

BREEDING, DISPERSAL, AND MIGRATION OF URBAN  
PEREGRINE FALCONS IN EASTERN NORTH AMERICA

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## ABSTRACT

The recovery of the Peregrine Falcon (*Falco peregrinus*) in eastern North America is a great conservation success, but the largely new urban population that it has produced has received remarkably little study. Satellite telemetry, detailed monitoring of active nests, and a review of archived nesting data since the resumption of breeding in the east were used to characterize aspects of the ecology of this rebuilding population.

The accuracy of small satellite transmitters was confirmed to be appropriate for tracking long-distance movements, and they were used to compare the dispersal and migration of 34 Peregrine Falcons. Adults from Alberta migrated farther than juveniles from eastern North America. Among the juveniles, those raised at natural nest sites or in rural habitat departed earlier, while males were much more likely to migrate long distances than females. Siblings varied considerably in their migratory strategies, and the one juvenile tracked over multiple years adapted his behaviour annually, suggesting that there are many factors involved in determining migratory movements in Peregrine Falcons, and that their relative importance may change with time.

In Ontario, the Peregrine Falcon population has grown to a record size, initially due to an intense captive-breeding and release effort, and more recently to considerable immigration from adjacent states. This influx resulted in a substantial dilution of the original *F.p. anatum* gene pool, in part because *anatum* juveniles appear to have been recruited to the breeding population at a lower rate. The shift was also facilitated by a small number of immigrant adults producing a disproportionate percentage of the offspring in southern Ontario.

In southern Ontario, nearly all nests have been on buildings in cities, reflecting the dramatic expansion of Peregrine Falcons into urban habitat throughout eastern North America. Pooling data from southern Ontario, Quebec, Massachusetts, Pennsylvania, and New Jersey revealed that productivity varied

considerably by region, but overall was similar at urban and rural sites. Within urban habitat, productivity was greater on buildings than on bridges and highest in nest boxes on covered ledges. While adults showed a bias toward nest sites facing between south and east, this did not translate directly into higher productivity, reflecting the complex variety of factors that influence nesting success. While building and vehicle collisions account for significant mortality among urban juveniles, human assistance through provision of nest boxes and rescues of grounded fledglings may offset these risks.

## RÉSUMÉ

Le rétablissement du Faucon pèlerin (*Falco peregrinus*) dans l'est de l'Amérique du Nord est un grand succès de conservation, mais la nouvelle population n'est pas bien connue. La télémétrie satellite, l'observation détaillée de nids en Ontario, et une analyse des données concernant les nids depuis le recommencement de la reproduction dans l'est de l'Amérique du Nord ont été utilisés pour caractériser des aspects de l'écologie de la population.

L'exactitude des petits émetteurs satellites pour la documentation des grands mouvements a été vérifiée, et ils ont été utilisés afin de comparer la dispersion et la migration de 34 faucons pèlerins. Des adultes de l'Alberta ont entrepris des migrations plus longues que des juvéniles de l'est de l'Amérique du Nord. Parmi les juvéniles, ceux des nids naturels ou des sites ruraux sont partis plus tôt, et les mâles avaient tendance à se déplacer sur de plus grandes distances. Les frères et sœurs ont démontré des stratégies plutôt différentes concernant la migration, et le seul juvénile suivi pendant plusieurs années a changé sa stratégie à chaque fois, suggérant que plusieurs variables ont de l'influence sur le comportement migratoire des faucons pèlerins, et que l'importance relative de ces facteurs peut changer progressivement.

En Ontario, la population du faucon pèlerin s'est agrandie à un niveau record, grâce à un programme vaste d'élevage en captivité, et plus récemment à l'immigration des individus des états contigus. L'arrivée de plusieurs adultes américains a causé une dilution de la composition génétique de la population qui était à l'origine entièrement de la sous-espèce *F.p. anatum*. C'était en partie parce que les juvéniles *anatum* avaient moins de succès à survivre à se reproduire; aussi, une minorité des adultes ont produit une majorité de la progéniture au sud de l'Ontario, et ils venaient presque tous des États-Unis.

Dans le sud de l'Ontario, presque tous les nids ont été situés sur des gratte-ciels, typique de l'expansion des faucons pèlerins dans les villes dans l'est de

l'Amérique du Nord. Analysant les données du sud de l'Ontario, Québec, Massachusetts, Pennsylvania, et New Jersey, il est évident que la productivité a varié par région, mais a été comparable entre les sites urbains et ruraux. En ville, la productivité était plus élevée sur les bâtiments que les ponts, et le plus élevé dans les nichoirs placés sur les rebords recouverts. Les adultes ont préféré les sites exposés au sud, sud-est, ou est, mais cette préférence n'a pas directement affecté leur productivité, reflétant la variabilité complexe des facteurs influençant le succès de reproduction. Les collisions avec les bâtiments et véhicules sont des causes importantes de mortalité parmi les juvéniles urbains, mais l'assistance humaine par la provision de nichoirs et les secours d'oisillons fondés peut décaler ces risques.

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## PREFACE AND STATEMENT OF ORIGINALITY

This thesis consists of five major chapters, all of which except the introductory literature review have been or will be submitted for publication in peer-reviewed journals. Since the thesis is manuscript-based, scientific names are provided in each chapter as appropriate, and some introductory material and methodology is repeated in two or more sections. However, to minimize duplication, a single literature cited section has been compiled.

Note that throughout this thesis, the term “eastern North America” is used to refer to Ontario, Quebec, Pennsylvania, New Jersey, and Massachusetts. While the original intent was to assess peregrines over a more geographically complete area, inconsistencies with data collection and the inability to negotiate data-sharing agreements with certain agencies resulted in the focus being restricted to a smaller subset of jurisdictions. However, with the exception of New York, these are the eastern provinces and states with the greatest number of urban Peregrine Falcons, and therefore can be expected to present a representative overview of the population as a whole.

The research comprising this thesis provides several original contributions:

- 1) This is the first study to investigate the movements of urban Peregrine Falcons, which have come to dominate the eastern population, but have yet to be documented in any detail.
- 2) This study is the first to use satellite telemetry to compare the migration patterns of captive-bred and wild-raised birds.
- 3) This study includes the first attempt to describe nest site preferences of urban Peregrine Falcons, and is one of few to evaluate their relative nesting success in different settings.

- 4) This is the first study to describe the extent to which management efforts such as the rescue of fledglings and the provision of nest boxes and trays affect the productivity and survival of peregrines.
- 5) This is one of few studies to evaluate the accuracy of satellite transmitters, and the first to assess variability over time and latitude.
- 6) This is the first study to evaluate the success of the Canadian *anatum* peregrine recovery program from the perspective of assessing the relative productivity of breeders and changes to the collective pedigree of a breeding population.

Collectively, this research provides a greater understanding of eastern peregrines, which can be applied to improving future management of the population.

## CONTRIBUTIONS OF COAUTHORS

This thesis includes four manuscripts that have been or will be submitted to refereed journals for publication. For all papers I am listed as the first author, having been solely responsible for the analysis of data and preparation of the manuscript; in all cases I was also directly involved in some to all of the data collection. Also for all papers, D.M. Bird is listed as the second author, in recognition of his support and assistance with the development of each paper as my thesis advisor.

G.L. Holroyd and M. Nash are co-authors on the first two papers, Chapter 3 (*Geographic and temporal variability in the accuracy of small satellite transmitters*) and Chapter 5 (*Dispersal and migration of juvenile Peregrine Falcons in eastern North America*). Holroyd initiated the satellite telemetry research program on peregrines in Alberta, upon which was based the eastern expansion of the project that supplied the bulk of my data. Nash was responsible for the initiative to expand this program into the east, and especially for coordinating the fundraising and logistics required to bring it to fruition.

T. Armstrong is a co-author on the third paper, Chapter 7 (*Origin, growth, and composition of the recovering Peregrine Falcon population in Ontario*). As the coordinator of the Ontario peregrine recovery program, Armstrong has played an instrumental role in the monitoring of the population, and compilation of much of the data used in the analysis.

T. French, F.A. McMorris, D. Brauning, and K.E. Clark are co-authors on the final paper, Chapter 9 (*Productivity, mortality, and management of urban Peregrine Falcons in eastern North America*). They coordinate the peregrine monitoring efforts in Massachusetts (French), Pennsylvania (McMorris and Brauning), and New Jersey (Clark), and contributed detailed data from each state to permit for a more regional overview.

## 1 General introduction

### 1.1 Breeding and migration strategies of Peregrine Falcons and other raptors in urban environments

#### 1.1.1 Peregrine population history

The Peregrine Falcon (*Falco peregrinus*; hereafter peregrine) is among the most widely naturally distributed bird species in the world, being one of only four that currently occur naturally on all five continents (Temple 1988, Cade 2003). Within North America, three subspecies have been recognized, each with a distinct historical breeding range: *F. p. pealei* along the north Pacific coast, *F. p. tundrius* in the subarctic and arctic, and *F. p. anatum* across the remainder of the continent (Enderson *et al.* 1995). More recently though, analysis has suggested that the *tundrius* and *anatum* subspecies are genetically indistinct (Brown *et al.* 2007).

Records indicate that peregrines were always uncommon to rare throughout most of their North American range, with a total population of approximately 10,000 pairs. Of these, Hickey (1942) estimated at least 350 pairs in eastern North America, and Kiff (1988) considered fewer than 1,500 in total belonged to the *anatum* subspecies. However, historical estimates were based on much less thorough surveys than modern inventories, and therefore are likely to have underestimated the population (Kiff 1988).

Peregrine productivity plummeted in the 1950s, and by 1964 the species was considered extirpated in eastern North America south of the tundra (Berger *et al.* 1969). It was later discovered that a few remote pairs remained present beyond this date, but the continental population dropped to as low as 324 confirmed pairs in 1975 (Fyfe *et al.* 1976). The North American decline was primarily attributed to reproductive impairment caused by exposure to dichlorodiphenyldichloroethylene (DDE), the primary metabolite of the

organochlorine pesticide dichlorodiphenyltrichloroethane (DDT) (Risebrough and Peakall 1988). DDE causes eggshell thinning by inhibiting certain enzymes responsible for supplying the eggshell with calcium as it forms in the oviduct (Fyfe *et al.* 1988). Severe decline or extirpation was observed for almost all populations where eggshell thinning exceeded 17% (Peakall and Kiff 1988). Similar concerns were expressed for other raptors, and contributed to the banning of DDT in North America in 1972 (Hickey 1988), though it was later suggested that other contaminants, most notably dieldrin, may have also contributed significantly to the decline of the peregrine (Nisbet 1988).

Subsequent to the North American ban, Henny *et al.* (1982) reported that migratory peregrines accumulated DDE primarily at their wintering grounds in Central and South America, though levels were sufficiently high to be of reproductive concern for only a small minority of individuals. DDT remains in use across parts of Central and South America, and migrant peregrines staging or wintering there continued to accumulate toxic residues (Baril *et al.* 1990, Johnstone *et al.* 1996), as a consequence of the high toxin concentrations of certain prey species (Fyfe *et al.* 1990). By 1994 migrant peregrines in Texas had significantly lower DDE residues when compared with levels from the late 1970s and early 1980s (Henny *et al.* 1996). Nonetheless, the potential remains for both survival and productivity to be impaired for long-distance migrants that happen to overwinter in areas where prey species are contaminated by DDE.

Considerable research into raptor propagation techniques in the late 1960s and early 1970s led to the development of a captive-breeding program that resulted in the release of over 2500 peregrines to the wild by 1985 (Cade 1988). In 1970, the Canadian Wildlife Service established a captive population of *anatum* peregrines by collecting 12 nestlings from the southern Northwest Territories and Yukon, southern Alberta and Labrador (Fyfe 1976). These birds formed the basis of the breeding population established at Wainwright, Alberta, to which several more *anatum* individuals were added over time (Fyfe 1988). Meanwhile

the American breeding program, coordinated by Cornell University, adopted a different approach, in which *anatum* birds represented a minority of breeders, supplemented primarily by the other North American subspecies, as well as *F.p. brookei* and *F.p. peregrinus* from Europe and *F.p. cassini* from South America (Barclay and Cade 1983).

The first releases of captive-bred juveniles took place in 1974 (Barclay 1988), and the peregrine has since undergone a dramatic recovery through most of its historical range (Enderson *et al.* 1995). In 1999, the species was removed from the Endangered Species List in the U.S. (Ambrose and Eberly 2000), and the *anatum* subspecies was downlisted to threatened status in Canada (Johnstone 1999), then further to special concern in 2007 (COSEWIC 2007). In some areas including the Yukon Territory and Mackenzie Valley of the Northwest Territories, the *anatum* population has fully recovered (Rowell *et al.* 2003). Nevertheless, the population continues to be closely monitored in most of its range, and some historically occupied areas such as cliffs in eastern Ontario have yet to be re-colonized.

### *1.1.2 Peregrine ecology*

Peregrines have historically been considered to be relatively solitary, cliff-nesting raptors, generally preferring remote and inaccessible nest sites (Ratcliffe 1988). Habitat associations range from tropical forests to arctic tundra, but a common feature is the proximity of open areas for hunting prey (White *et al.* 2002). Deforestation has been cited as a factor in the decline of many bird species (e.g. Martin and Finch 1995, Pimm and Askins 1995), but peregrines may actually benefit from it, in that they prefer open areas for hunting, while urbanization provides additional benefits through the creation of novel nest sites (Ratcliffe 1988). Whereas some other urban-nesting raptors require remnant patches of natural habitat for hunting (Stout *et al.* 2006b), peregrines are adept at hunting within the urban environment (DeCandido and Allen 2006).

Prior to the population crash, the majority of historical nest sites in North America were on cliffs. Only beginning in the 1930s did the first pairs settle in cities, with just six locations documented by the 1950s, including Montreal, Philadelphia, and New York (Groskin 1952, Hall 1955, Herbert and Herbert 1965). The most notable of these was a site in Montreal at which a single female with a series of three mates produced 22 young between 1940 and 1952 (Cade and Bird 1990). Monitoring of early urban nesting attempts indicated that their success tended to be poor (Herbert and Herbert 1969). Despite that, an increasing number of captive-bred young were released in cities as the recovery program progressed, largely because the risk of predation was lower than at rural locations (Barclay 1988), especially with respect to Great Horned Owls (*Bubo virginianus*), considered to be the greatest natural threat to peregrines (Herbert and Herbert 1965). Also factoring into the decision was the larger prey base in cities, especially the abundance of Rock Pigeons (*Columba livia*), heavily favoured by peregrines (Cade and Bird 1990). Prey abundance is widely considered to be positively correlated with the density of breeding peregrines (Beebe 1960, Nelson and Myres 1976, Ratcliffe 1993), perhaps in part because adult hunting success is in the range of 10 to 40% (Roalkvam 1985).

During the first decade of releases in Canada, the survival of juveniles to independence was similar at urban (89%) and rural (88%) sites (Fyfe 1988). Already by 1985, the number of peregrines breeding in North American cities was higher than at any point historically (Kiff 1988). Since then, the growth of the eastern population has continued to be far greater in urban areas, to the point that the majority of peregrines in midwest and eastern North America are nesting in cities (Martell *et al.* 2000). In some areas, such as southern Ontario and Ohio, all regularly occupied territories are in urban habitat.

Early observations also suggested that productivity at urban nests was similar to that at rural sites, with respective averages of 1.7 and 1.9 young per nesting attempt (Cade and Bird 1990). However, the dynamics of the urban population

remain largely unexplored, and further study of lifetime reproductive success and factors affecting survival rates is needed for both habitats (White *et al.* 2002). Recent observations suggest that there is potential for higher productivity in cities. Redig and Tordoff (1994b) reported the first instance of five young fledged from a nest, at a site in East Chicago, Indiana in 1994. As of 2007, 28 clutches of five had hatched in midwest cities, including an average of four per year since 2003; at nine sites this has occurred at least twice (Tordoff *et al.* 1999, 2001-2005; Redig *et al.* 2006, 2007).

Though peregrines have a tendency to return to habitat similar to that in which they were raised (Holroyd and Banasch 1990), relatively few of the urban juveniles produced in the 1980s were subsequently documented nesting as adults, raising speculation that cities may be a population sink. It has also been suggested that by exploiting urban habitats, the peregrine population in eastern North America could grow to exceed historical levels (Cade *et al.* 1996). The demography of the midwest peregrine population has been well-documented and suggests that the latter scenario is more likely (Tordoff and Redig 1997). However, as no comparable efforts have been made in the east, it remains unknown whether the situation is similar to that in the midwest.

