this degree was commonly observed in broods of peregrine falcons studied at Rankin Inlet. Asynchrony was particularly obvious in larger broods, however, even some broods of two showed a noticeable difference in the size of chicks at hatch. All broods of four chicks produced in 1983 and 1984 showed a spread of at least three days between the oldest and youngest members. Although the timing of hatch was difficult to ascertain accurately for all broods, the pattern of hatch observed most frequently included:

relative synchrony in the hatch of the first and second eggs, the third egg hatching a day to a day and one-half later, and the fourth egg hatching usually two days after the third. At one nest, time-lapse cameras revealed that the first egg of a clutch of four hatched during late a.m. July 13, the second hatched during late p.m. July 13, the third hatched during early p.m. July 15, and the fourth during late a.m. July 18. These patterns suggest that most females in the study population began effective incubation either shortly before or after laying the second egg. Considerable variation in the degree of asynchrony was observed however, as oldest and youngest members of broods were occasionally separated by as little as three days and in other cases by as much as five days.

Asynchronous hatching resulted in a wide range in size of the members of a brood; freshly hatched chicks weighed as little as 36 g while five day-old siblings weighed 100 to 140 g. These differences apparently introduced a competitive disadvantage to youngest members of some broods as these died in 45% (5/11) of broods of four chicks produced in 1983 and 1984. The last-hatched chick in one asynchronously-hatched brood of three chicks also died. All mortality occurred before the chicks were five days old. Mortality associated with asynchronous hatching accounted for a 7% (6/85) reduction in the total number of chicks hatched in 1983 and 1984. Starvation was implicated as the cause of mortality, as all chicks which eventually died were grossly underweight compared to nestlings of the same age but from different hatch positions. Evidence of fratricide has not been recorded in any species of the Falconidae (Newton 1979), and there was no evidence of this phenomenon in broods at Rankin Inlet. Only one dead chick was recovered; it apparently had been trampled into the loose substratum beneath the other chicks. At one nest where activity was monitored with a time-lapse camera, the adult female removed the dead chick from the nest, but later returned with the carcass and fed it to the remaining chicks in the nest. The lack of remains at other nests suggests that other dead chicks may have been treated in a similar manner.

A plot of weight gain through time for the surviving last-hatched young of broods of four (n=6) suggests that these individuals did not suffer a disadvantage through lack of access to food since weight gain during their first 30 days of life was similar to that of other siblings (Figures 4.1 and 4.2). This observation was supported by the lack of a significant difference in the slope of the straight-line portions of growth curves for chicks from all four hatch positions (Analysis of Covariance: Males (n=13) Equality of slopes F=1.41, $P=0.25$; Females

Figure 4.1 Relationship between weight and age in male nestling peregrine falcons of different hatch positions in broods that hatched asynchronously.

