ASPECTS OF THE POPULATION BIOLOGY OF TUNDRA PEREGRINE FALCONS (*Falco peregrinus tundrius*)

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ABSTRACT

A population of tundra peregrine falcons (*Falco peregrinus tundrius*) was studied over 4 breeding seasons at Rankin Inlet, NWT, Canada. Data from these 4 years were combined with data from the 10 previous consecutive seasons. As the study area and methodology were consistent during the entire study, I summarized and analyzed information from all 14 years to investigate paradigms in avian biology.

Levels and temporal trends of eggshell thinning, and organochlorine residues in egg contents, blood plasma of adults and juveniles, tissue samples, and prey species, were determined to: 1) assess the effect of contamination on the breeding performance of the peregrine population; 2) test predictions of a temporal decline in levels; and 3) test the hypothesis that contamination is due to the continuing use of organochlorines within the peregrines wintering range. Residue levels in peregrines and their prey, and eggshell thinning reflect a population that still is likely to experience some contaminant-related reproductive failures, however, the levels are not high enough to seriously affect production of the population. Contrary to predictions, no improvement in shell thickness was detected between decades and residue levels changed little. Results suggest that peregrines accumulate organochlorines on their wintering grounds, and also from contaminated aquatic species that range only within North America.

Parentage analysis of 55 broods (including 144 young) of peregrine falcons using single-locus minisatellite and microsatellite DNA profiling revealed a low frequency of extra-pair paternity (1.3% of young) but no intra-specific brood parasitism. The low frequency of extra-pair paternity justifies the use of traditional measures of reproductive success in this population but fails to support the hypothesis that floaters contribute substantially to their lifetime reproductive success before holding a territory. A low frequency of extra-pair paternity is consistent with studies of other raptors but fits poorly with the predictions of the Paternity Assurance Hypothesis; inconsistencies with this hypothesis are discussed.

The pattern of nesting territory occupancy and reproductive performance over 14 years was analyzed to determine the importance of density-dependent processes in regulation of the population, and test the predictions of two hypotheses explaining density-dependent fecundity. Breeding attempts at preferred territories (frequently occupied territories) produced young more often than attempts at avoided territories (infrequently occupied territories) supporting the hypothesis that occupation frequency is an indirect measure of habitat quality. Mean production of the population declined with increasing density because proportionally more breeding attempts occurred at infrequently occupied territories where the frequency of failure after laying or during brooding was high. Mean production at frequently occupied territories, however, did not change with density. Density-dependent fecundity was, therefore, consistent with predictions of the "habitat heterogeneity" hypothesis, but not the "interference" hypothesis.

14 adult peregrines were removed from their territories for 24 hours to test whether breeding densities were limited and elucidate the relative importance of territory quality and territoriality in population limitation. Rapid replacements at 11 territories provided evidence of a surplus of non-breeding adults (i.e. 'floaters') and population limitation. All six vacancies for females (at 5 good quality territories and one poor quality territory) were filled within 24 hours. Males were replaced at four good quality territories but only one of four poor quality territories. The observed pattern of territory defense and replacements in this population does not support territoriality as a main mechanism of population limitation. Instead, breeding densities may ultimately be limited by food, with the combination of individual and habitat quality determining whether a breeding attempt occurs at any given vacant territory.

I analyzed capture and resighting records of colour-banded adult peregrines collected from 1982 to 1995 to provide accurate estimates of survival using Cormack-Jolly-Seber capture-recapture methodology and traditional turnover methodology. Results were indicative of little or no difference in survival between males and females. Differences between estimates from the two methods were minimal. Low sample size of marked birds contributed to a lack of fit to the capture-recapture model, however, and assumptions of the model were not met. While capture-recapture methodology is a powerful technique for estimating population parameters, its practical application among raptor species may be limited by the sample size required and the difficulty of meeting assumptions implicit to the model. Estimates represent minimum survival because of the confounding effects of emigration.

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> "Step into the office. We just want a quick word."
>
> Gordon Court and Lloyd Davis, 1990 sometime.

So begun the epic adventure which ultimately resulted in this thesis. I now sit in front of this cursed computer in a fatigued state and wish that my brain cells could muster the energy to spark those synapses and stimulate an acknowledgments section replete with wit and kind sensitive thoughts about the people and events that got me where I am today (i.e. emotionally exhausted, overweight, out of shape, penniless, and unemployed). Instead, you will have to suffer through an unorganized section that has as much flow as the North Saskatchewan River in January.

> "Why, even my dustman couldn't fail to notice the complete lack of textural sanguine and dramatic sincerity...."
>
> Harry Enfield

Whether you intend to read it, use it as a door-jam or a potent cure for even the most severe insomnia, this tome does represent the accumulation of many things to me from thoughts to passions to liver damage to adrenaline-charged moments. Regardless of the poor attempt I make here to acknowledge all the inspiration, Scotch, help, and love I have received during my Ph.D., please accept me at my word that my heart contains what I fail to express in words. This Ph.D. is not my achievement but the result of work from many. I thank you all.

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"Stick to the coast!"

Mark Bradley

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Dedicated to the cycle of life and love, especially to:

my father
Len Johnstone
January 24th 1923 - November 4th 1994

and

my daughter
Francesca Johnstone
April 14th 1996 -

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. GENERAL INTRODUCTION

The peregrine falcon (*Falco peregrinus* Tunstall) is a crow-sized bird of prey having one of the largest natural distributions of any avian species. This species breeds on every continent, except Antarctica, and on most major islands, except New Zealand and Iceland (Hickey & Anderson 1969, White & Boyce 1988, Ratcliffe 1993). The lives of peregrines are inextricably linked to their prey, and their global distribution, in part, is the result of a correspondingly broad diet of predominantly avian species (Newton 1979, Erickson *et al.* 1988, Fyfe *et al.* 1990, Bradley & Oliphant 1991, Ratcliffe 1993). Where prey are available throughout the year, peregrines tend to be non-migratory. In high latitude breeding regions where prey are not available during winter, however, peregrines tend to be highly migratory with intercontinental movements approximating 15,000 km or more recorded for some sub-species (Kuyt 1967, Hickey & Anderson 1969, Court *et al.* 1988a, Schmutz *et al.* 1991, Ratcliffe 1993, Henny *et al.* 1996). Geographic variation in external morphology (i.e. size and colour) has led to the description of 19 subspecies (Stresemann & Amadon 1979, White & Boyce 1988). Three sub-species breed in North America: Peales peregrine (*F. p. pealei* Ridgway), American peregrine (*F. p. anatum* Bonaparte), and tundra peregrine (*F. p. tundrius* White).

The peregrine falcon is one of the most well studied of all raptor species, and potentially of all avian species. The popularity of the peregrine in the ancient sport of falconry (as early as 2000 BC, Ratcliffe 1993) first inspired detailed observation of the species. Many aspects of the species biology and ecology were perceptively described in the 13th century treatise on falconry by Emperor Frederick II (1248-50) of Hohenstaufen (Wood & Fyfe 1943). The detailed information collected by egg collectors, game keepers, amateur ornithologists, and falconers made a substantial contribution to the knowledge of peregrine breeding biology (Hickey 1942, Ratcliffe 1993). More recent studies included collection of long-term data on annual territory occupancy and breeding success among local peregrine populations (Hickey 1942, Bond 1946, Cade 1960, Herbert & Herbert 1965, Ratcliffe 1962). Such documentation was so extensive in some areas, notably parts of Great Britain and the eastern United States, that the break in these thoroughly established patterns of good reproductive performance and stable breeding populations became apparent after 1956 and widespread population declines were clear by the early 1960's (Hickey 1988, Ratcliffe 1988, Ratcliffe 1993). Moreover, egg breakage and disappearance, failure of incubated eggs to hatch, inexplicable death of chicks, small broods, the failure of pairs to lay, and apparent non-pairing were characteristic of the remaining breeding population (Ratcliffe 1988, 1993). Reproductive failure and dramatic declines in peregrines and other raptors were finally linked in the early 1960's to the introduction and widespread use of the organochlorine pesticides including dichlorodiphenyltrichloroethane (DDT), lindane, and dieldrin (Newton 1979, Ratcliffe 1963, 1967, 1993, Hickey & Anderson 1968). The necessity for a thorough understanding of pesticide accumulation and the effects of these contaminants on peregrine falcons has led to an enormous volume of information on the subject (Anderson & Hickey 1972, Peakall *et al.* 1975, 1990, Peakall 1976, 1990, Newton 1979, Cade *et al.* 1988, Baril *et al.* 1989, Newton *et al.* 1989, Peakall & Kiff 1988, Court *et al.* 1990, Fyfe *et al.* 1990, Noble & Elliott 1990, Ratcliffe 1993). These latter references constitute only a tiny fraction of the volume of related literature available. The population crash in Europe and North America prompted the landmark 1965 Madison Peregrine Conference (Hickey 1969). The subsequent efforts to restore the peregrine through captive breeding and reintroduction was outlined in the 1985 Sacramento Peregrine Conference (Cade *et al.* 1988). These events which acted as important catalysts for research efforts (Ratcliffe 1988).

The literature generated consists of natural history descriptions of different populations, surveys of population size and productivity, pesticide contamination and reproductive failure, migratory behaviour, and captive propagation and reintroduction. Nevertheless, major gaps remain in our knowledge of the ecology and population biology of peregrine falcons, including some of the most basic parameters required for a fundamental understanding of population dynamics, such as survival and recruitment. These gaps exist, in part, because research needs were only identified at the time when peregrines were becoming rare, or were already extirpated in some areas. In 1975, for example, a total of only 159 peregrine pairs were known to be breeding in southern Canada east of the Rocky Mountains and the United States (Fyfe *et al.* 1976, Johnstone *In press*). The scope and subject of studies, or their conclusions, have frequently been severely constrained by low numbers and highly dispersed populations breeding on inaccessible cliffs. It is not surprising, therefore, that the peregrine falcon has never generally been considered a suitable study species for experimental research on more general questions in avian population biology, despite extensive speculation in the literature on topics, such as population limitation.

Between 1991 and 1995 I studied a dense, easily accessible population of tundra peregrine falcons that breed around the hamlet of Rankin Inlet in the Keewatin District of the Northwest Territories, Canada. While the population is relatively small (24 territorial pairs, on average, are evident each spring), it has been intensively studied since 1980 (Court 1986, Court *et al.* 1988a, b, 1989, 1990, Bradley 1989, Bradley & Oliphant 1991, Bradley *et al.* In press, Duncan 1993). Survey methodology was carefully standardized between 1982-1995 resulting in a long-term data base on territory occupancy, productivity data, the identification of individuals breeding, recruitment, and collection of toxicological samples. The aim of this thesis was to fill some of the knowledge gaps for peregrines and examine some general theories in avian biology by using all data at my disposal, and by utilizing novel methods of experimentation and investigation.

For several decades, the single most important factor determining the outcome of a breeding attempt and the productivity of peregrine populations was the level of organochlorine contamination. In the absence of organochlorine contamination, populations remained stable; where there were high levels of contamination, productivity was very poor and populations declined (Newton 1979, Ratcliffe 1993) and in some cases were extirpated. An assessment of the accumulation and effects of persistent organochlorine compounds is, therefore, an important part of any investigation which has the reproductive performance of peregrine falcons as a major focus. In Chapter 1 (Johnstone *et al.* 1996, Muir *et al.* 1997), I document levels of organochlorines in peregrines and their prey at Rankin Inlet and assess their potential to affect breeding success. This study also fills an important knowledge gap in that there has been much speculation regarding the threat posed to migratory peregrine populations by the continuing use of organochlorines within their migratory and wintering ranges in Latin America (Burton & Philogene 1988, Fyfe *et al.* 1990, Noble & Elliott 1990); however, data to accurately assess this potential threat have been lacking. I assess this threat by determining temporal trends in levels of selected organochlorines between the 1980's and the 1990's, and comparing contaminant levels among three sub-populations of *F. p. tundrius* and their respective dietary intakes of contaminants to attempt to identify sources of contaminants.

A recent focus of behavioural ecology is the relationship of sperm competition with parental care, copulation behaviour, and mate guarding in different avian species. Mate guarding (i.e. when the male remains close to the female while she is fertile and prevents other males from inseminating his mate) and frequent copulation are considered alternative methods by which a male may assure paternity of the young it raises (Birkhead *et al.* 1987, Birkhead & Møller 1992, Møller & Birkhead 1992). The Paternity Assurance Hypothesis (PAH) predicts that birds which are prevented by ecological factors from closely guarding their mates, such as many diurnal and nocturnal birds of prey and colonial breeders, will use frequent copulation to ensure paternity. Studies of non-raptorial species support the hypothesis that, in the absence of mate guarding, frequent within-pair copulations are an effective strategy for assuring paternity (Birkhead & Møller 1992). Moreover, raptors do tend to copulate frequently (Møller 1987, Birkhead *et al.* 1987, Møller & Birkhead 1992, Birkhead & Møller 1992, Korpimäki *et al.* 1996). There have been few analyses of paternity among raptor species, however, to test predictions of the paternity assurance hypothesis (Decker *et al.* 1993, Swatschek *et al.* 1993, Warkentin *et al.* 1994, Korpimäki *et al.* 1996, Negro *et al.* 1996). Moreover, the raptor species studied so far provide a poor match with predictions of the paternity assurance hypothesis. Extra-pair parentage was generally rare, but the frequency of extra-pair copulations were correspondingly low, also. In the absence of extra-pair copulations, certainty of parentage is high without counter-measures. Further parentage studies of raptors are therefore required to thoroughly evaluate whether the paternity assurance hypothesis provides an adequate explanation of parentage, mate guarding and copulation behaviour, within this group. In Chapter 2 (Johnstone *et al.* In press) I determined the parentage of peregrine falcon broods using single-locus DNA profiling to test predictions of the paternity assurance hypothesis. Male peregrine falcons must provision their mates with food, and their frequent absences from the nest to hunt provide the female with potential opportunities for extra-pair copulations throughout her fertile period. The paternity assurance hypothesis suggests that, given frequent opportunities for EPCs, extra-pair parentage (EPP) should be high in the peregrine falcon, relative to guarding species (Birkhead and Møller 1992, Birkhead and Møller 1995, but see Dunn and Lifjeld 1994).

Population regulation and limitation of breeding densities, and their underlying mechanisms, have long been a central topic of debate in avian population ecology (Howard 1920, Andrewartha & Birch 1954, Hinde 1956, Lack 1956, 1966, Wynne-Edwards 1962, Brown 1969, Fretwell & Lucas 1970, Watson & Moss 1970, Sinclair 1989). The stability of breeding populations (in the absence of organochlorine contamination), rapid replacements of mates at nests, and anecdotal observations of a surplus of non-territorial non-breeding adults (often referred to as "floaters", Davies 1978) has long prompted speculation regarding how peregrine falcon and other raptor populations are regulated and whether they are limited (Ratcliffe 1962, Nelson 1977, Newton 1979, 1988, Court 1986, Hunt 1988). In general, models of peregrine population regulation and limitation in heterogeneous environments (Newton 1988, Hunt 1988) closely resemble the theoretical ideal despotic distribution model of Fretwell & Lucas (1970) and Fretwell (1972). They predicted that for a species occupying a heterogeneous environment, habitat associated with high fitness (i.e. good "quality" habitat) would be occupied at low densities, and as population density increases individuals would be forced to occupy habitat associated with increasingly lower fitness (i.e. poor quality habitat) until the quality of remaining available territories is so low that they are unsuitable for breeding attempts, and individuals become floaters instead. In Chapter 3 (Johnstone *et al.* MS1), I investigate the role and importance of density-dependent processes in regulation of the Rankin Inlet peregrine population and the underlying mechanisms, including the influence of habitat quality. In Chapter 4 (Johnstone *et al.* MS2), I test for population limitation by determining through withdrawal experiments (Newton 1992) whether a non-breeding surplus of adults exists.

One of the most fundamental parameters to an understanding of the dynamics of a population is survival. Considering the importance of this parameter, and its obvious need in management and conservation of the species, however, there are surprisingly few studies that include estimates of adult peregrine survival (or mortality) (Hunt 1988, Newton 1988, Wootton & Bell 1992, Pagel *et al.* 1996). Only recently has survival been estimated in three different populations through mark-recapture of individuals (Mearns & Newton 1984, Newton & Mearns 1988, Court *et al.* 1988, Court *et al.* 1989, Gould & Fuller 1995). Peregrines have been intensively banded and recaptured/resighted at Rankin Inlet for 14 years, providing one of the largest samples available for the species. In Chapter 5 (Johnstone *et al.* MS3), I estimate survival of adult male and female peregrine falcons by Cormack-Jolly-Seber (CJS) analysis of capture-mark-recapture data (Cormack 1964, Jolly 1965, Seber 1965, 1982, Burnham *et al.* 1987, Pollock *et al.* 1990, Lebreton *et al.* 1992) and turnover methodology (Mearns & Newton 1984), and provide a critique of the two methods.

Raptors have consistently proved to be difficult species through which to address paradigms in avian ecology mainly because of problems inherent with small samples and logistic problems, in general. This is especially true of peregrine falcons; their low population density and generally inaccessible nest sites make wild populations unattractive for intensive study. Fortunately, the peregrine falcons of Rankin Inlet represent a unique opportunity for study, in that the population is dense and easily accessible. Considering this opportunity and the fact that I was allowed access to another 10 years of information from the study area, I concentrated on those areas of raptor biology that have been poorly studied. As a consequence, this thesis covers a purposely diverse range of topics in raptor biology, in order to avoid yet another treatise on peregrine population size and productivity.

2. LONG-TERM TRENDS AND SOURCES OF ORGANOCHLORINE CONTAMINATION IN CANADIAN TUNDRA PEREGRINE FALCONS.

2.1 ABSTRACT

Levels of eggshell thinning, and organochlorine residues in egg contents, blood plasma of adults and juveniles, tissue samples, and prey species were determined for a population of migratory peregrine falcons (*F. p. tundrius*) breeding in the Canadian Arctic. Temporal trends were assessed by comparing data collected during 1991-1994, with data from 1982-1986, for the same population. Shells (n = 54) from 1991-1994 averaged 15% thinner than eggs produced prior to the introduction of DDT. No improvement in shell thickness was detected between decades. Mean DDE residue levels in eggs showed a decline from 7.6 mg kg (1982-1986) to 4.5 mg kg (1991-1994), but there was no significant change in ∑PCB residues. Moreover, the proportion of clutches with eggs exceeding critical ∑PCB, DDE, and dieldrin residue levels (10%) did not change between decades. Relative to Greenland and Alaskan populations, *F. p. tundrius* at Rankin Inlet show high levels of organochlorine contamination and little reduction in residues over the last decade. These tundra peregrines continue to be exposed to organochlorines in Latin America; although results also link relatively high levels in the study population with waterfowl species that do not leave Canada in winter.

2.2 INTRODUCTION

This paper reports on the toxicological assessment of a population sample of tundra peregrine falcons *F. p. tundrius* nesting around the hamlet of Rankin Inlet, Keewatin District, Northwest Territories, Canada and its prey species during the years 1982-1986 and 1991-1994. The results are used to assess the present impact of organochlorine contaminants (organochlorine insecticides and industrial polychlorinated biphenyls

(PCBs)) on breeding attempts of tundra peregrines, assess temporal trends in contamination, and identify the origin of contamination.

In many areas, peregrine falcons have recovered from dramatic population declines, following gradual decreases in contamination of their prey species. In North America, recoveries of *F. p. anatum* were subsequent to restrictions on use of organochlorines imposed over two decades ago (Cade *et al.* 1988, Peakall 1990). However, for populations of *F. p. tundrius* which winter in Latin America and feed on migratory species, the prospect of a reduction in contamination has seemed less certain and the impact on reproduction less clear due to the continued use of some organochlorines in these areas (Burton & Philogene 1988, Fyfe *et al.* 1990). This study is pertinent, as recent data on residues in *F. p. tundrius* in North America are lacking. No temporal studies of contaminant levels for a single population of *F. p. tundrius* exist, and attempts at trend analysis have been confused by haphazard data collection, resulting in samples that are temporally discontinuous and spatially disjointed (Peakall *et al.* 1990, Thomas *et al.* 1992). Such data are wrought with inherent sampling biases and perceived changes in contaminant levels may reflect geographical trends rather than true temporal trends.

The toxicological analysis of the Rankin Inlet *F. p. tundrius* population and its prey began in 1981. Court *et al.* (1990) reviewed data and samples from 1982-1986, and concluded that significant amounts of organochlorine pesticides and PCB residues were accumulating in the tissues of these Arctic-nesting peregrines and their prey. Eggshell thinning, levels of DDE residues in eggs, and levels of contaminants found in some prey species were all close to the critical levels considered to result in decreased production in peregrines (Peakall & Kiff 1988, Court *et al.* 1990, Peakall *et al.* 1990). Court *et al.* (1990) estimated that about 10% of all breeding attempts between 1981 and 1985 failed due to pesticide contamination, although the population itself remained productive and showed no evidence of decline.

In this study, I present data on samples collected between 1991 and 1994. Eggshell fragments representing 54 peregrine clutches, the contents of 28 whole peregrine eggs, blood plasma from 139 peregrines, tissue samples from seven peregrines, and whole body analysis of 70 individuals representing 12 prey species were assessed. The biological significance of this contamination was established by comparing levels of eggshell thinning and the detected levels of organochlorines in peregrines and prey species with levels considered critical to successful reproduction (Baril *et al.* 1990, Noble &

Elliott 1990, Peakall *et al.* 1990). I established temporal trends in organochlorine contaminants by comparing present levels with those published for the same population between 1982 and 1986 (Court *et al.* 1990). In an attempt to identify the origin of contamination, I compared the relative contamination of Rankin Inlet peregrines with two other populations of *F. p. tundrius*.

2.3 METHODS

Data were collected as part of the ongoing study of a small population of tundra peregrine falcons nesting within a 450 km^2 area around the hamlet of Rankin Inlet (62° 49'N 92° 05'W), Keewatin District, Northwest Territories, Canada. The population is productive; each year 14-25 pairs laid eggs (mean = 19), and successful pairs fledged a mean of 2.5 chicks (range 1.8-3.1) annually. There was no significant trend in either the number of pairs laying annually or the annual production of young per successful pair during the study period. Further details of the study area and population may be found in Court *et al.* (1988a, b).

To assess the thickness of eggshells, whole eggshells and eggshell fragments representing 54 clutches of eggs were collected from both unsuccessful and successful nests. Following the methods of Court *et al.* (1990) eggshell thickness was measured using a Leitz Wetzlar UWM Toolmaker's Microscope Micrometer, accurate to ±0.0025 mm. With fragment samples, mean eggshell thickness was determined from three chips selected at random from the collection at each nest. For whole eggs, measurements were taken from fresh chips taken at three places on the equator of the shell. At some nests, more than one egg was available for analysis. In these instances, three measurements were taken from each egg and then a mean thickness was calculated for the clutch. For statistical analysis this clutch mean was included in the data as a single value representing the clutch. Most measurements included the shell and the shell membrane. If the shell membrane was not present, 0.069 mm (average membrane thickness for 47 eggs, Court *et al.* 1990) was added to the shell thickness. Inter-observer reliability between Johnstone (1990's data) and Court (1980's data) at measuring eggshell thickness was confirmed by both measuring a random sample of eggshell fragments.

A sample of peregrine eggshells produced prior to the introduction of the organochlorine pesticides is not available for the Keewatin District. For comparative purposes, I compared the thickness of eggshells collected in this study with a weighted mean eggshell thickness calculated from three pre-pesticide collections of peregrine eggs from the Nearctic (Berger *et al.* 1970, Anderson & Hickey 1972, Walker *et al.* 1973). A weighted mean was used to allow for the difference in sample sizes used to calculate means for each study.

Whole addled peregrine eggs, blood plasma, and body tissues of peregrines, and representative prey species were collected for toxicological analysis. I measured levels of the following organochlorines: total polychlorinated biphenyls ($\sum$PCB); *p,p'*-DDT and its metabolites *p,p'*-DDE and *p,p'*-DDD; hexachlorobenzene (HCB); benzene hexachloride (α-BHC); oxychlordane; heptachlor epoxide (HCE); dieldrin; and mirex. Detection limits for PCB and organochlorines were 0.100 and 0.020 mg kg, respectively. PCB standards consisted of a 1:1 mixture of PCB 1254 and 1260, and $\sum$PCB quantification was based on the sum of the concentration of the 14 most abundant congener(s) groups. All toxicological analyses were conducted at the Health of Animals Laboratory, Food Animal Chemical Residues Section, Agriculture and Agri-Food Canada, Saskatoon. Preparation of samples, initial assay, and confirmatory gas chromatography-mass spectrometry analyses followed the methods of Won (1982), Won & Turle (1987) and Burse *et al.* (1983), as used by Court *et al.* (1990). The quality assurance program run by the Health of Animals Laboratory maintains analytical consistency between samples, validating a comparison between the data collected from 1991 to 1994 with the samples collected by Court *et al.* (1990). Approximately one recovery quality assurance (QA) sample was run with every 20 samples analyzed. Recoveries for PCB and organochlorines were all greater than 80% in all tissues, except for α-BHC (71-79%). Pesticide reference standards used for quantification were validated according to the Health of Animals Laboratory QA protocol.

Twenty-eight whole addled eggs were collected opportunistically from both successful and unsuccessful nests between 1991 and 1994. At successful nests, addled eggs were collected seven days after the hatch of the youngest nestling. Addled eggs were removed from unsuccessful nests only when it was clear that they had been abandoned. The eggs were wrapped in foil and then frozen until analysis. I treated moisture loss in eggs the same way as Court *et al.* (1990) (i.e. any eggs with less than 70% water content were eliminated from the sample). I compared mean water content of eggs and found no statistical difference between the sample of Court *et al.* (1990) and the eggs collected between 1991 and 1994; this validates a direct comparison of residue levels between the two samples. In six instances, more than one egg was collected from a clutch. Residues in each egg were measured separately, then a clutch mean for each residue was calculated. For statistical analysis this clutch mean was included in the data as a single egg representing the clutch. I lacked enough whole clutches from 1991 to 1994 to statistically assess whether within-clutch variation justified the presentation of residue levels from a single egg as being representative of the whole clutch. Pooling data with Court *et al.* (1990), I performed an analysis of variance on 12 clutches (Table 2.1). For all contaminants the 'within clutch variance' was small compared to the 'between clutch variance', supporting the premise that single eggs were representative of their respective clutches.