Within urban areas, Septon (2000) reported that as many as 74% of midwest territories remained occupied in winter, but only 3% of the individuals observed were juveniles. Anecdotal observations in the east agree that juveniles are scarce in winter, a somewhat surprising result given that the eastern population was historically not strongly migratory (Bollengier 1979). Since majority of peregrines released in the eastern United States were not from pure *anatum* stock, the eastern population is to some extent genetically distinct from the one that historically occupied this region (Temple 1988, Peakall 1990). As such, the migratory tendencies of the current population may differ considerably from historical patterns.

Despite significant increases to the peregrine population in much of North America, considerable resources remain allocated to promoting and monitoring its recovery, since in some regions numbers remain depressed (White *et al.* 2002). Already in 1985 it was estimated that more money had been spent on the recovery of the peregrine than on any other species (Kiff 1988), and additional expenses since then have been considerable. Arguments have been made more recently that funding for conservation should now be redirected to other species in more critical need of assistance (Restani and Marzluff 2002). Thus, it is important that any remaining conservation concerns relating to peregrines be pinpointed precisely to promote effective use of funds allocated to them.

### *1.1.3 Breeding requirements*

Food and shelter are basic needs largely responsible for limiting the distribution and abundance of most species (Bolen and Robinson 2003). For birds, the availability of suitable nest sites may also be a limiting factor, especially for those with specialized constraints. Peregrines fall into this category, as they require high ledges for nesting; they particularly favour the most prominent cliffs or other structures in an area (White 2006), reflecting the views of Hickey (1942) that traditionally occupied nest sites have characteristics that appeal strongly to all peregrines. Prey availability is often also a limiting factor for raptor populations (Newton 1998b). For example, at Langara Island, British Columbia where peregrines nest at unusually high densities, prey availability in the form of colonial seabirds is exceptionally high (Beebe 1960), showing a correlation between breeding density and prey supply also observed for peregrines elsewhere (Ratcliffe 1993).

The study of urban ecology has received increasing attention, highlighting the growing need to understand interactions of wildlife with human-dominated landscapes (Marzluff *et al.* 2001). Typically the expansion of urban areas results in loss of natural habitat and associated displacement of species that formerly occupied it, resulting in lower species richness (Marzluff *et al.* 1998). However,

in recent decades it has become apparent that a number of North American raptor species are thriving in urban environments, and in some cases have become more abundant in cities than in surrounding natural habitat. For example, the Red-shouldered Hawk (*Buteo lineatus*), long believed to require large woodlots for breeding (Crocoll 1994), has shifted to nest primarily in suburban areas in parts of Ohio and Kentucky, at an average distance of only 75 m from human residences (Dykstra *et al.* 2000). California populations of this species have shown higher productivity in cities than in rural areas (Bloom and McRary 1996), and similar results have been reported elsewhere in North America for Mississippi Kite (*Ictinia mississippiensis*; Parker 1996) and Eastern Screech-Owl (*Megascops asio*; Gehlbach 1996). Other raptors that have established substantial urban populations include Red-tailed Hawk (*B. jamaicensis*; Stout *et al.* 2006a), Cooper's Hawk (*Accipiter cooperii*; DeCandido 2005), Merlin (*F. columbarius*; Sodhi *et al.* 1992), and Burrowing Owl (*Athene culicularia*; Botelho and Arrowood 1996). Whether increasing urbanization has overall benefits for raptors is not yet clear. For example, while Cooper's Hawk has adapted to urban environments across much of North America (Rosenfield *et al.* 1996, Boal and Mannan 1998), the question remains whether such habitat acts as a source or a sink (Boal and Mannan 1999).

The urban environment includes many hazards that are rare or absent in natural settings. Most notably, buildings are a collision hazard, especially if constructed of reflective glass (Klem Jr. 1989). This hazard can be exacerbated by wind shear created through the artificial urban canyons formed by skyscrapers. Juveniles that become grounded as a result of their early flights may also be accidentally or intentionally harassed by people and/or their pets (Preston and Beane 1996). Low-flying juveniles are particularly vulnerable to collisions with vehicles. Power lines are also a concern, both through electrocution and direct impact (Dawson and Mannan 1995). Sweeney *et al.* (1997) found that collisions with vehicles, buildings, or power lines were responsible for 81% of injured peregrines brought to the Raptor Center at the University of Minnesota, while

Tordoff *et al.* (2000) reported that collisions with buildings or vehicles were the leading cause of mortality for peregrines in the midwest. The threat of poisoning is also a concern in some areas, especially where Rock Pigeons are targeted by control efforts, as the potential exists for toxins to be transferred to predators.

Conversely, raptors may benefit from settling in urban habitat. Although species richness in urban areas is typically lower than in natural surroundings, total biomass is often higher (Beissinger and Osborne 1982, Blair 1996, Marzluff *et al.* 2001). This is largely due to the high abundance of certain generalist species that thrive in human habitats, such as Rock Pigeon, European Starling (*Sturnus vulgaris*), House Sparrow (*Passer domesticus*), and Grey Squirrel (*Sciurus carolinensis*; Adams *et al.* 2006). Mortality in raptors often increases following dispersal, but Mannan *et al.* (2004) found a high rate of survival for Cooper's Hawks in Tucson, Arizona up to six months after fledging. They attributed this to the abundance of prey in the city, which may be of particular significance for juveniles, as they typically have lower hunting success than adults (Roalkvam 1985). In contrast, food is often a limiting factor in natural areas. One-quarter of deaths in a rural population of Red-tailed Hawks were determined to be a result of emaciation (Franson *et al.* 1996). The greater abundance of prey year-round in cities may also influence migration, as seasonal movements are generally stimulated by lack of food (Newton 2008). Given that there are considerable energetic costs to migration, as well as risks to health and survival associated with it, the existence of a stable food source that eliminates the need for migration may offer a considerable advantage to urban raptors.

For species that can adapt to nesting on buildings, cities offer an abundance of well-sheltered and protected nesting opportunities. These are often structurally superior to naturally occurring ledges on cliffs, providing a greater amount of flat surface area for nesting, and often having overhead cover. Additionally, such ledges are almost always inaccessible to mammalian predators, while some natural cliffs may not provide similar protection. Most of these features are

shared by bridges, though the availability of flat ledges varies considerably depending on architectural design.

Large cities may offer another advantage by virtue of their 'heat island' effect, with temperatures up to several degrees Celsius warmer than their surroundings (Bornstein 1968, Landsberg 1981). As cold temperatures have been implicated as a cause of nesting failure for raptors (Bradley *et al.* 1997), those individuals nesting in cities may have higher success, especially in particularly late or cold spring seasons. Another advantage may be the option to begin nesting earlier in the year, which may provide juveniles a longer period to acquire flight and hunting skills before dispersing or migrating in fall. This could also increase the chances of re-nesting successfully if a first attempt fails. Therefore, for species able to adapt to the threats associated with urban environments, city life offers a variety of advantages that may allow survival and productivity to equal or even surpass that in natural habitats.

#### *1.1.4 Migration ecology*

Migration is generally recognized as a seasonal movement, usually alternating between breeding and non-breeding areas and representing an adaptation to spatial and temporal variation in availability of resources (Dingle and Drake 2007). For most species, the key benefit of migration is easier access to food, and by extension, a greater likelihood of survival to the next breeding season (Sherry *et al.* 2005). However, it also may entail significant costs. Especially in the case of long-distance travels, the extra energy expenditure can be considerable, and may be particularly problematic for those species with limited opportunities to forage while migrating (Newton 2008). Long-distance migrants must also adapt to multiple ecosystems of varying suitability, each of which may feature different predators, prey, and sources of shelter (Bildstein 2006). Successful migration is dependent on being able to locate suitable habitat for breeding and wintering, timing departures and arrivals appropriately with respect

to availability of resources, and maintaining adequate physical strength throughout the journey (Newton 2008).

There is a continuum from species that are entirely migratory to others that are fully sedentary, with many occupying a middle ground where only some populations or individuals are migratory (Newton 2008). While migration may have evolved on multiple occasions, it is generally believed to have a genetic basis, and therefore variables such as the direction, distance, and timing of migration are considered heritable (Gauthreaux Jr. 1992, Rappole 1995, Berthold 2001). Many raptor species show differentiation in migratory strategies by age and sex (Mueller *et al.* 2000). Most commonly females migrate before males in fall and after them in spring (Bildstein 2006), but peregrines are among the few that tend to follow the reverse pattern (Hunt *et al.* 1975, Mearns 1982).

Environmental factors may also influence the development or inhibition of migratory behaviour in individuals. For example, since prey availability is a limiting factor for raptors, an increase in prey numbers during the non-breeding season could shift the costs and benefits of migration in favour of remaining sedentary. Such a change may also have an evolutionary aspect, in that individuals remaining on territory year-round are more likely to be able to claim prime nesting locations, and therefore may have greater productivity than migrants relegated to secondary habitat. This is reflected in the finding that most species migrate more rapidly on their return journey (Berthold 2001). Adults commonly migrate ahead of juveniles in fall, and in spring all species that have been studied also exhibit this pattern (Bildstein 2006). Adults often overwinter closer to their breeding grounds, permitting a quicker return (Mueller *et al.* 1977, Bildstein 2006). However, it has also been suggested that an earlier return to breeding grounds may be influenced by whether prey are less abundant en route than in the fall (O'Reilly and Wingfield 1995). Among raptors that are partial migrants, i.e. species in which fewer than 90% of individuals are migratory, juveniles may be more likely to disperse or migrate than adults, as they are

typically less able to compete successfully for limited food and shelter. Thus, sedentary juveniles of a partial migrant species may indicate a population that is below carrying capacity (Bildstein 2006).

Migratory strategies may adapt over time in response to changing availability of resources. For example, the prairie subspecies of Merlin (*F. c. richardsonii*) was historically a complete migrant, breeding in the boreal forest of western Canada and wintering primarily in Colorado and Wyoming (Warkentin *et al.* 2005). By the 1950s, substantial numbers were beginning to overwinter in Canadian cities, a change coinciding with the range expansion of House Sparrows and an increase in overwintering Cedar Waxwings (*Bombycilla cedrorum*) in response to the planting of fruiting ornamental shrubs (Oliphant and McTaggart 1977). Warkentin *et al.* (1990) suggested that there may be a genetic component to the determination of behaviour in this population of partial migrants, as the offspring of sedentary individuals tended to migrate less frequently.

Many raptors migrate in large flocks, annually following routes defined by major landscape features (Bildstein 2006), while others such as Osprey (*Pandion haliaetus*), Northern Harriers (*Circus cyaneus*), and peregrines show less hesitation in crossing large bodies of water and adopt more of a broad-front migration (Kerlinger 1985, Newton 1998a, Holroyd and Duxbury 1999, Bildstein 2006). More so than most other terrestrial birds, raptors take advantage of wind and air currents to help power their migration (Newton 2008). However, doing so also results in some degree of wind drift corresponding to prevailing winds, with juveniles especially likely to take advantage of this assistance. This behaviour is especially prevalent among soaring species such as buteos and vultures, but is evident to some extent even in species such as peregrines that have a more flapping flight (Bildstein 2006).

Diurnal migration is the norm for most raptors, as it is only during the day that warm thermals rise to enable efficient soaring. However, among species that

power their migration mostly through flapping flight, some nocturnal migration may occur (Bildstein 2006). Whereas many birds build up fat reserves before migration to power their flight, this increase is rarely substantial in raptors (Bildstein 2006). Peregrines in particular sustain their migration primarily through hunting along the way, often suspending travel at stopover sites rich in prey (Cochran 1975, Dekker 1980, Lank *et al.* 2003).

#### *1.1.5 Migration studies*

The study of migration has evolved considerably over time, aided by the development of new technology. Much of what is known about orientation and navigation has been learned from laboratory experiments involving pigeons and various passerines (Newton 2008). Such research has demonstrated strong directional preferences by migrants (Emlen and Emlen 1966), orientation by an internal magnetic compass (Wiltschko and Wiltschko 1972; Cochran *et al.* 2004), use of polarization patterns (Able 1993), and navigation by celestial compass (Sauer and Sauer 1960).

Displacement experiments have also been conducted to explore how birds respond to being moved off their usual migratory route. Most notably, Perdeck (1958, 1967) demonstrated heritability of migratory knowledge as well as homing ability in European Starlings by showing that displaced adults adjusted their trajectory to reach traditional wintering areas, while juveniles resumed travel in the same direction following displacement. Among the implications of these findings, reflected also in similar behaviour by a variety of other species, is that severe weather systems such as hurricanes may not cause adults to deviate from their ultimate destination, but juveniles may be more readily blown off course and end up far from traditional wintering grounds (Newton 2008).

For the most part, studies of migration in the wild have been observational rather than experimental. At their most basic, this involves visual counts at migratory hotspots (Newton 2008). This is particularly suitable for raptors, as they are

large, primarily diurnal migrants. Many species avoid crossing water bodies greater than 25 km in width, thus geographic bottlenecks occur where large numbers of migrants are concentrated between water and other physical features such as mountain ranges (Bildstein and Zalles 2005).

Peregrine migration has been studied in ever greater detail over the past several decades. As early as the 1960s some fidelity to migratory routes was recognized (White 2006). Records from raptor migration observatories show that the key areas for peregrine migration in North America include the mid-Atlantic coast south to Florida and the western coast of the Gulf of Mexico, with Assateague Island, Maryland and Padre Island, Texas being of particular significance as observation and banding sites (Enderson 1969b, Ward *et al.* 1988). Padre Island is especially important in spring, when it is the only site in North America where peregrines are known to concentrate regularly (Yates *et al.* 1988). The majority of records from these areas are of the *tundrius* subspecies, with only a few pertaining to individuals from the eastern *anatum* range. However, this pattern may simply reflect the banding effort on the breeding grounds, and the relative abundance of *tundrius* versus *anatum*; also, relatively little is known about movements during the spring migration of North American peregrines (Yates *et al.* 1988).

Until recently, leg bands provided the only opportunity to study the survival and movements of individual birds. Banding programs are often established at geographic bottlenecks or other sites where migrants are known to concentrate. Capturing individuals and affixing uniquely numbered bands creates the potential to recover these birds at distant locations, providing valuable information on individual movements. Despite the relatively low recovery rate for most species, banding data are the basis upon which most knowledge of migratory movements has been established (Newton 2008). A review of known peregrine band recoveries by Schmutz *et al.* (1991) showed that individuals from North America typically winter in Central or South America, with *tundrius* birds generally farther

south than *anatum* birds. However, the historical eastern *anatum* population was believed to be non-migratory or semi-migratory (Bollengier 1979), with recoveries of 70 adults or nestlings banded in the region prior to the DDT era including only one from south of the United States (Yates *et al.* 1988). Unfortunately banding analyses are hampered by low recovery rates; for example, of the raptors banded at Cape May between 1967 and 1993, only 1.5% have been reported again (Clark 1995). The introduction of coloured leg bands in 1973 was intended to address this issue (Ward 1976). Even so, fewer than 10% of individuals have been reported in comprehensive reviews (Schmutz *et al.* 1991, Clark 1995); the most recent summary indicates that of 36,569 peregrines banded between 1955 and 2000, 7% were subsequently recovered (Bildstein 2006). Furthermore, most birds are often reported only once, making it impossible to draw conclusions about the timing and routes of migration.

The advent of radio telemetry provided an opportunity to follow the movements of marked individuals in detail, without the need to recapture them. However, substantial drawbacks include the large investment of time required to relocate each individual, and the risk of losing track of a migrant if it moves too quickly and flies beyond the range of receivers (Hobson and Norris 2008). While some studies have successfully tracked migrants through use of aircraft and ground vehicles, radio telemetry is on the whole better suited to documenting local rather than migratory movements (Garton *et al.* 2001). Nonetheless, radio telemetry advanced the knowledge of peregrine migration significantly. Cochran (1975) followed a juvenile male from Wisconsin to Mexico over a period of 16 days in the fall of 1974, providing the first detailed description of migratory behaviour for this species. Subsequent radio telemetry work illustrated that this technology can be used effectively at a local level to identify areas of conservation importance by documenting habitat usage patterns (Hunt and Ward 1988).

Satellite telemetry represents a substantial advance over radio telemetry in that signals from the transmitter are automatically collected by orbiting satellites and

reported to researchers electronically, thereby eliminating the need to track individuals in person (Newton 2008). Thus, the position of an individual can be recorded at regular intervals over a period of up to a few years. This approach was first developed for mammals, and adapted to raptors in 1984 when transmitters became light enough for Bald Eagles (*Haliaeetus leucocephalus*) to wear; since then at least 26 other raptor species have been studied in this manner (Bildstein 2006). However, as transmitter weight should be limited to 3-4% of the individual's body weight, the technique still remains unavailable for smaller species (Newton 2008).