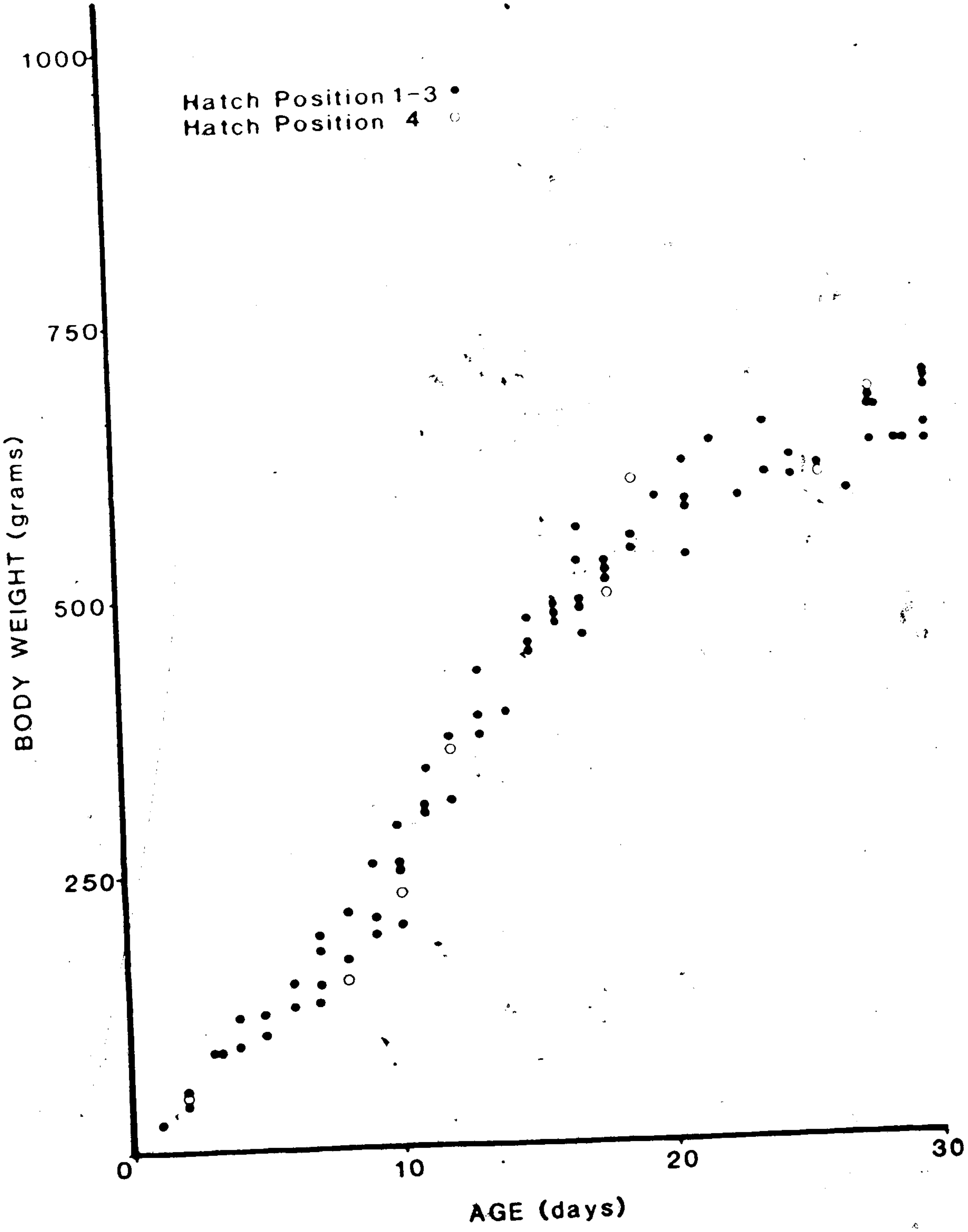
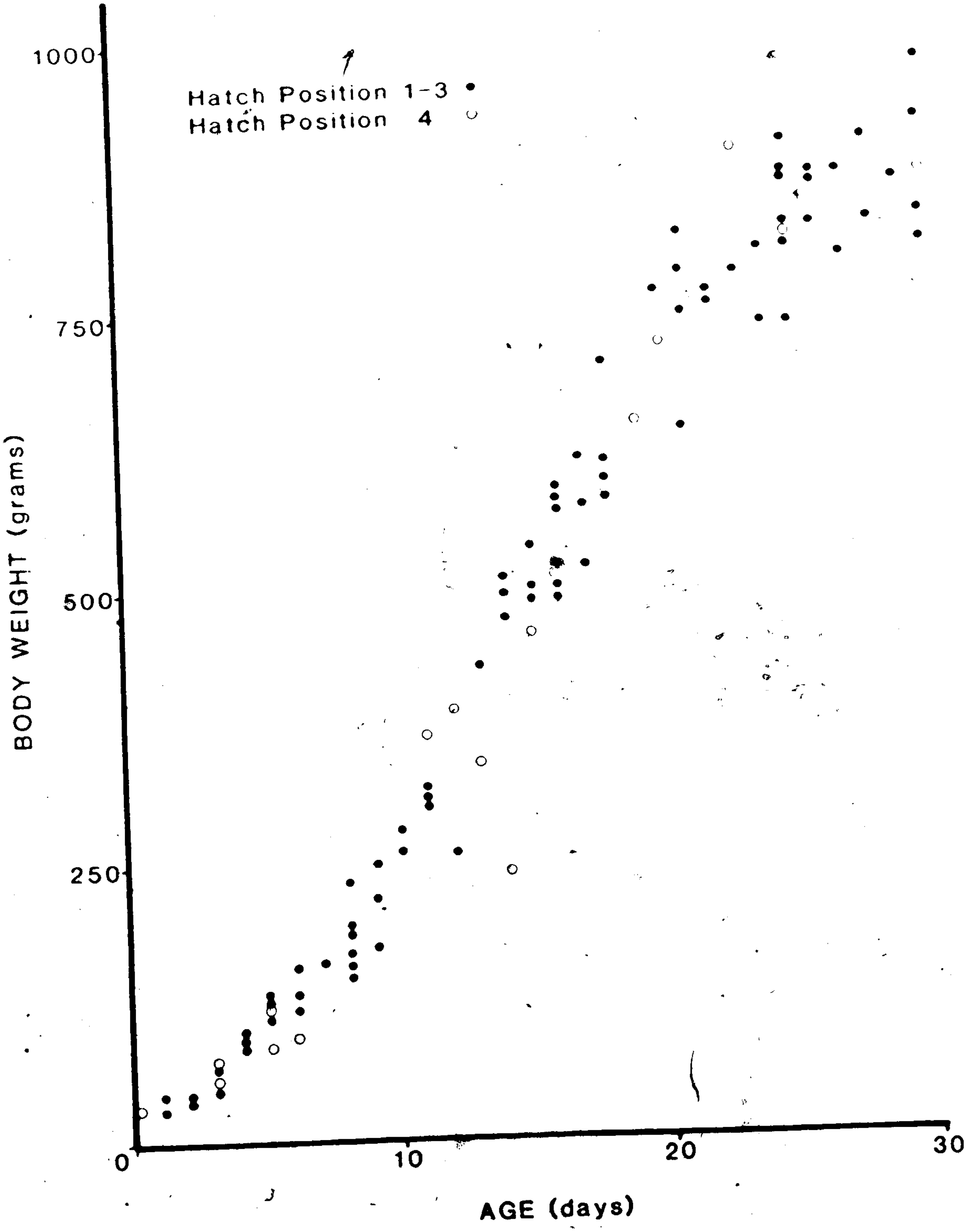