Egg contents were analyzed as follows: two 2-g sub-samples of the egg contents were taken, one of which was used for determination of sample dry weight by heating at 105°C to constant weight. The second sub-sample, used for analysis, was added to 20-g sodium sulphate in a mortar and pestle, ground to a free flowing powder and transferred to a glass column containing 2 cm sodium sulphate. The mortar and pestle were rinsed with hexane, which was added to the column. Sufficient dichloromethane:hexane (1:1) was then added to the column to just wet the contents. After standing one-half hour, the column was eluted with 300 ml dichloromethane:hexane (1:1). The eluate was collected and the volume reduced to near dry at 38°C using a rotary evaporator. The residue was transferred quantitatively to a graduated centrifuge tube and made to 8.0 ml using hexane. This was split into two 4-ml portions, one of which was used for lipid analysis by evaporation of the solvent at room temperature, followed by oven drying at 105°C for 10-20 min. The second 4 ml aliquot of eluate was transferred to an 8-g Florisil mini-column and eluted in sequence with hexane, 15% dichloromethane in hexane, 80% dichloromethane in hexane, collecting three fractions. The Florisil was used as supplied and the elution volumes adjusted to give the required elution pattern. Fraction 1 (hexane) was concentrated by evaporation to 10 ml, while the remaining two fractions were concentrated to 1 ml using an N-evap. All fractions were then analyzed by gas chromatography on a 30 m x 0.32 mm ID DB-608 capillary column, using a ^{63}Ni electron capture and nitrogen phosphorous detector and external standard calibration method. Positive findings were confirmed using a GC-MS system equipped with a 30 m x 0.25 mm ID DB-5 capillary column using positive or negative ion detection and electron impact or chemical ionisation mode, as appropriate.

Between 1991 and 1994 I live-captured adult peregrines and took blood samples from 26 males and 34 females. One to two cc of whole blood was collected from the brachial vein using a 23 gauge needle and 3 cc syringe. Blood samples were also collected from 79 peregrine and seven Rough-legged hawk (*Buteo lagopus*) nestlings prior to fledging. Whole blood samples were stored in 5 cc heparinized vacutainers until centrifuged 6-10 hours later. After spinning, blood plasma was stored frozen in 5 cc sterilized vacutainers until analysis. Briefly, the sample (0.25-1.5 ml) was transferred to a pre-weighed container and the sample weight was determined. 1 ml of methanol was added and mixed with the sample following this, the mixture was extracted two times with 5 ml hexane:ethyl ether (1:1). Each time, the extract was centrifuged at 1800 rpm for 6 minutes and the supernatant was removed. The combined supernatants were concentrated to 0.5 ml using a N-evap. The concentrated extract was then added to a 80 mm x 15 mm ID column containing 2.50-g Florisil topped by 1.5-g sodium sulphate. The column was eluted with hexane, 30% dichloromethane in hexane, and 80% dichloromethane in hexane, collecting each fraction. The fractions were evaporated to dryness on an N-evap and then dissolved in iso-octane. All fractions were analyzed by gas chromatography on a 30 m x 0.32 mm ID DB-608 capillary column with detection using a ^{63}Ni electron capture detector. Quantification was by external standard against a calibration mixture of known concentrations. Gas chromatographic confirmations were done by comparisons of chromatographic results on a 30 m x 0.32 mm ID DB-5 capillary column. GC-MS confirmations were performed as described above for the egg samples.

Between late May and early June of 1993 and 1994, up to ten adults of each of 10 common avian and two mammalian prey species were shot within the study area. Specimens were plucked (birds) or skinned (mammals), intestines were removed, and each was wrapped in foil and frozen until analysis. Each sample of each species was then ground with a Hobart chopper/grinder, sub-sampled and homogenized. Analysis for selected organochlorine residues proceeded as described above for the eggs, using 5-g analytical sub-samples.

Liver and breast muscle tissue from nestling peregrine falcons found dead within the study area were also collected. Analytical 5-g sub-samples of each tissue were used for analysis for organochlorine residues following the method described above for the eggs. The age of the nestling at death was recorded. For several nestlings where the precise date of hatching and date of death was not known an estimated age was calculated using the

Table 2.1. Analysis of variance on clutches from which at least two unhatched eggs were collected (1981-1994).

	Source of variation	Degrees of freedom	Sum of squares	Mean squares	*F*
ΣPCB	Between clutches	11	1.202	0.109	4.058***
	Within clutches	20	0.538	0.027	
	Total	31	1.74		
DDE	Between clutches	11	1.03	0.094	6.635***
	Within clutches	20	0.282	0.014	
	Total	31	1.313		
Dieldrin	Between clutches	11	0.089	0.008	3.266*
	Within clutches	20	0.049	0.002	
	Total	31	0.138		

Number of clutches = 12, number of eggs = 32. * $P < 0.05$, *** $P < 0.005$.

mean hatch date of the population (the mean date of clutch completion plus the mean incubation period (35 days; Court *et al.* 1988a) and the estimated date of death.

All residues in egg contents, plasma samples, and tissue of both prey and peregrines are expressed as mg kg wet weight of the samples. For statistical treatment, residue values below detection limits were included as recorded. A nil value or NO (not observed) was included when no analytical response was observed. The residue data were skewed in distribution (to the left), so for statistical comparisons, data were log transformed to more closely approximate a normal distribution. For the same reason, means reported for residue data are geometric, unless stated otherwise. Data of eggshell thickness, egg lipid content, and egg water content are normally distributed, so no transformation was necessary. Means for these data are arithmetic and reported with ± one standard deviation (S.D.). For comparisons of residue levels between decades, and between sexes, a Student's *t*-test (two-tailed) was performed on log-transformed data. Differences among data sets were considered significant when the probability value (*P*) was < 0.05. If sample sizes were small, an appropriate non-parametric test was used. Statistical analysis followed Sokal & Rohlf (1995) and Siegel & Castellan (1988).

While I measured residue levels of ten persistent organochlorine compounds, I restrict my discussion to those known to have serious effects on avian populations and for which critical levels have been estimated (Noble & Elliott 1990, Peakall *et al.* 1990, Furness 1993). I compare the levels of organochlorine residues I detected with critical levels derived from the literature in a review by Peakall *et al.* (1990).

2.4 RESULTS

2.4.1 Organochlorine Residues in Prey Species

Selected residues from whole body analysis of 10 avian and 2 mammalian prey species of peregrine falcons at Rankin Inlet (Bradley 1989, Bradley & Oliphant 1991) are summarized in Table 2.2. Analysis of the sample showed the continuing contamination of Arctic-breeding avian species by organochlorines but almost no contamination of mammalian prey species. Higher contaminant levels appear primarily related to the habitat and trophic level of individual species, and secondarily to migration range. Avian prey

Table 2.2. Selected organochlorine residues (mg kg wet weight) in prey species of peregrine falcons nesting at Rankin Inlet (1991-1994).

			Residues	
Species	N	ΣPCB	DDE	Dieldrin
Long-tailed duck	5	6.88	1.09	0.51
Clangula hyemalis		(2.88-18.88)	(0.61-3.75)	(0.02-4.02)
Black guillemot	8	0.38	0.17	0
Cepphus grylle		(0.13-0.65)	(0.10-0.24)	(0-0.02)
Northern pintail	4	2.11	0.47	0.09
Anas acuta		(0-5.40)	(0.09-0.91)	(0.03-0.26)
Semipalmated plover	5	0.40	0.50	0.02
Charadius semipalmatus		(0-2.06)	(0.10-1.07)	(0-0.11)
Semipalmated sandpiper	3	0.03	0.25	NO
Calidris pusilla		(0-0.10)	(0.04-0.70)	
Water pipit	5	0.14	0.69	NO
Anthus spinoletta		(0-0.79)	(0-9.50)	
Horned lark	7	ND	0.07	NO
Eremophila alpestris			(0-0.17)	
Lapland longspur	10	0.03	ND	NO
Calcarius lapponicus		(0-0.36)		
Snow bunting	2	ND	NO	NO
Plectrophenax nivalis				
Dunlin	1	NO	0.04	NO
Calidris alpina				
Arctic ground squirrels	7	NO	NO	NO
Spermophilus parryi				
Collared lemmings*	13	ND	ND	NO
Dicrostonyx groenlandicus		(0-4.17)	(0-0.11)	

* Contaminants were only found in one collared lemming who had levels (mg kg wet weight) of ΣPCB 4.17, DDE 0.11, DDD 0.07, and DDT 0.08.

ND means that the calculated mean level is below detectable limits, NO means no analytical response was observed.

species were grouped into seabirds, waterfowl, shorebirds, and passerines and then ranked by residue level. Within each group residue levels appeared related to migratory range, and most heavily contaminated were migrant species which occupy marine and aquatic habitats. Long-tailed duck (*Clangula hyemalis* formerly known as oldsquaw) and black guillemot (*Cepphus grylle*) migrate the least of all migratory species sampled yet rank first and fourth, respectively, in contamination. Both species are ocean-dwelling and feed on small fish and invertebrates. Long-tailed ducks winter in Hudson Bay, the Great Lakes, and along the Atlantic seaboard of Canada and the United States of America south to Chesapeake Bay (Bellrose 1976, Palmer 1976, Godfrey 1986). Black guillemot also winter on ice-free areas of Hudson Bay and along the Atlantic coast of Canada (Godfrey 1986).

Among the shorebirds, residues ranged from medium to low levels of contamination. The plover and sandpiper species winter in Latin America, as far south as southern Argentina and Chile (Godfrey 1986), and most show elevated contaminant levels, especially when compared to passerines. Passerines at Rankin Inlet rank as some of the least contaminated avian prey species. For example, only one of seven horned larks (*Eremophila alpestris*) and one of the ten Lapland longspurs (*Calcarius lapponicus*) sampled contained detectable levels of ΣPCB residues. The only exception to generally low residue levels in passerines was water pipit (*Anthus spinoletta*), a migrant which winters as far south as Guatemala. This is the only insectivorous passerine on the study area, and it contained the highest levels of DDE of all avian species sampled in this study. Snow buntings (*Plectrophenax nivalis*), which migrate shorter distances than other passerines, recorded the lowest residue levels.

ΣPCB, DDE, dieldrin, and heptachlor epoxide residues were detected in most of the avian species. Hexachlorobenzene was present only in black guillemots (geo mean = 0.10 mg kg, range 0.07-0.16), long-tailed ducks (geo mean = 0.10 mg kg, range 0.05-0.29), northern pintail (geo mean = 0.05 mg kg, range 0-0.08),and semipalmated plovers (geo mean = 0.01 mg kg, range 0-0.02),while α-BHC was only detected in long-tailed ducks (geo mean = 0.25 mg kg, range 0.05-0.75) and northern pintail (geo mean = 0.04 mg kg, range 0-0.64). Oxychlordane was detected (range 0.04-0.53 mg kg) only in water pipit, long-tailed ducks and northern pintail. Mirex was found in low concentrations (0.12-0.57 mg kg) in single specimens of water pipit, long-tailed duck and northern pintail. DDD and DDT were detected in the tissues of one long-tailed duck. While heptachlor epoxide, oxychlordane, DDD, DDT, hexachlorobenzene, α-BHC, and mirex were detected in some of the prey samples, the significance of such low level contamination on reproduction is difficult to assess. None of these compounds occurred in levels high enough to affect reproduction in peregrines (Baril *et al.* 1990).

Two mammalian species are commonly preyed upon by peregrines at Rankin Inlet (Bradley & Oliphant 1991). Neither Arctic ground squirrels (*Spermophilus parryi*)nor lemmings (*Dicrostonyx groenlandicus*) showed any organochlorine residues at detectable levels, except for a single collared lemming (Table 2.2).

Court *et al.* (1990) pooled samples for toxicological analysis. The low number of pools per species precludes a statistical comparison of residue levels in prey species to establish temporal trends, with the exception of two species. I compared residue levels in long-tailed duck and black guillemot sampled from 1982-1986 with 1991-1994 samples but at the stated level of statistical power I could detect no evidence for a change in residue levels in either species. Qualitatively, levels of ΣPCB, DDE, and dieldrin in most prey species sampled in the 1980's by Court *et al.* (1990) were similar, or even slightly lower, than in samples taken during the 1990's. The exception was long-tailed duck, where levels of these residues have increased slightly. Patterns of contamination concur between decades; waterfowl and marine species being the most contaminated, passerines the least, and water pipits showing the highest levels of DDE recorded (Court *et al.* 1990).

2.4.2 Eggshell Thickness

Measurements of eggshell thickness from Rankin Inlet are consistent with a population of peregrines that winters and migrates within a polluted environment, and feeds on a partly contaminated prey base on the breeding grounds. The mean thickness of eggshells collected between 1991 and 1994 was 15% thinner than the average pre-DDT shell thickness for peregrines from the Nearctic (0.306 ± 0.022 mm, n = 54 vs. 0.360 mm; Figure 2.1). The thinnest shell was 32% thinner than the average pre-DDT shell thickness for peregrines from the Nearctic. 28% (15/54) of the sample included eggs with shells thinner than critical levels (i.e. 17% of the mean pre-DDT shell thickness; Kiff 1988).

There was no evidence of improvement in eggshell thickness between the 1980's and 1990's. Mean eggshell thickness did not differ between 1982-1986 (mean 0.303 ± 0.022 mm, n = 62) and 1991-1994 (0.306 ± 0.022 mm, n = 54; Students *t*-test t_{114}=

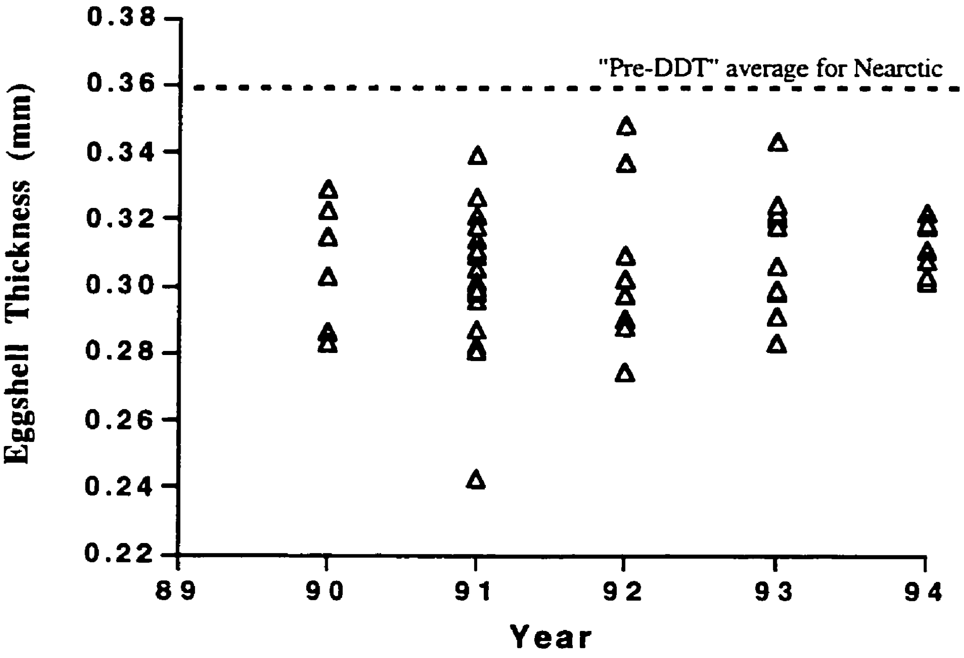

Figure 2.1. Eggshell thickness (mm) for tundra peregrine falcons nesting around Rankin Inlet, N.W.T. from 1990 to 1994 (n = 54 clutches).

-1.018, $P = 0.3107$). There was no difference in shell thickness among years 1991-1994 (ANOVA $F_{4,49} = 0.789$ $P = 0.5381$).

2.4.3 Organochlorine Residues in Eggs

A total of 28 peregrine eggs, representing 20 clutches, was collected for analysis between 1991 and 1994. Organochlorine residue levels in eggs are summarized in Table 2.3. Mean residue levels were below minimum critical levels, but 10% (two) of clutches included eggs with detected levels of ΣPCB, DDE, and dieldrin exceeding minimum critical levels (Peakall *et al.* 1990). In one egg levels of 45.63 mg kg ΣPCB, 28.05 mg kg DDE, and 1.37 mg kg dieldrin were recorded. In the other egg levels of 53.65 mg kg ΣPCB, 17.63 mg kg DDE, and 0.63 mg kg dieldrin were recorded. Pesticides tend not to occur singly in the environment, so that individual birds tend to accumulate contaminants collectively. Concentrations of organochlorines within eggs are strongly correlated (Table 2.4), so an egg that exceeded critical levels of one organochlorine tended also to exceed critical levels of the other contaminants.

Peregrine falcons with DDE residues in egg contents of 15 to 20 mg kg, tend to experience enhanced rates of reproductive failure (Peakall *et al.* 1975); two clutches (10%) in the sample contained eggs with residue levels exceeding these levels. One chick was produced from one of the two clutches, indicating that critical levels should not be construed as so rigid that they may be used to predict the success or failure of all breeding attempts. Variation in residue levels within some clutches was substantial enough that some eggs might hatch and others not.

I compared the mean levels of organochlorine residues in contents of eggs collected between 1982-1986 with those collected between 1991 and 1994 (Table 2.3). There was no significant change in mean ΣPCB or dieldrin levels in egg contents during this time. Mean DDE levels in egg contents decreased from 7.6 to 4.5 mg kg (wet weight) between the 1980's and the 1990's. This change made little or no difference to the shell thickness or annual reproductive success of the study population. Maximum values were still high, with 10% of clutches exceeding critical levels.

Table 2.3. Minimum critical residue levels and detected organochlorine residues (mg kg wet weight) in peregrine falcon eggs collected at Rankin Inlet during 1982 to 1986 (from Court *et al.* 1990) and 1991 to 1994.

		1991-1994 (n =20)		1982-1986			Difference (*P*)
Residue	Critical level[1]	Range	Mean	Range	Mean	n	between years
ΣPCB	> 40	1.67-45.63	8.31	1.95-47.76	8.74	36	0.72
HCB	> 4.0	0-0.17	0.03	0-0.15	0.03	22	0.7105
α-BHC		0-0.03	ND		ND	19	
Oxychlordane		0.04-0.91	0.21	0.08-0.80	0.21	21	0.5408
HCE	> 1.5	0.05-1.39	0.27	0.09-5.92	0.36	36	0.1038
DDE	15-20	0.76-28.05	4.45	1.79-29.27	7.59	36	0.0062
Dieldrin	> 1.0	0.05-1.80	0.36	0.13-1.66	0.41	36	0.1997
DDD		0-0.20	0.01	0-0.37	ND	22	0.2026
DDT		0-0.03	0.00	0-1.41	ND	36	0.0482
Mirex		0.06-1.82	0.50		NM		

[1] Following Peakall *et al.* (1990). NM= not measured, ND = the calculated mean level is below detectable limits.

Table 2.4. Correlation coefficients (*r* values) among concentrations of different organochlorine compounds in peregrine falcon eggs from 20 different nesting attempts from 1991 to 1994.

	ΣPCB	DDE	Dieldrin
ΣPCB	1.00		
DDE	0.917**	1.00	
Dieldrin	0.417*	0.516*	1.00

$*P < 0.05$, $**P < 0.001$

2.4.4 Organochlorine Residues in Blood Plasma

ΣPCB, oxychlordane, heptachlor epoxide, DDE, dieldrin, and mirex were all found at detectable levels in the plasma of adult peregrines (Table 2.5). These were in much lower concentrations than in egg contents. Adult females had significantly higher levels of DDE and ΣPCB than adult males, but there was no difference between sexes in any other residue levels (Table 2.5).

Only ΣPCB and DDE were found in detectable levels in the plasma of nestlings (Table 2.5), and in much lower concentrations than in the adults. Mean ΣPCB levels in nestlings were about one half of the levels in adult males, and almost one tenth the levels found in adult females. Plasma levels of DDE in male nestlings were positively correlated with DDE plasma levels in their mothers, but there was no significant relationship detected between DDE levels in female nestlings and levels in their mothers (Table 2.6). In contrast, plasma levels of ΣPCB in male or female offspring were not related to levels of ΣPCB in their mothers, although there was a positive association in plasma levels of ΣPCB between males and their female siblings (Table 2.6).

Previously, distinct differences in plasma levels of organochlorine residues at different times of the year were found (Court *et al.* 1990), so to establish temporal trends I restricted comparisons to samples taken after egg-laying during summer. In adult females sampled during summer, levels of DDE, dieldrin, and heptachlor epoxide were all less in samples taken during 1991-1994 than they were in 1982-1986 (Table 2.7). There was no evidence of a decrease in contamination by ΣPCB over the decade. However, the decreasing trend in these residue levels was not found in males. There was no significant difference in mean ΣPCB, DDE, dieldrin or heptachlor epoxide levels in male plasma during summer between decades. Also, there was no significant difference in DDE levels in the plasma of nestlings between 1982-1986 and 1991-1994 (Student's *t*-test, two-tailed t_{96}= -0.764 P = 0.2235. 1982-1986 mean = 0.030, range 0-0.02, n = 19; 1991-1994 mean = 0.059, range 0-2.697, n = 79). It is also clear that ΣPCB residues in peregrine nestlings have increased since the early 1980's. Court *et al.* (1990) could not detect ΣPCB in the plasma of nestlings at measurable levels, yet I recorded a mean ΣPCB residue level of 0.12 mg kg with a maximum value of 2.59 mg kg (Table 2.5).

Table 2.5. Organochlorine residues in peregrine falcon blood plasma samples taken at Rankin Inlet (mg kg wet weight) from 1991 to 1994.

Residue	Nestlings (n =79)		Adult Males (n =26)		Adult Females (n = 34)	
	Range	Geometric mean	Range	Geometric mean	Range	Geometric mean
ΣPCB	0-2.59	0.12	0-3.27	0.15	0-6.82	0.87**
Oxychlordane	0-0.07	ND	0-0.09	ND	0-0.14	0.02
HCE	0-0.04	ND	0-0.20	0.02	0-0.18	0.03
DDE	0-2.70	0.06	0.05-1.95	0.31	0-4.23	0.63*
Dieldrin	0-0.06	ND	0-0.30	0.03	0-0.37	0.04
Mirex	0-0.16	ND	0-0.34	0.02	0-2.14	0.08

* $P < 0.05$, **$P < 0.005$. Difference between adult males and females in mean plasma residue levels prior to laying in spring. ND means that the calculated mean level is below detectable limits.

Table 2.6. Correlation coefficients (*r* values) between residue levels in the blood plasma of 18 adult females and their offspring.

		Adult female		Offspring			
				Male		Female	
		ΣPCB	DDE	ΣPCB	DDE	ΣPCB	DDE
Adult female	ΣPCB	1					
	DDE	0.908***	1				
Male offspring	ΣPCB	0.083^{NS}	0.041^{NS}	1			
	DDE	0.593*	0.766**	0.391^{NS}	1		
Female offspring	ΣPCB	0.280^{NS}	0.005^{NS}	0.933***	0.177^{NS}	1	
	DDE	0.253^{NS}	0.024^{NS}	0.951***	0.185^{NS}	0.978***	1

* $P< 0.05$, **$P< 0.005$, ***$P< 0.0005$, NS= not significant.

Table 2.7. Geometric mean levels of organochlorine residues (mg kg wet weight) in the blood plasma of adult male and female peregrine falcons sampled during summer between 1982-1986 (Court *et al.* 1990) and 1991-1994 at Rankin Inlet.

Sex/Sampling Period	n	ΣPCB (range)	HCE (range)	DDE (range)	Dieldrin (range)
Males 1982-1986	19	0.47 (0-2.55)	0.09 (0.02-0.23)	1.03 (0.26-2.52)	0.08 (0-0.30)
Males 1991-1994	7	0.75 (0-3.27)	0.06 (0-0.20)	0.64 (0.18-1.76)	0.06 (0-0.30)
Differences t_{24}		-1.052^{NS}	0.803^{NS}	1.437^{NS}	0.53^{NS}
Females 1982-1986	50	0.75 (0-3.49)	0.08 (0-0.72)	0.80 (0.15-6.56)	0.10 (0.01-0.27)
Females 1991-1994	26	0.95 (0-6.82)	0.03 (0-0.18)	0.46 (0-4.23)	0.04 (0-0.37)
Differences t_{74}		-1.087^{NS}	2.642*	2.618*	3.299**

* $P< 0.05$, **$P< 0.005$, NS= not significant.

Table 2.8. Age at death (days old) and organochlorine residues (mg kg wet weight) in tissues of peregrine falcon chicks found dead at Rankin Inlet 1991-1994.

Age	Tissue	Residue				
		ΣPCB	HCE	DDE	Dieldrin	Mirex
22 days	Liver	1.58	0.08	0.99	0.06	0.07
	Breast	0.36	0.01	0.30	0.01	NO
24 days	Liver	30.61	0.34	18.30	0.23	0.82
	Breast	7.48	NO	5.70	NO	NO
25 days	Liver	37.89	1.09	14.39	0.45	1.81
	Breast	14.96	0.26	5.11	NO	NO
25 days	Liver	59.45	1.35	18.84	0.57	1.84
	Breast	57.30	0.84	16.95	0.13	1.31
25 days	Liver	18.80	1.11	7.47	0.79	NO
	Breast	24.10	0.17	7.48	0.19	NO
29 days	Liver	27.14	0.57	4.90	0.12	0.96
	Breast	7.38	NO	2.31	NO	0.96
31 days	Liver	3.98	0.13	2.04	0.06	0.79
	Breast	0.35	0.02	0.34	0.01	0.17

NO means no analytical response was observed.