By the early 1990s though, transmitter weight had been reduced sufficiently for use on peregrines. To date, three major studies of North American peregrines have been published based on satellite telemetry. Fuller *et al.* (1998) studied 61 adult *tundrius* individuals, and described their wintering areas, rates of travel, and typical routes. Britten (1998) documented the movements of 42 *anatum* females (27 adult and 15 juvenile) from western North America. McGrady *et al.* (2002) tracked 12 *tundrius* adults from their wintering grounds in Mexico to their breeding territories in the Arctic. None of these studies addressed either the eastern peregrine population, or the growing urban population, and they have provided only minimal documentation of the movements of juveniles.

Most recently, the analysis of stable isotopes has been introduced as a means of obtaining data on the movements of individuals (Hobson and Norris 2008). By determining the relative abundance of certain isotopes in fixed tissues, such as feathers, it is possible to determine a geographic range in which those tissues were grown by comparing them with global distribution patterns of the isotopes in question (Wassenaar 2008). Although inexpensive, the geographic resolution may be low unless multiple isotopes are combined, and the technique is still new enough that reference maps are as yet imperfect and the influence of physiological variation among species on the results is not yet well enough understood to ensure accurate interpretation of all results (Hobson and Norris

2008). For raptors, the technique remains somewhat problematic, as some results have shown rather improbable movements (Hobson 2008). An attempt by Lott and Smith (2006) to develop a reference base specifically for raptors suggests that they may accumulate or retain hydrogen isotopes somewhat differently than passerines, and this needs to be factored into any analyses. The successful use of stable isotope analysis for the study of migration is dependent on further development and evaluation of isotope mapping, with species-specific calibration as necessary to verify accuracy (Bowen and West 2008).

## **1.2 Research rationale**

The peregrine has been the subject of intense and expensive population recovery efforts spanning the past several decades. As a result, the species has been successfully reintroduced to eastern North America, with breeding numbers in some states and provinces now greater than ever before. However, the ecology of this re-established population remains poorly understood, and especially little is known about the life history of juvenile peregrines once they have gained independence.

Despite the hundreds of peregrines now breeding in eastern North America, knowledge of their survival rates and factors influencing their breeding success remains limited. Of particular interest are data pertaining to urban-nesting peregrines, which historically were a rarity, but have come to dominate the re-established population. The progress of peregrine restoration in the midwest region has been reported since 1986 by the Raptor Center at the University of Minnesota, through annual summaries of nesting attempts and periodic assessment of population trends. No comparable effort has been made for eastern North America, and it is unknown to what extent characteristics of the midwest population are applicable to the eastern population. A better understanding of these matters would permit more accurate predictions of population trends and may identify potential issues to target, should the population suffer another severe decline.

Migration is an important part of the life history of many birds. Previous peregrine migration studies using satellite telemetry have focused largely on western birds, and primarily on adult females. Research in the east has been limited mostly to individuals from the Arctic breeding population, observed while migrating through eastern North America. However, the breeding population in eastern North America is particularly diverse as a consequence of the several subspecies that contributed to the captive-breeding program, and may therefore differ considerably in its migratory characteristics. Satellite telemetry offers a unique opportunity to link the breeding and wintering sites of multiple individuals, as well as documenting the routes they follow on migration.

Although the eastern peregrine population has grown significantly since recovery efforts began in the 1970s, the species remains the subject of ongoing management in much of the region. Whether such efforts remain warranted should be evaluated, in light of the limited pool of resources available to address the needs of all species at risk. Any funds and time that are dedicated toward peregrines should be spent as efficiently as possible, which requires a solid understanding of the preferences of nesting peregrines and the forms of assistance that contribute the greatest to improving their survival and reproductive success.

A need therefore exists to assess the breeding and migration biology of eastern peregrines, not only to support their continued successful management, but also to identify approaches that could be applied to the recovery of other species at risk. Data on nesting attempts have been collected by volunteers and/or government agencies in several eastern provinces and states, providing an opportunity to assess factors affecting nest site selection and reproductive success, as well as causes of mortality. An expansion of both the geographic and demographic scope of telemetry research is required to begin understanding the movements of the eastern peregrine population and the tendencies of juveniles in comparison with adults.

### **1.3 Research objectives and hypotheses**

The eastern peregrine population has undergone great changes with respect to distribution, abundance, and ecology as a result of population recovery efforts, but its composition and dynamics remain rather poorly understood. My research was therefore concentrated around three main objectives: 1) documenting the dispersal and migration patterns of juvenile peregrines from eastern North America; 2) describing the recovery of peregrines in Ontario as a case study of the eastern population; and 3) evaluating factors influencing urban nest site selection and reproductive success.

#### *1.3.1 Peregrine dispersal and migration*

The first objective was to track and summarize the movements of marked peregrines. The primary focus was on juveniles from eastern North America, as their dispersal and migration had not previously been documented. To provide some basis for comparison, a smaller number of adults from western Canada were also included in the study.

Juveniles were expected to be migratory, as few are seen near eastern breeding sites in winter. Conversely, many adult peregrines in eastern North America are known to occupy their breeding territory throughout the year. Those adults that do migrate are expected to migrate more rapidly and directly than juveniles, due to their previous experience. Spring migration was expected to be more rapid and direct than fall migration for all individuals, as returning to breeding grounds early enough to claim a preferred nest site and mate significantly improves the potential for high reproductive success.

Peregrines from rural sites were expected to be more likely to migrate than those from urban locations, as prey availability tends to vary seasonally much more so than in cities where key prey species are mostly non-migratory. However, no difference was expected between captive-bred and wild-raised juveniles, as

adults do not normally accompany their offspring on migration, and therefore their presence or absence should have no bearing on migratory behaviour.

These hypotheses were investigated using satellite telemetry to document the movements of individual peregrines. A tangential objective was to evaluate the accuracy of satellite telemetry data and identify its benefits and limitations with respect to documenting migration.

### *1.3.2 Recovery of the Ontario peregrine population*

The second main objective was to describe the recovery of the Ontario peregrine population since breeding resumed in the wild in 1991. Historically Ontario supported only a small cliff-nesting population, but now a substantial new urban population has developed, as it has in Quebec and several eastern states. However, Ontario differs in that all captive-bred peregrines released in the province were of pure *F.p. anatum* stock, but by virtue of its location, it has received many immigrants from American states where most peregrines released were of mixed genetic lineage, involving *F.p. pealei*, *F.p. peregrinus*, and *F.p. tundrius*. Ontario was therefore selected for a case study of population recovery as it not only provided an opportunity to compare the growth of populations in rural and urban habitats, but also to explore changes in their genetic heritage over time, with the dominance of *anatum* individuals expected to decline over time as immigrants diluted the gene pool. The age at first breeding and average age of breeders were both expected to increase over time as more adults became available and prime territories became saturated in Ontario.

### *1.3.3 Urban nest-site selection and success*

The third objective was to identify factors influencing urban nesting success. Especially in urban areas, property managers and/or local biologists are often called upon to encourage peregrines to nest in certain areas, or to lure them away from unsuitable sites. Currently most such decisions are based on

educated guesses rooted in personal experience, but these may not necessarily reflect the actual needs or preferences of peregrines.

To identify priorities for future management efforts, the success of nesting attempts in eastern cities over the past quarter-century was evaluated with respect to a number of site characteristics. Nest site selection was hypothesized to be non-random, in that the choice of a location was likely related to the presence/absence or quality of various site attributes including ledge height, orientation, substrate, extent of shelter provided, and proximity to a major water body. It was expected that optimal nest sites result in greater productivity, as measured by the number of young fledged per nesting attempt. Some attributes were expected to be particularly conducive to success, such as the presence of overhead shelter from rain and snow, and east or southeast orientation providing exposure to morning sun and protection from afternoon heat.

The importance of human assistance to the recovery of the eastern peregrine population was also explored, as it has gone far beyond simply releasing captive-bred young. In many cities volunteers rescue fledglings that collide with buildings or otherwise come to the ground, an undertaking that may have a significant impact on both individual survival and the population growth rate. Additionally, the installation of nest trays and boxes may improve reproductive success through the provision of overhead cover and gravel, which is an ideal substrate for eggs. However, these urban advantages may be somewhat offset by additional sources of mortality, most notably collisions with buildings and vehicles. The known causes of death were therefore compiled for a subset of the eastern population to quantify the relative importance of various causes of mortality.

## **Connecting statement 1: Satellite telemetry as a method to Investigate dispersal and migration**

Banding programs and seasonal documentation of raptor numbers in migration at a number of key locations have yielded a basic framework of knowledge about peregrine movements. However, most such records provide the location of an individual at only a single point in time and space, and therefore do not generate sufficient data to determine the timing, rate, or specific routes of migration. Satellite telemetry has great potential to address these gaps in knowledge, but this technology also has limitations, and these need to be identified and respected to ensure the appropriate interpretation of data.

This manuscript is being submitted to the Journal of Field Ornithology, with co-authors D.M. Bird, M. Nash, and G.L. Holroyd.

## **2 Geographic and temporal variability in the accuracy of small satellite transmitters**

### **2.1 Abstract**

Satellite telemetry is being used increasingly in wildlife research, especially as the size of Platform Transmitter Terminals (PTTs) continues to be reduced. Limitations of the technology must be understood for data to be used accurately. In particular, the error associated with location estimates must be factored into the interpretation of results. We deployed 36 PTTs on Peregrine Falcons in Alberta and eastern North America between 1997 and 2005. Three models were used: 30 g and 20 g battery-powered PTTs and 18 g solar-powered PTTs. We received 15,505 location estimates during the study, 17% of which were considered to be of good quality (Argos location classes 1, 2, 3). The frequency of good-quality reports was negatively correlated with time elapsed since deployment of the PTT, and was generally higher at northern latitudes, though declining again north of 50°N. Solar-powered PTTs generated a significantly higher frequency of good-quality records. A subset of 387 data points from stationary PTTs was explored to estimate the error distance associated with each of the seven defined Argos location classes. Results generally agreed with published specifications, but even the highest location class was found to occasionally have errors as great as 33 km, and therefore single data points should be interpreted with caution. For both battery-powered and solar-powered transmitters, accuracy did not differ significantly between class A and class 0 records. However, 95% of class 1-3 records were within 3.26 km, and 68% within 1.31 km, suggesting that a moderate level of accuracy is possible if selectively using these points. For studies of a larger scale, such as the documentation of long-distance migration, the errors typically associated with lower quality location classes are relatively minor, therefore there is little risk in using class 0 and A data, and even class B data may be valuable. Within all Argos location classes, the mean accuracy was greater with solar-powered PTTs.

## 2.2 Introduction

Knowledge of wildlife movements expanded greatly with the development of radio telemetry, but such studies have limited practicality over large distances. The advent of satellite telemetry in the 1970s permitted researchers to begin remotely tracking the movements of individuals regardless of their pattern of movement (Kenward 2001). Research guidelines generally limit birds to carrying at most 5% of their body weight (Meyburg and Fuller 2007), therefore it was not until somewhat lighter platform transmitter terminals (PTTs) were developed in the 1980s that even the largest raptors and waterbirds could be studied (Jouventin and Weimerskirch 1990, Higuchi *et al.* 1996, Ely *et al.* 1997). As technology continued to permit PTT size to be reduced, species as small as the Peregrine Falcon (*Falco peregrinus*) began to be studied in the 1990s (Fuller *et al.* 1995).

Despite its advantages, satellite telemetry also has limitations, most notably with respect to the accuracy of locations, and it is important that these be assessed and documented. Errors in location estimation are a consequence of the manner by which data are received by satellites and processed by Argos (Service Argos, Largo, Maryland, USA). A number of previous studies have evaluated the accuracy of larger PTTs weighing 80 grams or more, with results generally indicating actual error rates greater than those specified by Argos (Fancy *et al.* 1988, Keating *et al.* 1991, Mate *et al.* 1997, Brothers *et al.* 1998). Smaller PTTs are expected to be less accurate on average, as they typically have lower power and therefore succeed less frequently in transmitting multiple signals to satellites. Britten *et al.* (1999) evaluated 30 g PTTs on Peregrine Falcons between 1993 and 1995, concluding that they had considerable error, and were not recommended for research requiring an accuracy of better than 35 km.

Since the review by Britten *et al.* (1999), the size of the smallest PTTs has continued to decrease. We compared battery-powered 30 g and 20 g PTTs and solar-powered 18 g PTTs, evaluating the accuracy of data by using stationary

PTTs. Additionally, we assessed these three PTT models with respect to the frequency of good-quality signals reported by each, in relation to their lifespan, season, and latitudinal position.

### **2.3 Methods**

For a study on the dispersal and migration of Peregrine Falcons (*Falco peregrinus*; see Chapter 5) we attached PTTs to 27 juveniles and seven adults between 1997 and 2005. We primarily targeted juveniles from the lower Great Lakes region (Ontario, Quebec, New York, and Pennsylvania), but also included seven adults from Alberta. Most of the juveniles were equipped with PTTs after being retrieved from the ground uninjured, or following brief periods of rehabilitation for minor injuries. We fitted another five juveniles with PTTs prior to fledging, around 32 days of age, and used mist nets or bow nets to trap the remaining birds. PTTs were deployed between May and October each year, with the majority applied in June and July.

All PTTs were manufactured by Microwave Telemetry (Landover, Maryland, USA). We compared a 30 g battery-powered model ( $n = 14$ ), 20 g battery-powered model ( $n = 11$ ), and 18 g solar-powered model ( $n = 11$ ). All PTTs were programmed to be on for 8-10 hours at a time, with duty cycles of one active period every 3-10 days for battery-powered units, and every 1-3 days for solar-powered units.

We attached PTTs to each bird as a backpack, using a harness of either Teflon ribbon ( $n = 11$ ; Bally Ribbon Mills, Bally, Pennsylvania, USA; Fuller *et al.* 1995), or neoprene ( $n = 25$ ; Britten 1998). The fit of each harness was checked, and if necessary adjusted, at several points during the 30-45 minute attachment procedure. We observed each bird following release, and in one case in 1998 recaptured a juvenile to adjust the fit of the harness, but otherwise noticed the birds having no discomfort or difficulties in adjusting to flight with the transmitter.

Each PTT typically emits a signal once per minute, which is received by one of the Argos-affiliated National Oceanic and Atmospheric Administration (NOAA) polar-orbiting satellites when it is within range. At least two messages are required for the satellite to estimate a location, and four or more are needed for the estimate to be considered accurate (Argos 2007). The relative distance between the PTT and the satellite changes with each transmission, causing the frequency of the received signal to vary. Argos uses Doppler analysis to interpret these shifts in frequency and estimate the single location from which the signals were emitted (Fancy *et al.* 1988, Argos 2007). Regardless of the number of messages received, each location estimate includes a second location that is symmetrical to the first, on the opposite side of the satellite's ground track. Argos determines the more probable coordinates with approximately 95% accuracy by comparing them with previous locations, transmitter velocity, and the rotation of the earth (Harris *et al.* 1990).

We received data from Argos through the Automated Distribution System (Argos 2007), and transferred records to an Excel spreadsheet, where duplicate entries were eliminated. We also confirmed the plausibility of all points by calculating the rate of travel between points, as recommended by Britten *et al.* (1999). In the few cases where ambiguity between two options could not be resolved beyond any doubt, the data point was discarded.

Each data point is assigned a location class (LC) by Argos, reflecting its estimated accuracy (Table 2-1). Errors are assumed to be bivariate normal and equal along both the x and y axes. The straight line distance is therefore greater, and is calculated according to the bivariate normal distribution (Keating *et al.* 1991). For each PTT, we calculated the percentage of locations classified as good (LC 1,2,3) and compared these over time of year, months elapsed since deployment, latitude, and PTT model.

Table 2-1. Location classes as defined by Argos (adapted from Keating *et al.* 1991 and Argos 2007)

LC	Quality	Estimated accuracy (m) for 68% of locations (univariate / bivariate)	Number of messages used to calculate location
3	Good	<150 / 226	4 or more
2	Good	150-350 / 226-528	4 or more
1	Good	350-1000 / 528-1510	4 or more
0	Adequate	>1000 / 1510	4 or more
A	Adequate	No estimate of accuracy	3
B	Poor	No estimate of accuracy	2
Z	Poor	Invalid location	n/a (location rejected)

### 2.3.1 Stationary transmitters

One 30 g transmitter was intentionally left to broadcast from a stationary position in Alberta for two months in fall 1999 to experimentally test the accuracy of data. An additional six transmitters provided data from stationary locations in Ontario ( $n = 5$ ) and Maryland ( $n = 1$ ) for variable periods of time as a result of bird mortalities. We calculated the distance between each reported location and the known location; in the case of three transmitters for which the exact location could not be found, we estimated it as the centroid of all class 2 and 3 reports received following mortality.