Hatch Position 1-3 ●
Hatch Position 4 ○
1000
750
500
250
BODY WEIGHT (grams)
0
10
20
30
AGE (days)

Figure 4.2 Relationship between weight and age in female nestling peregrine falcons of different hatch positions in broods that hatched asynchronously.


Hatch Position 1-3 ●
Hatch Position 4 ○
BODY WEIGHT (grams)
1000
750
500
250
0
10
20
30
AGE (days)

(n=11) Equality of slopes $F=0.19$, $P=0.89$). It is possible that the last-hatched young, although they survived and grew normally, may have been slightly delayed in their initial weight gain very early in life (less than five days old), however, the data were insufficient to test for such differences.

i) The Source of Mortality in Last Hatched Young

The loss of some of the last-hatched members of asynchronously hatched broods on the study area raises two questions. First, does the brood reduction observed here happen for the same reasons it does in other raptor species, namely from a lack of available food for parents and hence young, or do late-hatched chicks starve for other reasons? Second, if the gross food supply available is not linked to brood reduction, then why do some last-hatched young survive while others do not?

Considering the broad spectrum of food potentially taken by peregrine falcons, both in the Rankin Inlet population and in others, it is difficult to believe that any pair of falcons would fail because of lack of food. Burnham (1975) conducted censuses of breeding passerines in the vicinity of peregrine nests in Greenland. He found some areas where passerine abundance was very low relative to others and concluded that the absence of successful breeding pairs of peregrines in these areas was related to the lack of abundant prey. Considering this, it is possible that individual pairs in some populations of peregrines might occasionally attempt to nest in areas of low prey abundance. Such pairs might lose entire broods or late-hatched brood members to starvation. The peregrines at Rankin Inlet nest at a density more than ten times greater than that recorded by Burnham (1975). Thus, the likelihood of only certain pairs being affected by variations in local density of prey species is low because their wide-ranging foraging flights could potentially take them to all parts of the study area. Indeed, observations of foraging flights of peregrines on the study area suggest that birds from different pairs may occasionally forage over the same ground. Moreover, the peregrines at Rankin Inlet displayed a broad spectrum of prey use, supplementing their diet of small birds with black guillemots and mammals such as arctic ground squirrels and lemmings. Mammals and colonial sea birds were not available to supplement peregrine diets in the population studied by Burnham (1975).

Although never quantified, the abundance of passerines (both adults and fledglings) during the period when brood reduction occurred in the study population, also makes it difficult to believe that mortality occurred because the pair had difficulty in obtaining food. Indeed, at some nests sites where last-hatched members of broods died, freshly cached carcasses of prey species were found near the nest on the very day that mortality occurred. Support for this also comes from the fact that surviving chicks, although still facing a size disadvantage, showed no difference in growth rate compared with that of older siblings. These observations suggest that, unlike many other raptors showing brood reduction associated with asynchronous hatching, the lack of adequate food resources available to the parents is not a factor in the death of late-hatched brood members. Additional support for this conclusion is given below.

Since food availability seems unrelated to brood reduction in peregrine falcons, perhaps mortality of the youngest members of broods occurs because these birds simply face a mechanical disadvantage, through their smaller size and lesser developed powers of co-ordination, in obtaining food during feedings. Why then would some late-hatched young live and others die? One obvious explanation could be the degree of asynchrony in any given brood; perhaps the larger the age spread in the young, the higher probability of brood reduction. Such conjecture was not supported by the observations at Rankin Inlet, where many of the last-hatched chicks that survived were members of the most asynchronous broods (ie: those broods with a five day spread in age between first and last-hatched chicks). It seems more probable that differential survival of these late-hatched young might be more closely linked to conditions at the nest during the early life of the nestlings, particularly with regard to parental care.