2.4.5 Organochlorine Residues in Peregrine Tissue

Liver and breast muscle samples were collected from seven peregrine falcon chicks that were found dead in their nests between 1991 and 1994. Organochlorine residues for these samples are reported in Table 2.8. Most nestlings carry a considerable load of contaminants relative to their ages (only about 20 to 30 days).

2.5 DISCUSSION

2.5.1 Present Level of Contamination and Biological Significance

Our suite of measurements of residues from the peregrine falcon, the terminal carnivore in the avian component of this Arctic ecosystem, showed the presence of organochlorine contaminants at detectable levels in all tissues sampled. Organochlorine residues were also detected in the whole body analysis of 10 avian prey species of this predator. In most species, residues were found at low levels, but peregrine falcons are extremely sensitive to organochlorine contaminants and are known to experience reproductive failure as a consequence of dietary intake of contaminants at relatively low levels (Peakall 1976, Newton 1979, Peakall *et al.* 1990, Ratcliffe 1993).

The absence of residues, at detectable levels, in the blood plasma of seven rough-legged hawk nestlings that feed primarily on local mammalian prey, confirm the findings that arctic mammalian species contribute little organochlorine contamination. Mammalian species represent a substantive source of relatively 'clean' prey for peregrines at Rankin Inlet; microtine rodents and Arctic ground squirrels account for up to 33% of prey biomass for the population in any one year (Bradley & Oliphant 1991). In years of peak microtine abundance, mammals may represent an even greater portion of the diet and a portion which would contribute little to a peregrine's body burden of organochlorine contaminants (Bradley & Oliphant 1991, Court *et al.* 1988a, b).

Organochlorine residue levels in some avian prey at Rankin Inlet are high enough to affect the reproductive success of peregrines. Baril *et al.* (1990) concluded that only three compounds in prey species, DDE, ΣPCB, and dieldrin, are likely to affect reproduction. I found that critical dietary levels of ΣPCB for peregrines (5 mg kg; Baril *et al.* 1990) were exceeded in long-tailed duck. Maximum detected levels of ΣPCB residues in northern pintail also exceeded critical ΣPCB levels. Mean DDE residue levels in long-tailed duck exceeded critical levels (1 mg kg; Baril *et al.* 1990) while the sample of water pipits and semipalmated plovers included individuals with levels also exceeding critical levels. Critical levels for dieldrin (0.1 mg kg; Baril *et al.* 1990) were exceeded in long-tailed duck, northern pintail, and some semipalmated plovers. High residue levels recorded in long-tailed duck are consistent with other studies; Braune (1994) listed long-tailed duck as the most heavily contaminated waterfowl in the Northwest Territories.

Considering the dietary levels of contaminants for peregrines at Rankin Inlet, it was not surprising that over one-quarter of the falcon eggs sampled had shells thinner than critical levels. For the peregrine, a review of 30 different studies showed that populations declined or had been extirpated in every case where shell thinning had exceeded 17% below normal (Peakall & Kiff 1988). The mean thickness of eggshells collected at Rankin Inlet between 1991 and 1994 was 15% thinner than the pre-DDT shell thickness for peregrines from the Nearctic.

Peakall *et al.* (1975) concluded that DDE concentrations of 15-20 mg kg wet weight in peregrine eggs were associated with 20% eggshell thinning. Peakall *et al.* (1990) examined the relationship between the percentage of eggs containing organochlorine concentrations greater than the estimated critical values, and the status of the peregrine population. They reviewed data collected between 1965 and 1986 from all three peregrine subspecies, *F. p. tundrius*, *F. p. pealei*, and *F. p.. anatum* in Canada, and concluded that in almost all cases where the percentage of eggs with critical DDE levels approached 50% or greater the population was declining. If DDE residue levels, on average, are less than the 15-20 mg kg wet weight, productivity is usually sufficient to maintain population size (Peakall *et al.* 1975, 1990, Newton *et al.* 1989). At Rankin Inlet, mean residue levels of 28 eggs, representing 20 clutches were well below minimum critical levels, and the population remains productive. However, 10% of clutches (two) included eggs with detected levels of ΣPCB, DDE and dieldrin exceeding critical levels (Peakall *et al.* 1990). I conclude that ranges of residue levels are such that a few breeding attempts at Rankin Inlet each year may fail because of organochlorine contamination. The frequency of organochlorine-related failure will be low, and certainly well below the levels likely to result in population decline.

2.5.2 Contamination in comparison with other populations

Compared to other *F. p. tundrius* populations, peregrines around Rankin Inlet show higher levels of contamination. At Rankin Inlet, mean DDE levels in post-laying plasma samples from after-second-year females are three to four times higher and mean ΣPCB residues are three to five times higher than in Greenland (Jarman *et al.* 1994). Rankin Inlet peregrines also show higher DDE levels than *F. p. tundrius* from the Colville River drainage, Alaska (T. Swem & S. Ambrose unpublished data *pers. comm*, Swem 1994). A sample of eggs from 13 clutches collected between 1990 and 1991 from Alaska averaged 3.3 mg kg DDE with a maximum recorded level of 5.3 mg kg (Swem 1994). Mean DDE levels are similar (3.3 vs. 4.5 mg kg) in the two populations, but maximum levels differ substantially (5.3 vs. 28.1 mg kg). None of the eggs from the Alaskan sample exceed critical limits whereas 10% of clutches from Rankin Inlet contain eggs exceeding critical limits for DDE. I consider that the greater variation in residue levels in eggs from Rankin Inlet is reflective of a diet of prey species occupying widely different trophic levels. Peregrines in Rankin Inlet have access to species that forage in marine, aquatic, shoreline, and tundra habitats. More heavily contaminated prey species, those occupying marine and aquatic habitats, are less common in the diet of Alaskan peregrines (Baril *et al.* 1990, White & Cade 1971).

2.5.3 Temporal trends

Contrary to predictions, I could find no evidence of sharp declines in contaminant levels in Arctic-breeding peregrine falcons and their prey species at Rankin Inlet. Contaminant levels measured at Rankin Inlet reflect a population that still experiences some reproductive failures related to organochlorine contamination. Mean residue levels of dieldrin and ΣPCB in eggs have not shown change between decades. The proportion of clutches with eggs exceeding critical ΣPCB and dieldrin residue levels (10%) has not changed between decades. Mean DDE residues in peregrine eggs have decreased between decades, but the difference, while of statistical significance, is of marginal biological significance. The inverse relationship between DDE levels and eggshell thickness is described by the log of DDE residues in egg contents to eggshell thickness (Court *et al.* 1990). Therefore, using the formula provided by Court *et al.* (1990), the 41% decline in DDE residues only predicts a 3% increase in eggshell thickness. The proportion (10%) of eggs in the sample with DDE residue levels exceeding critical levels has not changed since the study was initiated by Court *et al.* (1990) in the early 1980's.

Analysis of eggshell thickness concurs with the assessment above; eggshell thickness shows no improvement between decades. Residue levels in the plasma of adult males and chicks concur with the trends found in egg residues and eggshell thickness. There has been no decrease in plasma residue levels of ΣPCB, DDE, or dieldrin between decades; in fact, there is evidence of an increase of ΣPCB residue levels in chicks. The temporal trends in plasma residue levels of adult female peregrines are less clear and conflict with the rest of the data set. Levels of ΣPCB residues in the plasma of adult females have not changed between decades, but DDE, dieldrin, and heptachlor epoxide residues have decreased within this time period.

The lack of a strong declining trend in contaminant levels is in direct contrast to other *F. p. tundrius* populations, and also *F. p. anatum* (Cade *et al.* 1988, Kiff 1988, Peakall *et al.* 1990, Court 1993). Studies of *F. p. tundrius* in both Greenland and Alaska, document clear decreases in residue levels within the last decade (Jarman *et al.* 1994, Swem 1994). This suggests that contaminant levels in prey species utilized by peregrines at Rankin Inlet are not declining as rapidly as the other *tundrius* populations.

2.5.4 Origins of contaminants.

Twenty years after the restriction of DDT use in the northern hemisphere, some breeding attempts by peregrine falcons continue to fail because of organochlorine contamination. Most studies attribute present organochlorine contamination in this raptor to the exposure of both peregrines and their migratory prey to contaminants on wintering grounds in Latin America. I partly concur; the contaminants found in Rankin Inlet peregrines do not originate on their breeding grounds. However, comparison of the results of this study with studies of *F. p. tundrius* in Greenland and Alaska provides some evidence that not all pollutants originate from Latin America.

Differences in contaminant levels among peregrine populations must be explained by differential accumulation of contaminants in diet by either: 1) differences in residue levels of non-migratory prey taken on the breeding grounds; 2) differences in exposure to organochlorines on the wintering grounds in Latin America; 3) differences in contaminant levels of migrant species taken on the breeding grounds (Springer *et al.* 1984). I reject the hypothesis that contaminant levels in non-migratory prey contribute to Rankin Inlet peregrines having higher contaminant levels relative to the Greenland and Alaskan populations of *F. p. tundrius* for two reasons. First, non-migratory species such as microtine rodents, Arctic ground squirrels, and rock ptarmigan *Lagopus mutus*, constitute a much higher proportion (up to 40% of biomass) of the diet of Rankin Inlet peregrines relative to the other populations (Bradley & Oliphant 1991). Non-migratory prey represent a small portion of the peregrine diet in Alaska and Greenland. Mammals are reported as being taken less than 1% of the time by peregrines in Alaska and Greenland (White & Cade 1971, Swem 1985, Burnham & Mattox 1984). Non-migratory avian prey species in Alaska, Greenland and Rankin Inlet are solely represented by ptarmigan species, but account for only small proportions of the total diet (Cade *et al.* 1968, Springer *et al.* 1979, Burnham & Mattox 1984, Falk *et al.* 1986, Court *et al.* 1990, Bradley & Oliphant 1991). In Greenland, migratory passerine species total over 90% of the peregrine diet by biomass, but rock ptarmigan are also taken (Burnham & Mattox 1984, Falk *et al.* 1986). In Springer *et al.* (1979), willow ptarmigan (*Lagopus lagopus*) accounted for only 6% of prey remains at peregrine nests on the Colville River, Alaska. Secondly, non-migratory prey species at Rankin Inlet are essentially free of organochlorine contaminants (this study; Court *et al.* 1990). I conclude that non-migratory species represent a significant portion of the diet of Rankin peregrines, but are largely free of contaminants and should help to lower contaminant levels, relative to other populations.

Population-based differences in contaminant levels may be related to differences in exposure to organochlorines on the wintering grounds in South America, however data regarding migratory routes and migration ranges provide some evidence that contradicts this conjecture. Band returns and recent satellite tracking of *F. p. tundrius* from Alaska, Greenland, and Rankin Inlet indicate that migratory routes and wintering areas for peregrines in South America overlap greatly between populations (Burnham & Mattox 1984, Yates *et al.* 1988, T. Swem unpublished band return data, *pers comm.*; W. Seegar & J. Dayton unpublished satellite telemetry data of Rankin Inlet and Greenland peregrines, *pers comm.*). If populations overlap in migratory route and wintering ranges, then exposure to contaminants should be similar. Differences in diet between individuals will be evident but, on average, populations should have equal likelihood of accumulating contaminants from their prey during migration and while on the wintering grounds. On this basis, I reject the hypothesis that differences in contaminant levels between Greenland, Alaska, and Rankin Inlet peregrines are due to differences in accumulation of contaminants during migration and while on the wintering grounds.

Our third hypothesis is that contaminant levels differ between populations because of differences in contaminant levels of migrant species taken on the breeding grounds. The differences in migrant species and their relative contaminant levels preyed on by Rankin Inlet, Alaskan, and Greenland peregrines are substantial. Studies of peregrine prey show an association between residue levels and the habitat or trophic level occupied by each species (Newton 1979, Newton *et al.* 1989, Baril *et al.* 1989, 1990). Species associated with marine and aquatic habitats tend to have higher residue levels (Baril *et al.* 1989, 1990), but are under-represented in Alaskan and Greenland diets. In Rankin Inlet the greatest contributor to contaminant loads in local peregrines are long-tailed ducks. This is the most heavily contaminated of any prey species on the breeding grounds. They are also the greatest single contributor to the diet of peregrines there, accounting for up to 25% of the peregrine diet by biomass (Bradley & Oliphant 1991, Duncan 1993). Northern pintail and black guillemot further increase the contribution of contaminants from marine and aquatic species at Rankin Inlet.

Waterfowl are a minor part of the diet of *F. p. tundrius* in Alaska. Four studies list waterfowl as ranging from 0 to 5% of the diet of peregrines (by numbers) on the Colville River, Alaska (White & Cade 1971, Springer *et al.* 1979, Dittrick & Swem 1981, Swem 1985). While waterfowl are available, the study populations of Alaskan peregrines subsist primarily on passerines (White & Cade 1971). Yet, passerine species, with the exception of insectivores, tend to contain lower residues, reflective of their trophic level (Burnham & Mattox 1984, Baril *et al.* 1989, Court *et al.* 1990). Passerine species also tend to make up the greatest portion of peregrine diet in Greenland. Burnham & Mattox (1984) found that four passerine species make up over 90% of the Greenland peregrines diet by biomass. One passerine species alone, Lapland longspur, accounts for 70% of the diet in Greenland. Only trace amounts of long-tailed duck in the diet of Greenland peregrines were noted, and remains were found at only one nest out of thirteen (Burnham & Mattox 1984). Burnham & Mattox (1984) found low residue levels in a number of prey species taken on the study area and concluded that the levels of DDE in peregrine eggs and the correlated degree of eggshell thinning did not result from feeding on prey in the nesting area.

I conclude that the high contaminant levels in Rankin Inlet peregrines relative to study populations of *F. p. tundrius* in Greenland and Alaska can be attributed neither to differential accumulation of contaminants during migration/wintering, nor to the contamination of non-migratory prey on the breeding grounds. Evidence suggests that they are, in part, due to differences in the use of migratory species on the breeding grounds which tend to be more contaminated, especially seabirds and waterfowl.

Curiously, the greatest single source of organochlorine contaminants on the breeding grounds, long-tailed ducks, are one of the least migratory species preyed upon at Rankin Inlet. Long-tailed duck do not range to where persistent organochlorines, such as DDT, are used. They winter in the Great Lakes, and along the Atlantic seaboard of Canada and the United States of America south to Chesapeake Bay (Bellrose 1976, Palmer 1976, Godfrey 1986). Palmer (1976) even notes long-tailed duck as a regular winterer in ice-free areas of Hudson Bay. Therefore, I conclude that continued organochlorine contamination of the top avian carnivore in this Arctic ecosystem is as much related to the continued contamination of waterfowl and seabird prey species that range only within North America, than to continued pesticide use in South America. Further decreases in organochlorine contamination of peregrines breeding at Rankin Inlet in the Northwest Territories of Canada are primarily related to declines of these contaminants in marine and aquatic ecosystems within North America, and secondarily to a decrease in use of organochlorines in Latin America.

3. PARENTAGE OF PEREGRINE FALCON BROODS AS DETERMINED BY MINISATELLITE AND MICROSATELLITE DNA PROFILING.

3.1 ABSTRACT

The parentage of 55 broods of peregrine falcons (a total of 144 young) was examined using single-locus minisatellite and microsatellite DNA profiling to: 1) investigate the accuracy of traditional measures of an individual's reproductive success; 2) test predictions of the Paternity Assurance Hypothesis (PAH) in a dense raptor population; and 3) assess whether non-territorial adult peregrines (floaters) contribute to their lifetime reproductive success before holding a territory. Extra-pair paternity (EPP) was detected, but at a low frequency (1.3% of young); this is consistent with studies of other raptors, but fits poorly with the predictions of the PAH. The low rate of EPP justifies the use of traditional measures of reproductive success in this population with high confidence. Peregrines may use distant guarding and frequent copulation as complementary paternity guards; the high probability that intruders will be detected may reduce the frequency of EPCs and the frequency of females accepting EPCs. No evidence of intra-specific brood parasitism was found, but rapid mate-switching was detected on three occasions. The mechanism of social dominance and territoriality is discussed in the light of competition for good quality nests.

3.2 INTRODUCTION

Traditionally, measures of reproductive success in monogamous avian species have assumed that young in a nest are genetically related to the adults attending that nest. However, many studies which examined the genetic parentage of young have shown that this assumption can be erroneous, and that some young are related to only one or neither of the pair attending the nest (Wetton *et al.* 1987, Westneat *et al.* 1990, Birkhead & Møller 1992, Graves *et al.* 1993). Estimates of an individual's reproductive success, whether for a single breeding attempt or a lifetime, may be seriously confounded by the presence of extra-pair young. As part of a long-term study of the population dynamics of tundra peregrine falcons, *F. p. tundrius*, in Arctic Canada (Court 1986, Court *et al.* 1989), I sought to determine the error in estimates of annual and lifetime reproductive success (Newton 1989a) attributable to the extra-pair parentage of young.

Extra-pair parentage of young may result from: 1) fertilization of the egg by a male other than the individual in attendance at the nest (extra-pair paternity, EPP); or 2) the "dumping" of fertilized eggs in a nest by extra-pair females (intraspecific brood parasitism). Given the importance of the nesting cliff as a focus for courtship and copulation, the extreme tenacity of females to their nesting cliff once established on territory, and the vigorous antagonistic response to females intruding on the territory (Nelson 1977, Ratcliffe 1993, Court 1986), intraspecific brood parasitism in peregrines is unlikely.

Nevertheless, the frequency of EPP could be relatively high in the peregrine falcon. The Paternity Assurance Hypothesis (PAH) suggests that mate guarding is the primary means by which birds assure paternity of their young (Birkhead *et al.* 1987, Møller & Birkhead 1992a). Male peregrines, however, must provision their mates with food, and their frequent absences from the nest to hunt provide the female with potential opportunities for EPCs throughout her fertile period. The PAH suggests that, given these frequent opportunities, the frequency of EPCs, and consequently EPP, should be high in the peregrine falcon relative to guarding species (Birkhead & Møller 1992, Birkhead & Møller 1995, but see Dunn & Lifjeld 1994).

The PAH also predicts more EPCs, and thus EPP, in populations of high density, because territorial intrusions will be more frequent (Møller 1985, Birkhead *et al.* 1987, Birkhead & Møller 1992). Therefore, I would expect the frequency of EPP in this study population of peregrine falcons to represent an upper estimate for the species because: 1) it is one of the densest populations on record, at about one pair per 19 km^2; 2) the limited distribution of suitable nesting habitat within the study area further results in pairs nesting in close proximity (as little as 600 m apart); 3) intrusions by non-territorial adult peregrines at nest sites are frequent (Court 1986, J. Ball & Johnstone, unpublished data); and 4) there is a known, non-territorial, non-breeding surplus of mature peregrines or 'floaters' in this population (Chapter 5).

Here, I review results of DNA analysis of seven individual hypervariable loci in order to determine the proportion of extra-pair young in broods of peregrine falcons at Rankin Inlet and, where possible, to assign parentage. I use these results to: 1) assess the accuracy of traditional methods of estimating reproductive success by determining the frequency of extra-pair young; 2) assess the prediction that extra-pair young will more likely result from EPP than intraspecific brood parasitism in this species; 3) assess the prediction of the Paternity Assurance Hypothesis that the frequency of EPP should be relatively high in a population of diurnal raptors compared with guarding species; 4) assess the intraspecific prediction of the PAH that EPP should be frequent in a population where nesting territories are closely spaced; and 5) examine evidence for floaters contributing to their lifetime reproductive success before holding a territory. I discuss the parentage of young with regard to: 1) observations of copulation behaviour in this and other raptorial species; 2) the accuracy of traditional measures of reproductive success; and 3) sperm competition theory.

3.3 METHODS

3.3.1 Study Area and Data Collection

Data were collected as part of a long-term study of tundra peregrine falcons breeding within an area of 450 km^2, near the hamlet of Rankin Inlet (69° 49'N, 92° 05'W), on the western coast of Hudson Bay, Northwest Territories, Canada (Court 1986, Court *et al.* 1988a, b, Bradley & Oliphant 1991, Johnstone *et al.* 1996). Since 1982, as part of annual population monitoring, attempts were made to catch and band any unbanded peregrines, establish the identity of pairs holding territories, and record the outcome of all breeding attempts (Court *et al.* 1989).

By 1991 the majority of peregrines in the breeding population were banded, although blood samples for DNA analysis had not been collected from them. Between 1991 and 1994, I attempted to trap and collect a blood sample from all adults on territories. The breeding population in these years consisted of 26, 26, 28, and 28 territorial pairs respectively. Most females (27/45) were trapped after laying, either late in incubation or over young, while most males (20/27) were trapped prior to laying. To limit possible abuses, trapping methods are not described. I also took blood samples from 8 male and 4 female 'floaters' (potential extra-pair fathers or egg-dumpers) that were trapped during withdrawal experiments (Johnstone MS, Chapter 5). All unmarked peregrines were banded when they were caught.

I collected blood samples for DNA analysis from 153 chicks representing 58 broods. Brood mortality, associated with storms, can be high in this arctic-breeding population (Bradley *et al.* In press), so, to maximize the sample, I collected blood from chicks at the earliest opportunity. I took blood samples as soon as the development of peripheral vasculature in chicks enabled collection (6-15 days), and when dry, relatively warm weather ensured a safe visit to the nest. To ensure that archived DNA samples matched an individual chick's band number, I tagged each chick in a brood with a small numbered leather leg strap at the time of sampling. This identified the chick, along with its blood sample, until it had grown large enough to apply a standard U. S. Fish and Wildlife Service metal band and an anodized aluminium alpha-numeric colour band. Blood samples of chicks that died before fledging were identified using the leather leg strap number and the nest site number.

With chicks, blood was collected after veni-puncture of a wing using a 25 gauge needle and a 1 ml syringe. Blood samples were obtained from adults from the brachial vein, with a 3 ml syringe and a 23 gauge hypodermic needle. Four to six drops of whole blood were collected into 2 ml Nalgene® cryo-tubes containing 95% ethanol. Samples were kept at ambient temperature in the field and during transportation back to the laboratory where they were stored at -18°C until analysis.

I recorded the reproductive histories of banded individuals in the population following Court *et al.* (1988a). I identified individuals occupying territories by reading their alpha-numeric colour bands using a telescope. Most individuals were identified prior to laying. When poor weather conditions or an individual's behaviour prevented identification, I attempted to trap that individual either prior to laying, during incubation, or over chicks.

It was not always possible to positively identify the individuals at nest sites, or to trap all of them to get blood samples. Of 58 broods, 19 were produced at nest sites where the resident pair had been both visually identified and sampled, 17 originated from territories where the female had been sampled but the male had not, whilst the converse was true for only four broods. Three broods were raised at different nest sites at which neither of the adults had been sampled. At the remaining 15 broods, the identity of one or both adults could be inferred from occupancy of the site in preceding or subsequent years. Either an unbanded adult had occupied the territory for one or more years before an unbanded individual was banded there, or the same banded individual had been recorded at the nest for one or more years before an unidentified bird bred there. Given the nest site fidelity shown by peregrines, and the low rate of turnover of individuals on territories (Court *et al.* 1989), it seemed reasonable to assume that it was the same individual on all occasions; it had simply taken more than one year to successfully trap it, or I had not been able to verify the band number in one year. In the first case, I included the individual who was finally banded at the nest as the putative parent in the year(s) immediately preceding, when an unbanded bird bred there. In the second case, I assumed that the unidentified occupant was the individual that had bred on the territory in the year(s) immediately prior. I then checked the single-locus profile of the putative parent against the chicks in the brood for incompatibilities. If the individual was not compatible as parent, I could not exclude that this was attributable to EPP or intraspecific brood parasitism; alternatively the assumption may have been incorrect and a turnover in territory holders may have occurred. However, if the putative parent was compatible then I could exclude the occurrence of either EPP or intraspecific brood parasitism in the brood.

3.3.2 Single-locus DNA Profiling

Single-locus DNA profiling is a method of investigating familial relationships with discriminatory power that can equal multi-locus DNA fingerprinting, but without some of its inherent limitations. Multi-locus fingerprinting requires DNA samples from both putative parents and their offspring to confidently exclude extra-pair parentage, and the side-by-side comparison of banding patterns. However, in studies of wild populations, it is not always possible to obtain samples from key adults. Individuals, or members of one sex, may be more resistant to trapping than others, or concerns about disturbance to individuals during the breeding season may prevent intensive trapping efforts. In most studies of peregrine falcons, fewer adult males are caught than females (Mearns & Newton 1984, Ward *et al.* 1988, Court *et al.* 1989). Also, the requirement of side-by-side comparison of banding patterns creates difficulties when trying to assign parentage from a large pool of potential parents. Using single-locus DNA profiling, it is usually possible to exclude extra-pair parentage, when samples from only one adult are available, or for groups of three or more siblings when samples from neither adult were obtained (Wetton & Parkin 1997). Single-locus DNA profiling also allows a database of the profiles of individuals in a population to be built which can be screened to identify the actual parents of extra-pair young (Wetton *et al.* 1995).

3.3.3 Laboratory Analyses

DNA was extracted as described previously (Wetton *et al.* 1995), restricted with *Mbo* I, assayed fluorometricaly and diluted to 150 ngμl^{-1} with 2x BPB loading dye (4% Ficoll 400, 40 mM EDTA, 0.05% bromophenol blue, 0.05% xylene cyanol FF). 1.5 μg of genomic DNA along with 10 ng of an internal marker, consisting of a 4:1 mix of 1 Kilobase DNA ladder (Gibco/BRL) to lambda DNA digested with *Xho* I, was loaded onto a 20 x 22 cm 0.8% agarose gel in TAE buffer (40 mM Tris, 40 mM acetic acid, 1 mM EDTA (pH 8.0)) and electrophoresed at 48 V for 44 h until fragments < 2 kb were lost from the end of the gel. DNA was Southern blotted onto Zetaprobe GT nylon membrane (Bio-Rad) and fixed by baking at 80^{o}C *in vacuo* for 120 min.