All statistical analyses were conducted using SPSS 9.0 (SPSS Institute, 1998, Chicago IL). Kruskal-Wallis and Mann-Whitney tests were used to compare distributions, while Spearman's Rho statistic was used to explore correlations among independent variables (Zar 1999).

## 2.4 Results

The 36 PTTs generated a total of 15,505 records. The frequency of good-quality signals ranged from 7% to 42% for individual PTTs. Overall, good-quality signals accounted for 17% of all points, LC 0 for 30%, LC A for 12%, and poor quality classes for 41% (Figure 2-1). The frequency of LC 0, 1, and 2 was above

average for the solar-powered PTTs and below average for the two battery-powered models, while the reverse was the case for LC A, B, and Z. LC 3 reports were rare for all PTTs, exceeding 3% for only two units, and averaging 1.2% or less per model.

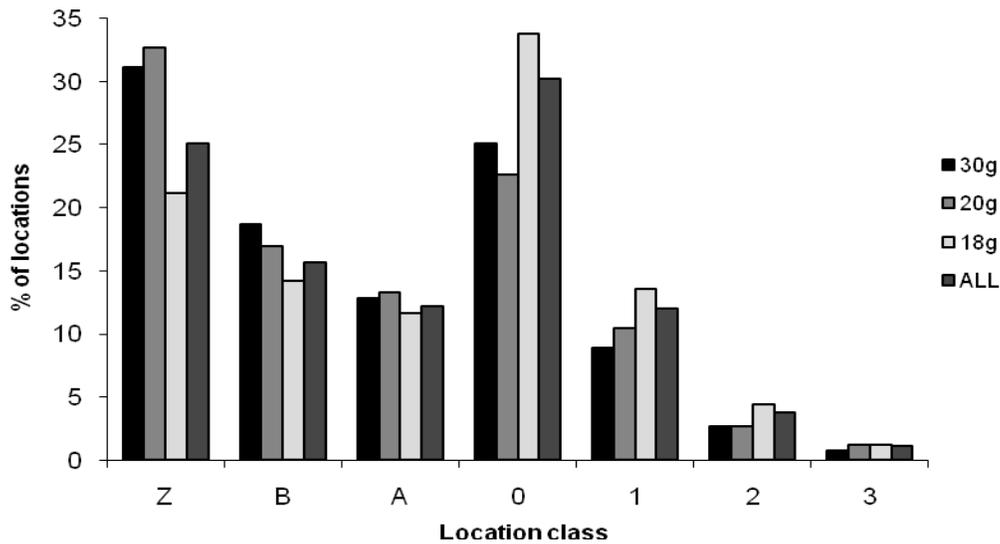


Figure 2-1. Frequency of Argos location classes reported by each PTT model

#### 2.4.1 Variation over time

Pairwise correlations among time, Julian date, and days elapsed since transmitter deployment were all low (Spearman's Rho < 0.25), therefore accuracy was assessed independently for each of these potential influences.

The frequency of good-quality signals varied seasonally, generally peaking from August through November, declining through winter to a low point in April, and then rebounding thereafter (Figure 2-2a). Seasonality was less evident when also including classes 0 and A in the analysis (Figure 2-2b). The solar-powered transmitters provided the most consistent results, with 58% to 68% of data among the top five classes each month, whereas the 30 g and 20 g battery-powered transmitters fluctuated over ranges of 22% and 32%, respectively, but always remained lower than the solar-powered units.

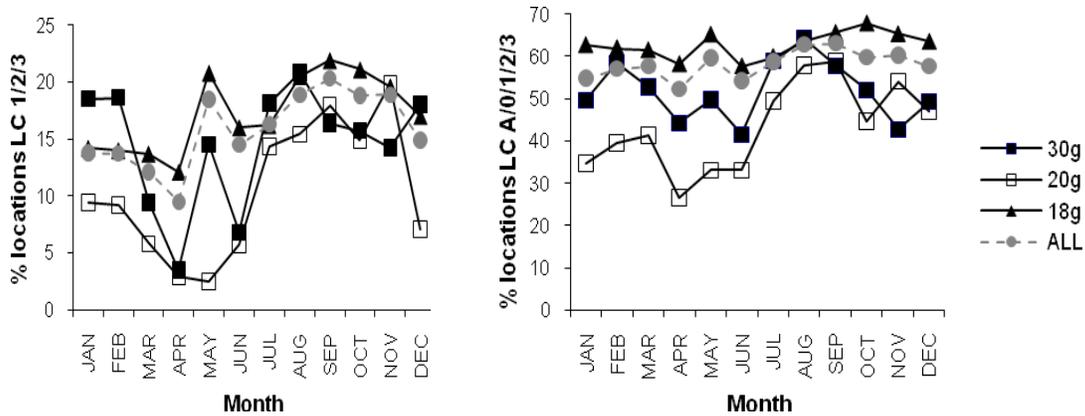


Figure 2-2. Monthly frequency of a) good; and b) good and adequate quality locations

There was a significant and fairly steady decline over time in the frequency of good-quality signals for both 30 g (-1.2% / month,  $r^2 = 0.76$ ,  $F_{1,15} = 48.1$ ,  $P < 0.001$ ) and 20 g (-1.4% / month,  $r^2 = 0.80$ ,  $F_{1,12} = 49.3$ ,  $P < 0.001$ ) battery-powered transmitters (Figure 2-3). The frequency of good-quality records was below 10% by the fifth month for 20 g PTTs, and by the eighth month for 30 g PTTs. The frequency of good-quality signals from the 18 g solar-powered transmitters showed no trend over time ( $r^2 = 0.4\%$ ,  $F_{1,21} = 0.87$ ,  $P = 0.77$ ). Beyond six months, the solar-powered PTTs consistently outperformed both battery-powered models.

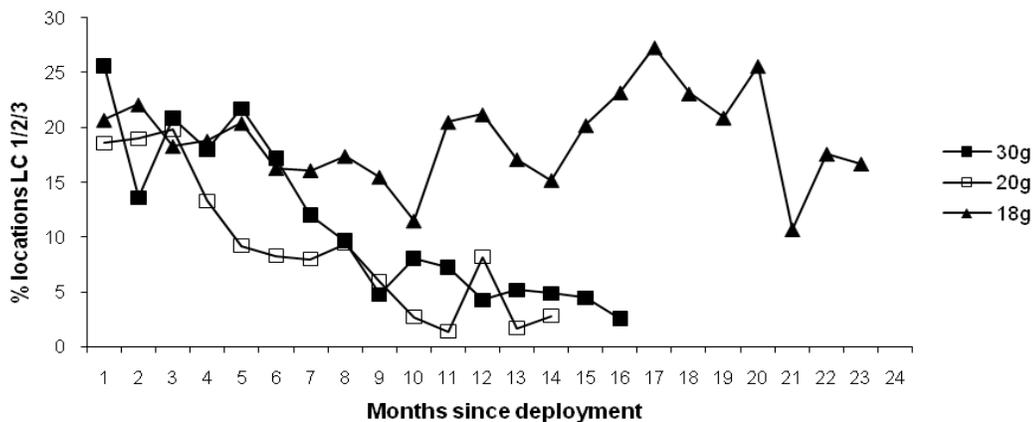


Figure 2-3. Frequency of good-quality locations over time by PTT model, limited to periods with at least 50 data transmissions per month

### 2.4.2 Variation with latitude

The majority of data were received from PTTs between 40° and 49° N (54%) or between 30° and 39° N (30%). Locations south of 30°N accounted for less than 7% of reports, and over two-thirds of these were from individuals wintering between 10° and 20°N. All of the individuals carrying solar-powered PTTs remained between 10° and 50°N.

Overall the distribution of location classes differed significantly by latitude ( $\chi^2_{42} = 442.5, P < 0.001$ ). For battery-powered PTTs, good-quality locations were most frequent between 40° and 50°N, and significantly lower elsewhere (Figure 2-4). The frequency of good-quality locations did not differ significantly by latitude for solar-powered PTTs. LC Z reports were more frequent than expected by chance north of 50°N and south of 20°N, while good-quality reports were more frequent than expected only between 20°N and 50°N.

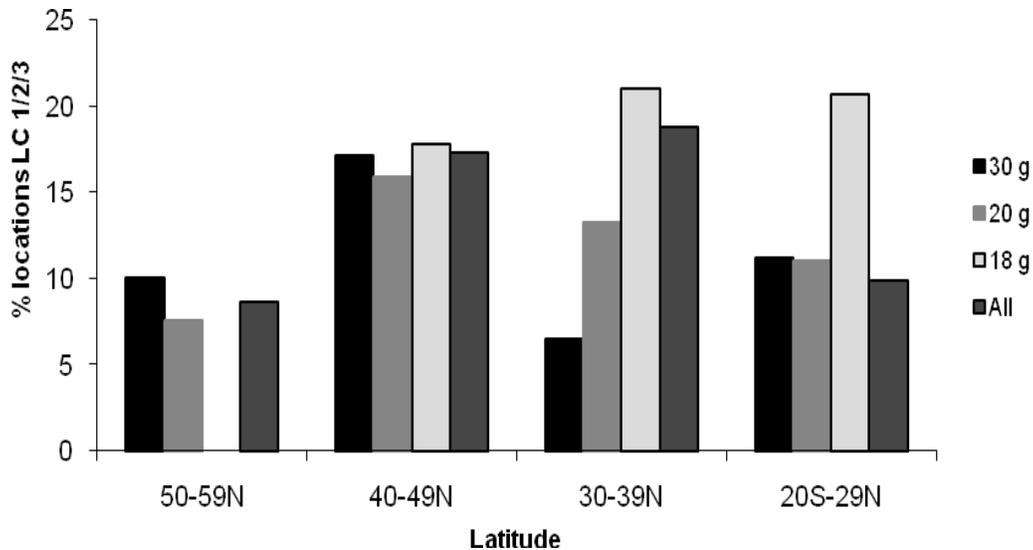


Figure 2-4. Frequency of good-quality locations by latitude; note that no 18 g transmitters operated north of 50°N. Data from south of 30°N are grouped due to small sample size.

### 2.4.3 Accuracy evaluation

Of 569 reports received from stationary transmitters, 197 were assigned LC Z, and for all but 15 of these, no location was estimated. Table 2-2 summarizes the error associated with each location class for the data from the seven stationary PTTs. Each LC had at least one report within 0.5 km of the true location, and one at least 4.0 km away from it. Location error differed across location classes (Kruskal-Wallis = 190.4,  $df = 6$ ,  $P < 0.001$ ). There was no difference in accuracy between LC 0 and LC A ( $Z = 0.83$ ,  $P = 0.40$ ), but both LC 0 ( $Z = 3.28$ ,  $P < 0.001$ ) and LC A ( $Z = 3.80$ ,  $P < 0.001$ ) were significantly less accurate than LC 1, LC B was significantly less accurate than LC A ( $Z = 7.20$ ,  $P < 0.001$ ), and LC Z was significantly less accurate than LC B ( $Z = 2.774$ ,  $P = 0.006$ ).

Table 2-2. Minimum, maximum, and mean error (km) between reported and actual locations for data from seven stationary PTTs

Location class	<i>n</i>	Minimum error	Maximum error			Mean error		
			100%	95%	68%	100%	95%	68%
Z	15	0.42	705.12	677.07	187.70	204.51	168.75	58.86
B	100	0.50	256.83	120.47	24.02	30.62	22.39	7.47
A	98	0.08	135.23	17.25	3.38	5.55	3.01	1.36
0	42	0.34	57.72	13.80	3.15	4.98	3.25	1.57
1	63	0.00	5.51	3.26	1.31	1.25	1.07	0.71
2	42	0.14	4.02	1.41	0.75	0.70	0.59	0.38
3	27	0.00	33.32	0.98	0.27	1.50	0.28	0.14

The maximum error of all points, as well as within one (68%) and two (95%) standard deviations, generally followed the  $Z > B > A > 0 > 1 > 2 > 3$  sequence outlined by Argos, except for class 3 at the 100% scale, due to one significant outlier. Mean error at each scale also generally followed this pattern, though at the 95% and 68% scales, class A locations were on average slightly closer to the true location than class 0 locations.

For 68% of data points, the longitudinal error was greater than the latitudinal error. On average, the longitudinal error was 109% greater than the latitudinal error, with the discrepancy greatest for class Z readings at 159%, and least for class A at 48%.

The accuracy of individual PTTs varied significantly (Kruskal-Wallis = 61.1, df = 6,  $P < 0.001$ ), with mean error distances ranging from  $7.4 \pm 2.3$  km for PTT 24863 to  $31.1 \pm 15.1$  km for PTT 5260, both 30 g battery-powered PTTs. Individual PTTs also showed varying departures from the expected pattern of accuracy (Table 2-3). Most notably, in three of seven cases, the mean error for LC A was less than half that of LC 0, and for PTT 15113, LC 1 had the lowest mean error, while LC 3 had a greater mean error than LCs A, 0, 1, and 2.

Table 2-3. Mean error (km) by location class for each stationary PTT

PTT	Z	n	B	n	A	n	0	n	1	n	2	n	3	n
5260	77.9	3	154.3	3	5.1	4	3.9	4	1.6	8	0.2	2		
15113	282.8	3	25.1	35	4.6	22	2.0	7	0.9	22	1.2	9	7.1	5
15114	320.4	1	20.8	8	1.4	12	1.2	3	0.8	5	0.6	2		
15117	223.6	4	20.6	18	1.7	19	3.8	4	1.5	9	0.7	10	0.6	3
24427	6.4	1	40.3	24	14.4	23	4.5	14	2.0	5	0.9	3		
24863	43.7	2	16.0	4	3.2	11	18.7	4	1.5	7	0.6	5	0.2	4
59782	677.1	1	19.4	8	1.0	7	3.8	6	1.1	7	0.4	11	0.2	15
ALL	204.5	15	30.6	100	5.5	98	5.0	42	1.2	63	0.7	42	1.5	27

The distance within one standard deviation of error (68%) ranged from 1.0 to 11.8 km. All PTT models reported errors of greater than 300 km at least once. As large outliers can strongly skew means, the three models were compared within two standard deviations of error (95%). Accuracy was found to differ significantly among them (Kruskal-Wallis = 12.62, df = 2,  $P = 0.002$ ), with the solar-powered PTTs reporting the smallest mean error of  $5.4 \pm 0.9$  km, while the battery-powered units had mean errors of  $6.4 \pm 2.0$  km (20 g) and  $8.2 \pm 1.2$  km (30 g).

## 2.5 Discussion

In general, our assessment of data accuracy reflects the hierarchy of location class quality outlined by Argos (2007). Our results confirmed that LCs 1-3 are significantly more accurate than lower classes. Therefore the frequency of LC 1-3 data can be used as an indicator of PTT accuracy, and data from these classes should be preferentially used for plotting locations. However, while the 68<sup>th</sup> percentile error associated with LC 1 was 13% lower than specified by Argos (2007), it was 32% and 16% higher, respectively, for LC 2 and LC 3.

### 2.5.1 Accuracy of location classes

Vincent *et al.* (2002) tested four 100 g battery-powered PTTs and reported that the accuracy of LC A was comparable to LC 1 and better than LC 0. We found no overall difference between LC A and LC 0, though for some individual PTTs, LC A was considerably more accurate, and for others the opposite was true. LC 1 was more accurate than either LC 0 or LC A, consistent with Argos (2007) specifications. Although we found the accuracy of LC B to be significantly lower than other classes, we concur with Vincent *et al.* (2002) that such data may be of value when plotting long-distance movements, especially when omitting them might leave long gaps of coverage. The mean error of 31 km that we found to be associated with LC B would be a minor issue if assessing the pattern of migration of an animal covering several hundred kilometres per day.

Britten *et al.* (1999) previously assessed the accuracy of LCs B, A, and 0, recognizing that data in these classes commonly represent the majority of records received from small PTTs. While they reported 68<sup>th</sup> percentile errors for LC B, A, and 0 of 98.5, 6.8, and 11.5 km, our results showed much greater accuracy, with corresponding errors of 24.0, 3.4, and 3.2 km, respectively. One potential explanation for this difference is that their study took place in a mountainous region, where altitudinal variation was greater. Also there was more potential for interference from the landscape, as Keating *et al.* (1991) reported that PTT errors were much greater when in valley bottoms. An

alternate possibility is that our results benefited from improved algorithms used by Argos for calculating location, updated in 1994 to permit the interpretation of locations from only two or three messages (D. Stakem, Argos, pers.comm.).