Analyses of time-lapse films of activities recorded at three nests on the study area allowed a limited assessment of these conditions (Table 4.5). From the small sample of nests, it appears that the female most likely to have the entire brood survive was the most attentive in terms of time spent at the nest and number of feedings given per day. Again, the number of feedings per day could indicate a lower rate of delivery of food to a brooding female, perhaps indicating a lack of food available to the pair, either in absolute terms, or in relative terms that reflect the foraging ability of the male. As previously discussed, a lack of prey in absolute terms is not well supported, nor is it likely in relative terms as some of the pairs that lost young had prey cached nearby on the day mortality occurred. It seems more probable that the differences observed are not related to food supply at all, and simply reflect variability in the attentiveness

Table 4.5 Parental care of asynchronously hatched broods of peregrine falcons for the five days after the youngest brood member hatched

Nest site	Parameters	Day 1	Day 2	Day 3	Day 4	Day 5	Mean	Fate of last hatched
1	Feedings per nestling	2.3	2.3	2.0[1]	2.0	3.0	2.3	
	Inattentive period	4%	4%	14%	15%	46%	17%	DIED
	Mean temperature (°C)/ Total precipitation(mm)	9.8/0.0	12.4/0.0	14.0/0.0	15.2/0.6	9.7/0.8	12.2/0.3	
2	Feedings per nestling	1.5[1]	2.0	1.8	2.0	2.3	1.9	
	Inattentive period	18%	19%	26%	12%	23%	20%	DIED
	Mean temperature (°C)/ Total precipitation (mm)	16.7/0.0	18.8/0.0	15.7/0.0	16.4/0.6	12.2/0.0	16.0/0.12	
3	Feedings per nestling	2.5	2.8	3.3		3.0	2.9	
	Inattentive period	<1%	2%	8%	[illegible]	15%	6%	LIVED
	Mean temperature (°C)/ Total precipitation (mm)	11.4/0.0	15.3/0.0	16.7/0.0	18.8/0.0	15.7/0.0	15.6/0.0	

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[1] denotes day on which last hatched nestling died

of different females to their broods.

Another difference between nests, noted from the films, involved the size of the prey items fed to broods during the observation period. At the nests where brood reduction occurred, all prey items used were of a small size (small enough to be held in one foot of the adult female) and were probably small passerines (prey remains at these nests showed a heavy use of juvenile Lapland longspurs). Passerines were also fed to the brood where no mortality occurred, however, arctic ground squirrel carcasses were brought to the nest on three separate occasions during the five day observation period. It is possible that during feedings, the older and more coordinated chicks receive most of the food during the early portion of the feeding. The smallest chick might only receive food when the older chicks were satiated and stopped begging for food. With a large prey item, all members of the brood could be fed, but with a prey item the size of a juvenile passerine, little would remain after the older three chicks had been fed. If older chicks took food at each feeding, it is easy to see how younger members of broods fed exclusively on small prey, might be continually deprived, lose condition, and die. Intensive study, involving more time-lapse studies of feeding patterns at nests with broods of four chicks, is needed to adequately address the relationship of prey size on differential mortality of last-hatched nestlings.

Analyses of time-lapse film sequences revealed another phenomenon that may contribute to the mortality of the smallest nestlings. At one nest, a brood of four was produced on a broad ledge (0.75 m X 3.0 m) which faced southwest. Weather during the period of observation at this nest often included mid-day temperatures of above 20°C. During the early morning hours, members of the brood were 'huddled' under the brooding female. However, during inattentive periods later in the day the older brood members dispersed from the immediate vicinity of the scrape, apparently in response to lack of shade. When the female arrived back at the ledge, the three older chicks moved under her, where they were shaded. The fourth and youngest chick, apparently not as mobile, remained stationary less than a metre away. On one occasion the female attempted to shade the youngest chick, but quickly returned to the group of older nestlings. Consequently, the smallest nestling lay exposed to direct sunlight for several hours. On two subsequent feedings, the female returned directly to the group of older chicks; and the smallest individual, still located less than a metre from the other chicks, was ignored. The female did not assemble all members of the brood until shortly before dusk. The last-hatched individual was dead by the next morning.