Inserts isolated from the peregrine charomid clones c*Fpe*MS1 and c*Fpe*MS17, the merlin clones c*Fco*MS2, c*Fco*MS4 and c*Fco*MS19 and the kestrel clone c*Fti*1 (Wetton & Parkin 1997) were labelled with [α^{32}P]-dCTP by random priming (Feinberg & Vogelstein 1980) and hybridized sequentially after removal of the preceding probe. Prehybridization, hybridization, washing and probe stripping followed standard protocols (May *et al.* 1993), competitor DNA was not used, and final washes were at a stringency of 0.1x SSC, 65^{o}C. A final hybridization with random primed internal size marker allowed estimation of allele sizes.

PCR amplification of the CCAT$_n$ tetramer repeat locus *Fpe*μ1 was achieved using 5ng of DNA (1μl of *Mbo* I digest in 2x BPB diluted 1:29 with 10mM Tris, 1mM EDTA) per 25μl PCR reaction comprising 20 pmoles of each primer
(*Fpe*μ1F 5'TGTAAGTGGTGTTAAAACAG3' and
Fpeμ1R 5'GATATTAATTCCAAAGTCCA3'), 0.2 mM each of dATP, dGTP, dTTP and 0.05 mM dCTP, 0.25μCi[α^{32}P]-dCTP, 3mM $MgCl_2$, 20mM $(NH_4)_2SO_4$, 0.01% (w/v) Tween, 75mM Tris-HCl pH 9.0 and 0.2 units "Red Hot" DNA polymerase (Advanced Biotechnologies). After an initial denaturing step of 180 s at 94^{o}C, the reaction proceeded for 30 cycles as follows; 45 s at 94^{o}C, 60 s at 58^{o}C then 90 s at 72^{o}C (DNA Thermal Cycler PTC-100, MJ Research). The PCR products were electrophoresed through 6 or 8% denaturing polyacrylamide gels and visualised by autoradiography after an overnight exposure. Allele sizes were determined by comparison with standards of known length.

3.3.4 Parentage Analysis

All seven loci display extensive variation (mean = 16 alleles, range 7-27) and heterozygosities ranging from 0.77-0.95. Composite profiles are effectively individual specific (probability of profile identity between unrelated individuals $P < 2 \times 10^{-9}$). Consequently, the probabilities of failing to identify cases in which one or both members of an assigned pair are actually unrelated to a nestling are very low (overall one parent false inclusion probability: excluding linked loci (*F*MS2 & *F*MS4) 1.86×10^{-4}, including all loci 1.47×10^{-5}; overall two parent false inclusion probability: excluding linked loci 1.01×10^{-6}, including all loci 1.55×10^{-8} (Wetton & Parkin 1997, following Bruford *et al.* 1992, and Gundel & Reetz 1981)).

Nestling alleles which did not match those of the adults identified at the nest site were used to screen a genotype database of all sampled adults in an effort to identify the true biological parents. The loci used were *F*µ1, *F*MS2, *F*MS17 and c*Fti*1, a 3% error in length estimation was allowed for when matching putative parental and offspring minisatellite alleles run on different gels. Potential matches were confirmed by running samples in adjacent lanes and probing with *F*MS1, *F*MS4 and *F*MS19.

3.4 RESULTS

Results of the parentage analysis of 58 broods of peregrine falcons are shown in Table 3.1. The profiles of 50 broods fitted expectations based upon them being the offspring of a single pair of adults, and showed a predictable degree of similarity among years within sites in accordance with the observed changes in territory occupant. Apart from a single nestling displaying a slight band shift at one locus (*F*MS1) which was attributed to *de novo* mutation of the paternal allele, all other incompatibilities were mirrored at several loci. Sixteen young from seven broods mismatched with one of their putative parents at between five and all seven loci (mean = 6.2), indicative of either EPP, intraspecific brood parasitism, mate switching subsequent to the breeding pair being identified or mis-identification of the attendant adults. All members mismatched with one of the assigned adults in six of the seven broods. In three cases the identity of the excluded parent (two

Table 3.1. Comparison of relationships between adults and nestlings as determined by observational and genetic means.

The identity of each adult peregrine attending a brood was either confirmed by contemperaneous observation; inferred from previous or subsequent residence on the territory, or was unknown (included in this category were some banded individuals who were never bled). The remaining cells show the number of broods (and nestlings) for which the expected relationships were confirmed (legitimate) or disproved. Two cases of EPP were noted each in broods of mixed paternity, with some nestlings being compatible with the resident male. Six further broods were entirely incompatible with one sampled adult, either as a result of rapid mate-switching (RMS) or mis-assignment of adults where contemperaneous observational data was lacking.

Male	confirmed	confirmed	inferred	inferred	confirmed	unknown	unknown	unknown
Female	confirmed	inferred	inferred	confirmed	unknown	confirmed	inferred	unknown
Legitimate	16 (47[a])	1 (1)	2 (6)	8 (23)	4 (8)	16 (42[b])	-	3 (9)
EPP	1 (1[a])	-	-	-	-	1 (1[b])	-	-
Inferred male mis-assigned	-	-	-	1 (1)	-	-	-	-
RMS	2 (5)	-	-	1 (3)	-	-	-	-
Inferred female mis-assigned	-	1 (3)	-	-	-	-	1 (3)	-
IBP	-	-	-	-	-	-	-	-

[a] A single brood of mixed paternity consisted of one EPY and one legitimate offspring

[b] A single brood of mixed paternity is thought to consist of one EPY and two legitimate offspring sired by the resident male (see text).

females and one male) had been inferred solely from their occupancy of the site in another year. Thus, it is probable that pair composition had changed in the intervening period and the adult had simply been mis-assigned. However, in the other three cases there was strong contemporaneous observational data to confirm that the excluded adults were resident on the nesting territory prior to egg laying. For example, a combination of profiling and observational data gave evidence that mate-switching occurred at one nest on two occasions between early occupation of the study area and egg-laying. In 1991 and 1992, female 'A' was trapped and identified at Nest Site 12, and DNA profiling confirmed her as the genetic mother of broods in both years. In 1993 and 1994, female 'A' was again identified at Nest Site 12 and trapped, 26 days and 16 days respectively, prior to the first egg being laid. Observation of courtship behaviours and copulation provided evidence that she had settled on the territory in both years, but DNA profiling revealed so many mis-matches (6 or 7) with all six chicks that she was rejected as the mother of broods in 1993 and 1994 . In 1995, a different female ('B') who had been sampled in 1991 at another site was positively identified at Site 12. This female had been selected from the database as a potential parent of both broods at Nest Site 12 in 1993 and 1994, and this was confirmed using three further single locus probes. Thus, I conclude that female 'A' was displaced from her territory by female 'B' prior to egg-laying in both years.

Similarly 'C', a banded but unbled female, was identified at Nest Site 53 in 1991 when she raised a brood of three, but appeared to have been replaced by female 'D' in 1992 who was trapped and subsequently observed there, on three successive days, approximately three weeks prior to egg laying. However, the genetic mother of the two young raised in 1992 was not female 'D' but the same female as produced the three young in 1991, presumably the unsampled female 'C'. Once again, rapid mate switching (RMS) appears to be the most likely explanation.

In each case where rapid mate switching has been assumed, the territorial male was confirmed as the father of the entire brood. If the eggs had been dumped it would imply that the parasitic female had been fertilized by the resident male (quasi-parasitism). However, such occurrences are extremely rare in birds having been recorded only in the white-fronted bee-eater (*Merops bullockoides*: Wrege & Emlen 1987) and the zebra finch (*Taeniopygia guttata*: Birkhead *et al.* 1990) despite the detection of intraspecific brood parasitism in many species. The sole report of intraspecific brood parasitism in falcons involved lesser kestrel (*F. naumanni*) eggs totally unrelated to the parasitized pair, furthermore only a single egg was involved in each brood (Negro *et al.* 1996), and pairs of this species nest within a few metres of each other. I found no conclusive evidence of straightforward intraspecific brood parasitism among the 88 young which were compared with observationally confirmed attendant females, suggesting that it accounts for less than 1.1% (1/88) of young, if it occurs at all.

At one nest site there was evidence of mixed paternity within a single brood. Two broods were sampled from Nest Site 77, in 1991 and 1994. The male identified in 1991 was never bled though his mate was, whilst an unbanded male was observed on the territory in 1994 and the identity of his mate was unknown. Single locus profiling confirmed that the female seen in 1991 was the mother of that brood but was unrelated to the 1994 brood. From the remaining bands it was possible to reconstruct the profile of the male that had sired all of the 1994 brood and two of the three young in 1991. The remaining nestling shared none of its paternal alleles with its nest mates in either brood. Three paternal alleles were observed at four loci, one at each locus being unique to the same 1991 nestling, but no male could be found in the database matching either of the partial paternal profiles. The most parsimonious explanation is that the anomalous 1991 nestling was sired extra-pair by a non-resident male whilst the other two were sired by a male who was resident throughout the four year period, though I cannot exclude the converse possibility that a single non-resident extra-pair male sired all five young which share a father.

The final brood in which there was direct evidence of genetic mismatch with the attendant adults comprised two young, one of which showed evidence of EPP. Whilst one chick was wholly compatible with both adults, its nestmate was incompatible with the attendant male at seven out of 11 single locus markers (data not shown). The adult male at the nest was trapped and banded eight days before the first egg was laid, it was identified by telescope just prior to egg-laying, and it was identified again while defending the nestlings. The same male was also identified, and trapped once, at the same nest site in two subsequent breeding seasons. As I can exclude mis-identification of the adult or rapid mate-switching prior to egg-laying, I conclude that this represents a true case of EPP, suggesting a rate of 1.3% (1/78 in fully sampled pedigrees). Furthermore, using the genotype database, the nearest neighbouring male was identified as the true sire; this was confirmed with additional single locus probes (probability of false paternal inclusion $< 5 \times 10^{-5}$; Wetton & Parkin 1997). The proximity of the two nests (1200m) and the topography between them would have provided the cuckolding male with the opportunity to observe the neighbouring nest to establish the presence or absence of the territorial male, and consequently, the opportunity for furtive undetected EPCs.

3.5 DISCUSSION

3.5.1 Mate switching

Occasional cases of mate switching between occupation of the breeding grounds (15-25 May) and egg-laying (about June 7th) occurred in the study population between 1982 and 1995. However, because opportunities to read band numbers after egg-laying are rare, I could not eliminate the possibility that mate switching occurred more frequently than band records indicated. Parentage analysis of broods revealed three instances between 1991 and 1994 where mate switching occurred after territory occupants had been identified visually before egg-laying.

One incident of mate switching also gave some interesting insight into competition for nest sites and dominance hierarchies. Female 'B' was first trapped over a brood of three chicks in 1991. In 1992 she bred at this same nest, but all four of her nestlings died before fledging. DNA profiling confirmed her as the genetic mother of both these broods. In 1993, she had moved about 1.7 km to another nest and a different male. Coincidentally, female 'B' was the subject of a territorial withdrawal experiment on June 2nd of that year (Chapter 5). During her temporary confinement, she was quickly replaced by an unbanded female. Upon her release, female 'B' did not regain her territory. DNA profiling provided evidence that she then moved approximately 17 km to Nest Site 12, where she displaced female 'A', and laid the first of three eggs on June 15th, 1993.

Most population studies of peregrines and other raptors assume that, when a bird does not return to the nest where it has bred for one or more years, it has died, unless caught at another nest (Mearns & Newton 1984, Newton & Mearns 1988, Court *et al.* 1989, James *et al.* 1989). Also, it is often assumed that once an individual has bred at a nest it will return there, and will have the social dominance to successfully compete for the territory until senescence or death. Yet, this case of mate switching indicates otherwise: females that have bred previously may not breed in a given year, and previous occupancy of a site does not guarantee future ownership. Following the removal experiment, female

'B', an experienced breeder, either could not regain her nest or opted to move elsewhere. Although originally at a poor quality nest she then moved to the highest quality nest in the study area (as ranked by years occupied and production) where she displaced a female ('A') that had bred at that site for at least two years. Female 'A' was not recorded breeding elsewhere in that year, or the year following, when female'B' again prevented female 'A' from breeding at Site 12.

The reasons for female 'A' not retaining her breeding place are not clear. There is little to suggest that physical size is responsible for the difference in dominance between the two females. In the spring of 1993 female 'B' was actually 50-g lighter than 'A', although she had a slightly greater (by 7 mm) wing chord. It has been hypothesized that older or more experienced birds may be more dominant; I cannot test this hypothesis, since neither female was banded as a nestling it is impossible to assess their age. An alternative explanation is that the female 'A' was perhaps sick or in poor condition and thus unable to afford the cost of defending the territory. With the risk of fatal fights, a female in such condition may opt not to breed in the interests of long-term production. The presence of female 'A' on the territory in the second year implies an intent of breeding, although she was again displaced by female 'B' or opted not to breed for a second year running, allowing female 'B' to occupy the vacancy. On average, females at Rankin Inlet have a breeding career of only 2.9 years (Chapter 4), and female 'A' was first banded in 1991 as an after-second-year breeding adult, so it also possible that this represents a case of reproductive senescence.

3.5.2 Intra-specific Brood Parasitism

The absence of intraspecific brood parasitism in this study supports the hypothesis that intraspecific brood parasitism is unlikely in raptors because of the extreme tenacity of the female to her nest prior to, and throughout, her fertile period. Moreover, the lack of tolerance to female territorial intruders at this time (Newton 1979) also makes intraspecific brood parasitism unlikely at Rankin Inlet.

3.5.3 Frequency of Extra-pair Paternity

The frequency of EPP varies widely in monogamous avian species (see Table 12.2 in Birkhead & Møller 1992). Birkhead & Møller (1992) predicted that the rate of EPC and EPP in non-mate guarding species should be higher than in species which guard their mates closely. This prediction is supported by data from some species (Møller & Birkhead 1992b, Møller & Birkhead 1993), but is not well supported by studies of colonial seabirds or raptors. Birkhead & Møller (1992) identify species in these groups as being constrained from guarding their mates.

The results of this study fit the predictions of the PAH poorly because, given the frequent opportunities for EPCs in a dense population with a surplus of breeding age birds, one would predict relatively frequent EPP. The low frequency of EPP (1%) documented in this study, however, conforms with results from parentage studies of other raptors: 3% for lesser kestrel, *F. naumanni* (Negro *et al.* 1996), 2% for Eurasian kestrel, *F. tinnunculus* (Korpimäki *et al.* 1996), and 0% for Eleonora's falcon, *F. eleonorae* (Swatschek *et al.* 1993), black vulture, *Coragyps atratus* (Decker *et al.* 1993) and merlin, *F. columbarius* (Warkentin *et al.* 1994). All of these studies show a poor fit with predictions of the PAH, and justify, in these species, the assumption of traditional methods of measuring individual reproductive success; namely that young in a nest are genetically related to the pair attending the nest.

3.5.4 Floaters

Many studies have identified a surplus of non-territorial adults, and speculate about breeding strategies that these individuals may pursue (Smith 1978, Newton 1992, Zack & Stutchbury 1992, Rohner 1996). It has been suggested that competition for good quality, or 'source', nest sites (i.e. those associated with high 'fitness'- high rates of survival and high reproductive success) creates this surplus. Rather than attempt to breed at a nest associated with poor fitness, individuals may forego breeding until a good quality nest becomes available (Newton 1992). For male floaters, an alternative strategy to waiting for a good quality nest or breeding at a poor quality nest, would be to gain EPCs with a female at a good quality nest. However, the low rate of EPP and intraspecific brood parasitism in this study is evidence that floaters rarely contribute to their lifetime success before holding a territory.

3.5.5 Paternity Guards

The low frequency of EPP in this population suggests that either peregrines use efficient paternity guards or that they have little need of them. Male peregrines may use frequent copulation to assure paternity. Raptors tend to copulate much more frequently than non-raptorial species (Møller & Birkhead 1991, Birkhead & Møller 1992, Korpimäki *et al.* 1996) and there is some evidence that peregrines also copulate frequently. Data are very limited however and previously published estimates (Ratcliffe 1993, Birkhead *et al.* 1987, Møller 1987, Sodhi 1991), which vary by an order of magnitude, are based on a single study of captive peregrines (Wrege & Cade 1977). In a preliminary study of copulation behaviour, J. Ball & R. Johnstone (unpublished data) estimated mean daily copulation frequencies of 7.1 ± 6.9 copulations/day based on the observation of 15 pairs of peregrines at Rankin Inlet for a total of 83 hours between territory occupation and the laying of the penultimate egg of the clutch. While this frequency is lower than most other published estimates (Wrege & Cade 1977, Ratcliffe 1993, Birkhead *et al.* 1987, Møller 1987, but see Sodhi 1991), it represents the only quantitative data available for wild peregrines, and provides evidence that peregrines copulate frequently.

In non-raptorial species, frequent within-pair copulations seem to be an effective strategy for ensuring paternity (Birkhead & Møller 1992). In raptors, however, the evidence is equivocal. While many raptors copulate frequently (but see Simmons 1990) and EPP is rare (0-5% of offspring), in general, the frequency of EPC is also correspondingly low (0-7% of all copulations) compared to other taxa (Simmons 1990, Korpimäki *et al.* 1996).

Although the breeding and hunting ecology of peregrine falcons and other raptors may seem to exclude the use of mate guarding as a means to assure paternity, I suggest that tundra-nesting peregrines attain a functional level of distant mate guarding. Korpimäki *et al.* (1996) concluded that Eurasian kestrels, *F. tinnunculus*, may effectively guard their mates from a distance, and hypothesized that other open-country raptors may guard similarly. In the exposed, featureless landscape of this study area, movement or any flight displays at nests will be visible to peregrines foraging at considerable distances. Anecdotal observations during trapping attempts of the rapid appearance/return of a bird to its mate support the hypothesis of distant mate guarding. I concur with Korpimäki *et al.* (1996) that some raptors may use frequent within-pair copulation and mate guarding as complementary, rather than alternative, means of assuring paternity.

3.5.6 Territorial Intrusions

A peregrine that detects an intruder on its territory reacts with threatening behaviour, and usually overt aggression, including physical, occasionally fatal, conflict (Cade 1960, Hall 1970, Nelson 1977, Newton 1979, Court 1986). Intuitively, attempts to solicit EPCs or dump eggs should therefore be surreptitious; not in full view of the territorial pair. Yet, intrusions by a third adult, when both members of the breeding pair are present at the nest, are frequent at Rankin Inlet (61 in 195 hours of observation, Court 1986). The sperm competition hypothesis proposes that territorial intrusions are attempts to gain EPCs with the territorial female (Birkhead & Møller 1992), but observations from Rankin Inlet (Court 1986) show that: 1) intrusions occur when both partners are present at the nest (0.31 intrusions/hour); 2) close to 40% of intruders are female; 3) intrusions by males are most frequent before the females fertile period (0.38 intrusions/hr pre-fertility vs. 0.06 intrusions/hr during fertile period); and 4) intrusions when both of the pair are present rarely, if ever, result in EPCs. These observations do not fit with the predictions of the PAH and suggest that intrusions are for some other purpose.

Observations at Rankin Inlet suggest that vigorous antagonistic responses to intruders may not be a response to the threat of extra-pair parentage, but are efforts to repel individuals challenging the territory holder for a place to breed. Birkhead & Møller (1992), in general, are dismissive of intrusions being attempts to obtain territories, but they also restrict their argument to intruders looking only for vacancies at territories. Data from Rankin Inlet suggest that intruders may actively compete for a place to breed with a bird already established on territory. A nest site is essential for breeding, but, for successful reproduction, the quality or 'fitness' associated with a nest site is equally important (Newton 1991, Newton 1992, Newton 1994, Johnstone Chapter 4 & 5); this results in competition for high quality nest sites. This predicts that intruders should consist of non-territorial males and females, as well as territorial birds from lower quality nests. It also predicts that intrusions may occur at any time prior to laying, although they will tend to peak shortly after all birds arrive on the breeding ground and decline once the dominance hierarchy is established. The data from Rankin Inlet (Court 1986, Chapter 3 & 5), including the mix of male and female intruders, the peak in intrusion frequency, the occurrence of mate-switching before egg-laying, and the presence of floaters in years when not all of the available nest sites are occupied, support this alternative explanation of the function of intrusions.

To ensure that they are not displaced, males should guard their territory. Mate guarding may, therefore, be co-incidental to guarding a territory. The rapid return of males and females to their nests during disturbances (trapping, for instance), prior to the fertile period when the threat of extra-pair parentage is low (*pers. obs.*, M. Bradley, G. Court *pers. comm.*) suggests that mate guarding may be secondary to territory guarding.

3.5.7 Frequency of Extra-pair Copulations

EPCs are rarely observed in this population of peregrines. During the pre-laying period and until the third egg was laid, J. Ball & R. Johnstone (unpublished data) recorded 31 within-pair copulations, but no EPCs. Thus, from these data, EPCs account for less than 3.2% of all copulations. Studies of other raptors also note similarly low frequencies of EPCs (0-7%; Korpimäki *et al.* 1996), compared with guarding species (Birkhead & Møller 1992). With so few EPCs, the certainty of parentage is high, so I cannot entirely agree with the supposition that frequent copulation is primarily a strategy employed by raptors to assure paternity (Birkhead & Møller 1992, Birkhead *et al.* 1987). A strategy to ensure parentage is redundant when the likelihood of extra-pair copulation is low.

It is also important to note that few studies of copulating raptors were able to distinguish between 'successful' EPCs, in which the cloacae actually touch, and unsuccessful EPC attempts. Negro *et al.* (1992), studying a colony of lesser kestrels, recorded one of the highest frequencies of EPCs (6.7%) among raptors, but noted that none of the 30 EPCs with paired females were successful. Negro *et al.* (1992) suggested that the lack of reaction by paired males while extra-pair males solicited, or copulated with, their mate, in full view of them, was attributable to their high confidence in paternity: if no sperm is transferred to the female, then sperm competition does not occur. Although logistically difficult, future studies should aim to distinguish attempted EPC from successful EPC.

Sperm competition theory, and the PAH, poorly predict the frequency of EPCs in raptor species studied to date. The lack of fit may be, in part, related to the severe consequences of being caught. Unlike non-raptorial species, a cuckolding male peregrine detected on a territory at Rankin Inlet soliciting EPCs may incur physical injury, even death (Court 1986). Similarly, with successful fledging of young raptors conditional on substantial paternal investment; the threat of a male with-holding or decreasing paternal care, due to uncertainty of paternity following detection of an EPC, may exceed any potential benefits which a female may accrue by accepting EPCs (Møller & Birkhead 1993, Birkhead & Møller 1992, Negro *et al.* 1992, Whittingham *et al.* 1992, Dixon *et al.*

1994). In two raptor species, attempts at EPC failed because of resistance, a lack of co-operation, or aggression by the pair (Korpimäki *et al.* 1996, Negro *et al.* 1992). Unlike other species (McKinney *et al.* 1984), male raptors are unlikely to be able to 'force' EPCs on unwilling females, as females are usually larger in size than males (Newton 1979). The alternative hypothesis, that raptors tend not to enter into EPCs because of the costs incurred if they are detected, would predict an inverse relationship between the likelihood that an EPC is detected by the territorial male, and the frequency of EPCs. A comparison of open country with forest dwelling raptors may provide a good test of this, whenever sufficient data become available.

Three alternate hypotheses to the PAH have been proposed to explain variation in copulation frequency in birds. The fertilization hypothesis (Birkhead *et al.* 1987), which proposes that copulation occurs only as often as necessary to fertilize eggs, may be rejected given the high copulation frequency observed in peregrine falcons. Similarly, the predation hypothesis (Birkhead 1979) which proposes that copulation frequency is related to the risks of predation during copulation is also weak. This hypothesis requires that birds are sometimes killed by predators during copulation. While it cannot be rejected, it is difficult to accept that an event so rare that it has never been documented (Birkhead & Møller 1992) could act as a powerful selective force for such an energetically expensive behaviour among a group of predators.

Finally, the social pair-bond hypothesis proposes that frequent copulation may serve to establish, reinforce, and maintain the pair bond, result in reproductive synchronization between partners, and accelerate the breeding cycle (Nelson 1965, Brockway 1966, Newton 1979, Birkhead & Møller 1992). The frequency and pattern of copulations, including a long period and peaks in frequency prior to the female's fertile period, may be associated with a pair-bond function in osprey *Pandion haliaetus* (Birkhead & Lessells 1988), goshawk *Accipiter gentilis* (Møller 1987), and lesser kestrel (Negro *et al.* 1992). For migratory populations nesting at high latitiudes, acceleration of the breeding cycle by frequent copulation may be very important. At Rankin Inlet the breeding season is extremely compressed; the earliest that peregrines have been seen on the study area is 10 May (Court *et al.* 1988a), most pairs do not appear on territories until 23-30 May, yet the mean lay date is only 9 June (S.D. = 4.16 days, Bradley *et al.* In press). Earlier re-occupation and laying is not advantageous (Bradley *et al.* In press) because of very cold weather and the absence of migratory prey species which have not yet returned from wintering, but laying cannot be delayed by much if chicks are to fledge before poor weather sets in once again during August. Frequent copulation would be well worth its expense energetically if it provides a behavioural mechanism which advances the onset of the females fertile period and sperm production in the male, which ultimately may maximise the likelihood of fledging young.