We found that longitudinal error was on average more than twice as great as latitudinal error, a pattern comparable to that documented by Keating *et al.* (1991) and Vincent *et al.* (2002), and contrary to the Argos (2007) claim that latitudinal and longitudinal error are expected to be equal. This can have practical implications for effectively focusing effort when searching for a downed transmitter. Similar to Vincent *et al.* (2002), we found that the difference was least pronounced for LC A.

### 2.5.2 Variability in data

We documented considerable variability in accuracy among individual PTTs. Whereas Keating *et al.* (1991) reported a three-fold difference in 68<sup>th</sup> percentile error in a study of 10 PTTs and Fancy *et al.* (1988) documented a five-fold difference among 12 PTTs, there was an 11-fold difference between the best and worst of our seven stationary PTTs. This high variability in results between PTTs may have been influenced both by differences in the actual performance of individual units, and by their location. A variety of factors may affect the accuracy of data, including the distance of the PTT from the satellite ground track, the elevation of the PTT, and the number of signals received by the satellite (Fancy *et al.* 1988, Rodgers 2001). The latter in turn may be influenced by the animal's surroundings (B. Henke, North Star Science and Technology, pers.comm.). Most of our stationary units were on dead birds, and while some were in an open landscape, others were in forested habitat, where there was greater probability of interference with the transmission of signals. Under normal conditions of use, the researcher has no way of knowing such sources of error, let alone quantifying them, and therefore each data point should be viewed with some caution.

Keating *et al.* (1991) predicted that sampling frequency, and correspondingly accuracy, would be greatest at high latitudes, and lowest near the equator, due to the polar orbit of the satellites resulting in more overlapping coverage near the poles (Fancy *et al.* 1988, Argos 2007). Our results were partially consistent with this, peaking between 40°N and 50°N and gradually declining to the south, but also to the north. This pattern primarily reflected the results from the battery-powered PTTs, as the solar-powered PTTs were on birds that remained mostly between 30°N and 50°N, and showed minimal differences related to latitude.

In addition to performing more consistently over varying latitudes, we found that solar-powered PTTs had significantly greater accuracy than battery-powered PTTs. This difference was particularly apparent over time, in that the frequency of good-quality results declined by over 1% per month for battery-powered PTTs, but remained fairly stable over time for solar-powered units. This is to be expected since low battery voltage is among the factors contributing to reduced accuracy (Britten *et al.* 1999). The lower frequency of good-quality data from battery-powered PTTs in winter and early spring may simply reflect the decline in output of these units over time. Our results therefore suggest that solar-powered transmitters are superior in terms of both longevity and accuracy. However, we caution that our results are based on studying the Peregrine Falcon, a species that tends to perch in the open, with ample opportunity for solar cells to fully power the PTT. Such units may be less advantageous for species that spend considerable time in dense cover, where the ability of the solar panels to recharge the PTT may be more limited.

Reduced power is just one of the many factors that can limit the accuracy of data generated by satellite transmitters. While location classes are generally a good indicator of the quality of an individual data point, our results demonstrate that occasionally even those marked as good-quality can have an associated error at least one order of magnitude greater than expected, and that 5% of data points among LC 1, 2, and 3 have an error of at least 1 km. While the voltage of the

PTT at the time of each transmission is recorded, other factors such as interference from habitat or weather, and variability among individual PTTs are more difficult to predict, and therefore there is no way to truly evaluate the accuracy of any individual data point. We therefore agree with Britten *et al.* (1999) that researchers should resist the urge to use single satellite telemetry points for local scale analysis such as habitat usage. However, given that the mean error associated with good-quality location classes is under 1.5 km, and for adequate-quality location classes is under 5.6 km, an individual animal's use of a particular location can be determined with some confidence if multiple independent reports indicate very similar coordinates.

Since we began our study, GPS PTTs have become available, which reliably report locations accurate to within 100 m or less. Issues of location uncertainty can therefore be eliminated through using such PTTs. The smallest GPS PTT currently available weighs 22 grams, while conventional solar-powered PTTs are now available in sizes as small as 9.5 grams (Microwave Telemetry Inc, Landover, MD). Therefore until technology progresses further, researchers using satellite telemetry on species weighing less than 500 – 600 g will need to continue considering how best to interpret data from conventional satellite telemetry, taking into account the sources of variability we have identified.

## **Connecting statement 2: Satellite telemetry as a tool to investigate movements of the eastern Peregrine Falcon population**

Satellite telemetry is currently the only technique that permits researchers to concurrently collect data on the movements of multiple individuals, regardless of their location. The limited precision of lightweight satellite transmitters precludes their use for detailed assessment of habitat use, but the data they provide are more than adequate for describing large-scale patterns of movement. The lack of knowledge about the dispersal and migration of individuals in the recovering eastern Peregrine Falcon population can be effectively addressed using satellite telemetry.

This manuscript is being submitted to *The Condor*, with co-authors D.M. Bird, M. Nash, and G.L. Holroyd.

## **Dispersal and migration of juvenile and adult Peregrine Falcons in southern Canada and northeastern United States**

### **3.1 Abstract**

Satellite telemetry was used to track 27 juvenile Peregrine Falcons (*Falco peregrinus*) from eastern North America and 7 adults from Alberta. All adults and 52% of juveniles remained near the nest site until migration, while most of the other juveniles staged elsewhere before migrating. Complete fall migration data were recorded for 21 individuals, and partial data were obtained for three others. Date of departure ranged from early July to mid-November. Distance traveled also varied considerably, from four individuals that remained within 100 km of their origin to 11 individuals that each flew a total of over 4000 km. Among juveniles, males migrated significantly farther than females, but three of four individuals that stayed local were males. Most long-distance migrants from Alberta skirted the Gulf of Mexico, while eastern birds either crossed it or island-hopped across the Caribbean. Most individuals wintered in the United States, with smaller numbers in Canada, South America, Mexico and the Caribbean. Wintering and natal habitat were similar for 87% of birds. Full spring migration data were obtained for 10 individuals. In most cases, the cumulative distance traveled was shorter in fall than spring, and all but one of the individuals wintering south of the United States passed along the Texas Gulf Coast on the way north. In two cases where wild siblings from the same nest were tracked, movements were quite similar, but on three other occasions where hatched siblings were tracked, behaviour differed considerably among them. Only two individuals were tracked over a period of greater than one year; both showed fidelity to winter and breeding territories. Fourteen juveniles and one adult were known or presumed to have died during the study. Of those for which cause of death could be determined with some certainty, up to three individuals were victims of hurricanes, four collided with vehicles or transmission lines, and two were taken by predators.

### 3.2 Introduction

The Peregrine Falcon (*Falco peregrinus*; hereafter peregrine) has been a species of conservation concern since its drastic mid-twentieth century decline linked to DDT contamination, and has been monitored extensively on its breeding grounds (e.g. Berger *et al.* 1969, Barclay 1988, Cade *et al.* 1996, Corser *et al.* 1999, Rowell *et al.* 2003). Detailed studies of wintering behaviour have also been conducted (Enderson *et al.* 1995, Septon 2000, McGrady *et al.* 2002). However, the effective conservation and management of a migratory species requires that its year-round movements and requirements be well understood (Bennetts *et al.* 1999, Sillett and Holmes 2002, Webster and Marra 2005).

Migration has long been the most difficult part of the peregrine's annual life cycle to document in detail. Considerable banding effort, especially at Assateague Island, Maryland (Berry 1971, Ward *et al.* 1988) and Padre Island, Texas (Hunt *et al.* 1975, Chavez-Ramirez *et al.* 1994, Seegar *et al.* 2003) has provided a basic framework of knowledge, including evidence that some individuals show fidelity to either the Atlantic coast or Gulf coast flyways (Yates *et al.* 1988). Except for rare direct recoveries, banding data provide little information about the pace or route of migration. Tracking with radio telemetry beginning in the mid 1970s provided greater detail, but its inherent logistical challenges limited application to relatively local studies (Hunt and Ward 1988, Enderson and Craig 1997) or longer-distance tracking of lone individuals (Cochran 1975).

With the advent of sufficiently light satellite transmitters in the early 1990s, researchers began to study peregrine migration in greater detail. Fuller *et al.* (1998) tracked 26 individuals from breeding sites in the Arctic and 31 captured on migration at Assateague Island or Padre Island; all were adults and 55 of 57 were females. Britten *et al.* (1999) studied 27 adult and 15 juvenile females from breeding areas in Alaska and the Colorado Plateau. McGrady *et al.* (2002) followed one male and 11 female adults from a wintering site in coastal Mexico.

None of these studies specifically targeted the eastern North American population, which has undergone the most dramatic declines and increases over the past half-century. Most also focused primarily on females, since in earlier years the lightest platform transmitter terminals (PTTs) were too heavy for males, and far more adults were studied than juveniles. Yet in many species, migration strategies differ among sexes and/or age groups (Kerlinger 1989, Berthold 2001). Our primary objective was therefore to describe the dispersal and migration of juvenile peregrines in eastern North America. Moreover, this population provided an opportunity to explore differences between urban and rural peregrines, as well as between captive-bred and wild-raised juveniles. Additionally, we aimed to assess causes of mortality and determine how these relate to migration.

### **3.3 Methods**

#### *3.3.1 Study area*

Thirty-six PTTs (Microwave Telemetry Inc., Columbia, Maryland) were deployed on 34 peregrines between 1997 and 2005 (Appendix A). Our study was aimed primarily at juvenile peregrines ( $n = 27$ ), with only a small number of adults studied for comparative purposes ( $n = 7$ ). The majority of juveniles studied were from southern Ontario ( $n = 17$ ), with smaller numbers from Quebec ( $n = 2$ ), New York ( $n = 3$ ), or Pennsylvania ( $n = 5$ ); the adults were all from Alberta. One individual from southern Ontario continued to be tracked as an adult, receiving new PTTs in its second and third summers. Birds were defined as being urban if released or raised on buildings, and rural if released or raised on cliffs.

#### *3.3.2 Transmitter attachment*

To fit peregrines with transmitters, most were either trapped intentionally ( $n = 22$ ), rescued opportunistically shortly after fledging ( $n = 5$ ), or selected prior to release from rehabilitation for minor injuries ( $n = 2$ ). All transmitters were attached as backpack harnesses. Seven of the eight American birds were fitted with transmitters prior to fledging, at around 30-32 days of age. In the first three

years of the study, transmitters were attached using a Teflon ribbon harness (Bally Ribbon Mills, Bally, Pennsylvania) as described by Kenward (2001). Subsequently, a softer and more flexible neoprene harness adapted from Britten *et al.* (1999) was used on all other birds. All individuals in the study were also fitted with a standard USFWS band and a colour alphanumeric band (Acraft Sign and NamePlate Company, Edmonton, Alberta) on opposite legs for visual recognition. Due to several PTT numbers being reused during the course of our study, most individuals are referred to by their band number or a name given by project sponsors.

The combined weight of the transmitter and harness was limited to 5% of the body weight of the individual carrying it. During the first four years of the study, both 30 g ( $n = 14$ ) and 20 g ( $n = 11$ ) battery-powered transmitters were used, with the lighter units generally reserved for males. An 18 g solar-powered model was first used in the fifth year, and for the majority of deployments thereafter ( $n = 11$ ).

### 3.3.3 *Data collection and analysis*

A variety of duty cycles were employed, with data received every three to four days during migration and three to 10 days during winter from battery-powered transmitters, and every one to three days throughout the year from solar-powered transmitters.

Data were transmitted to National Oceanic and Atmospheric Administration (NOAA) satellites and processed by Argos as described by Fancy *et al.* (1988). Activity sensors were included on all transmitters, indicating when a unit became stationary due to either death of the bird or failure of the harness. Data received after a transmitter had become stationary were omitted from analysis. Data were filtered on a daily basis to eliminate duplicate transmissions and inaccurate points. In most cases, a single location per day was plotted for each bird. If multiple data points were received in a day, the most accurate was typically

selected by choosing the one with the highest LC class as identified by Argos (increasing quality in the series Z, B, A, 0, 1, 2, 3; Argos 2007). On days when no good-quality (1, 2, 3) readings were received, adequate-quality class 0 or A data were used, based on the review of Vincent *et al.* (2002) and analysis of the data from this study (see Chapter 3). During migration only, class B readings were used if no better quality data were available, as the degree of error was likely to be small relative to the scale of study (Steenhof *et al.* 2005). If on any day the highest accuracy was shared among two or more data points, the first was arbitrarily selected for inclusion. In rare cases when the transmitter was broadcasting over several hours during a period of active migration, all locations of class A or better were plotted to estimate the hourly rate of travel.

Date of dispersal was identified as the first date on which an individual was at least 10 km away from its natal site without returning during the subsequent duty cycle. A destination was defined as an area occupied for at least one week. Date of departure was considered the last known date on the summering or wintering grounds, while date of arrival was the first day on which the individual was reported at its destination. Fall and spring were defined for each individual by the timing of its movements, rather than by calendar date. Winter and summer were defined as the intervening periods between migrations. A season was considered complete if data were received throughout its entire duration. Distance and duration were not assessed for incomplete migrations, but rate and efficiency of travel were calculated for the portion completed. Direct distances were calculated as the straight line displacement between start and end points, while cumulative distances were calculated using the single best point each day to reflect the total distance traveled. Rate of migration was calculated using cumulative distances, and efficiency of travel was calculated as the ratio of cumulative distance to direct distance. For individuals tracked longer than one year, data from only the first year were used for comparison with other individuals.

As some data were not normally distributed, the Mann-Whitney U test was used to compare groups (Zar 1999). Statistics were calculated using SPSS 9.0 (SPSS Institute, Chicago IL). Significance was set at  $\alpha = 0.05$ . All results are presented as mean  $\pm$  standard error.

### **3.4 Results**

Between 18 and 3413 data points were received for each of the 34 individuals tracked, for a total of 14,936 locations. Of these, 17% were considered good-quality (location class 1, 2, 3), and an additional 42% were adequate-quality for plotting locations (location class 0, A). The duration of tracking ranged from one week to 32 months.

#### *3.4.1 Mortalities*

Fourteen juveniles and one adult are known or presumed to have died while wearing a PTT (Table 3-1). The adult was lost during a hurricane in the western Caribbean, and transmissions also ended abruptly for two juveniles that were last recorded in the same area the following year as a hurricane approached. Three individuals were killed by collisions with vehicles, all after at least one month. One male was found dead below electrical wires after half a year. The remaining eight individuals were not recovered, and the telemetry data did not permit cause of death to be deduced with certainty, though circumstantial evidence suggested that one fell down a chimney, while two others were predated.

#### *3.4.2 Post-fledging movements:*

Post-fledging movements were documented for all juveniles except one that fell victim to predation within its first week of flight. Those from rural nests tended to leave their natal territory at a younger age ( $72.3 \pm 15.2$  days,  $n = 3$ ) than juveniles from urban sites ( $87.1 \pm 4.3$  days,  $n = 19$ ), but the difference was not significant ( $U = 20$ ,  $P = 0.23$ ). Similarly, there was a slight but non-significant difference between wild-raised ( $81.3 \pm 6.4$  days,  $n = 12$ ) and captive-bred ( $89.5 \pm$

5.2,  $n = 10$ ) birds ( $U = 45.5$ ,  $P = 0.42$ ). Age of departure was similar for males ( $86.3 \pm 5.5$  days,  $n = 11$ ) and females ( $83.8 \pm 6.6$  days,  $n = 11$ ;  $U = 59$ ,  $P = 0.78$ ).

Table 3-1. Timing and nature of mortalities of peregrines while wearing PTTs

Individual	Age at death (months)	Sex	Date of death	Cause of death
5735b	Adult	F	Nov 1998	Hurricane
Lincoln	5	M	Nov 1999	Hurricane
Eco	5	M	Nov 1999	Hurricane
Maryann	3	F	Aug 2000	Unknown (chimney?)
Pinnacle	4	F	Oct 2000	Unknown
Magellan	7	M	Jan 2001	Collision with power line
Sarah	3	F	Aug 2001	Vehicle collision
Trillium	2	M	Jul 2001	Unknown
Dieppe	3	M	Sep 2001	Vehicle collision
Horus	2	M	Jul 2002	Unknown (predation?)
Destiny	3	F	Aug 2002	Unknown
Hope	3	F	Aug 2002	Unknown
Richmond	7	M	Jan 2003	Unknown
Hafoc	10	M	Mar 2005	Vehicle collision
Skye	4	F	Sep 2005	Unknown (predation?)