These observations suggest that the size of nest ledges, in combination with weather conditions, might also affect the probability of brood reduction at certain nests. One might expect to see higher survivorship of late-hatched chicks at small nests, for example, stick nests where young could not disperse in the manner described above. From the data collected in 1983 and 1984, of the five nests of four chicks where brood reduction occurred, all but one involved broad open ledges. Of the six nests where the fourth-hatched chicks survived, all but one involved the use of a stick nest. Also, in support of this hypothesis, a marked female produced an asynchronous brood of four on a broad open ledge (1.5 m X 3.0 m) in 1983 and, on the same cliff, produced an asynchronous brood of four on a small sticknest in 1984. In 1983, the youngest member of the brood was lost; in 1984 all members of the brood survived to fledging.

ii) The Adaptive Significance of An Asynchronous Hatch in the Study Population

It is clear that asynchronous hatching is widespread in the study population and that the brood reduction it induces can have a significant impact (25-33% reduction) on the annual production of those pairs involved. As this represents an atypical condition for the species, it is instructive to ask why this condition exists in the study population and in other populations of *Falco peregrinus* nesting at high latitudes. Explanations of this phenomenon can be drawn at both proximate and ultimate levels. For example, a proximate cause of asynchrony might be linked to the severe environmental conditions faced by these birds during laying. Although this is possible, in an ultimate sense there may be some real adaptive significance to this tendency, similar to that proposed for other species (Lack 1954, Hussell 1972).

Weaver and West (1943) suggested that the reason for the early onset of incubation in some species of arctic birds was to protect the first-laid eggs from freezing. Although more recent work by Hussell (1972) has dismissed this possibility in arctic passerines, the inclement weather often seen at Rankin Inlet during the laying period of peregrines certainly makes this a plausible explanation for the asynchronous hatching observed in the study population. Snow, freezing rain, and sub-freezing mean daily temperatures are not uncommon during the laying period (June 1-15) at Rankin Inlet (Table 2.3). It is possible that, under such conditions, adult females in this population cover the first-laid eggs sufficiently to initiate incubation. If severe weather conditions were the direct cause of asynchrony in the study population, one might also expect the degree of asynchrony observed in broods to vary with the micro-climatic conditions of nest cliffs. Nests sheltered from snow and wind, with southern exposure, and located under overhanging rock might be expected to show broods of relative greater synchrony. Observations at Rankin Inlet did not support this conjecture. Of the 11 asynchronous broods of four chicks produced in 1983 and 1984, four were on ledges that faced north (brood reduction occurred at one nest) and seven were on ledges that faced south or south-west (brood reduction occurred in four nests).

In terms of the ultimate causes of asynchronous hatching in the study population, it is instructive to consider the patterns observed at Rankin Inlet in relation to the two major hypotheses advanced to explain asynchronous hatching in birds: the "brood reduction" hypothesis proposed by Lack (1954) and the "predation hypothesis" of Hussell (1972). Lack (1954) proposed that asynchrony is an adaptation promoting brood reduction in times of food shortage, and is most often seen in those species utilizing a prey-base that is variable over time. The nature of prey selection by peregrines and the relative synchrony of broods of this species in other parts of the world (Ratcliffe 1980) suggests that food supply during the nesting period of this species is secure. It follows then, that if asynchrony occurs in this species, it may not happen for the same reasons as it does in other species. Do observations of asynchronous hatching in peregrine falcons nesting at Rankin Inlet suggest otherwise?

From the data on productivity (Tables 2.5-2.8), it appears that the study population responded to increased prey abundance in 1985 through a rise in the percentage of pairs laying, a slight increase in the percentage of pairs producing young, a slight increase in brood size, and a substantial increase in the number of pairs breeding in the study area. The increase in the number of breeding pairs is similar to other raptor species, many of which show asynchronous hatching, that undergo local fluctuations in breeding numbers which are synchronous with fluctuations in the numbers of their primary prey (Galushin 1974). However, the similarity between the peregrines and species adapted to irregular food supplies, at least in terms of response to increased prey abundance, ends here.

Raptorial birds showing asynchronous hatching and brood reduction, and dependent on an unstable food source, would be expected to show measurable differences in breeding success from year to year. Presumably a good portion of this variability is caused by differences in clutch size in different years (Newton 1979), but differential survival of members in asynchronous broods must also contribute to this variability. Unfortunately, most studies of these raptors relate brood sizes that were measured after most of the mortality of very young chicks would have occurred. Indeed, studies showing the difference between number of young hatched and number of young fledged in asynchronously-hatched broods seem very rare. However, Bechard (1981) showed that the number of young Swainson's hawks fledged in any year of his study was lower in areas where prey abundance was lower. He attributed the lower production in these areas to brood reduction induced by asynchronous hatching and concluded (pp.240): "...a dearth of food increased the incidence of brood reduction." It is reasonable to assume that similar reductions would occur in other raptor species utilizing a fluctuating prey base and showing asynchronous hatching in those years when overall food abundance dramatically decreases. The great variability in annual clutch size and brood size for a Norwegian population of the rough-legged buzzard (*Buteo lagopus*) studied over a number of years suggests such a trend (Hagen 1969, in Newton 1979).