3.5.8 Conclusions

In general, sperm competition theory and the PAH poorly predict the behaviour of the peregrine falcon and other raptors studied to date; copulation frequencies in these birds are high, but the frequency of EPP is low and corresponds with the low frequency of EPC. The poor fit may be related, in part, to the ability of some raptors to guard their mates from a distance. Studies of raptors which examine the relationship between the frequency of EPC, and the likelihood of EPC detection, may help elucidate a confounding effect. While it cannot be entirely rejected, I conclude that the PAH does not presently provide an adequate explanation of the high frequency of copulation in some diurnal raptors, including tundra-nesting peregrine falcons. I reject the fertilization hypothesis and the predation hypothesis as explanations of the high copulation frequency in some raptors, but consider that the social pair-bond hypothesis may best explain the frequency and pattern of copulations.

4. DENSITY-DEPENDENT FECUNDITY IN TUNDRA PEREGRINE FALCONS THROUGH FAILURES AT POOR-QUALITY TERRITORIES.

4.1 ABSTRACT

I examined patterns of nesting territory occupancy and reproductive performance over 14 yrs in a population of tundra peregrine falcons, *F. p. tundrius*, to identify the importance of density-dependent processes in population regulation, and test the predictions of two hypotheses explaining density-dependent fecundity. The frequency by which a territory was occupied was an indirect measure of habitat quality, in that more breeding attempts at preferred territories (frequently occupied territories) produced young than attempts at avoided territories (infrequently occupied territories). Mean production declined with increasing population density because proportionally more breeding attempts occurred at infrequently occupied territories (i.e. poor quality habitat), where the frequency of attempts failing after laying or during brooding was high, relative to frequently occupied territories. Increases in density, however, were not associated with changes in the mean production at frequently occupied territories. Density-dependent fecundity in this study was consistent, therefore, with predictions of the "habitat heterogeneity" hypothesis, but not the "interference" hypothesis which proposes that decreases in mean fecundity result from a relatively uniform decrease in habitat quality.

4.2 INTRODUCTION

Most studies of density-dependent fecundity in animal populations (Lack 1966, Sinclair 1989) have focused on its existence, and importance in population regulation, but limited attention has been given to the proximate mechanisms through which reproductive rates become inversely related to density (Dhondt *et al.* 1992). Density dependence explains that, in the absence of an infinite supply, the availability of limiting resources declines as the density of individuals competing for them increases, resulting in commensurate declines in fitness parameters (Andrewartha & Birch 1954, Lack 1966).

The availability of resources may, however, be determined by factors other than competitor density; in some environments, the availability of a resource may vary spatially and/or temporally throughout the landscape. For territorial species in heterogeneous environments, the potential reproductive success and survival of an individual may be determined, in part, by its competitive ability at securing and utilizing resources ('individual quality': Coulson & Porter 1985, Coulson & Thomas 1985, Newton 1989a,b) and, also, by the availability of critical resources within the defended boundaries of the habitat that it occupies (i.e. 'habitat or territory quality': Högstedt 1980, Van Noordwijk & DeJong 1986).

Two different hypotheses have been proposed to explain how density-dependent fecundity arises in territorial species. The "interference" hypothesis proposes that a hostile social environment, resulting from increasing agonistic encounters and interferences, leads to a uniform decrease in habitat quality and corresponding decrease in fecundity throughout the population (Lack 1966, Fretwell & Lucas 1970, Dhondt & Schillemans 1983). The habitat heterogeneity hypothesis, however, predicts that the decline in mean population fecundity is the result of an increasing proportion of breeding attempts occurring in poor-quality habitat (Andrewartha & Birch 1954, Dhondt *et al.* 1992, Kadmon 1993). Both hypotheses predict habitat specific fecundity, but the habitat heterogeneity hypothesis predicts that fecundity will not decrease in high quality habitats with increasing density, whereas the interference hypothesis predicts that a decrease in mean population fecundity will, in part, be due to a decline in high quality habitat. Implicit to both hypotheses is that habitat quality varies at the scale of a home range or territory of an individual (Dhondt *et al.* 1992).

In some studies of territorial birds, variation in habitat quality has been inferred from differences in the frequency by which a nest or territory is occupied, and is supported by a positive association between the frequency of occupation and reproductive success (Newton 1979, 1991, Lewis & Zwickel 1980, Møller 1982, 1983, Korpimäki 1988, Matthysen 1990, Ferrer & Donazar 1996). The underlying rationale is that, assuming that animals act in a way to maximize fitness, territories associated with high fitness (i.e. high quality habitat) should be occupied whenever possible. In a heterogeneous environment, therefore, high quality habitat should be occupied in preference to poor-quality habitat.

Here, I report the results of a 14-year population study of tundra peregrine falcons (*F. p. tundrius*). The aim was to identify the importance of density-dependent processes in population regulation and gain an understanding of the mechanisms involved. I tested the assumption that the frequency by which a territory is occupied is a measure of its quality by testing for differences between frequently and infrequently occupied nests in parameters of reproductive success. I compared: the outcome of breeding attempts, clutch size, brood size, mean production, total individual production, lifetime production, mean duration of breeding career, and recruitment. Mean production of frequently and infrequently occupied territories were compared to determine whether they represented reproductive 'sinks' or 'sources' (Pulliam 1988, Danielson 1992). I then tested for density-dependent effects in reproductive parameters and assessed whether changes could be best explained by the habitat heterogeneity hypothesis or by the interference hypothesis.

4.3 METHODS

4.3.1 Territory Occupancy Surveys

This study was conducted in a 450 km^2 area around the hamlet of Rankin Inlet, Keewatin District, Northwest Territories, Canada (62°49'N 92°05'W) during the years 1982-1995 inclusive. The area is described in detail elsewhere (Court *et al.* 1988a, b, 1989). Each year, in early spring (May 15-June 10), the entire study area was systematically surveyed by snowmobile for territorial pairs of peregrines (Court *et al.* 1998a). Occupants of territories were identified by reading their alpha-numeric colour bands with a telescope. Following Postupulsky (1974) and Court *et al.* (1998a), 1) a territory is defined as an area that contained one or more nest sites within the range of a known or inferred pair of actual or potential breeders, and 2) an occupied territory was a territory or nest site where one pair of birds was present at some time during the breeding season, although eggs may not have been present, and where the presenec of birds was made obvious by defence behaviour exhibited towards conspecifics and potential predators, including humans. Any territorial adult that had been first banded as a nestling on the study area was noted as a recruit, following Mearns & Newton (1984) and Court *et al.* (1989). Attempts were made to trap and band any unmarked falcons. Regular visits were subsequently made to territories to establish continued occupancy and record clutch size, brood size, and

Figure 4.1. Location of frequently (solid circles) and infrequently (open circles) occupied nesting territories (n=39) used between 1982 and 1995 around Rankin Inlet. Circles joined by lines indicate alternate nest sites within a territory.

production (i.e. the number of young fledged) following Court *et al.* (1988a, b). The outcome of 330 breeding attempts which occurred at 39 different nesting territories was recorded (Fig. 4.1). I considered a breeding attempt to be any instance in which a male and female peregrine defended a territory together; implicit to this definition is that a breeding attempt may fail before any eggs are laid. A breeding attempt was considered to be "successful" when one or more nestlings survived to the age of banding (28 days). Nests were visited after banding to account for any mortality between banding and fledging. Production is defined as the total number of young fledged or raised to an advanced stage of development (35 days).

4.3.2 Statistical Methods

Parametric techniques were used when the inherent assumptions were met. Non-normal data were analyzed using appropriate non-parametric techniques (Siegal & Castellan 1988). For all statistical tests, a P-value >0.05 was considered to be not significant. All comparisons were two-tailed, unless stated otherwise.

4.3.3 Territory Occupancy

Nesting territories were divided into *frequently* and *infrequently* occupied, based on their histories of occupancy. Frequently occupied nesting territories were those occupied more (9-14 years inclusive) than the mean occupation frequency (8.5 years), while infrequently occupied territories were those occupied less (1-8 yrs. inclusive) than the mean occupation frequency.

4.3.4 Reproductive Parameters

Mean production was calculated: 1) per territorial pair (i.e. total production of territory divided by the number of years in which the territory was occupied), and 2) per successful pair (i.e. total production of territory divided by the number of years in which young were banded). Many breeding attempts failed before young fledged, so the inclusion of attempts which failed to lay, hatch eggs, or produce young (i.e. values of zero) seriously biased means for clutch, brood, and production per territorial pair, respectively. Therefore, I also calculated and compared: mean clutch size per laying pair, mean brood size per pair for which eggs hatched, and production per successful pair, at frequently and infrequently occupied territories, respectively. I also calculated and compared the frequency of attempts which laid, hatched eggs, or produced young between frequently and infrequently occupied territories.

4.3.5 Frequent and Infrequent vs. Sink and Source

In 'source' habitat, reproduction exceeds mortality on average and a net surplus is produced. In 'sink' habitat, however, the opposite is true; some reproduction occurs but, on average, it is not sufficient to match mortality and a net deficit results (Danielson 1992). Calculations of whether a net reproductive surplus or deficit occurred were based on: 1) the knowledge of an equal sex ratio among fledgling peregrines ($z = 0.958$, $n = 430$ young from 174 broods, $P = 0.337$), therefore, the average number of young males or females produced per nesting attempt can be taken as half the mean number of young produced; 2) 33% of fledglings surviving to breeding age themselves (based on the mean of two estimates of pre-breeder survival, Newton & Mearns 1988); 3) annual mortality of adult peregrines of 0.28 (mean of two estimates calculated from turnover data and capture-recapture methodology, Chapter 6). Territories which produce a mean of 1.7 ($0.28 \div 0.5 \times 0.33$) or more young annually can, therefore, be considered reproductive sources, while those annually producing less than 1.7 young on average are reproductive sinks. When comparing the proportion of sources and sinks among frequently and infrequently occupied territories, a frequency value of less than 5 prevented the use of a Chi-square test for a 2 x 2 contingency table, and a Fisher exact test was used in its place (Siegal & Castellan 1988).

4.3.6 Lifetime production & breeding career duration

Total production for individual birds was estimated for 128 banded peregrines (80 females and 48 males) by summing the number of young produced by an individual in all its breeding attempts on the study area. For 13 individuals, total individual production is an estimate of lifetime reproductive success as their breeding history was recorded from recruitment until disappearance from the breeding population, and thus, assumed senescence or mortality. For the remaining 115 individuals, total individual production is a censored estimate of lifetime reproductive success, because some of these individuals were still breeding in 1996 (M. Bradley, unpublished data), the production of the individuals prior to banding is not known, and the fate of the individual (i.e. breeding elsewhere, senescence, death) when it has not been sighted in the population for one or more years is unclear.

Low sample size precluded a comparison of lifetime reproductive success between frequently and infrequently occupied territories, but not for mean total individual production. For statistical purposes I included all 128 individuals in the comparison of total individual production between frequently and infrequently occupied territories. Comparisons of mean individual production between frequently and infrequently occupied territories were potentially biased by the tendency for the reproductive histories of many individuals to be recorded at frequently occupied territories, and few individuals at infrequently occupied territories. For example, the individual production of 65 different females representing 21 frequently occupied territories was compared with the individual production of 15 different females representing 18 nests. To provide some degree of independence for the effect of territory quality on an individual, I calculated the mean production of individuals for each territory, assigned that mean production value to each individual, and then compared these means. The same procedure was used when comparing mean duration of breeding career (i.e. the number of years in which an individual was recorded breeding), between frequently and infrequently occupied territories.

4.3.7 Density dependence in fecundity

Associations between population density (number of territorial pairs in the study area) and parameters of reproductive performance were assessed using Spearman rank-order correlation coefficient. In two years, dramatic fluctuations in population parameters were associated with strong density-independent effects. In 1985 the maximum number of pairs laying was recorded and the productivity of the population doubled. This was linked to a super-abundance of microtine rodents, an important prey item of peregrines at Rankin Inlet (Court *et al.* 1988a, Bradley & Oliphant 1991). At this extreme latitude for the species, the population is subjected to very poor weather during the breeding cycle and in 1986 severe weather had a demonstrable effect on reproductive and population parameters. Mean lay dates 10 days later than normal, high egg mortality, high chick mortality and, ultimately, low productivity were associated with severe blizzards (Bradley *et al.* In press). Such strong density-independent factors may confound any analysis of the relationship between density and reproductive parameters. Therefore, I present the results of two analyses; one which includes the full data set, and a second which excludes 1985 and 1986. The latter analysis accepts losses due to storms and fluctuations in microtine rodent abundance in other years as inevitable noise.

4.4 RESULTS

4.4.1 Occupation Frequency

No more than 29 of the 39 available nesting territories were occupied in any single year (range 19-29, mean = 24, n = 14), giving a maximum annual occupancy of 74% (29/39). Territories were only occupied for 8.5 years (range 1-14, n = 39) of the 14 year study, on average (Fig 4.2). A total of 21 nesting territories (Fig. 4.2) was occupied 9 to 14 years and thus termed "frequently occupied territories". The remaining 18 territories were occupied in 1 to 8 years; these territories were termed "infrequently occupied territories".

The pattern of territory occupancy over the years was not the result of independent random occupation of territories each year. Peregrines settled in frequently occupied territories more often than expected by chance, while infrequently occupied territories were occupied less often than expected by chance ($\chi^2_1 = 102.6$, $P < 0.0001$) implying a preference for frequently occupied and an avoidance of infrequently occupied territories.

4.4.2 Occupation Frequency vs. Reproductive Performance

Breeding attempts at frequently occupied territories made an important contribution to the total production of the population (82%, 352/430 fledglings over 14 years). Young produced at 4 frequently occupied territories alone accounted for 25% (104/430) of the production of the entire population over the study. On average, each territory in the study area produced a total of 11.0 young (range 0-30, n = 39) during the study, however, there was great variation in the total production of each territory (Fig. 4.3). Most (66.4%) of the variation in production was related to territory occupancy (Fig 4.4.). Breeding attempts at frequently occupied territories also produced more young annually, on average, than attempts at infrequently occupied territories (Table 4.1), consistent with the hypothesis that occupation frequency reflects habitat quality.

Results indicate that the difference in mean annual production was not the result of true differences in the size of the brood reared to banding, as there was no significant difference between frequent and infrequently occupied territories in the mean annual production per successful pair. Instead, the difference may partly be explained by the

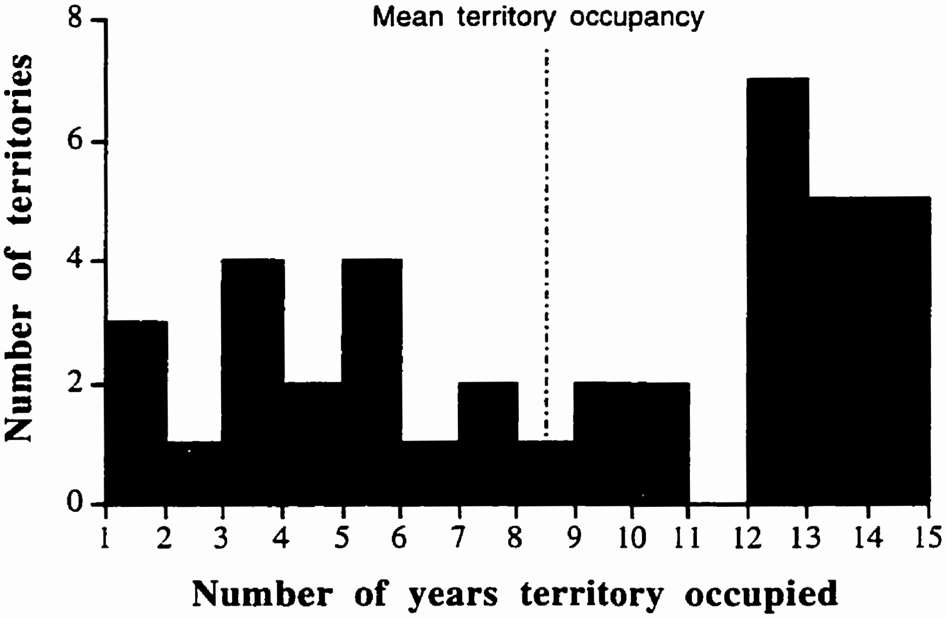

Figure 4.2. Occupation frequency of 39 different nesting territories which remained continuously available at Rankin Inlet from 1982-1995. Dotted line indicates mean occupancy frequency (8.5 years).

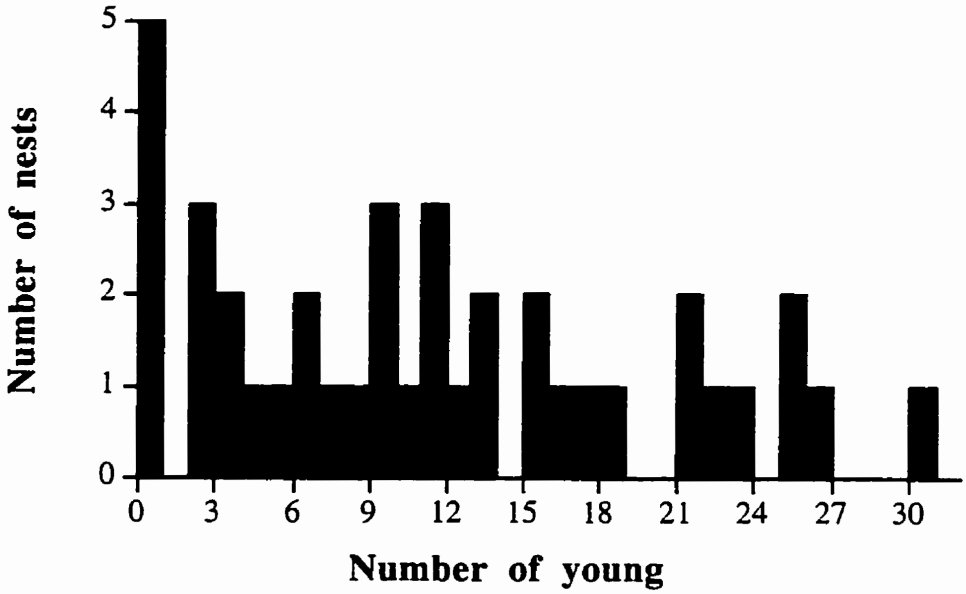

Figure 4.3. Total number of young produced at 39 different peregrine nesting territories which remained continuously available at Rankin Inlet 1982-1995.

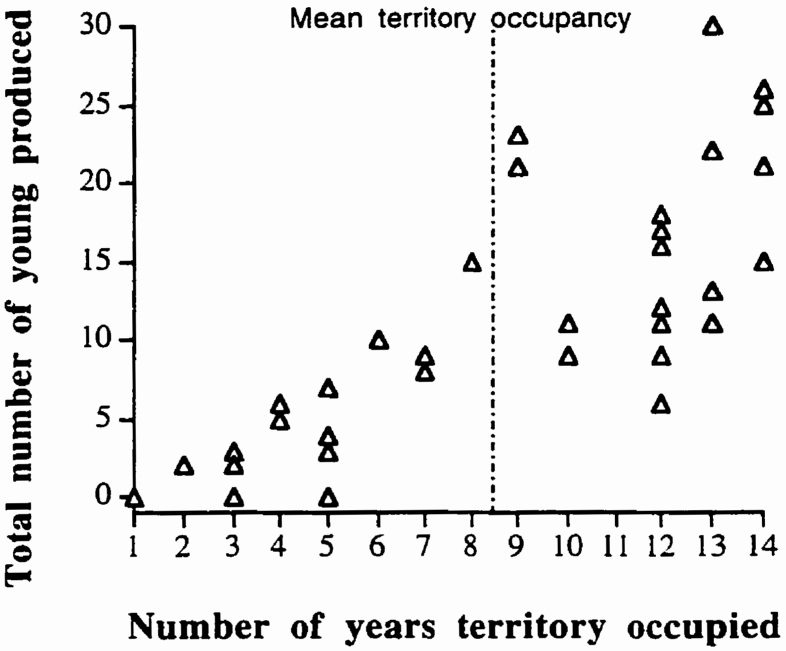

Figure 4.4. Total number of young produced (*YP*) at 39 different peregrine nesting territories in relation to occupation frequency (*O*) between 1982-1995. On a linear regression, $YP = 1.532O - 1.939$, with *O* explaining 66.4% of the variation in *YP*- values ($P = 0.0001$). Dotted line indicates mean occupancy frequency (8.5 years).

Table 4.1. Outcome of breeding attempts by peregrine falcons on 21 frequently and 18 infrequently occupied territories.

	Territory occupancy		Difference*	*P*
	Frequent	Infrequent		
Total number of breeding attempts	257	73		
Mean clutch size (range)	3.4 (1-4)	3.2 (1-4)	$U = 5411$	0.2784
Mean brood size (range)	2.9 (1-4)	3.0 (1-4)	$U = 2964$	0.4028
Mean total production of territory (range)	16.9 (6-30)	4.2 (0-15)	$U = 19$	0.0001
Mean production per successful pair (range)	2.5 (1-4)	2.4 (1-4)	$U = 2134$	0.5711
Mean production per territorial pair (range)	1.4 (0.5-2.6)	0.8 (0-2.1)	$U = 104$	0.0164
Attempts (%) in which eggs were laid	214 (83)	55 (75)	$\chi^2{}_1 = 2.37$	0.1237
Attempts (%) in which eggs hatched	170 (66)	38 (52)	$\chi^2{}_1 = 4.85$	0.0277
Attempts (%) in which young fledged	145 (56)	32 (44)	$\chi^2{}_1 = 3.62$	0.0571

* Differences in means calculated by Mann-Whitney *U*-test. Differences in proportions between frequent and infrequently occupied territories: Chi-square test for 2 x 2 table.

frequency of failures among breeding attempts at frequently and infrequently occupied territories and subsequent differences in the number of attempts having production values of zero. Breeding attempts at frequently and infrequently occupied territories were equally likely to lay a clutch, however, a higher proportion of attempts at infrequently occupied territories failed before hatch. Moreover, the difference in the proportion of breeding attempts failing before young reach banding age is close to statistical significance.

Female peregrines which bred at frequently occupied nests produced more young on average during their breeding careers than those breeding at infrequently occupied territories (Figure 4.5; frequently occupied mean = 4.7, range 1-11, n = 65; infrequently occupied mean = 3.0, range 1-10, n = 15; difference Mann-Whitney-*U* test $U = 284.5$, $P = 0.0122$). This is explained mainly by the positive association between total individual production and the number of breeding attempts an individual made (i.e. breeding career length) (Spearman rank-order correlation coefficient: $r_S = 0.748$, n = 80, $P = 0.0001$), and females at frequently occupied territories having a longer breeding career (Table 4.2). While approaching significance, the differences among males in total individual production and breeding career length between frequently and infrequently occupied territories were not statistically significant (individual production: frequently occupied mean = 3.9, range 1-9, n = 39; infrequently occupied mean = 1.9, range 0-3, n = 9; difference Mann-Whitney-*U* test $U = 247.5$, $P = 0.0562$). However, breeding careers of comparatively few individual males at infrequently occupied territories were recorded. The total individual production of males was positively associated with breeding career length (Spearman rank-order correlation coefficient: $r_S = 0.647$, n = 48, $P = 0.0001$). The mean breeding career length of individuals at frequently occupied territories suggests that the almost continual occupancy of these territories is explained by a number of individuals breeding there for only a few years each rather than an individual occupying it for a long time.

Few (4.6 %) of the 430 individuals that were banded as young were subsequently recorded as breeding adults (i.e. recruits). The mean age at recruitment for males was 4 years (range 2-8 yrs, n = 16), and for females, 3 years (range 3-5 yrs, n = 4). All the female recruits and 13 male recruits had been produced at frequently occupied nests. There was no evidence, however, that fledglings produced at frequently occupied nests were more likely to survive to breed than fledglings from infrequently occupied nests. The proportion of recruits produced at frequently occupied nests (17/20) did not differ

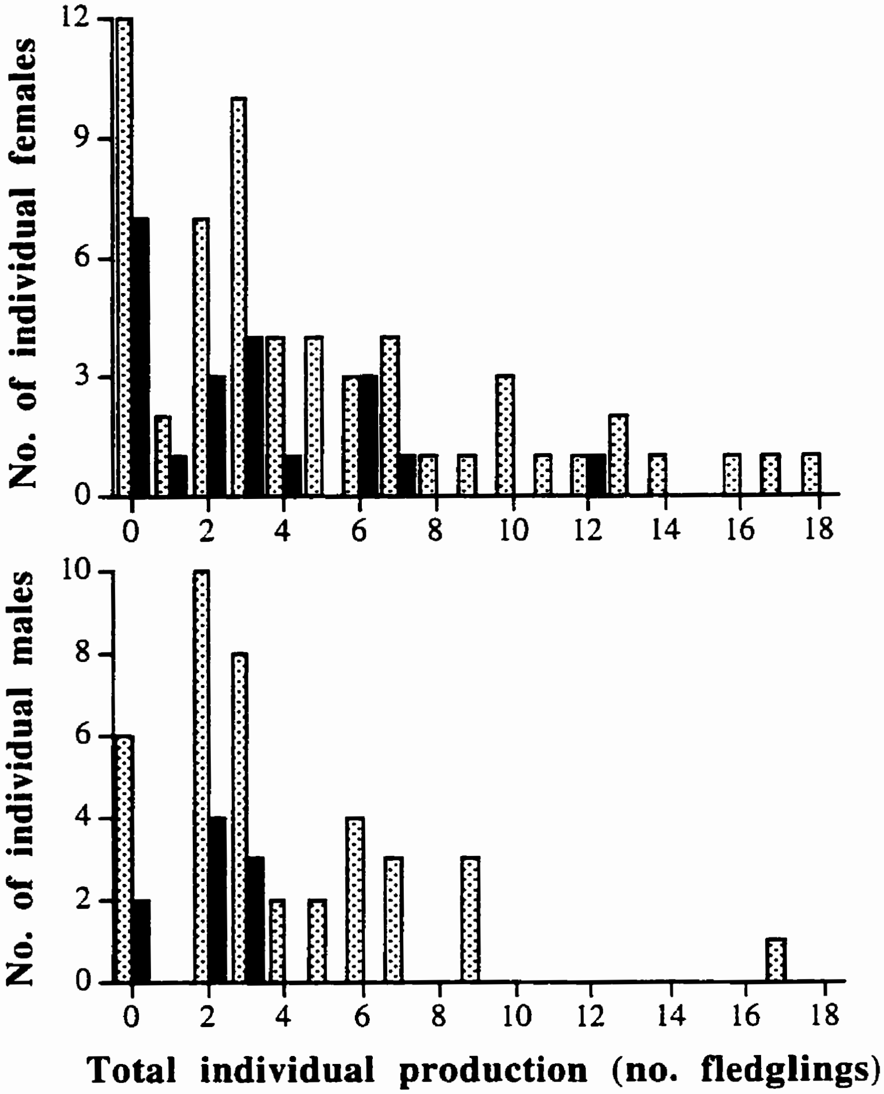

Figure 4.5. Total individual production for 48 different males and 80 different females breeding at frequently occupied territories (light shaded bars) and infrequently occupied territories (solid black bars).