The post-dependence behaviour of juveniles followed one of five patterns (Table 3-2). In three patterns, individuals remained at their natal site; at one extreme, five juveniles did not disperse or migrate at all, although they did take some exploratory flights ranging as far as 150 km. Four of these birds died within their first year, while the PTT was removed from the other in mid-winter for re-deployment on another bird. Two of these birds were from hack releases and stayed behind after their siblings departed, but the other three were from wild nests, and were not chased away by their parents.

Table 3-2. Post-independence movement patterns of juvenile peregrines (F=female, M=male). Distances are presented as means  $\pm$  1 SE.

	<i>n</i>	Distance to staging site (km)	Maximum roaming distance (km)
Local movements only	5 (2F, 3M)	0	78.6 $\pm$ 28.2
Local movements, then migration	3 (1F, 2M)	0	124.0 $\pm$ 77.7
At natal territory until migration	5 (3F, 2M)	0	<5
Staging elsewhere prior to migration	Urban - 6 (2F, 4M)	44.0 $\pm$ 13.3	36.0 $\pm$ 12.1
	Rural - 3 (2F, 1M)	61.7 $\pm$ 0.3	14.0 $\pm$ 9.0
	Wetland - 2 (1F, 1M)	137.5 $\pm$ 97.5	93.0 $\pm$ 3.0
Random wandering	2 (1F, 1M)	n/a	230.0 $\pm$ 21.0

Another eight individuals remained near their natal territory temporarily, but did ultimately migrate. Three of these undertook exploratory flights prior to migration that extended as far as 274 km, but in each case in directions different from that in which they ultimately migrated. Such flights almost always lasted only one duty cycle, in most cases less than four days. The period between initial exploratory flights and onset of migration ranged from 23 to 53 days. The other five juveniles remained within 5 km of their natal site until they migrated. Both groups included a mix of males and females, and of wild-raised and captive-bred individuals. This direct departure pattern was also followed by all adults in the study.

The most common pattern of behaviour, exhibited by 11 individuals, was to disperse to a staging site shortly after becoming independent. Six settled in an urban area; all of these were hacked ( $n=5$ ) or raised ( $n=1$ ) in cities. Another three settled in agricultural landscapes, while the final two staged at large wetlands; all but one of these birds were also from cities. Except for one wild urban female that dispersed 235 km to her staging site, others all moved less than 70 km. Most often ( $n = 4$ ) the staging site was southwest of the natal site, but there was no consistent pattern, with others being to the north ( $n = 1$ ),

northeast ( $n = 1$ ), east ( $n = 2$ ), west ( $n = 2$ ), and northwest ( $n = 1$ ). Five of the 11 individuals in this group died or were injured at their staging site; those that survived to migrate did so after spending 22 to 79 days there.

The final pattern was observed for only two birds that dispersed from their natal territory and did not return, but also did not settle at a staging site. They wandered in a seemingly random manner for a period of three to four weeks, until both died from vehicle collisions. Although the maximum range from the natal site was no more than 251 km for either individual, the minimum cumulative distance traveled was between 600 and 700 km for each bird.

### *3.4.3 Fall migration*

Nine of the juveniles (six females, three males) died prior to migration, and one of the PTTs on an adult failed in late summer. Four juveniles monitored through to winter did not migrate, remaining in southern Ontario ( $n = 3$ ) or New York ( $n = 1$ ). The movements recorded by the remaining 20 individuals are summarized in Table 3-3.

The displacement between departure and arrival locations varied from 177 to 9998 km, and differed considerably by age, sex, origin, and habitat (Table 3-4). The median displacement was more than an order of magnitude greater for adults than juveniles. Among juveniles, median displacement by males was nearly four times greater than for females. However, of the four birds that did not migrate at all, three were males. The median displacement by captive-bred birds was almost four times greater than for wild-raised birds. Statistical comparison of the displacement of urban and rural juveniles was not possible due to the latter group being represented by a single individual, but the median displacement of urban juveniles was similar.

Table 3-3. Origin, destination, timing, distance, and duration of fall migration for all individual peregrines that migrated

Name	Year	Age / Sex	Origin		Destination		Distance		# days	Rate (km/da)
			Location	Date	Location	Date	Dire	Tota		
5735a	97/9	Ad F	Peace Point AB	21	Veracruz MEX	11	477	482	22	219
5735b	98/9	Ad F	Fort Chipewyan AB	20	SW Caribbean <sup>1</sup>	8	577	746	49	152
Lincoln	99/0	Juv	Guelph ON	20	Panama <sup>1</sup>	10	376	415	22	189
Eco	99/0	Juv	Richmond Hill ON	30	Panama <sup>1</sup>	3	379	507	34	149
Nate	99/0	Juv	Richmond Hill ON	29	Cartagena COL	13	371	494	46	107
24424	99/0	Ad F	Fort Chipewyan AB	23	Chable MEX	24	482	530	29	183
24427	99/0	Ad F	Edmonton AB	29	Culiacan MEX	11	325	332	12	277
24868	99/0	Ad	Fort Chipewyan AB	15	Iguaba BRA	12	999	119	58	207
Lionheart	01/0	Juv	Richmond Hill ON	26	Charleston SC	26	123	203	31	66
Lightning	01/0	Juv	Richmond Hill ON	16	San Francisco DR	21	286	364	34	107
Ruby	01/0	Juv	Charleston Lake	10	New York City NY	19	483	485	9	54
Y3	02/0	Juv	Harrisburg PA	29	Cape Charles VA	31	330	332	3	111
4C	02/0	Juv	Harrisburg PA	16	Newark NJ	21	259	335	5	67
4A	02/0	Juv	Pittsburgh PA	1 Jul	Bridgeton NJ	6 Jul	419	717	5	143
W2	02/0	Juv	Pittsburgh PA	11	Philadelphia PA	8	388	119	28	43
15116	02/0	Ad	Drumheller AB	6	Cabruta VEN	13	647	977	97	101
Teedee	03/0	Juv	Kitchener ON	9	New York City NY	6	580	944	26	36
5259	03/0	Juv	Pittsburgh PA	26	Cleveland OH	30	177	177	4	44
Miriam	03/0	Juv	Toronto ON	18	Detroit MI	28	328	845	40	21
Richmond	03/0	Juv	Richmond Hill ON	26	Edisto SC	5	125	141	9	157

*Individuals tracked again in subsequent years:*

24424	00/0	Ad F	Fort Chipewyan AB	27	Chable MEX	23	481	488	27	181
Nate	00/0	Ad	Richmond Hill ON	17	Cartagena COL	18	372	451	31	144
Nate	01/0	Ad	Mississauga ON	27	Cartagena COL	16	369	497	20	244

<sup>1</sup>-last known location before individual was killed in or during a hurricane

Most of the ten birds undertaking long-distance (>1000 km) migrations traveled fairly directly south (Figure 3-1). Only in two cases did the cumulative distance traveled between points exceed the direct distance between departure and arrival points by more than 35%. Adults took more direct routes (mean extra distance  $16.9 \pm 9.2\%$ ,  $n = 5$ ) than juveniles ( $34.6 \pm 10.9\%$ ,  $n = 4$ ), but the difference was not significant ( $U = 4$ ,  $P = 0.22$ ). All but one of the western birds skirted around the Gulf of Mexico. All eastern birds heading that far south

crossed it, either directly, possibly using oil platforms for resting and/or feeding, or via an island-hopping route through Florida and the Caribbean islands. The only western peregrine to attempt a Caribbean crossing perished in a hurricane northeast of Panama. Among the ten short-distance migrants, there was considerably more variation in direction and patterns of movement (Figure 3-2). Three males and three females had a greater longitudinal than latitudinal displacement.

Table 3-4. Median and mean displacement (km) of peregrines during fall migration, summarized by age, sex, origin, and habitat

	Group	<i>n</i>	Median displacement	Mean displacement	U	<i>P</i>
Age	Adult	5	4821	5864 ± 1152	1	0.02
	Juvenile	12	451	1003 ± 329		
<i>Juveniles only:</i>						
Sex	Female	5	330	341 ± 50	5	0.04
	Male	7	1236	1475 ± 499		
Origin	Wild	6	359	317 ± 36	0	0.02
	Captive	6	1244	1688 ± 534		
Habitat	Urban	11	419	1050 ± 356	n.a.	n.a.
	Rural	1	483	483		

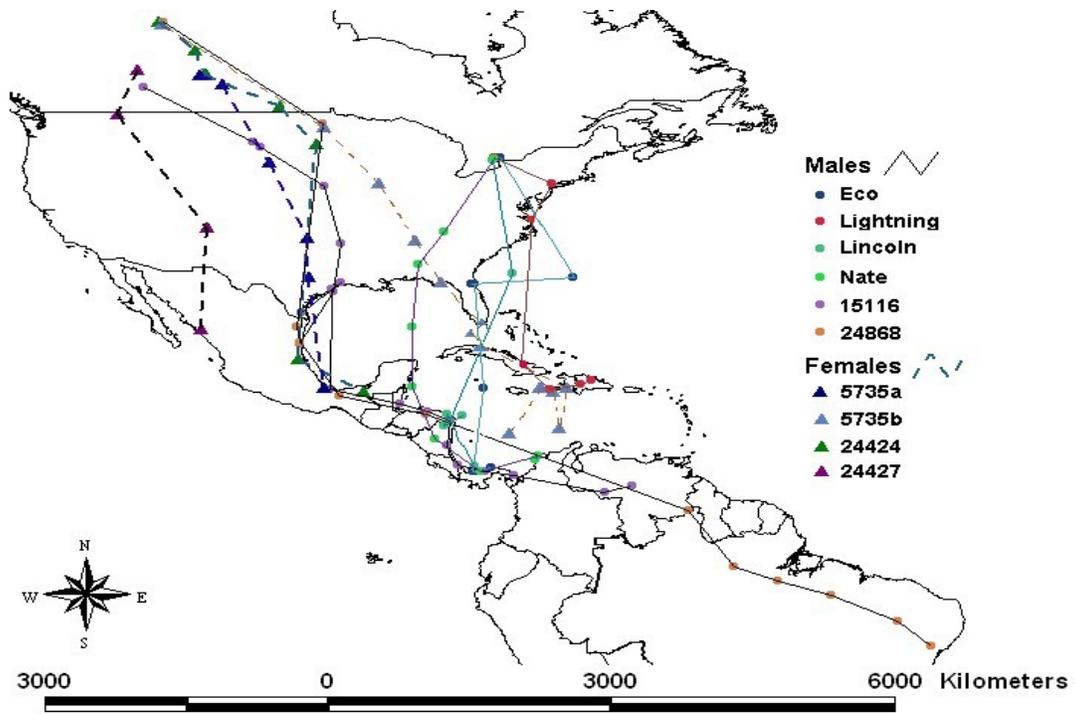


Figure 3-1. Routes followed by long-distance peregrine migrants during fall

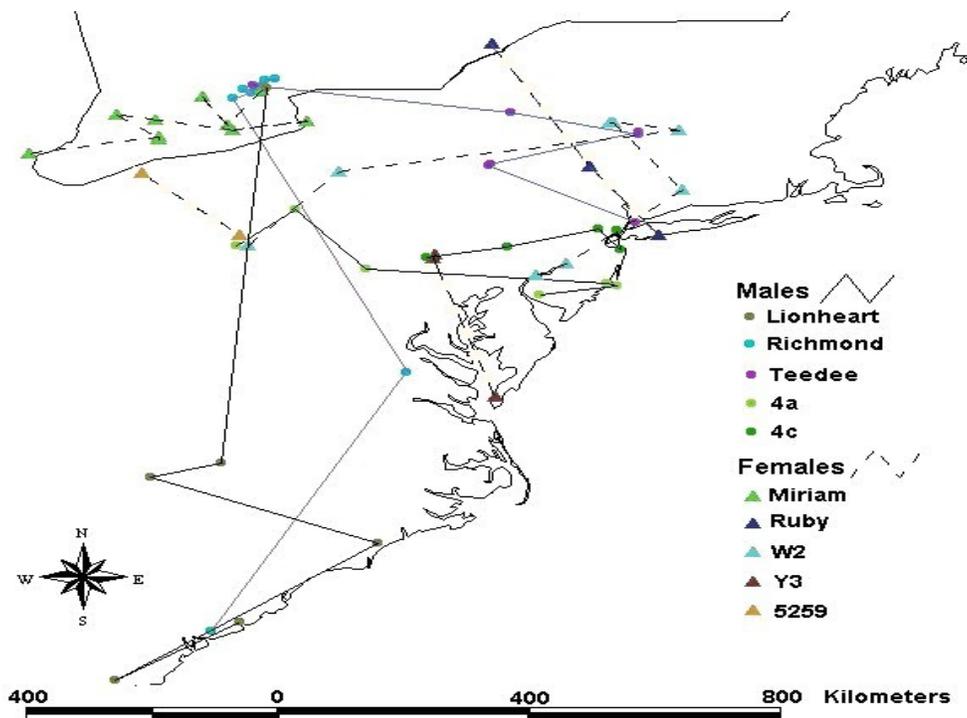


Figure 3-2. Routes followed by short-distance peregrine migrants during fall

In general, the mean displacement of individuals was positively correlated with the latitude of their natal or breeding territory (Figure 3-3). The shortest migration by an individual from north of 45°N was 3253 km, while the longest migration from south of 43°N was 419 km.

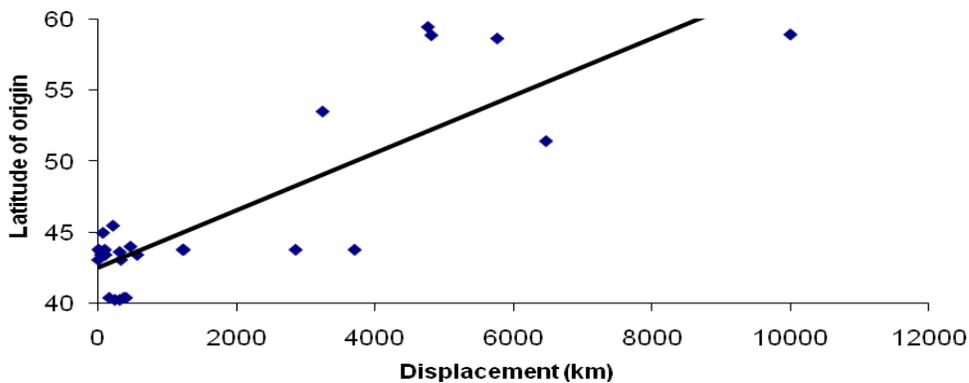


Figure 3-3. Line of best fit ( $r^2 = 0.71$ ;  $F_{1,28} = 67.53$ ,  $P < 0.001$ ) showing the correlation between latitude of origin and distance of migration by peregrines

Date of departure varied from July for four of the five juveniles from Pennsylvania to mid-November for two of the southern Ontario juveniles. The median date of departure was 23 September, but only half of migrants departed within one month before or after that date. The median departure date was slightly but not significantly earlier for adults (Table 3-5). Among juveniles, the median and mean departure dates for females were seven and three weeks earlier than those of males, but the difference was not significant due to the small sample size and one female being the latest of all juveniles to migrate. The median departure date for wild-raised juveniles was over ten weeks earlier than for captive-bred individuals, and this difference was weakly significant.

Duration of migration ranged from 3 to 97 days. The Pennsylvania juveniles were the quickest to reach their destinations, with all but one of them doing so within five days. Two Ontario juveniles also completed their migration in less than 10 days. Overall, short-distance migrants reached their destinations in an

average of  $15 \pm 5$  days, while long-distance migrants took an average of  $38 \pm 9$  days ( $U = 13$ ,  $P < 0.05$ ).