From Chapter 2, the population of peregrines showed no significant difference in clutch size, brood size, or number of young fledged per territorial pair over the five years of the study. In this period, there were two years, 1983 (poor spring weather) and 1985 (increased prey abundance), when reproductive success of individual pairs might have shown large fluctuations. These results suggest that survivorship of last-hatched peregrine nestlings within asynchronously-hatched broods did not vary from year to year, a primary difference between the peregrines at Rankin Inlet and what one would expect in other raptors showing asynchronous hatch and brood reduction as an adaptation to a variable food resource. This conclusion is also supported by the fact that the proportion of broods of four young in the study population did not increase dramatically in 1985, a year of greater food availability (Table 2.7). Indeed, the slightly larger brood size in this year was apparently caused by the greater proportion of broods of three, with fewer broods of two and one. Detailed investigation of chick mortality in 1983 and 1984 showed that broods were never reduced beyond the last-hatched chick and that mortality of last-hatched young in a brood of three was rare. This suggests that it was hatching success, rather than survival within broods, that improved in 1985.

Unfortunately, detailed information on hatch success could not be obtained in 1985, so comparison with that for 1983 and 1984 was impossible. However, from the raw data, a comparison of the reduction from clutch size to brood size (ie: that reduction which did not result from asynchronous hatching) in 1985 against that for 1983 and 1984 suggests that relatively more eggs hatched in 1985. A reduction from clutch to brood that was not associated with asynchronous hatching could be identified in 8 of 28 (29%) successful nests in the 1983/1984 sample, but similar reductions could be identified in only 2 of 20 (10%) of successful nests in 1985.

Mebs (1964) in his study of the common buzzard (*Buteo buteo*) also noted an increase in hatching success during years of increased prey abundance. He found that 15% of eggs failed to hatch in years of low food availability, while only 5% failed to hatch in years of abundant food. Decreased hatching success in years of low food abundance suggests some effect of the nutritional condition of the adults in these years (Newton 1979). This is supported by the experiments of Hochachka (1985) who investigated the effects of supplemental food on the reproductive success of black-billed magpies (*Pica pica*). Pairs provided with supplemental food before and during incubation did not show significantly larger clutch sizes compared to controls, but did fledge significantly more young. Hochachka (1985) was unable to identify any differences in egg quality in the two groups, and concluded that the difference in the numbers of young fledged was most probably affected by the quality of care provided to both eggs and young. He believed such quality was mediated by the nutritional state of the adults. Similarly, increased availability of prey for peregrines nesting at Rankin Inlet in 1985 may have contributed to improved condition of adults. This may have been manifested in either a higher rate of fertility, or more likely, improved care of eggs during incubation. This provides at least one explanation for the apparent improvement in hatching success observed in this year.

From the previous sections, it is clear that survivorship of last-hatched young did not vary significantly from year to year, despite differences in prey abundance. Thus, the patterns here do not suggest an adaptation in keeping with Lack's (1954) brood reduction hypothesis. However, one further explanation of the ultimate reason behind asynchrony in this population is seen in an adaptation of Hussell's (1972) nest predation hypothesis. Hussell (1972) proposed that parent birds, by starting incubation with the first egg, reduce the time to fledging for young from first-laid eggs, and thereby reduce the risk of losing these chicks through predation.

Cade (1960) proposed that the peregrine was limited in its northern distribution by the length of its breeding cycle and by the time over which conditions for successful breeding (weather and prey availability) exist in northern areas. Peregrines nesting at the very limits of the species range or in extreme climates, such as that at Rankin Inlet, have a very restricted period of time in which to complete breeding. This is particularly evident when one considers the very short period of time that fledglings have to gain independence before migration begins (Chapter 2). Perhaps, as proposed by Hussell (1972), by initiating incubation with the first egg, the time to fledging for some young could be reduced by as much as six days. For the peregrine, this would allow earlier fledging dates for some members of broods and hence provide a longer period in which to be fed by adults and possibly gain independence well before migration begins. Pairs employing this strategy might have more young survive, though, through time, increased survivorship of young fledged earlier would have to more than compensate for the losses of late-hatched young. Unfortunately such conjecture is difficult to address quantitatively, particularly in consideration of the amount of time involved and the logistical difficulties of working with such small populations and with raptors in general.