Table 4.2. Mean length of breeding career (in years) of adult peregrines breeding at frequently and infrequently occupied territories.

Sex	Mean tenure (range)		Difference (*U*)*	*P*
	Frequently occupied nests	Infrequently occupied nests		
Male	2.7 (1-5) n = 39	2.0 (1-4) n = 9	240.5	0.0842
Female	2.9 (1-5) n = 65	2.2 (1-4) n = 15	325.5	0.0446

* Mann-Whitney *U* test

from expected given the proportion of the population produced at frequently occupied territories ($\chi^2_1 = 0.046$, $P = 0.8303$).

A net reproductive surplus was recorded at 8 (21%) different territories, while a net reproductive deficit was recorded at the remaining 31 territories. Therefore, 33% of frequently occupied territories (7/21) and 6% of (1/18) infrequently occupied territories could be deemed source territories, and the remainder, reproductive sinks. The difference in the proportion of source territories relative to sinks between frequently and infrequently occupied territories was statistically significant (Fisher exact test $P = 0.0373$, n = 39).

4.4.3 Breeding Population Density and Reproductive Parameters

The population of peregrines at Rankin Inlet fluctuated among years by up to 21% of the mean annual number of territorial pairs (mean = 24, range 19-29, n = 14) and 32% of the mean annual number of laying pairs (mean = 19; range 14-25; n = 14) and,overall, showed a positive growth trend over 14 years (r = 0.75, $P = 0.002$).

Associations between population density (i.e. the number of territorial pairs) and reproductive parameters are summarized in Table 4.3. The mean brood size and production of young by territorial pairs was inversely related to the size of the breeding population. The lack of any significant association between population size and these same means calculated only for pairs which actually laid a clutch, hatched young, and produced young, respectively, indicates that differences are due to the number of breeding attempts which fail. This is supported by the positive association between population size and the percentage of attempts which fail to hatch eggs, or fail to produce young (Table 4.4).

There was a significant relationship between density and the percentage of breeding attempts occurring at infrequently occupied nests; as the breeding population increased a higher proportion of breeding attempts took place on infrequently occupied nests (Spearman rank-order correlation coefficient: $r_s = 0.800$, n =14, $P = 0.0039$; excluding 1985 & 1986 $r_s = 0.774$, n =12, $P = 0.0103$). Also, as the number of breeding attempts occurring at infrequently occupied territories increased, the mean occupation frequency of infrequently occupied territories decreased (Spearman rank-order correlation coefficient: $r_s = -0.68$, n =14, $P = 0.0143$; excluding 1985 & 1986 $r_s = -0.738$, n =12, $P = 0.0144$);

Table 4.3. Association between population density (number of territorial pairs in the study area) and parameters of reproductive performance in the Rankin Inlet peregrine population 1982-1995 (Spearman rank-order correlation coefficient).

Association of population density with:	All years (n = 14)		Excl. 1985 & 1986 (n = 12)	
	r_S	P	r_S	P
Mean per territorial pair				
Clutch size	-0.365	0.2106	-0.502	0.0961
a) frequently occupied territories only	-0.276	0.3188	-1.313	0.1893
b) infrequently occupied territories only	-1.704	0.0884	-0.597	0.0478
Brood size	-0.388	0.1623	-0.580	0.0546
a) frequently occupied territories only	-0.591	0.5546	-0.986	0.324
b) infrequently occupied territories only	-0.670	0.0158	-0.761	0.0116
Production	-0.503	0.0695	-0.763	0.0114
a) frequently occupied territories only	-1.245	0.2132	-0.569	0.0592
b) infrequently occupied territories only	-0.681	0.0141	-0.763	0.0114
Mean per successful pair				
Clutch size	-0.178	0.5206	-0.286	0.3425
a) frequently occupied territories only	-0.144	0.6037	-0.281	0.3506
b) infrequently occupied territories only	-0.206	0.4568	-0.214	0.4770
Brood size	-0.054	0.8468	-0.133	0.6592
a) frequently occupied territories only	-0.124	0.6551	-0.234	0.4376
b) infrequently occupied territories only	-0.216	0.4351	-0.031	0.9191
Production	-0.376	0.1749	-0.569	0.0593
a) frequently occupied territories only	-0.242	0.3830	-0.396	0.1893
b) infrequently occupied territories only	-0.401	0.1479	-0.500	0.0972

Table 4.4. Association between population density (number of territorial pairs in the study area) and failure of breeding attempts in the Rankin Inlet peregrine population 1982-1995 (Spearman rank-order correlation coefficient).

Association of population density with:	All years (n = 14)		Excl. 1985 & 1986 (n = 12)	
	r_S	*P*	r_S	*P*
% Attempts failing to lay	0.381	0.1692	0.535	0.0763
a) frequently occupied territories only	0.282	0.3101	0.399	0.1862
b) infrequently occupied territories only	0.423	0.1277	0.586	0.0520
% Attempts failing to hatch	0.445	0.1082	0.661	0.0284
a) frequently occupied territories only	0.208	0.4531	0.359	0.2332
b) infrequently occupied territories only	0.641	0.0209	0.735	0.0147
% Attempts failing to produce	0.586	0.0345	0.786	0.0091
a) frequently occupied territories only	0.293	0.2906	0.488	0.1059
b) infrequently occupied territories only	0.695	0.0122	0.798	0.0081
%Attempts at infrequently occupied territories in which eggs were laid that hatched	-0.690	0.0129	-0.721	0.0167
%Attempts at infrequently occupied territories in which eggs hatched that young fledged	-0.595	0.0318	-0.597	0.0478

indicating that the least frequently occupied territories were occupied at the highest population densities. Moreover, the proportion of attempts at infrequently occupied territories which failed to produce young increased as the number of infrequently occupied territories used increased (Spearman rank-order correlation coefficient: $r_S = 0.634$, n =13, $P = 0.028$; excluding 1985 & 1986 $r_S = 0.678$, n =11, $P = 0.0321$).

Mean production declined with increasing density because the proportion of breeding attempts failing to produce young increased (Fig. 4.6 and Table 4.4). The strong association between population size and the proportion of breeding attempts failing was attributable to failures at infrequently occupied territories. The proportion (%) of attempts at infrequently occupied territories which failed to hatch eggs or produce young was positively associated with population density, however, and the association with the proportion of attempts failing to lay was nearly significant. Breeding attempts at infrequently occupied territories were associated with a poorer frequency of success at hatching and producing young, relative to frequently occupied territories (Table 4.1); moreover, the proportion of attempts at infrequently occupied territories in which: 1) a clutch was laid and eggs hatched, and 2) in which eggs were hatched and young subsequently survived to the age of independence, decreased with increasing population size (Table 4.4). No statistically significant association was found between population density and the proportion (%) of attempts among frequently occupied territories failing to lay, hatch, or produce young.

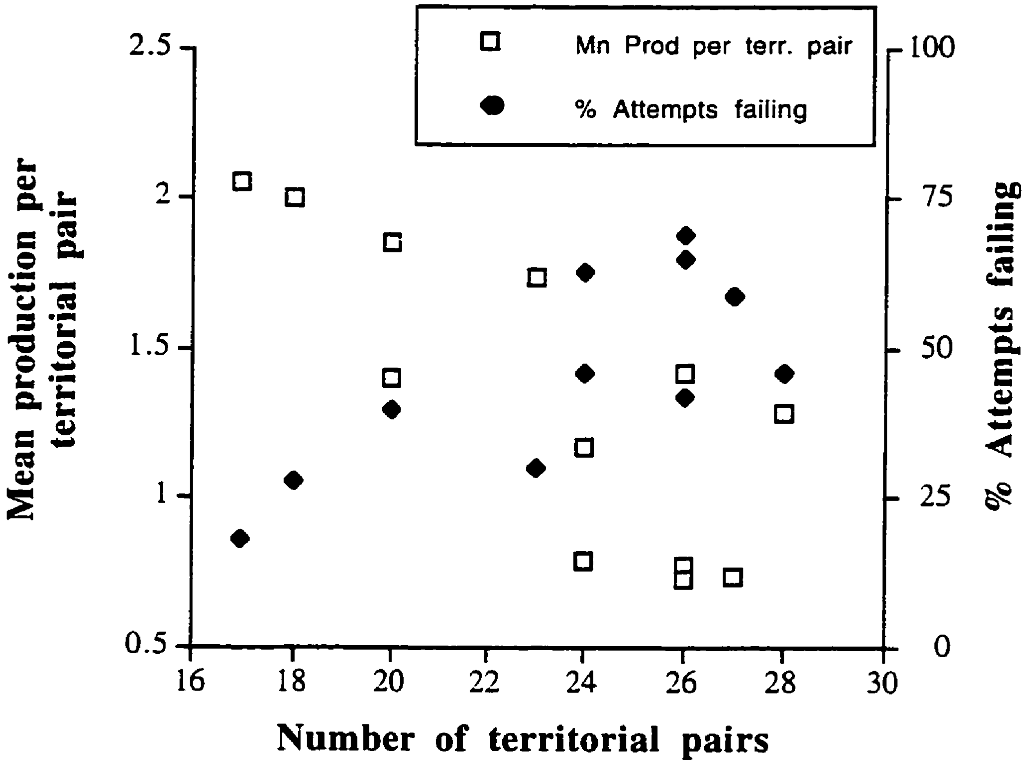

Figure 4.6. Changes in mean annual production per territorial pair (number of young) and percentage of breeding attempts that fail to produce young with population density (number of territorial pairs) of tundra peregrine falcons at Rankin Inlet 1982-1995.

4.5 DISCUSSION

By definition, good-quality habitat is that associated with high fitness, while poor-quality habitat is that associated with low fitness (Fretwell & Lucas 1970, Morris 1989). At Rankin Inlet, differences in reproductive parameters (proxies of fitness) between peregrines breeding at frequently and infrequently occupied territories were consistent with a heterogeneous environment and an ideal despotic distribution (Fretwell & Lucas 1970). Assuming that adult survival is not lower on frequently compared to infrequently occupied territories, greater fitness rewards were likely to accrue to individuals breeding at frequently versus infrequently occupied territories for threee reasons: 1) individuals breeding at frequently occupied territories produced more young per breeding attempt, on average, than individuals at infrequently occupied territories; 2) young produced at frequently occupied territories were not of inferior quality (i.e. young from frequently occupied territories have the same probability that they will survive to breed themselves, as young produced at infrequently occupied territories); 3) individuals attempting to breed at frequently versus infrequently occupied territories are more likely to produce an annual net reproductive surplus than a deficit, (i.e. they are more likely to be breeding at a reproductive 'source' rather than 'sink'). Frequently and infrequently occupied territories may therefore be considered good and poor-quality habitat, respectively.

Individual females breeding at frequently occupied territories also had longer breeding careers than females at infrequently occupied territories and, in accordance with the positive association between breeding length and total production, their total production was greater. This is also indicative that occupation frequency reflects habitat quality, but the evidence is more equivocal than mean annual production data, as it assumes that when an individual has disappeared from the breeding population that it was dead. Given the mobility of peregrines, their potential for distant dispersal, and the small size of the study area, an individual may have simply moved instead, and may have been breeding beyond the limits of the study area.

Habitat quality can only be determined by the performance of the individuals which occupy it (Newton 1991), so the higher reproductive performance of frequently relative to infrequently occupied territories observed at Rankin Inlet may be explained by: 1) frequently occupied territories attracting good-quality individuals (i.e. fitness is largely determined by individual quality, independently of any attributes of the territory itself); 2) that some attribute(s) of frequently occupied territories confer better performance on individuals that breed there (i.e. fitness is largely determined by territory quality, independently of individual quality); or 3) some combination of individual and territory quality. While the differences in reproductive performance between frequently and infrequently occupied territories are consistent with variation in attributes of the territories themselves, they may be equally well accounted for by variation in the performance of individuals.

The reasons underlying the poor hatchability of clutches laid at infrequently occupied territories, and poor survival of broods to independence are difficult to elucidate. In many species of birds, the breeding performance of inexperienced individuals is poor, but improves with age (Kluijver 1951, Finney & Cooke 1978, Newton 1979, Coulson & Thomas 1985). If a dominance hierarchy exists among breeding age peregrines and it is age-related, then older more experienced individuals may be able to secure a place to breed at high quality territories, leaving inexperienced birds with the option of breeding where the chances of successfully breeding are lower. Unfortunately, a paucity of known-age individuals in the population precludes me from comparing the age of birds occupying different habitats and comparing the performance of birds in a single age class between habitats.

Some physical attribute of infrequently occupied territories may also predispose breeding attempts at such territories to failure. The multiplicity of factors and interactions potentially involved, however, in quantitatively describing a territory of a highly mobile species that occupies a broad range of nesting habitat, occupies a large home range, and utilizes an extensive prey base, does not avail itself to statistical treatment (Court *et al.* 1988a, Bradley & Oliphant 1991).

Some interaction between territory and individual quality is likely. If habitat was homogeneous, but individual quality varied, differences in reproductive performance between frequently and infrequently occupied territories would not be predicted: over time enough good and poor-quality individuals would breed at any given territory that no association between occupancy and fitness parameters would be apparent. Some attribute(s) of frequently occupied territories must attract good-quality birds, instead. Alternately, if fitness rewards were determined mainly by territory quality, an interaction with individual quality is still predicted if individuals can assess habitat quality before choosing a place to breed. In this scenario, individual fitness would be determined by the competitive ability to gain a good-quality territory.

Regardless of the underlying mechanisms, differences in reproductive performance between frequently and infrequently occupied territories provide evidence of habitat heterogeneity. As individuals breeding at frequently occupied territories are likely to accrue greater fitness benefits than individuals at infrequently occupied territories, the assumption that occupation frequency provides a measure of territory quality is supported.

The mean production of the peregrine falcon population at Rankin Inlet was inversely related to population density. Mean annual production of the population decreased because of an increase in the frequency of breeding attempts failing, similar to the pattern shown in nuthatch *Sitta europaea* L. (Nilsson 1987); not because of a decrease in the number of eggs in a clutch, young in a brood, or the number of nestlings in a brood which survived to the age of independence. The positive association between population density and reproductive failure was, in turn, attributable to the proportion of breeding attempts occurring at infrequently occupied territories. The size of the breeding population increased because more peregrines bred at infrequently occupied territories. Moreover, breeding attempts at infrequently occupied territories failed more frequently than attempts at frequently occupied territories, and the proportion which failed to hatch eggs, or produce young, increased with population density.

The density-dependent reproductive performance of peregrines falcons at Rankin Inlet was consistent with predictions of the habitat heterogeneity hypothesis (Dhondt *et al.* 1992), but not the "interference" hypothesis, in that the decline in mean production of the breeding population was attributable to an increasing proportion of breeding attempts occurring at infrequently occupied territories where breeding attempts have the greatest likelihood of failing (i.e. poor-quality habitat). The "interference" hypothesis was rejected as the prediction that reproductive performance would decrease across all habitats was not met; reproductive performance among frequently occupied territories did not decline with increasing population density.

In most studies where it has been found, density-dependent fecundity is manifested by a reduction in size of the clutch or the number of young in a brood (Sinclair 1989), but at Rankin Inlet, it was the total number of reproductive failures that increased with population density. This was not entirely unexpected, as clutch and brood sizes in falcon species generally show less variation between years than other raptor and other avian species, but the frequency of desertion tends to vary (Newton 1979, Court *et al.* 1988a, Newton & Mearns 1988, Ratcliffe 1993).

It is not clear why more entire clutches or broods fail at infrequently occupied territories. Identification of the proximate and ultimate reasons underlying this 'all or nothing' phenomenon is problematical. Failure of a breeding attempt is associated with complete abandonment of the nesting territory by attending adults within a couple of days, and little physical evidence is left from which the fate of the brood or clutch may be determined. The possibility that the death of one of the breeding pair during the breeding season forced abandonment by the remaining adult cannot be discounted if the adults are not recorded in the breeding population again. Eggs or corpses of chicks are rarely found, except in cases where catastrophic weather events, such as severe blizzards or rain storms, force immediate abandonment (Bradley *et al.* In press). The absence of eggs or chicks is difficult to interpret; while it may represent cases of predation, predation may have occurred after abandonment. Moreover, adult peregrines are known to eat their own failed eggs or dead offspring (Newton 1979, Court *et al.* 1988a, Ratcliffe 1993). Also, a lack of gross differences in the physical features of successful and unsuccessful nest sites (Court *et al.* 1988a, M. Bradley unpublished data) suggests that frequently and infrequently occupied territories are, on average, equally susceptible to predation events or catastrophic weather events.

Newton (1979) concluded that among raptor species, many clutch desertions and nestling deaths were ultimately attributable to the inability of the male to keep the female and brood supplied with enough food. The pattern of failures at infrequently occupied peregrine territories at Rankin Inlet suggests that enough resources were available to produce a clutch but not enough were available to maintain enough condition to incubate the eggs, and then provision the young until independence. This is consistent with the general pattern of failures found among raptor species (Newton 1979), in that breeding attempts generally fail early in the season.

Population density is inextricably linked to food supply (Newton 1979, 1988). High population densities and, therefore, breeding attempts at infrequently occupied territories, can only be supported in years when good food conditions exist. To account for the pattern of reproductive performance observed, food availability for individuals at frequently occupied territories must not change with population density, while at infrequently occupied territories it must initially be close to levels critical for successful breeding, or decrease during the breeding season.

Depression in food availability at infrequently occupied territories is, in part, consistent with prediction of the ideal-despotic model of density-dependent habitat selection which predicts that dominant individuals maintain the variation in fitness rewards by preventing further density-dependent reduction in habitat quality through territoriality (Fretwell 1972, Halama & Dueser 1994). This is inconsistent, however, with the model of territoriality for tundra peregrine falcons at Rankin Inlet and elsewhere, (Cade 1960, Court 1986, Ratcliffe 1993), in that: 1) only a small core area of about 250m radius immediately around the nest cliff is always vigorously defended against conspecific intruders, and 2) anecdotal observations and circumstantial evidence suggests that hunting ranges are economically undefendable and probably not exclusive. Dominant individuals, therefore, may not be able to prevent depletion of food resources. This would infer that differences in food availability between frequently and infrequently occupied territories would be attributable to the relative ability of individuals occupying those territories at acquiring food.

Newton (1979) attributed nest desertions among raptors early in the breeding season to poor-quality individuals failing early, leaving only the superior individuals to breed. Moreover, it was considered that young birds would generally have a more difficult time achieving the body condition necessary to breed, than older birds. The competitive struggle for a place in the breeding population (Newton 1988, Chapter 5) may mean that peregrines of poor-quality, whether because of age, inexperience, or ranking low on the dominance hierarchy, only get the opportunity to breed in high-density years when there are sufficient resources available to initiate a breeding attempt at a poor-quality territory. Moreover, many of these breeding attempts subsequently fail because of their inability to continue to secure sufficient resources for successful breeding. The frequency of reproductive failures among infrequently occupied peregrine nesting territories at Rankin Inlet is, in part, parsimonious with food shortage as the ultimate cause of reproductive failure. Investigation of this "all or nothing" phenomenon is a priority for future research.

5. "FLOATERS" IN A TUNDRA PEREGRINE FALCON POPULATION: EVIDENCE AND MECHANISMS OF POPULATION LIMITATION.

5.1 ABSTRACT

There is extensive anecdotal evidence that peregrine falcon breeding densities are limited, but the presence of a non-breeding surplus has never been established by experimentation. After the breeding population had settled, I removed 14 adult tundra peregrine falcons from their territories for 24 hours to test whether breeding densities were limited and elucidate the relative importance of territory quality and territoriality in population limitation. Rapid replacements at 11 territories were indicative that a surplus of non-breeding adults (i.e. 'floaters') existed even though there were unoccupied territories available in all years of the study. All six vacancies for females, at 5 good quality territories and one poor quality territory were filled within 24 hours. Males were replaced at four good quality territories but only one of four poor quality territories. The observed pattern of territory defense and replacements in this population does not support territoriality as a main mechanism of population limitation. Instead, breeding densities may ultimately be limited by food, with the combination of individual and habitat quality determining whether a breeding attempt occurs at any given vacant territory.

5.2 INTRODUCTION

An important aspect of avian population ecology is the limitation of breeding densities and the mechanisms which underlie this phenomenon. Data from a wide variety of avian species indicate that territoriality is an important proximate mechanism by which breeding densities are limited (Hinde 1956, Brown 1969, Watson & Moss 1970, Patterson 1980, Hannon 1988, Newton 1992). The underlying rationale is that, as an area becomes saturated, further individuals or pairs are deterred or prevented from settling by the behaviour of those already occupying territories. As a territory is usually a prerequisite for breeding, individuals that are prevented from settling are either forced to breed elsewhere, or become "floaters" (i.e. a non-territorial, non-breeding surplus of adults) (Davies 1978). The observation from some studies, however, of a non-breeding surplus despite the availability of 'vacant' nesting territories suggests that mechanisms other than territoriality may explain density limitation in some populations or species, for example variation in the quality of habitat available, especially in terms of the related food supply (Bendell & Elliott 1967, Manuwal 1974, Newton & Marquiss 1991, Newton 1992).

For peregrine falcons (*F. peregrinus*) occupying a heterogeneous environment, Newton (1988) hypothesized that habitat quality may provide a mechanism by which breeding densities are limited. Newton (1988) predicted that in a heterogeneous environment, only good quality nesting territories (i.e. those associated with high fitness) will be occupied at low population density. As population density increases, further birds will be forced into progressively poorer quality territories until the quality of remaining available territories is so low that they are unsuitable for breeding attempts, and the additional birds become floaters. This ideal despotic model of nest site selection (Fretwell & Lucas 1970, Fretwell 1972) provided a good explanation of population density limitation in European sparrowhawk *Accipiter nisus* (Newton 1991, Newton & Marquiss 1991), but it has never been tested with empirical data on peregrines.

Analysis of 14 years of territory occupancy and reproductive performance data from this study area (Chapter 4) confirmed some of Newtons' (1988) predictions. Specifically, at low population densities nesting territories generally associated with a high frequency of reproductive success were occupied and, as population density increased, the proportion of breeding attempts occurring at nesting territories associated with a low frequency of reproductive success increased. Moreover, there were unoccupied territories in every year of the study; on average, only 24 of the 39 different territories were occupied in any one year, and at maximum, only 29 territories were occupied. Anecdotal observations at peregrine territories at Rankin Inlet (Court 1986, pers. observation) and elsewhere (Nelson 1977, Newton 1979, Ratcliffe 1993) have often noted the presence of non-territorial peregrines in the immediate vicinity of occupied territories prior to laying and it has been speculated that these individuals were floaters searching for vacancies. Nevertheless, the presence of floaters in peregrine populations has never been tested experimentally.

Here, I report the results of a removal experiments (Newton 1992) in which 14 'vacancies' were created experimentally at peregrine territories. The aims of this study were to: 1) establish whether breeding densities in a population of tundra peregrine falcons, *F. p. tundrius*, were limited by determining through removal experiments whether a non-breeding surplus exists, and 2) elucidate the relative importance of territoriality and habitat quality in population limitation. In this paper I present an alternate hypothesis to explain how breeding population limitation arises.

5.3 METHODS

This study was conducted in an area approximately 450 km^2 around the hamlet of Rankin Inlet, Keewatin District, Northwest Territories, Canada (62°49'N 92°05'W) between 1991 and 1995. The area is described in detail elsewhere (Court *et al.* 1988a, b, 1989). The breeding population is unusually dense (Court *et al.* 1988b), with an average of one territorial pair per 18.75 km^2, and a maximum density of one territorial pair per 15.5 km^2. Compared to other populations of *F. peregrinus*, the breeding season of peregrines at Rankin Inlet is also very compressed. Peregrines return from migration in mid-May, before the snow cover is gone from nesting ledges, and prior to the return of their migratory prey species (Court *et al.* 1988a). The period of courtship and mating is brief with the first eggs being laid in the last few days of May (mean lay date of 14 years-June 8th).

Each year, from May 15th, the entire study area was systematically surveyed by snowmobile for territorial pairs of peregrines. Occupants of territories were identified by reading their alpha-numeric colour bands with a telescope. Attempts were made to trap and band any unbanded falcons (Bloom 1987, Court *et al.* 1988a). Territories were visited regularly following the establishment of a pair in order to record the clutch size, brood size, and production (i.e. the number of young fledged) following Court *et al.* (1988a, b). Territories were classified as "good" quality (i.e. those occupied in 9-14 years) or "poor" quality (i.e. those occupied in only 1-7 years of the 14 year population study), based on the frequency of occupancy over the period 1982-1995. Breeding attempts at frequently occupied territories produced young more often than attempts at infrequently occupied territories (Chapter 4).