Table 3-5. Median and mean dates for onset of fall migration by peregrines, summarized by age, sex, origin, and habitat

	Group	<i>n</i>	Median	Mean	U	<i>P</i>
Age	Adult	6	10 Sep	8 Sep $\pm$ 6 days	34.0	>0.1
	Juvenile	14	26 Sep	13 Sep $\pm$ 13 days		
<i>Juveniles only</i>						
Sex	Female	5	10 Aug	31 Aug $\pm$ 24 days	16.5	>0.1
	Male	9	30 Sep	22 Sep $\pm$ 15 days		
Origin	Wild	6	23 Jul	16 Aug $\pm$ 23 days	9.5	<0.1
	Captive	8	8 Oct	6 Oct $\pm$ 10 days		
Habitat	Urban	13	29 Sep	17 Sep $\pm$ 16 days	n.a.	n.a.
	Rural	1	10 Aug	10 Aug		

Adults migrated more than twice as rapidly as juveniles, while among juveniles males traveled at twice the speed of females (Table 3-6). Overall rate of migration was more rapid for long-distance migrants ( $161 \pm 17$  km/day,  $n = 15$ ) than short-distance migrants ( $61 \pm 14$  km/day,  $n = 8$ ;  $U = 8$ ,  $P < 0.01$ ). Among the long-distance migrants there was considerable variation in the rate of travel during different phases of migration. Two individuals traveled most rapidly during the first quarter of migration, and two others were traveling fastest during the last quarter of their migration; more typically, the rate of travel was greatest during the middle half. The most rapid travel recorded was 658 km/day by an adult male entering the middle part of its migration. In three cases, a series of data points showed steady movement over the course of a transmission window of between 2.25 and 7.5 hours; mean rate of travel during these periods ranged from 24 to 48 km/h.

Table 3-6. Median and mean rates of fall migration by peregrines, summarized by age, sex, origin, and habitat

	Group	<i>n</i>	Median	Mean km/day	U	<i>P</i>
Age	Adult	6	195	191 ± 25	3	<0.01
	Juvenile	14	86	91 ± 15		
<i>Juveniles only:</i>						
Sex	Female	5	43	54 ± 16	8	<0.1
	Male	9	108	112 ± 18		
Origin	Wild	6	54	69 ± 18	14	>0.1
	Captive	8	108	108 ± 21		
Habitat	Urban	13	107	94 ± 16	n.a.	n.a.
	Rural	1	54	54		

#### 3.4.4 Winter residency

Wintering locations were identified for 18 individuals, with the majority ( $n = 11$ ) in the United States, and others in Mexico ( $n = 3$ ), Canada ( $n = 2$ ), Colombia ( $n = 1$ ), and the Dominican Republic ( $n = 1$ ) (Figure 3-4). An additional five individuals were either in or headed for South America when contact was lost from their transmitters. All but one of those wintering in the United States or Canada were within 15 km of either the Atlantic Ocean, Lake Ontario, or Lake Erie; the other was on Delaware River, 75 km upstream from Delaware Bay. Those in Mexico and the Dominican Republic were all 40 to 80 km from the nearest coast, and were not near any other major water bodies.

Complete winter data were received for 11 individuals, with data over at least four months for another two (Table 3-7). Wintering locations of these birds ranged from 43°N (Rochester, New York) to 10°N (Cartagena, Colombia). All individuals settled into a winter territory for at least three months. One individual, adult female 24424, shifted 75 km north to a second location by the coast for the final five weeks of winter, and a juvenile male, Lightning, shifted 50 km northwest for the final two weeks of winter. The remainder stayed in the same area throughout winter, though all roamed away from their core area at least

occasionally. Juveniles wandered more frequently and over longer distances, with 80% of data points within  $18.3 \pm 2.4$  km of the centre of their winter territory ( $n=10$ ), compared to  $12.2 \pm 1.9$  km for adults ( $n = 3$ ;  $U = 7$ ,  $P > 0.1$ ).

Table 3-7. Locations of wintering peregrines and distance (km) of satellite telemetry points from the centre of their winter territory

Name	Age	Season	Location	90% radius	80% radius
5735a	Ad	Sep 97 – Mar 98	Veracruz MEX	37.1	15.9
Nate	Juv	Nov 99 – Mar 00	Cartagena COL	11.5	7.3
Nate	Ad	Nov 00 – Feb 01	Cartagena COL	10.1	5.1
24424	Ad	Sep 99 – Jan 00	Chable MEX	24.0	10.3
	Ad	Jan 00 – Feb 00	Laguna Pom MEX	19.6	9.8
24427	Ad	Oct 99 – Mar 00	Culiacan MEX	22.0	10.3
Magellan	Juv	Oct 00 – Feb 01 <sup>1</sup>	Toronto ON	32.5	22.7
Lionheart	Juv	Nov 01 – Mar 02	Charleston SC	14.1	10.9
Lightning	Juv	Nov 01 – Feb 02	San Francisco DR	55.4	32.7
Ruby	Juv	Aug 01 – Apr 02	New York City NY	21.6	14.8
Y3	Juv	Aug 02 – Mar 03	Cape Charles VA	17.4	12.3
4C	Juv	Aug 02 – Mar 03	Newark NJ	31.0	21.7
4A	Juv	Sep 02 – Feb 03	Bridgeton NJ	23.1	21.6
W2	Juv	Sep 02 – Feb 03	Philadelphia PA	26.2	13.7
Hafoc	Juv	Oct 04 – Mar 05 <sup>1</sup>	Rochester NY	62.5	25.0

<sup>1</sup> - died during the winter

The over-wintering birds showed a significant preference for familiar habitat during winter ( $\chi^2_1 = 6.27$ ,  $p < 0.05$ ). Both of the cliff-nesting adults occupied a rural setting during winter, while the one cliff-hacked juvenile over-wintered adjacent to New York City, but remained primarily in the natural habitat of Jamaica Bay. Of the 10 birds from cities, only two juveniles over-wintered in rural habitat: a female from Harrisburg, Pennsylvania, near the tip of the Delmarva Peninsula, Virginia, and a male from Pittsburgh, Pennsylvania in the agricultural part of southern New Jersey near Bridgeton.

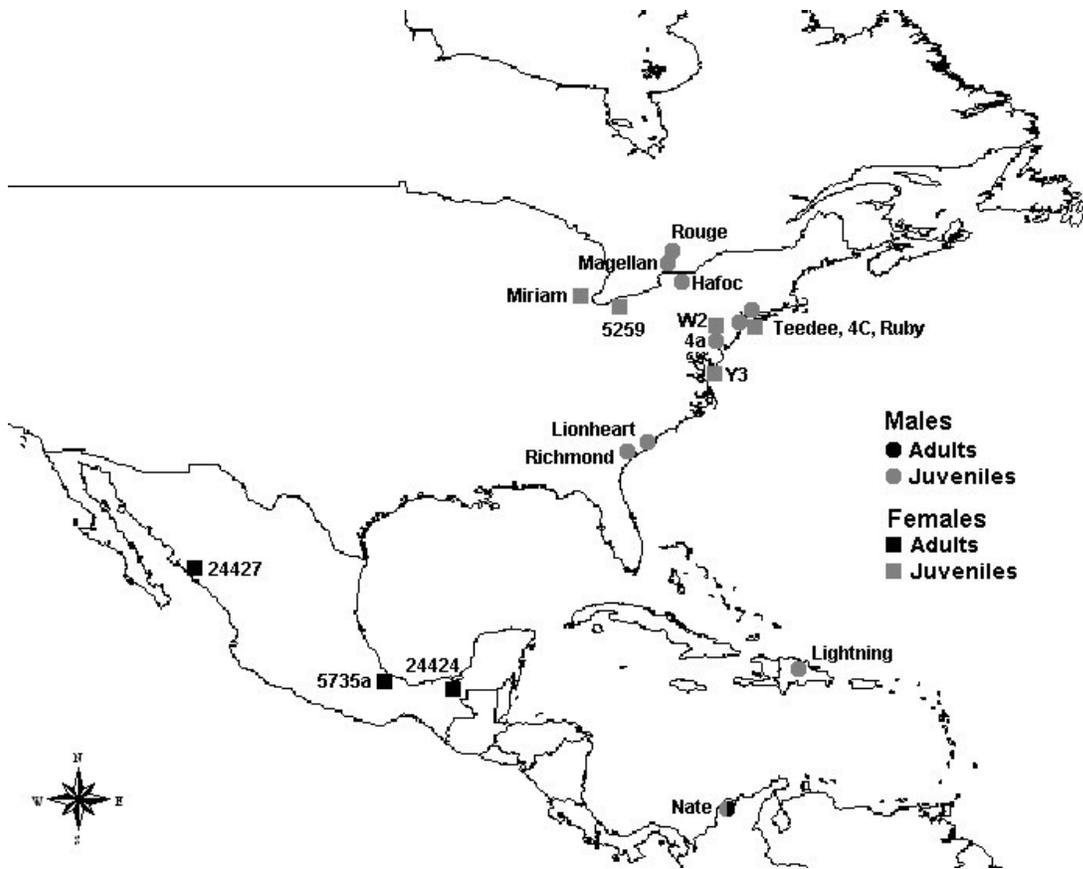


Figure 3-4. Locations of 18 overwintering peregrines as identified by satellite telemetry

### 3.4.5 Spring migration

Data were received throughout the spring season from 11 transmitters, including one male in two consecutive years, and two juveniles from Pennsylvania that remained at their wintering location throughout spring and into summer, indicating that their fall movement represented dispersal rather than migration. The spring migration of the remaining individuals is summarized in Table 3-8.

Date of departure varied from late February to mid-April, with birds wintering farther south leaving earlier than those farther north. The fastest of the long-distance migrants completed its northbound migration in just 8 days, at a mean speed of 423 km/day. At the opposite extreme, one individual took two months to reach its summer territory, but as data were not received between 22 April and

23 May, it is possible that the migration may have been as much as four weeks shorter than recorded. Adults ( $252 \pm 86$  km/day,  $n = 3$ ) traveled faster in spring than juveniles ( $96 \pm 26$  km/day,  $n = 6$ ;  $U = 2$ ,  $P < 0.1$ ). The slowest of the juveniles was a female that spent nearly a month traveling from Virginia to New Jersey, involving many back and forth movements. As in fall, some individuals were fastest at either end of the journey, while the majority traveled most quickly in the middle. All but one of the individuals wintering in Mexico or South America passed along the Texas gulf coast on their northbound migration.

Table 3-8. Origin, destination, timing, distance, and duration of spring migration for all individual peregrines that migrated

Name	Year	Origin		Destination		Distance (km)		# days	Rate (km/day)
		Location	Date	Location	Date	Direct	Total		
5735	97/9 8	Veracruz MEX	10 Mar	Peace Point AB	16 Apr	4753	5511	36	153
Nate	99/0 0	Cartagena COL	30 Mar	Richmond Hill ON	5 May	3701	7135	36	198
24424	99/0 0	Chable MEX	27 Mar	Fort Chipewyan AB	29 Apr	4804	5996	34	176
24427	99/0 0	Culiacan MEX	19 Mar	Edmonton AB	27 Mar	3253	3382	8	423
Nate	00/0 1	Cartagena COL	24 Feb	Mississauga ON	1 Apr	3686	5734	35	164
Lionheart	01/0 2	Charleston SC	14 Mar	Mississauga ON	14 Apr	1214	1438	31	46
Lightning	01/0 2	Santiago DR	22 Mar	North York ON	23 May	2820	5342	62	86
Ruby	01/0 2	New York NY	13 Apr	Trenton ON	18 Apr	481	481	5	96
5258	02/0 3	Cape Charles VA	29 Mar	Atlantic City NJ	26 Apr	275	1328	29	46
15114	02/0 3	Bridgeton NJ	19 Apr	Hamilton ON	1 May	567	983	12	82

Comparisons between fall and spring movements are summarized in Table 3-9. All adults returned to the territories they had occupied the previous summer,

while the four captive-bred juveniles each went back to within 5 - 120 km of their release site. The two wild-raised juveniles did not show such fidelity, with the male settling 310 km north of the Pittsburgh nest where he was raised, and the female establishing a territory 240 km southeast of her natal site in Harrisburg.

Table 3-9. Comparison of fall and spring migration characteristics for peregrines tracked by satellite telemetry in both seasons

Name	Age	Cumulative distance (km)		# days		Rate (km/day)	
		Fall	Spring	Fall	Spring	Fall	Spring
5735	Ad	4828	5511	22	36	219	153
Nate	Juv	4940	7135	46	36	107	198
24424	Ad	5309	5996	33	33	183	182
24427	Ad	3324	3382	12	8	277	423
Lionheart	Juv	2036	1438	31	31	66	46
Lightning	Juv	3643	5342	34	62	107	86
Ruby	Juv	485	481	9	5	54	96
5258	Juv	332	1328	3	29	111	46
15114	Juv	717	983	5	12	143	82

The cumulative distance traveled was nearly identical in fall and spring for two birds, 30% shorter in spring for one, and 13% to 300% longer in spring for the remainder. In some cases, the longer distance was a result of the birds staying over land in spring, while crossing large bodies of water such as the Gulf of Mexico in fall. The relative duration of spring and fall migration varied considerably between individuals, with no patterns apparent. On average, adults migrated more rapidly in spring than fall (by  $34 \pm 62$  km/day) and juveniles migrated more slowly ( $-6 \pm 25$  km/day), but there was considerable variability.

#### 3.4.6 Multi-year observations

Only two individuals were tracked for more than one year. A breeding adult female from northern Alberta (24424) was tracked from July 1999 to December

2000. It was faithful to both summer and winter territories, dates of departure and arrival for fall migration differed by only four days between the two years, and the rate of travel was consistent, i.e. 183 km/day and 181 km/day.

The other individual was a captive-bred male (Nate) first tracked as a juvenile, and monitored by telemetry through to February 2002, then observed visually on a regular basis until being killed in a territorial battle with another male in 2005. During the three years he was tracked by telemetry, he maintained a small winter territory centered in the same part of Cartagena, Colombia. His arrival there was consistently within a five-day span in mid-November, but each year the date of departure from his summer territory became later, and the duration of migration correspondingly shorter (Table 3-10). In contrast, the duration of spring migration was similar over two years, but five weeks earlier in the second year.

The routes taken by Nate differed somewhat over time (Figure 3-5). He crossed the Gulf of Mexico on the way south the first year, whereas in subsequent years he minimized the distance over water by flying along Florida and crossing to the Yucatan peninsula via Cuba. Similarly, the two spring migration routes differed, with a much more direct line taken from Texas to Ontario the second year.

Table 3-10. Comparison of migration characteristics across years for the male peregrine, Nate

Origin	Destination	Departure	Arrival	# days	Distance (km)	Rate (km/day)
<i>Fall</i>						
Richmond Hill	Cartagena	29 Sep 1999	13 Nov 1999	46	4940	108
Richmond Hill	Cartagena	17 Oct 2000	18 Nov 2000	31	4517	144
Mississauga	Cartagena	27 Oct 2001	16 Nov 2001	20	4928	244
<i>Spring</i>						
Cartagena	Mississauga	30 Mar 2000	5 May 2000	36	7135	198
Cartagena	Mississauga	24 Feb 2001	1 Apr 2001	35	5734	164

In the summer of 2001, Nate established a territory with a mate in Mississauga, Ontario, 40 km southwest of his release site, but did not breed, and he again migrated to Colombia in October. The following years they did breed successfully at the same location, and he no longer migrated, instead remaining on territory throughout the year.

#### *3.4.7 Sibling comparisons*

Four pairs and one set of three siblings were included in our study to compare the movements of related individuals. The two pairs of wild-raised siblings, both from Pennsylvania in 2002, showed a fair level of similarity in their behaviour. In each case, the siblings departed within two weeks of each other, and undertook comparable short-distance migrations southeast to the Atlantic coast.

The results were considerably different for captive-bred birds. Of three brothers released at Richmond Hill in 1999, two departed within a day of each other in late September and followed broadly similar routes south as far as Panama, but the third sibling did not migrate at all. In 2001, both males from Richmond Hill migrated, leaving 10 days apart; one went as far as the Dominican Republic while the other stopped in South Carolina. In 2003, the male from Richmond Hill migrated to South Carolina, while his sister remained at the hack site for seven more weeks and then moved only a short distance west to Detroit, Michigan.