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V. Conclusion

The population of peregrine falcons nesting at Rankin Inlet, N.W.T., offered a unique opportunity to investigate some poorly known aspects of the biology of this species. The fact that individuals were color marked allowed a detailed description of territory use, both in terms of patterns of occupancy and turnover of territorial pairs. More importantly, observable territorial behavior in this population provided some insight into the way in which this population, as well as those of other raptor species, may be limited. The relative accessibility of nests allowed detailed documentation of both total and partial nesting failures, information that is difficult to obtain with any accuracy in most other populations. The body of information obtained over the years of this study is discussed in a variety of contexts in various chapters of this thesis, and it would be redundant and not particularly productive to attempt to summarize all of this information here. However, it may be interesting to point out a few of the unique aspects of the reproductive biology of this population and discuss their implications in terms of what is known of the biology of peregrines and ecology of raptorial birds in general.

From even the most cursory examination of the natural history of the peregrine falcons at Rankin Inlet, described in Chapter 2, it is clear that this population is unique in several respects. The density of the breeding population is among the highest on record, and represents the most concentrated population of peregrines recorded breeding at arctic latitudes. Somewhat acharacteristically for peregrines, this density is attained without a strict feeding specialization on super-abundant colonial prey species. However, the density of pairs at Rankin Inlet tends to indicate that an abundant source of food is available to the population. This abundance appears more a function of the breadth of the spectrum of prey taken by pairs in the area, rather than any single numerous prey species. Like other populations, a large proportion of all available avian prey species is utilized, however, mammals are also used to supplement the diet.

The extensive use of mammals in the diet of peregrines is uncommon, and tends to highlight the considerable plasticity of this falcon in terms of prey selection. The very adaptable nature of the peregrine in terms of prey use gives some indication as to why this species has been so successful in colonizing such a wide variety of habitats throughout the world.

The productivity of the population, in terms of young produced per successful pair and young produced per territorial pair, is also among the highest on record, an observation that again suggests an abundant food supply. Additionally, these parameters of reproductive success did not vary significantly from one year to the next, suggesting that food supply was stable enough to allow relatively constant reproductive output for pairs in the study population over all years of the study. This observation, particularly in view of the unstable or irregular nature of arctic ecosystems, again suggests a distinct advantage to the broad spectrum of prey use demonstrated by the falcons nesting at Rankin Inlet.

In contrast to the conclusions reached above, the high frequency of asynchronous hatching seen in the study population, at least in terms of Lack's (1954) brood reduction hypothesis, initially suggested that the food supply available to pairs in the study population is unstable. Detailed investigation of asynchronous hatching and associated mortality of last-hatched young indicated that there was little evidence to conclude that brood reduction in this study population occurred for the same reasons as it apparently does in other raptors showing asynchronous hatching and utilizing an unstable food resource. Thus, the occurrence of hatching asynchrony in these birds does nothing to alter the impression that the productivity and density of the population of peregrines at Rankin Inlet was related to an abundant and reliable prey base.

In view of this constant productivity and the relative constancy in the size of the study population between 1981 and 1984, and in keeping with theories on limitation of breeding density in peregrines and other raptors (Ratcliffe 1962, 1969, 1980, Nelson 1977, 1978, Newton 1976, 1979), it could have been suggested that the density of pairs at Rankin Inlet in these years was limited to below the carrying capacity of the area. In this study, there existed a rare opportunity to evaluate evidence either supporting or negating this contention. First, the investigation of patterns of territory use and turnover of adults established that falcons in the population showed that most territories were regularly occupied and that falcon pairs demonstrate strong fidelity to nest sites. Second, observations of territorial behavior and color marked adults established that pairs did compete with other falcons for territories each spring and that some adult birds were excluded from the breeding population. Third, observations of territorial interactions of peregrines provided some evidence that territoriality could be linked to the spacing of pairs in the population, giving some support to the hypothesis that some raptor populations are limited by a shortage of nesting habitat created by the territorial nature of the birds themselves.

If the density of any raptor population was limited in relation to the carrying capacity (food supply), it would follow that increases or decreases in food supplies should be associated with commensurate changes in density. This has been noted in some raptors adapted to irregular food supplies (Pitelka et al. 1955, Village 1983), but is seldom observed in species, like the peregrine, adapted to a stable food supply. In such species, territory size would be expected to change over very broad expanses of time with slow changes in the abundance of food. However, at Rankin Inlet in 1985, this conjecture could be evaluated using the peregrine, as there was a profound, short-term increase in prey abundance as populations of microtine rodents peaked in this year. Considering the peculiar use of mammalian prey by falcons in this area, this change in rodent abundance rather fortuitously represented a "natural experimental" change in the carrying capacity of the environment. Under such conditions, a model of population limitation based on food supply and territoriality would have predicted a reduction in the levels of aggression around traditionally used nest sites, more birds from the non-breeding sector of the population would be expected to obtain territories, and population density should increase. Unfortunately, the rate of territorial interactions in 1985 could not be measured, thus, comparisons with that of previous years was not possible. However, the dramatic increase in the density observed at Rankin Inlet in 1985 did support this model. Also, a very large proportion of members of pairs making up this increase were not birds produced in the study area in any of the previous four years. This, in consideration of the level of philopatry seen in this species, represented additional evidence for the existence of a considerable number of non-breeding adults. Thus, the prey-related increase in the population density of the peregrines nesting at Rankin Inlet, combined with the body of evidence for the existence of reproductively capable non-breeding birds obtained in both 1985 and other years, represents strong circumstantial evidence that the density of this raptor population is limited. Investigations before 1985 suggested that limitation operated through a shortage of nesting sites created by territoriality, and the patterns observed in 1985 suggested that expressions of territoriality and territory size were mediated through the food supply.