I experimentally created vacancies at 14 territories by trapping and temporarily confining the original occupant of the territory. Observations were then made to determine whether the vacancies were filled by new birds. Three removals were done in 1992, 6 in 1993, 3 in 1994, and 2 in 1995. Removals were done after all the territories were settled, but before egg-laying, and after the occupants of the majority of territories in the study area and all the territories immediately surrounding the site of the removal had been identified by reading their alpha-numeric colour bands with a telescope. This was done to control for the possible movement of near neighbours to the vacancy. Individuals were caught following Bloom (1987), placed on a perch in a darkened, ventilated wooden box, and held for up to 24 hours. One individual was released after 7:55 hours had elapsed, due to an approaching storm which threatened the safety of the captive bird, and field personnel. Before each captive individual was released, the territory was re-surveyed for occupants. A replacement was considered to have occurred if 1) another individual was present at the nesting cliff or ledge, and 2) behaviours consistent with a pair bond (prey deliveries, ledge displays, copulations, defense of territory against intruding conspecifics or others) were observed. If the replacement bird was banded, I attempted to identify it using a telescope; if not, I attempted to trap and band it. In three cases, the nest was continually observed until replacement occurred, and the time elapsed between removal and replacement was noted. I recorded the outcome of the dispute for ownership upon release of the original territory holder, and the territory was visited again after laying to confirm the identity of the occupant.

5.4 RESULTS

Removal experiments provided evidence of a non-breeding surplus of males and females in the population. Results of removal experiments are summarized in Table 5.1. Vacancies were filled at 11 out of 14 nests (79%) within 24 hours, and behaviours consistent with formation of a pair bond were observed in each case. The male which was held for only 7:55 hours was not replaced within that time. One of the replacement birds was a subadult; the rest were in adult plumage and were, therefore, a minimum of two years of age. All six vacancies for females, of which five were at frequently occupied nests, were filled. Males were replaced at all four frequently occupied nests, but only one of the four vacancies at infrequently occupied nests were filled (difference in male replacement frequency between frequent and infrequent occupied nests: Fisher exact test, two-tailed, $P = 0.143$). Each of the original male territory holders regained its territory at the end of the detainment, however two of the original female occupants did not regain their territories from the replacement females upon release. Both replacement females bred successfully, raising two young each to independence. The fate of one of the displaced/replaced females is unknown; it has neither been trapped nor identified by spotting scope in annual surveys of the population since 1994. Evidence from DNA fingerprinting (Johnstone *et al.* In press, Chapter 3) indicates that the other replaced female moved to another nest site in the same season, successfully usurped the female residing there, mated with the resident male and fledged young in that year and the year following.

Two replacement birds, one female and one male, which were expelled from the territory after the release of the original occupant subsequently entered the breeding population in 1996 (M. Bradley *pers comm.*), one and two years respectively, after the initial removal experiment in 1995. In both cases, the birds were recorded at nests other than the one where the removal experiment(s) took place. Two vacancies at frequently occupied nests were occupied by banded males but they were not identified. In both cases I was able to exclude the event that males from immediate neighbouring territories had moved into the vacancies because they were still present on their territories at those times.

Table 5.1. Summary of results of removal experiments in which adult peregrine falcons were removed from their territories for 24 hours.

Sex removed	Territory Quality	Replacement	Territory regained	Date of removal	Days before laying	Comments
Female	Good	Yes	Yes	27/5/93	9	
Female	Good	Yes	Yes	1/6/95	8*	
Female	Good	Yes	Yes	1/6/95	8*	
Female	Good	Yes	Yes	7/6/92	5*	5:06 hours until replacement
Female	Good	Yes	No	2/6/93	7	
Female	Poor	Yes	No	31/5/94	6*	
Male	Good	Yes	Yes	8/6/92	8	3:38 hours until replacement
Male	Good	Yes	Yes	26/5/93	12	
Male	Good	Yes	Yes	31/5/93	9	
Male	Good	Yes	Yes	28/5/94	11*	
Male	Poor	Yes	Yes	30/5/94	9*	Replaced by subadult
Male	Poor	No	Yes	25/5/93	14	
Male	Poor	No	Yes	8/6/93	-1*	
Male	Poor	No	Yes	1/6/92	9	Held 7:55 hours then released

* Denotes cases in which no eggs were laid, so the date of removal was compared with the mean lay date for the population for that year. Lay dates were obtained following Court *et al.* (1988a).

5.5 DISCUSSION

Removal experiments have been used in a wide variety of species to indicate the existence in the population of non-territorial individuals which are capable of breeding, but are prevented from doing so by the lack of a territory (see review by Newton 1992). When a vacancy created by a removal experiment is filled, it is usually regarded as evidence of a non-breeding surplus (Newton 1992). It is important, however, to establish the origin and status of replacement birds to distinguish a true surplus from birds moving from other territories or migrants stopping over at a vacant territory.

Vacancies at peregrine territories at Rankin Inlet were filled rapidly. Rapid replacements at nests have been recorded elsewhere in peregrines (Newton 1979, Ratcliffe 1993) including anecdotal reports of replacement within 24 hours of female peregrines in the Scottish Highlands after they were shot at their nests (Macintyre (1960) in Newton 1979, Ratcliffe 1993), and also in a wide variety of other raptors (Newton 1979, Village 1983, Bowman & Bird 1986, Newton & Marquiss 1991). In non-raptorial species, the rapid replacement of territory holders has been documented 'within minutes' in red-winged blackbirds *Agelaius phoeniceus* (Orians 1961, Eckert & Weatherhead 1987), and within hours in great tits *Parus major* (Krebs 1977), and willow warblers *Phylloscopus trochilus* (Hogstad 1989).

In these experiments, movements between territories were not detected or suspected. I cannot exclude the possibility that the two replacement males that were banded (but not identified) had moved from distant territories within the study area, but it is equally possible that both were banded individuals from the floating population (on average, 58% of territorial males and 75% of territorial females in years were banded during years that removals were done). Ringed males, and to a lesser extent females, are likely to occur in the floating population given: 1) the large number of young banded over the study period; and 2) the high frequency at which locally produced males appear as recruits after a turnover in the occupant(s) of a territory (author's unpublished data). This suggests that such birds may be somewhere near to capitalize on the death or movement of the previous occupant by occupying the vacancy created (see also Smith 1978, Zack 1990, Zack & Stutchbury 1992).

The inference that replacement birds were from a non-breeding surplus was supported by the following: 1) the late stage at which the experiments took place, soon after all the territories were established, reduces the likelihood that replacements were merely birds which had not yet settled. By this time, breeding birds should have already been established on their territories, and well into the courtship period. 2) Laying dates for other peregrine populations farther north are similar to those at Rankin Inlet (Alliston & Patterson 1978, Calef & Heard 1979) which decreases the likelihood that the replacements were migrating birds still on their way to more distant breeding grounds. 3) Unbanded replacement birds were most likely to come from a non-territorial portion of the population. 4) One replacement individual was a subadult, an age class that has never been recorded holding territories in the study population. 5) Most replacement birds were unable to retain the territories after the release of the original territory holder. This is consistent with the hypothesis that floaters are individuals which lack the experience, physical characteristics, age, or social dominance to gain a breeding place, and therefore are unlikely to be successful in competing with the previous occupant for ownership of the territory. 6) Some replacement birds which did not retain their territories after the original territory holder was released have been recorded in the breeding population in subsequent years. This concurs with the idea that floaters are excluded from breeding until they have attained qualities which make them competitive in securing a place in the breeding population (i.e. they have risen in the queue for 'inheriting' a territory (Wiley & Rabenold 1984, Zack & Stutchbury 1992)), or an increase in food supply allows a larger breeding population. Any migrating peregrine which opportunistically capitalized on a vacant territory, in comparison, would be less likely to be recorded in the population again.

The two cases where replacement birds bred successfully provides evidence that at least some individuals of the surplus are physiologically capable of breeding. Furthermore, there is no reason to suspect that the adult replacement birds would not have gone on to breed if they had remained on territory after the release of the territory holder. In most studies where replacements have proceeded to breed, however, their success was much lower than the rest of the territorial population (Dhondt & Schillemans 1983, Newton 1992). Anecdotal observations of replacements at peregrine nests have previously recorded surplus birds proceeding to breed. Gamekeepers on grouse moors in Britain noted that when a female peregrine was shot at a nest, generally the male re-paired within 24 hours and females were even recorded taking over the incubation of eggs or rearing of young (Ratcliffe 1993). Moreover, replacement was sometimes so rapid that the eggs remained viable. Hickey (1942) cited a case where both the male and female at a nest were successively shot, and the replacements were so rapid that the two new birds eventually raised a brood to which neither was related. Subadult peregrines have been recorded breeding in captive breeding programs (Wrege & Cade 1977), and also in the wild (Newton 1979, Newton & Mearns 1988, Ratcliffe 1993), so it is possible the replacement subadult that I recorded may have gone on to breed, given the opportunity. I conclude that the results of the removal experiments are indicative of a non-breeding surplus of both sexes in the population.

A removal experiment tests not only for the presence of surplus individuals able to occupy a territory when one becomes available, but also for the existence of density limitation (Newton 1992). When replacement follows removal, it is usually concluded that the density of the breeding population is limited by territoriality (i.e. that further individuals are prevented or discouraged from securing a territory by the behaviour of those already holding territories) (Newton 1979, Newton 1992). However, before territoriality or any other factors hypothesized to limit density can be considered, a surplus of both sexes must be demonstrated as breeding densities may also be limited by an unequal sex ratio (Newton 1992); this condition was met in this study.

The presence of surplus male and female breeding age peregrines at Rankin Inlet leads me to conclude that breeding density is limited. The role of territoriality, however, in limitation of the density of the breeding population is less clear as a non-breeding surplus of adults occurs despite the existence of vacant nesting habitat. Intuitively, the non-breeding surplus should utilize vacant nesting places, yet in any one year a minimum of 25% (10/39) of all territories remained vacant. Territoriality should only be accepted as the proximate mechanism of population limitation in this population if the behaviour of birds already on territory prevents occupation of unoccupied territories (i.e. the supposedly 'vacant' nest sites are actually within the boundaries of one or more neighbouring territories and the behaviour of territorial birds prevents floaters from settling there, as per the predictions of Ratcliffe (1962) and the "ideal-despotic" model of habitat distribution) (Fretwell & Lucas 1970, Fretwell 1972). These territories would only become available for use when the boundaries of neighbouring territory(s) change (e.g. if territory size shrinks when there is an increase in food availability or when the neighbour is a less aggressive individual that will allow another to breed in closer proximity). In some avian species, documented changes in territory size have been associated with agonistic characteristics and/or spatial requirements varying between individuals and also with fluctuations in food supply (Cade 1960, Dhondt 1971, Ralph & Pearson 1971, Newton 1979, Enokkson & Nilsson 1983, Davies & Lundberg 1984, Newton 1992, Ratcliffe 1993).

Ratcliffe (1962) proposed that territoriality acted as a proximate mechanism of population regulation in non-migratory peregrine populations in Great Britain by near neighbours preventing the occupation of suitable nesting habitat. The model of territoriality for the peregrine population at Rankin Inlet, however, provides poor support for this hypothesis. Tundra peregrines maintain small nesting territories—areas which include a small hill, rock outcrop, or one or more cliff(s), in which courtship and nesting occur, and from which intruding conspecifics are repelled (Cade 1960, Court 1986). Each territory may include a number of suitable places to nest, so over a number of breeding seasons, several alternate nest sites or adjacent cliffs may be used. Conspecifics are strictly excluded from an area ca. 250m radius immediately surrounding the nest site (Court 1986) and also from alternate nest sites, although Cade (1960) noted that particular features within an individual's home range such as favoured perches from which to hunt may also be defended. Some hunting occurs within the exclusive zone around the nest, but the area is too small to contain sufficient prey to be for the purposes of monopolizing food resources, and most hunting must take place outside of this area. Following Hinde (1956) and Nelson (1977), the territories maintained by peregrines at Rankin Inlet are, therefore, mainly Type B (i.e. defended area provides one or more nest sites but most of the food is obtained elsewhere), but may range to Type B-A (i.e. defended area provides nest site and a significant part of hunting occurs within the defended area). For some breeding pairs, the location and distance of likely hunting grounds relative to nesting territories (unpublished radio telemetry data, M. Bradley) suggests that hunting ranges are not exclusive. Peregrines occupying territories on islands in the study area must do the majority of their hunting on the mainland or its margins, in which case much of the home range would be economically undefendable. Moreover, removals were made just prior to laying, a period during which males should spend as much time as possible in the immediate vicinity of the nest site to guard their nesting territory against intruders and prevent extra-pair copulations (Chapter 3).

Territoriality results in the exclusion of other peregrines occupying suitable nesting places within the core nesting territory, but provides an inadequate explanation for floaters being excluded from unoccupied habitat. The model of territoriality and the pattern of nest site occupation in this population is suggestive of a pre-emptive model of habitat use (Pulliam & Danielson 1991) in that territorial behaviour may prevent individuals from being usurped from the breeding population but does not limit the use of potential nesting habitat outside the defended area or the likely reproductive success in that habitat. I propose that, in this population at least, territoriality may be a competitive process or mechanism, that determines which individuals out of the entire pool of possible breeders secure and maintain a place in the breeding population, rather than a proximate mechanism determining the density of breeders.

An alternate explanation of population limitation is that floaters do not utilize unoccupied nesting territories because they are actually unsuitable for occupation (Hunt 1988, Newton 1991). Newton (1991) hypothesized it was the combination of individual quality (which was related to the ability to find food) and habitat quality (which was related to food availability) that determined whether a replacement or a breeding attempt at any given territory occurred. A 'high quality' individual thus had the option of breeding in good or poor habitat as it was able to find sufficient food to breed in either. A 'low quality' bird, however, could only gather sufficient resources in good quality habitat to breed. Floaters were considered less competent (i.e. poorer quality) individuals, an assumption supported by the lower reproductive success of replacement birds (Newton & Marquiss 1991, Newton 1992), thus only the occupants of territories associated with a plentiful food supply (i.e. good quality habitat) were replaced in some studies (blue grouse *Dendragapus obscurus*, Lewis & Zwickel 1980; American kestrel *F. sparverius*, Bowman & Bird 1986; European sparrowhawk *A. nisus*, Newton & Marquiss 1991). Floaters presumably remained non-breeders rather than replacing birds at poor quality territories or using unoccupied territories.

Overall, the pattern of replacement and territory occupancy at Rankin Inlet is consistent with the hypothesis that the combination of habitat and individual quality determines whether a vacancy is occupied, even though the link between habitat quality and food supply is less demonstrable for peregrine territories at Rankin Inlet, than for some other species (Newton 1992). In the absence of exclusive hunting territories, intuitively it would be predicted that the ability of an individual at gathering food (an important component of individual quality) should have more importance in influencing whether a breeding attempt or replacement occurred at any particular territory than the inherent qualities of the habitat associated with a territory (including food supply). Nevertheless, vacancies were always occupied at territories associated with good reproductive performance, but not always at those associated with poor reproductive success. Thus, the individual quality of floaters was always sufficient to occupy a vacancy, for the purposes of attempting to breed, at a territory associated with good reproductive performance (i.e. good quality territory) but apparently it did not always exceed the threshold necessary to attempt to breed at a territory associated with poor reproductive performance. By inference, the suitability (Fretwell & Lucas 1970) of vacant territories was therefore below the threshold of any pair of individuals in the non-breeding surplus in the years that the removal experiments were done, although in at least one out of the 14 year population study fluctuations in suitability allowed the occupation of these territories where breeding attempts were usually untenable.

At Rankin Inlet, the size of the breeding population and the total number of young produced by the population fluctuates substantially between years, unlike most peregrine populations for which stability in size in considered the norm (Court *et al.* 1988b, Newton 1988, Ratcliffe 1993, Bradley *et al.* In press, Chapter 3). The variability has been linked, in part, to fluctuations in microtine rodent populations, an important prey item of this peregrine population (Court *et al.* 1988b, Newton 1988, Bradley & Oliphant 1991). In an environment where habitat quality fluctuates among years, it is predicted that poor quality individuals, for whom reproduction is normally intenable, will attempt to breed in years of exceptional prey availability. The observation that individuals which entered the breeding population at high population densities (i.e. years of high prey abundance) tended to fail in their breeding attempts (Chapter 3), concurs with this prediction. Moreover, it supports the hypothesis that the population is ultimately limited by food supply, and at a proximate level, by a lack of individuals of sufficient quality that are able to secure enough resources to breed.

The division of labour in peregrines and many other raptors during the breeding season suggests that male quality may be more important than female quality in determining whether replacement or a breeding attempt occurs at a poor quality territory. As males provision the female with food through courtship, egg-laying and incubation, the energetic demands of a poor quality female may be met by a good quality male. It has been noted or suggested that floaters are mainly young, inexperienced birds (Newton 1992, Zack & Stutchbury 1992) which are coincidentally susceptible to failure, but I was not able to investigate this because of a lack of known age individuals. Newton (1989b) noted that the age of first breeding among European sparrowhawks was higher on good territories than on poor ones, which concurs with the hypothesis that mainly young birds are relegated to breeding at poor territories or become floaters. Priorities for future research include investigating whether males replace individuals at poor quality territories less frequently than females do, and comparing 1) the body condition of males and females, and 2) provisioning rates, among good and poor quality territories.

In summary, these removal experiments were indicative that a non-breeding surplus of males and females exists in this peregrine population and, therefore, that the breeding population is limited. The proximate mechanism through which the size of the breeding population is adjusted to the amount of food available in a given year is unclear. Since only a relatively small area in the immediately vicinity of the nest is defended vigorously, territoriality is unlikely to prevent floaters from occupying all vacant territories. The observation that individuals entering the breeding population in years of high population density generally had a poor breeding performance (Chapter 4) suggests that the population may be proximately limited by a lack of competent individuals that are able to secure sufficient resources to breed in the available habitat (i.e. individual quality), and ultimately by food supply (i.e. habitat quality). Examples of floaters subsequently being 'promoted' to the breeding population suggests that individual quality may change with age, which concurs with the hypothesis that the non-breeding surplus may consist largely of young or inexperienced birds.

6. SURVIVAL ESTIMATES FOR MALE AND FEMALE TUNDRA PEREGRINE FALCONS USING TURNOVER AND CAPTURE-RECAPTURE METHODOLOGY.

6.1 ABSTRACT

There is a lack of accurate survival estimates for peregrine falcons despite the need for these in species management and conservation. From 1982 to 1995, adult tundra peregrine falcons at Rankin Inlet, Canada were marked with alpha-numeric colour bands and the occupants of breeding territories were subsequently identified. I estimated survival from the capture-recapture/resighting histories of 55 males and 88 females using Cormack-Jolly-Seber capture-recapture methodology and from turnover data. Results were indicative of little or no difference in survival between males and females. Differences between estimates from the two methods were minimal. Low sample size of marked birds contributed to a lack of fit to the capture-recapture model. While capture-recapture methodology is a powerful technique for estimating population parameters, its practical application with raptor species may be limited by the sample size required and the difficulty of meeting assumptions implicit to the model. Estimates represent minimum survival because of the confounding effects of emigration.

6.2 INTRODUCTION

Many management, ecological, and evolutionary questions in current biological studies require an understanding of the dynamics of animal populations. Yet, accurate estimates of key determinants of population dynamics, life history parameters such as survival and reproductive rates, are rarely available for vertebrates. For species which are relatively long-lived or occur at low densities, such as many birds of prey, realistic estimates may only be gained after intensive study of a population for many years. The breeding biology of peregrine falcons, *F. peregrinus*, has been well studied (Newton

1979, Cade *et al.* 1988, Ratcliffe 1993), but there is a lack of accurate estimates of survival despite the need for such estimates in population modelling and species management (Hunt 1988, Newton 1988, Wootton & Bell 1992, Pagel *et al.* 1996). Moreover, most published estimates of peregrine survival are for females only (Ambrose & Riddle 1988, Newton & Mearns 1988, Gould & Fuller 1995, but see Nelson 1988).

Court *et al.* (1989) presented estimates of adult male and female mortality from a 7-year population study of tundra peregrine falcons *F. p. tundrius* breeding in the Canadian Arctic. Here, I present the results of an intensive banding and recapture/resighting study of the same population over 14-years. The aim was to update previous estimates using a larger sample, improve the accuracy of estimates using current capture-mark-recapture modelling techniques, and test for habitat specific differences in survival. Elsewhere, I demonstrated that breeding attempts at infrequently occupied territories failed more often than attempts at frequently occupied territories, and speculated that some individuals may become "floaters" rather than breed at poor quality territories (Chapter 3, Chapter 4). I also sought to establish whether breeding at infrequently occupied territories incurred costs in terms of an individuals survival (Conroy 1993), by comparing survival among individuals breeding at frequently and infrequently occupied territories.

Historically, raptor studies have estimated mortality and survival from estimates of the turnover of adults identified on nesting territories (Mearns & Newton 1984, Newton 1986, Newton & Mearns 1988, Ambrose & Riddle 1988, Court *et al.* 1989, James *et al.* 1989). Gould & Fuller (1995) warn that traditional methods of estimating survival are inherently biased and fail to utilize all available data, however, and recommend Cormack-Jolly-Seber (CJS) models for more rigorous analysis of capture-mark-recapture data and less biased survival estimates (Cormack 1964, Jolly 1965, Seber 1965, Seber 1982, Burnham *et al.* 1987, Pollock *et al.* 1990, Lebreton *et al.* 1992). They also facilitate statistical comparisons of survival between habitats, in comparison with turnover data (Conroy 1993, Newton *et al.* 1993b). I report annual survival estimates for male and female peregrines calculated from the two methods to highlight differences in methodology, and to allow comparison with previously published estimates for peregrines, and other raptor species.

6.3 METHODS

6.3.1 Study Area and Survey Methods

The study population of peregrines nests within a 450 km^2 study area around the hamlet of Rankin Inlet, Keewatin District, Northwest Territories, Canada (62°49'N 92°05'W). It was studied between 1981 and 1995 and is described in detail elsewhere (Court *et al.* 1988a, b, 1989). Each year, in early Spring (May 15-June 10), the entire study area was systematically surveyed by snowmobile for territorial pairs. Because of its small size and gentle terrain, it is logistically a simple task to systematically search the entire study area for territorial pairs, not just historic or frequently used nest sites. Also, potential nesting habitat within this area is extremely limited. Much (200 km^2, 44%) of the study area is accounted for by Hudson Bay, which remains frozen at this time of year, and much of the land is also covered in ice and snow until well after egg-laying, limiting snow-free nesting habitat. Against this backdrop, territorial peregrines are obvious.

Throughout each field season, an attempt was made to mark any unbanded individuals with U.S. Fish and Wildlife Service aluminum leg bands, and blue anodized aluminum alpha-numeric colour bands. Each year, banded individuals were identified using a telescope, or occasionally, by being recaptured. Most captures of males were made in spring, prior to egg-laying, while females were also caught during incubation and nestling stages. When nesting territories were identified and occupied, they were visited regularly to establish the outcome of the breeding attempt. All young were banded late in the nestling stage.

6.3.2 Turnover

Maximum mortality estimates, and thus minimum survival estimates, were calculated from turnover frequency following Mearns & Newton (1984) and Court *et al.* (1989). Turnover is defined as the proportion of territories where identified individuals were caught (or seen) in successive years that do not contain the same individual in the second year (Mearns & Newton 1984). Mortality, and its converse survival, was estimated from this proportion with an adjustment for the known movements of banded individuals within the study area. This estimate is biased high because only territories in which birds could be identified in successive years were included (Court *et al.* 1989, James *et al.* 1989, Gould & Fuller 1995), yet only four out of 39 different territories were occupied for all 14 years of the study (Chapter 4). Following Court *et al.* (1989), I provide a second estimate of mortality to account for this bias, where vacancy at a territory in a year succeeding identification was considered mortality. Standard error of the survival estimate was calculated following Gould & Fuller (1995).

6.3.3 Capture-Recapture Methodology

I used the programs RELEASE 2.4 (Burnham *et al.* 1987) and SURGE 4.0 (Pradel & Lebreton 1991) to analyze data, following the methods of Lebreton *et al.* (1992). TESTS 2 and 3 of RELEASE were used to test goodness-of-fit of the data to the assumptions in the global capture-recapture model. These assumptions are: 1) the probability of capture is the same for all individuals present in a population during a sampling period, 2) every marked individual of a cohort present in a population immediately after a sampling period has the same probability of surviving until the next sampling period, 3) emigration is permanent, 4) marks are not lost and all are reported, and 5) all samples are instantaneous and each release is made immediately after the sample. TEST 2 tests for statistical independence among individuals of the same age and sex cohorts, while TEST 3 tests whether previously released individuals have the same future fates as newly released individuals (Burnham *et al.* 1987).

Maximum likelihood estimates of survival and recapture probability were calculated from capture-recapture/resighting data using Cormack-Jolly-Seber open population models in SURGE (Pollock *et al.* 1990, Lebreton *et al.* 1992, Burnham *et al.* 1995). Only the capture-resighting histories of adult peregrines were included for analysis, as there is some evidence that survival rate among juveniles, or 'pre-breeders' is markedly lower (Newton & Mearns 1988). Despite marking a large number of young, I was not able to estimate survival among pre-breeding peregrines. Only 20 of the 430 peregrines banded as young were subsequently recorded in the breeding population. I did include the capture-recapture histories of these 20 recruits in SURGE analysis. The year in which they were first sighted as adults was treated as their first capture.

SURGE fits a probabilistic model to the capture-recapture data. The model computed by SURGE is specified by the user who chooses the variables influencing survival and/or recapture probabilities. I included sex, time (year), and territory occupancy as variables. Territory occupancy was included as a variable as it is predicted that individuals captured and released at infrequently occupied territories are less likely to be resighted than individuals at frequently occupied territories. Occupation frequency is also an indirect measure of territory quality, in that breeding attempts at frequently occupied territories were successful (i.e. young were fledged) more often than attempts at infrequently occupied territories (Chapter 3). As there were only 20 known-age individuals in the population I did not consider the effect of age. Akaike's Information Criteria (AIC, Akaike 1973, Anderson *et al.* 1994), a numerical measure based on the deviance and the number of parameters in a model, and likelihood ratio tests (LRT, Burnham *et al.* 1987) were used to identify models that best described the data.

6.4 RESULTS

6.4.1 Survival Estimates Based on Turnover

Of 130 territories in which males were identified in successive years at Rankin Inlet, in 96 cases (74%) it was the same individual in the second year and in 34 (26%) it was a different one. I cannot attribute all turnover to mortality because males were recorded moving between territories. Adjusting this turnover estimate for 8 known movement yields a mortality estimate of 0.20 (26/130). Assuming that territory vacancy was due to the death of the previous resident (Court *et al.* 1989), then of 143 territories in which males were identified in successive years, 104 held males that were alive in a later year. This yields a maximum mortality estimate of 0.27 (39/143). Minimum survival of adult male peregrines was therefore estimated at 0.727 (104/143) with a S.E. of 0.037.

Of 207 territories in which females were identified in successive years, in 144 (70%) it was the same individual in the second year, and in 63 (30%) it was a different one. Females were also recorded moving between territories. Adjusting this turnover estimate for 13 known movement yields an estimate of mortality for females of 0.24 (50/207). Again, assuming that territory vacancy was due to the death of the previous resident, then of 226 territories in which females were identified in successive years, 157 survived to a later year; making the maximum mortality estimate 0.31 (69/226). Minimum survival of adult females was therefore estimated at 0.694 (157/226) with a S.E. of 0.031.

Turnover for both sexes combined was 29% (97/337). Accounting for 21 known movements, mortality was 0.23 (76/337). Assuming that territory vacancy was the result of mortality, maximum mortality was estimated at 0.29 (108/369). Minimum survival for male and female adult peregrines combined, therefore, was estimated at 0.707 (261/369) with a S.E. of 0.024.

6.4.2 Survival Estimates Using Capture-Recapture Methodology

Capture-recapture data were collected from 55 male and 88 female adult peregrines at Rankin Inlet. The small size of the sample precluded separate goodness-of-fit analyses for the male and female data. For both sexes combined goodness-of-fit tests indicated a lack of fit of the data to the capture-recapture model at the cohort and sub-cohort level (χ^2_{20}= 37.41, P = 0.0105 and χ^2_{34}= 56.27, P = 0.0095 for TESTS 2 and 3, respectively) and overall fit of the data to the model was inadequate (χ^2_{54} = 93.68, P = 0.007 for TEST 2 + TEST 3; Burnham *et al.* 1987).

Although the data did not fit, I considered that for comparative purposes further analysis was warranted with knowledge of lack of fit. Model $\phi\, p_S$ fit the data best (i.e. had the lowest AIC value, Table 6.1) which indicated that sex, time, or territory occupancy had no effect on survival (ϕ) but recapture probability (p) differed by sex. The model with the next lowest AIC, model $\phi_S\, p_S$ which indicated that survival differed between sex, was also competitive as it did not differ significantly from model $\phi\, p_S$ (Likelihood ratio test χ^2 = 1.66, df = 1, P = 0.198).

Recapture probabilities were 0.817 for females (SE = 0.038) and 0.652 for males (SE = 0.052) for the most parsimonious model ($\phi\, p_S$); and 0.822 for females (SE = 0.037) and 0.638 for males (SE = 0.054) for the competitive model ($\phi_S\, p_S$). Survival estimates from both models are summarized in Table 6.2.

Table 6.1. Capture-recapture models used to estimate survival of tundra peregrine falcons at Rankin Inlet, Canada: 1982-1995. Models were generated from the program SURGE and are listed in order of increasing AIC (Akaike's Information Criteria). NP is the number of estimable parameters.

Model[1]	NP	Deviance	AIC
$\phi\ p_{s}$	3	652.73	658.73
$\phi_{s}\ p_{s}$	4	651.07	659.07
$\phi_{t+s}\ p_{s}$	17	632.53	664.53
$\phi_{t}\ p_{s}$	16	634.30	666.30
$\phi_{t+s+q}\ p_{s}$	18	630.64	666.64
$\phi_{t*s*q}\ p_{s}$	56	584.40	696.40
$\phi_{t*s*q}\ p$	55	590.83	708.83
$\phi_{t*s*q}\ p_{t*s*q}$	108	527.05	743.05

[1] Model subscripts indicate time (t), sex (s) or territory occupancy (q) effects on survival (ϕ) or recapture (p). An "*" indicates full sex, territory quality or time-effects, whereas "+" indicates a reduced model in which sex, territory quality or time-effects are additive.

Table 6.2. Mean (S.E.) survival estimates for tundra peregrine falcons at Rankin Inlet, Canada using two different methods.

METHOD	Male	Female	Combined
Turnover*	0.727 (0.037)	0.694 (0.031)	0.707 (0.024)
Capture-recapture**	0.765 (0.038)	0.701 (0.032)	0.725 (0.023)

* Following Mearns & Newton (1984) and applying a correction for territory vacancies following Court *et al.* (1989). **Survival estimates for both sexes combined represent the most parsimonious model in SURGE; separate male and female survival estimates orginate from a competitive model (see text).

6.5 DISCUSSION

Accurate estimates of population parameters are important for species conservation and management decisions. Published estimates of peregrine survival have mainly been limited by small samples and uncertain error (Ambrose & Riddle 1988, Enderson & Craig 1988, Nelson 1988, Wootton & Bell 1992). I was able to calculate survival estimates for male and female tundra peregrine falcons by turnover and capture-recapture analysis of a relatively large sample for the species.

Estimates of survival of peregrine falcons at Rankin Inlet are low in comparison with most other studies of the species (Table 6.3). Differences may be attributed, in part, to biological differences among populations (e.g. migratory vs. non-migratory populations), and/or bias associated with the different population surveys. Gould & Fuller (1995) provide estimates for tundra peregrines in Greenland which may be considered closely comparable with the population studied here because of similarities in their biology (Burnham & Mattox 1984, Court *et al.* 1988a, b, 1989, Bradley & Oliphant 1989, Mattox & Seegar 1988). Mearns & Newton (1984), however, studied a non-migratory peregrine population which was also recovering from the effects of organochlorine pesticide contamination. Assuming there is some cost related to annual inter-continental migration, survival is predicted to be higher in the non-migratory populations studied by Mearns & Newton (1984), and Nelson (1988, 1990) than among populations of highly migratory tundra peregrines. The low estimates of survival from Nelson (1988, 1990) are difficult to explain. Nelson (1990) explained that low survival among Langara Island peregrines, relative to other studies, were the result of the severe environmental conditions to which the population is exposed. Peregrines at Rankin Inlet, however, are also exposed to poor conditions on the breeding grounds (Bradley *et al.* In press), as well as being highly migratory. The large sample included in this study, relative to others, however, may give an increased degree of accuracy to survival estimates. The small size of the study area, relative to the areas surveyed in Mearns & Newton (1984) and Gould & Fuller (1995), however, may counteract this as the bias associated with emigration from a small study area is likely to be larger.

The high nest site fidelity of breeding peregrines in most studies implies that emigration is usually low (Mearns & Newton 1984, Ratcliffe 1993). Among the Rankin Inlet population, however, 14% (8/55) of males and 15% (13/88) of females were known to have moved between territories. Moreover, the frequency of detected movements under-

Table 6.3. Mean annual survival estimates of peregrine falcons from different studies.

STUDY	Male	Female	Combined
This study*	0.73	0.69	0.71
— **	0.765	0.70	0.725
Court *et al.*(1989)*	0.85	0.81	0.83
Mearns & Newton (1984)*	—	0.91	0.89
Nelson (1988, 1990)	0.74	0.63	
Gould & Fuller (1995)**	—	0.79	—

*Derived from mortality estimates calculated from turnover data.

** Calculated from Jolly-Seber capture-recapture methodology.

estimates emigration. Even small movements (0.5-20 km) could place a marked bird beyond the limits of this small study area. Estimates of the age of first breeding also suggests that adults may move from one breeding place to another. Of 16 males that were banded on the study area as nestlings, 6 (38%) were 6 years or older when they were first recorded as adults in the breeding population (median 4 years, range 2-8). This seems an inordinate delay to the age of first breeding considering that: 1) peregrines are capable of breeding as yearlings (Ratcliffe 1993), and 2) males only made an average of 2.3 breeding attempts at Rankin Inlet (range 1-9, n = 59). Even if competition for nesting territories delays breeding (Chapter 4), it seems likely that these individuals may have bred elsewhere before settling on the study area. Survival estimates from both techniques must be regarded as minimum values, therefore, because the effects of emigration cannot be separated from the estimate (i.e. emigration and mortality are indistinguishable).

Variation in population survey methodology may also contribute to differences in survival estimates among studies. This may account, at least in part, for the differences in survival estimates between Gould & Fuller (1995) and this study. At Rankin Inlet the population is surveyed as peregrines re-occupy the breeding grounds at the completion of migration, but Greenland populations are not surveyed until after egg-laying. Elsewhere, it was found that: 1) 18% (61/330) of all breeding attempts at Rankin Inlet over a fourteen year period failed before eggs were laid, and 37% (122/330) failed before hatch (Chapter 4); and 2) breeding attempts at territories that were occupied infrequently experienced a higher frequency of failure. Moreover, complete abandonment of a territory is associated with failure; members of pairs are rarely seen at a nest site following failure. Estimates from populations which are not surveyed before laying may be biased high, therefore, because the sample will tend towards including mainly the capture-resighting histories of individuals breeding at frequently occupied or "high-quality" territories, for whom the probability of recapture and possibly survival is higher, at the expense of capture-recapture histories of individuals breeding at poor quality sites where recapture is less likely and survival may be lower. The difference in survival and recapture probabilities between Rankin Inlet and Greenland population of tundra peregrines is parsimonious with this explanation.

I concur with Gould & Fuller (1995) that capture-recapture methodology represents a powerful tool in improving our understanding of raptor population dynamics. Estimates of survival from Cormack-Jolly-Seber capture-recapture modelling are less biased than estimates from turnover data because: 1) more information is used; and 2) it is not assumed that vacancies at nesting territories without replacement are due only to emigration (Gould & Fuller 1995). In this study, however, I found that survival estimates from turnover data closely approximated those from capture-recapture methodology when the latter bias was simply corrected for by assuming that vacancies at territories were the result of mortality (Court *et al.* 1989), despite the associated difference in sample size.

Survival estimates for tundra peregrine falcons using capture-recapture methodology were inaccurate because of small samples of marked birds, and all assumptions of the model were not met. Capture and recapture episodes are assumed to be instantaneous which is unrealistic. Limiting capture and resighting periods to a short time period may contribute to fulfilling this assumption (DeStefano *et al.* 1994). However, I found that incubation and brooding periods were ideal for trapping and banding female peregrines. It is also assumed that marks are not lost and all are reported. I cannot entirely eliminate the possibility that bands are not lost, however, the frequency of such an event must be very low. I have never recorded instances in which a bird marked with USFWS band had lost its alpha-numeric colour band. Colour bands do wear over time which makes reading a worn band difficult from a distance; in this study I was able to re-capture all such individuals to replace the colour band. The assumption that all marks are reported was not met. Despite a powerful telescope, skilled field personnel, and intensive efforts, it was not possible to get close enough to a few marked individuals each year to read their bands, and some of these individuals were not trapped. Also, emigration is not always permanent; one female first banded as a breeding adult in 1986 was not recorded in the population again until 1990 (at a different territory).

Capture-recapture modelling may represent "stronger, more sophisticated analyses" (Gould & Fuller 1995) than turnover analysis, however, the use of this technique among raptor species may be restricted. Begon (1983) succinctly described the dilemma: "mathematical sophistication does not, in itself, guarantee the practical utility of an ecological technique". Capture-recapture methodology requires large numbers of marked birds and high recapture/resighting rates over a long period; conditions infrequently met in studies of raptors (DeStefano *et al.* 1994). I caution those designing population studies that the accuracy of survival estimates are heavily dependent on the quantity and quality of the available data. My estimates were inaccurate because of small sample sizes. For raptor species which are secretive, or exist in low numbers and are highly dispersed, such as many endangered species, the samples required by Cormack-Jolly-Seber analyses may be difficult or practically impossible to collect. Simpler techniques such as turnover appear more attractive but are also fraught with inherent biases and the assessment of confidence in the estimates is difficult (Begon 1983). I emphasize the recommendations of Begon (1983) and DeStefano (1994) that field ecologists should closely consider the biology and behaviour of their study species when designing a study to ensure that the assumptions are only marginally violated.

For some species, the confounding influence posed by emigration may be an overriding limitation in the interpretation and application of raptor survival estimates regardless of the method of calculation. Without an estimation of emigration rates (Lebreton & North 1993, Baker *et al.* 1995), and correction for this, the survival estimate may be of limited use as it will be biased low. Population surveys should be conducted over a geographic area that is sufficiently broad to encompass movements, or emigration should be estimated by remote telemetry. Estimation of emigration is a priority for future research. For migratory populations of peregrine falcons and other highly mobile raptors, satellite telemetry may provide the only practical method through which the relative influence of emigration on survival estimates may be elucidated (Bunck & Pollock 1993, Kenward 1993).

7. GENERAL DISCUSSION

More than two decades after the use of organochlorines was restricted within North America, tundra peregrine falcons at Rankin Inlet continue to accumulate organochlorine contaminants through dietary intake. Contaminant levels and levels of eggshell thinning reflect a population that is still likely to experience some reproductive failures related to organochlorine contaminants. The levels are not high enough, however, to seriously affect the productivity of the population, on average. The effects of contamination on annual productivity of the population are minor, in comparison with fluctuating prey availability or severe weather (Bradley *et al.* In press). Organochlorine contamination can no longer be considered a factor seriously limiting production of the population or long-term stability. I found no evidence of sharp declines over the last decade in residue levels in peregrines or their prey, contrary to predictions. This concurs with research from a variety of marine and terrestrial ecosystems and other species which indicates that levels of persistent organochlorines in the environment have decreased substantially over the last three decades but over the last decade have leveled off (Elliott *et al.* 1989, Government of Canada 1991, Newton *et al.* 1993a, Beck *et al.* 1994, Muir *et al.* 1996, 1997, Jensen *et al.* 1997). Continuing contamination of *F. peregrinus* and their prey is usually attributed to the use of organochlorine pesticides within their wintering range in central and South America. At Rankin Inlet, however, I found that relatively high residue levels for the subspecies were linked to contaminated waterfowl and seabird species that range only within North America. This research provides evidence that continued contamination may be attributed to both 1) the present use of organochlorines within the tundra peregrine's wintering range and that of their prey, and 2) sustained loads of contaminants still present within North American ecosystems. As this population functions close to a DDT-free population it is suitable, therefore, for addressing more general questions in avian biology.

The low incidence of pesticide-induced reproductive failures made it possible to access a large number of peregrine falcon broods for parentage analysis. Parentage analysis revealed a low rate of extra-pair paternity (1.3% of young) and indicated that intra-specific brood parasitism is even rarer (<1.1% of young), if it occurs at all. Intuitively, the tenacity of females to the nesting cliff during courtship and laying would seem to preclude opportunities for intra-specific brood parasitism. In order to provision the female with prey during this period, however, males must spend time foraging away from the immediate vicinity of the cliff. The paternity assurance hypothesis predicts that this provides opportunities for extra-pair copulations, and to counteract the resulting probability of uncertainty of parentage, peregrines will copulate frequently to displace or devalue the sperm of their competitors (Birkhead *et al.* 1987, Birkhead & Møller 1992, Møller & Birkhead 1992). The low frequency of extra-pair paternity found in this study partially supports this hypothesis. So far, however, studies of parentage and copulatory behaviour in raptors generally do not support all of the predictions of the paternity assurance hypothesis. Consistent with predictions of the paternity assurance hypothesis, rates of extra-pair paternity among those raptors studied to date are low (Decker *et al.* 1993, Swatschek *et al.* 1993, Warkentin *et al.* 1994, Korpimäki *et al.* 1996, Negro *et al.* 1996). Rates of extra-pair copulation, however, are also low. Moreover, they correspond relatively closely to rates of extra-pair paternity. When extra-pair copulations are rare or infrequent the certainty of parentage is high, therefore, it is difficult to accept frequent copulation as a means of assuring paternity. The frequency of extra-pair paternity found in this study cannot be considered unequivocal support for the paternity assurance hypothesis. There is some evidence that extra-pair copulations are infrequent at Rankin Inlet. Moreover, the pattern of territorial intrusions, including the frequency, temporal distribution relative to the females fertile period, the frequency of intrusions by females, and blatant intrusions in the presence of the territorial male, suggest that intrusions are not for the purposes of seeking extra-pair copulations. The poor fit of the paternity hypothesis to raptors studied to date may be related, in part, to the ability of some raptors to guard their mates from a distance, in combination with the threat of injury to detected intruders. More detailed studies of other raptor species are necessary before the paternity assurance hypothesis can be accepted as a satisfactory explanation of mate guarding and copulation behaviour in raptors, and I urge other researchers to vigorously pursue this avenue of enquiry. Detailed studies of mate guarding, copulation frequency and the estimation of extra-pair copulation frequency are research priorities for this study population.

Through accessing pairs of peregrines for parentage analysis I was able to get detailed information on nest site occupancy, and the reproductive performance of individuals. This study gave important insight into habitat use, population regulation and limitation. Variation in habitat quality (presumably owing to prey availability) and individual quality (i.e. the ability of an individual to secure resources) appear to be important factors in nesting territory selection, and population limitation and regulation at Rankin Inlet. Preferred nesting territories were associated with a higher frequency of success at producing young than territories that were avoided, supporting the hypothesis that occupation frequency is an indirect measure of territory quality. The pattern of territory selection closely matched some predictions of the ideal despotic model of habitat selection in that good quality territories were occupied at low population densities, then as numbers increased, increasingly poor quality territories were occupied (Fretwell & Lucas 1970, Fretwell 1972). Krebs' (1971) study of great tits (*Parus major*) (but see Lemel 1989), and Newtons' (1991) study of sparrowhawks (*A. nisus*) also supported the ideal despotic model. The presence of floaters is indicative that the suitability of territories eventually declines to the point where breeding attempts are no longer tenable, and remaining individuals become a non-breeding surplus (Brown 1964, 1969, Davies 1978, Perrins & Birkhead 1983); another prediction of the ideal despotic distribution.

Reproductive rates are inversely related to density in many populations. Sinclair (1989) found a decrease in clutch size with density in 26% of 19 bird studies, but the underlying mechanisms have received little attention. Reproductive performance did not decline with increasing density at all peregrine territories. Instead, similar to the pattern observed in Spanish imperial eagles, *Aquila adalberti*, (Ferrer & Donazar 1996), density-dependent fecundity in the Rankin Inlet peregrine population was directly related to the increasing proportion of breeding attempts occurring at poor quality territories with increasing density; thus supporting the habitat heterogeneity hypothesis (Dhondt *et al.* 1992, Kadmon 1993). Most studies of density-dependent fecundity in avian species have purposely focused on species with large and variable clutch sizes. Peregrine clutches are small and vary little in size in comparison with many species studied to date, however, this did not preclude density-dependent fecundity. The study of density-dependent fecundity may well benefit from further study of the frequency of breeding attempt failures in comparison with population density among other species.

The role and importance of territoriality in population regulation and limitation has been emphasized in most discussions of population regulation and limitation in avian species. Similarly, the ideal despotic model predicts that dominant individuals (i.e. those at good quality territories) prevent density-dependent resource depletion through territoriality. Evidence from peregrines at Rankin Inlet, however, is equivocal. While other peregrines may be prevented from nesting at, or close to, good quality territories, it is not clear whether territorial behaviour limits the use of nesting habitat outside the defended area or the likely reproductive success there. Also, hunting ranges may be economically undefendable. In the absence of exclusive hunting ranges, dominant individuals at Rankin Inlet may not be able to prevent depletion of food resources. The pattern of reproductive performance and nesting territory selection may, therefore, be better explained by a pre-emptive model of habitat use (Pulliam & Danielson 1991), in that territorial behaviour may prevent individuals from being usurped from the breeding population but does not limit the use of nesting habitat outside the defended area or the likely reproductive success in that habitat. In this scenario, the ability of an individual male at finding available prey and provisioning his mate would be an important determinant of the reproductive performance associated with a territory. Poor performance at territories only occupied at high densities would therefore be explained, in part, by these individuals being of poorer quality. In other species, floaters were mainly young, inexperienced birds which tend to be susceptible to failure (Newton 1992, Zack & Stutchbury 1992). The comparison of age at breeding, lifetime reproductive success, body condition, and provisioning rates between good and poor quality territories might partly contribute to an understanding of the influence of individual quality.

Ecotoxicology, parentage, and population studies required that individual peregrines were identified. As a consequence, the Rankin Inlet peregrine population is the most extensively banded population in the world. This allowed a unique opportunity to examine population parameters. Survival is the most basic parameter, along with reproductive success, through which an understanding of population dynamics of a species may be gained. For rare or endangered species, accurate survival estimates are important for population modeling which is often a key component of species management and conservation. The accurate estimation of survival, however, remains one of the most difficult tasks that face population biologists. The logistic and/or methodological difficulties are especially apparent for those studying raptors which frequently exist in low numbers and are often highly-dispersed. Moreover, most raptors are capable of distant movements or dispersal between years and which creates uncertainty regarding a marked individual's fate (i.e. whether it has died, emigrated, or even been missed in the population survey) when it is not resighted or recaptured. The peregrine falcon is one of the most studied of all avian species, yet few estimates of survival exist. Most published estimates are severely limited by small samples and/or uncertain error, and survival of male peregrines remains virtually unknown. This study provided estimates of minimum survival for male and female adult peregrine falcons calculated from one of the largest samples available for the species. The results indicated little or no difference in survival between males and females, and confirm that peregrines are a long-lived species. These estimates must be regarded as minimum values, however, as the effects of emigration cannot be separated from the estimate. Capture-recapture modeling present advantages in estimating survival over traditional turnover analysis, however, both techniques are severely limited when estimates of emigration are not available. Application of capture-recapture modeling necessitates an extraordinary logistical commitment, however, recent examples in other species demonstrate that this approach can be very value for estimating population parameters and comparing survival among habitats, age-classes, and sexes (Bell *et al.* 1993, Kenward 1993, Lebreton & North 1993, Newton *et al.* 1993b, Forsman *et al.* 1996, Raphael *et al.* 1996, Reid *et al.* 1996).

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IMAGE EVALUATION
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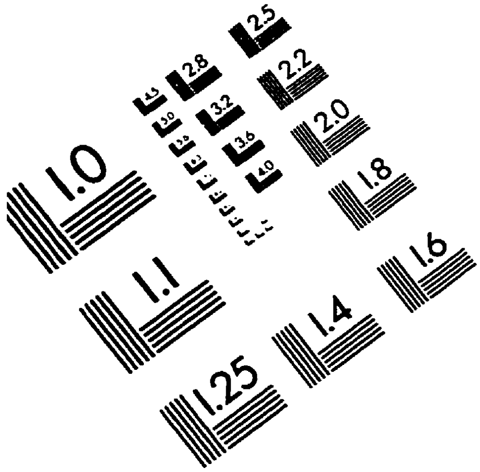

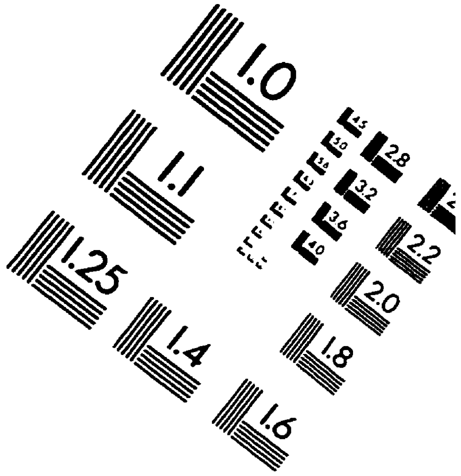

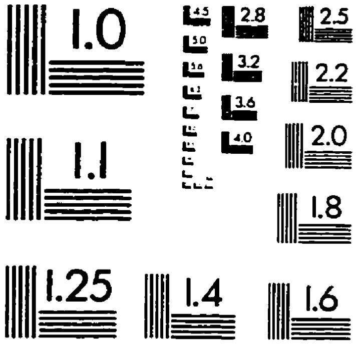

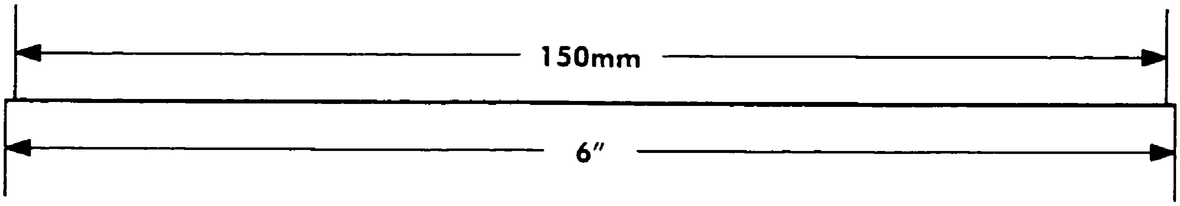

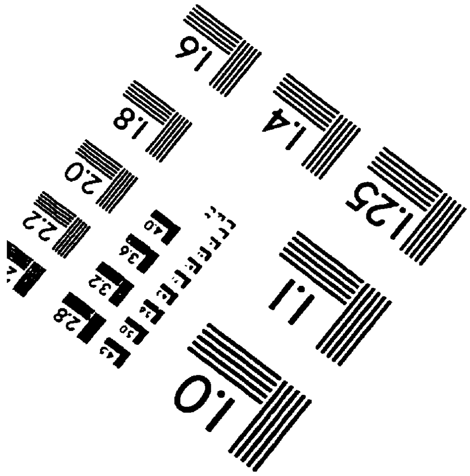

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