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APPENDIX I. List of vertebrate species encountered on the Rankin Inlet study area, 1981-1985.

Status - BL = breeds locally M = migrant R = range extension
Abundance - C = common UC = uncommon R = rare A = accidental

Birds		Status	Abundance
Arctic loon	*Gavia arctica*	BL	C
Red-throated loon	*Gavia stellata*	BL	C
Tundra swan	*Cygnus columbianus*	BL	C
Canada goose	*Branta canadensis*	BL	C
Brant	*Branta bernicla*	M	R
White-fronted goose	*Anser albifrons*	BL	UC
Snow goose	*Chen caerulescens*	BL	C
Mallard	*Anas platyrhynchos*	R	R
Northern pintail	*Anas acuta*	BL	C
Green-winged teal	*Anas crecca*	R	R
Greater scaup	*Anthya marila*	R	R
Oldsquaw	*Clangula hyemalis*	BL	C
Common eider	*Somateria mollissima*	BL	C
King eider	*Somateria spectabilis*	BL	UC
Red-breasted merganser	*Mergus serrator*	BL	UC
Rough-legged hawk	*Buteo lagopus*	BL	C
Gyrfalcon	*Falco rusticolus*	BL	R
Peregrine falcon	*Falco peregrinus*	BL	C
Rock ptarmigan	*Lagopus mutus*	M	C
Sandhill crane	*Grus canadensis*	BL	C
Semipalmated plover	*Charadrius semipalmatus*	BL	C
Lesser golden plover	*Pluvialis dominica*	BL	UC
Ruddy turnstone	*Arenaria interpres*	M	R
White-rumped sandpiper	*Calidris fuscicollis*	M	C
Baird's sandpiper	*Calidris bairdii*	M	C
Least sandpiper	*Calidris minutilla*	BL	R
Dunlin	*Calidris alpina*	BL	UC
Semipalmated sandpiper	*Calidris pusilla*	BL	C
Buff-breasted sandpiper	*Tryngites subruficollis*	M	R
Red phalarope	*Phalaropus fulicaria*	BL	R
Pomarine jaeger	*Stercorarius pomarinus*	R	R
Parasitic jaeger	*Stercorarius parasiticus*	BL	UC
Long-tailed jaeger	*Stercorarius longicaudus*	BL	R
Glaucous gull	*Larus hyperboreus*	M	UC
Herring gull	*Larus argentatus*	BL	C
Thayer's gull	*Larus thayeri*	M	UC
Arctic tern	*Sterna paradisaea*	BL	UC
Black guillemot	*Cepphus grylle*	BL	C
Snowy owl	*Nyctea scandiaca*	BL	UC
Short-eared owl	*Asio flammeus*	BL	UC

Horned lark	*Eremophila alpestris*	BL	C
Bank swallow	*Riparia riparia*		A
Common raven	*Corvus corax*	BL	R
Common grackle	*Quiscalus quiscula*		A
Water pipit	*Anthus spinoletta*	BL	C
Myrtle warbler	*Dendroica coronata*		A
Blackburnian warbler	*Dendroica fusca*		A
Palm warbler	*Dendroica palmarum*		A
Hoary redpoll	*Carduelis hornemanni*	BL	UC
Savannah sparrow	*Passerculus sandwichensis*	BL	R
White-crowned sparrow	*Zonatrichia leucophrys*	R	R
Lapland longspur	*Calcarius lapponicus*	BL	C
Snow bunting	*Plectrophenax nivalis*	BL	C

Mammals

Ermine	*Mustela erminea*	R
Arctic fox	*Alopex lagopus*	UC
Polar bear	*Ursus maritimus*	R
Ringed seal	*Pusa hispida*	C
Bearded seal	*Erignathus barbatus*	R
Brown lemming	*Lemmus sibricus*	
Collared lemming	*Dicrostonyx groenlandicus*	
Arctic ground squirrel	*Spermophilus parryii*	C
Arctic hare	*Lepus arcticus*	UC
Barren-ground caribou	*Rangifer tarandus*	UC