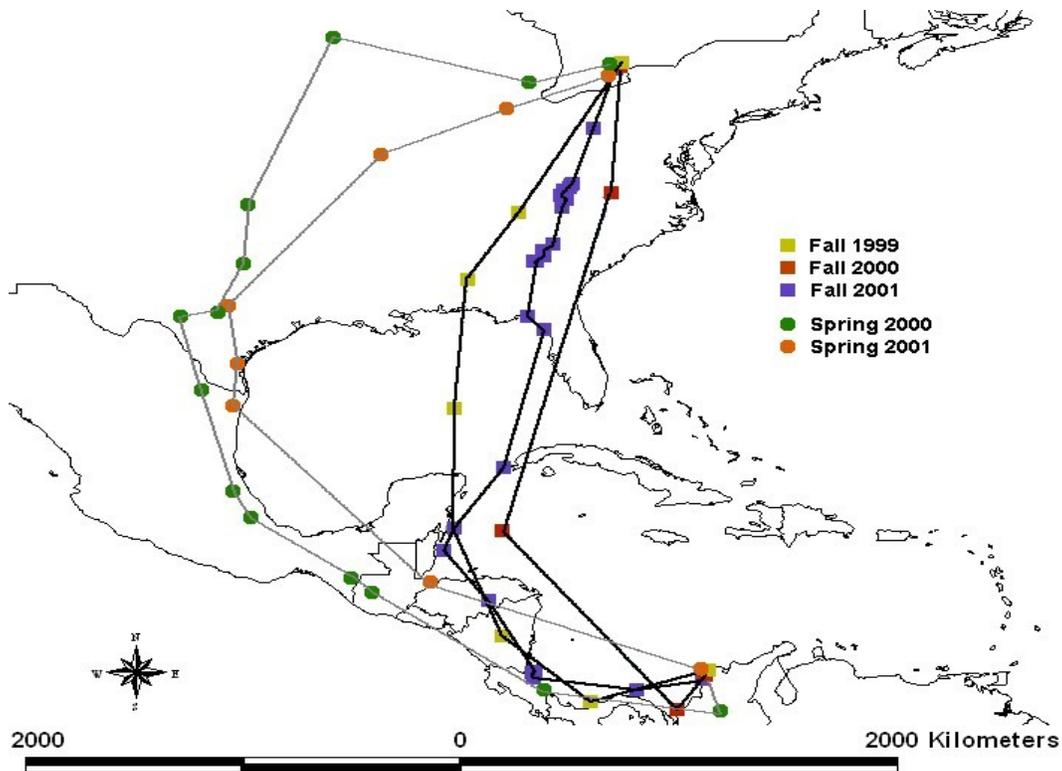


Figure 3-5. Comparison of routes over three fall and two spring migrations by the male peregrine Nate

### 3.5 Discussion

We observed considerable variability among the 34 individuals in our study. While few general conclusions can be drawn about the migratory behaviour of peregrines from our data, it is evident that age, sex, origin, and summer habitat of individuals may all have some degree of influence on migration. However, as all adults were from Alberta, we cannot separate effects of age and geography, and results relating to these factors must be interpreted with caution. To properly test for differences by age, an adequate sample of adults and juveniles from a single geographic area would need to be tested.

#### 3.5.1 Migration patterns

We found no difference in the timing of migration between juveniles and adults, which is consistent with observations at Assateague Island (Ward *et al.* 1988). Adults in our study migrated significantly farther than juveniles and traveled more than twice as rapidly, generally following more direct routes. Similarly, Hake *et*

*al.* (2001) observed that juvenile Honey Buzzards (*Pernis apivorus*) made many more changes of direction during migration, and took roughly 50% longer than adults to cover a similar distance. The more efficient travel of adults may to some degree reflect learned behaviour. Rapid migration, especially in spring, may also be an adaptation to return to breeding territories before potential competitors, and maintain an advantage in any battle for control of the territory. Ward and Laybourne (1985) observed that adult peregrines hunt more shorebirds on migration than do juveniles, and Newton (1979) suggested that variability in migration patterns by age or sex may be related to differences in food availability and preferences. However, considering the wide variety of prey targeted by peregrines, it seems unlikely that any such differences are great enough to influence migratory behaviour significantly.

Among juveniles, males traveled much greater distances than females. Whereas Ward *et al.* (1988) reported an earlier peak of males than females with a sample size of over 4700, we observed the opposite pattern, albeit our sample size of 24 was too small for the difference to be significant, given the variance observed.

Captive-bred juveniles in our study delayed their departure longer than wild-raised birds. This may be partly due to not being forced out of their territory by parents, but could also reflect an abundance of prey at sites selected for releases (Alonso *et al.* 1987, Watson 1997). Wild-raised birds undertook only short movements in fall, with 419 km being the greatest displacement, contrasting sharply with the captive-bred birds, all of which migrated a greater distance, the shortest being 483 km. The captive-bred birds were all from pure *anatum* lineage, while the wild birds were either known or strongly suspected to be of mixed heritage. These results therefore suggest that there may be a genetic component to migration in peregrines.

Juveniles from cliffs departed sooner than those in urban habitats. This is to be expected, given the seasonal fluctuations in availability of prey at rural sites compared to the year-round abundance of prey in cities. However, we caution that our sample size of rural birds ( $n = 4$ ) was too small to assess this difference with confidence.

Long-distance migrants in our study traveled at a mean rate of 165 km/day southbound and 178 km/day northbound, comparable to the 141 to 204 km/day reported by previous satellite telemetry studies on peregrines in both North America (Fuller *et al.* 1998, McGrady *et al.* 2002) and Eurasia (Ganusevich *et al.* 2004). Our rates of travel may have been somewhat underestimated, since they were based on cumulative distances between consecutive data points, and when these were several days apart, it is likely that the actual distance traveled exceeded the straight line distance to some degree. The faster pace of migration in spring is also consistent with previous studies on peregrines (Fuller *et al.* 1998, McGrady *et al.* 2002) and Prairie Falcons (*F. mexicanus*) (Steenhof *et al.* 2005). Our limited data on hourly rates of travel were near the lower end of the 35 to 70 km/hour range reported by Cochran and Applegate (1986) using radio telemetry.

All of the adults for which both fall and spring routes were documented returned to the same breeding territory, while all captive-bred juveniles went back to within 120 km of their release sites, reflecting the traditionally accepted tendency of peregrines to show natal philopatry (Temple 1988). Wild-raised juveniles established summer territories at least 240 km away, more typical of the pattern recently observed in the northeast, where most breeding adults with known origins settle a considerable distance from their point of origin.

As we only tracked two individuals for more than one year, we cannot draw any strong conclusions about long-term patterns of migratory behaviour of individuals. In both cases, strong fidelity was shown to wintering sites, and in the

absence of evidence to the contrary, it is likely that this is common for peregrines. The differences between juvenile and adult migration strategies were exemplified by Nate, the male we tracked over three years. In his second fall, he shortened the duration of migration by almost one-third, and improved his routing by flying via the Florida Keys and Cuba, rather than risking the longer open water crossing across the Gulf of Mexico as he did the previous fall. By his third fall, he had established a breeding territory and departed even later, with his rate of migration over twice as rapid as it had been as a juvenile. The fact that in subsequent years, after breeding successfully he ceased migrating reflects the plasticity of migratory behaviour in peregrines. It suggests that migration is practiced only when its benefits outweigh its costs, and that the risk of leaving a territory undefended may be greater than the cost of overwintering in the north.

### *3.5.2 Dispersal patterns*

Unlike migration, the timing and nature of dispersal from natal territories showed few patterns related to sex, origin, or habitat, despite varying considerably. While just over half (52%) of juveniles retained their natal territory as a home base until migrating, most of the others spent at least a few weeks at a separate staging area prior to migration. Those staging in urban areas may have been scouting for future breeding territories, since one of those individuals returned to the same location in its second summer. The two that staged at wetlands were likely attracted by a concentration of migratory waterfowl and shorebirds, as there were no suitable nesting possibilities near either location. Agricultural areas also lack nesting options, and while birds may be common there, most are typically small passerines rather than waterfowl or shorebirds. Of note perhaps, all three juveniles that staged in agricultural areas died within a month of settling there. Given that starvation is thought to be a common cause of death for young raptors (Newton 1979), it may be that these individuals were not sufficiently skilled hunters to kill enough small and agile prey. Contamination by agricultural pesticides is another possible explanation for their deaths.

### 3.5.3 *Geographic areas of importance for peregrines*

Several birds in our study crossed the Gulf of Mexico or traveled hundreds of kilometres over the open waters of the Atlantic Ocean. Whereas many raptors avoid crossing large bodies of water, peregrines are known to show little hesitation in this regard and have frequently been recorded offshore (Kerlinger 1985, White *et al.* 2002). In particular, oil platforms in the Gulf of Mexico have recently been reported to provide important resting and feeding opportunities for migrant peregrines (Russell 2005).

Long-distance migrants in our study followed a variety of routes, but two areas frequented by several individuals were the coasts of Texas and Florida along the Gulf of Mexico. Lott (2006) reported a mean annual count of 1908 peregrines at Curry Hammock State Park in the Florida Keys from 1999 to 2004, a number far higher than at any other North American raptor watch. However, at most four of the migrants in our study may have passed there, suggesting that despite the large numbers reported, the site may record only a minority of North American peregrines annually. The birds in our study that may have passed through the Florida Keys were in the area between 22 October and 6 November, considerably later than the median date of 3 October, peak date of 7 October, and 80% passage period of 26 September to 17 October reported by Lott (2006).

In spring, the west coast of the Gulf of Mexico has long been recognized as the only concentration of northbound peregrine migrants in North America (Yates *et al.* 1988). Our study supported this claim, as at least five of seven individuals that wintered south of the United States passed through this area, though their routes diverged quickly just to the north, generally moving from there to their summer territories in a fairly direct line. This pattern of movement reflects previous radio telemetry studies by Yates *et al.* (1988).

Yates *et al.* (1988) also concluded that a 'loop migration' in which peregrines migrate south along the Atlantic coast and north along the Gulf coast was rare,

based on just four recoveries in Texas out of 105 recoveries of birds banded on the east coast. However, in our study, both of the migrants that went south through Florida came back north via Texas, suggesting that it may be more common than previously believed. As spring migration is more rapid, it is likely that a smaller proportion of individuals linger long enough to be captured on their northbound travels, possibly accounting for them being undersampled in the previous study. While other raptors such as Osprey (*Pandion haliaetus*) (Hake *et al.* 2001) and Bald Eagle (*Haliaeetus leucocephalus*) (Laing *et al.* 2005) have been found to take a more direct route during spring migration compared to fall, our results suggests that the opposite is more often true for peregrines, especially for those following the loop migration pattern.

Also, most of the banding of migrants along the Atlantic coast takes place at Assateague Island, Maryland, which is believed to heavily sample the peregrine populations of Greenland and the eastern Canadian arctic (Enderson 1969a, Ward *et al.* 1988). This was supported by our telemetry data, which showed most individuals from the Great Lakes area following a more inland route along the Appalachians, with only two birds possibly passing over Assateague Island. Therefore, it may be that the arctic population rarely follows the 'loop migration' pattern, while the temperate eastern population does so more commonly.

Most individuals in our study showed a strong preference for coastal locations in winter, consistent with historical observations from eastern North America (Enderson 1965, Bonney Jr. 1979), band recovery data from throughout the wintering range (Schmutz *et al.* 1991), and telemetry findings from a Virginia-based study (Watts *et al.* 2002). The size of the winter territories observed in our study was similar to the mean radius of 10-14 km reported for peregrines wintering in south Texas (Enderson *et al.* 1995). As in their study, we found adults more likely to be sedentary or hold small territories than juveniles. This may reflect their dominance in displacing juveniles from the most productive

territories, or simply that adults as more experienced hunters do not require as large a prey base.

#### *3.5.4 Factors influencing migration*

Peregrines nesting in temperate eastern North America were historically non-migratory or weakly migratory (Enderson 1965), and therefore the large number of individuals from our study overwintering in the United States or Canada was to be expected. However, the tendency of almost all the captive-bred birds in our study to migrate long distances suggests that while they were of pure *anatum* ancestry, they were not necessarily representative of the historical eastern population. Rather, their movements had more in common with the Alberta birds we studied, perhaps a consequence of the initial captive-breeding population being dominated by peregrines from northwestern Canada (Fyfe 1988). Our results showing that more northern birds had a greater tendency to migrate long distances than those breeding farther south in eastern North America may simply reflect the pattern seen in Europe, where peregrines in the central and southern part of the continent migrate little if at all, but those from the north undertake long movements (Mearns 1982).

The influence of weather on the migratory behaviour of birds has been well documented (Titus and Mosher 1982, Kerlinger 1989, Bildstein 2006), but at few locations are peregrines sufficiently abundant to establish clear links between their passage and local weather patterns. One exception is Assateague Island, where the only weather conditions positively correlated with peregrine migration were increasing rain and decreasing barometric pressure (Titus *et al.* 1988). This is counter to the conditions favoured by most other raptors, and suggests that peregrines are less limited by inclement weather. Extreme conditions can still be an important factor, as reflected by as many as three individuals in our study that died while caught in hurricanes over the Caribbean. Slack and Slack (1981) suggest that peregrines may adapt the routing of their migration due to weather, and this was seen on at least two occasions in our study. A northbound migrant, adult female 24424, returned to North Dakota for a week after

encountering an April 2000 snowstorm in Manitoba, while the juvenile male, Lightning, flew to Haiti from Cuba in November 2001 to escape Hurricane Michelle approaching from the west, and thereby became the only individual in our study to winter in the Caribbean. Seegar *et al.* (2003) also documented hurricane avoidance by a peregrine.

### 3.5.5 Mortality

Half of the 28 juveniles in our study are known or presumed to have died within their first year of life. A review of 88 band recoveries by Yates *et al.* (1988) found that 62.5% of mortalities occurred during the first fall or winter, while first-year mortality for peregrines around the world has been variously reported as ranging from 30% to 70%, the highest extreme occurring in North America (Enderson 1969b, Mebs 1971, Olsen and Olsen 1988, Ratcliffe 1993). Thus, the results of our telemetry study actually show a higher rate of survival than expected. In a study of Alaskan Golden Eagles (*Aquila chrysaetos*), McIntyre and Collopy (2006) found a high level of survival during the post-fledging dependence period, with only one of 48 individuals dying prior to dispersal. Similarly, just one of our 28 juveniles died during that period. Mortality was greatest during the first few months of independence, a pattern also observed in a study of juvenile peregrines in Virginia (Watts *et al.* 2002). However, our results are somewhat biased in that a majority of birds were fitted with PTTs during their post-fledging dependence period, and individuals that had already died during early flights were therefore not part of the sample population. While storms claimed three individuals in our study, anthropogenic factors in the form of vehicle and power line collisions took a greater toll, accounting for at least four mortalities.

### 3.5.6 Study limitations and recommendations

Satellite telemetry provides a good description of long-distance travels, but is less well-suited to accurately assessing local movements (Chapter 2; Britten *et al.* 1999). As such, individual points during migration were not analyzed with respect to precise location or habitat type. Despite this, there was enough

clustering of data points at both summer and winter territories to permit at least a coarse assessment of habitat usage for some of the birds. The high level of fidelity of both urban and rural-raised individuals to similar environments on their wintering grounds is consistent with previous observations of low interchange between urban and cliff-nesting populations in the east (Cade and Bird 1990). The coexistence of these sympatric yet largely genetically separated populations could ultimately have interesting implications, potentially resulting in divergence if exchange between them remains minimal.

Financial and logistical restrictions precluded a balanced distribution of PTTs among our study populations, and this limited the power of some of our statistical analyses. In particular, too few rural birds were studied to permit a valid comparison between their migratory habits and those of urban birds. While the differences were not statistically significant, in several cases they were substantial enough to suggest a real pattern, worthy of further investigation. Similarly, while we studied only a few sets of siblings, it may be significant that those from wild nests shared similar migratory behaviour, while those that were captive-bred differed moderately to greatly. In the case of an individual remaining at the hack box, this may happen because of the absence of adults to drive it away, but differing behaviours among those that do migrate are less easily explained. Similar variability in migratory strategies has been noted previously in peregrines by Yates *et al.* (1988) and in Bald Eagles by Harmata (2002). While it has been demonstrated that migratory tendencies are heritable in some species (Berthold and Querner 1981), and this has been assumed to apply to peregrines (e.g. Schmutz *et al.* 1991), other factors may evidently override genetics. Further study of this, including satellite tracking of entire families, would be desirable.

Another priority for further study is to track more individuals over several years to investigate changes in migratory behaviour over time. Any future telemetry research should collect data on a daily basis, as the gaps in travel resulting from

the three- to 10-day duty cycles in our study left many potentially interesting details of migration undocumented. Also, as PTTs with precise GPS capability continue to become lighter, it will become possible to use these units on peregrines, permitting accurate assessment of their habitat usage during all parts of their life cycle.

Not all research into peregrine migration requires the use of satellite telemetry. Long-term standardized observational counts have been shown to provide a good index of population trends (Bednarz *et al.* 1990). Our results indicate that a substantial number of eastern peregrines migrate to or across the Caribbean. A better understanding of this population could be achieved by further expanding the network of raptor migration monitoring stations in that area, such as the trial sites established in Cuba in 2001 (Santana *et al.* 2003).

### **Connecting statement 3: Implications of variable dispersal and migration on the structure and composition of recovering populations**

Satellite telemetry has revealed that there is considerable variability in the migratory behaviour of individual peregrines in eastern North America, with some remaining sedentary while others undertake short or long-distance migrations. Such differences may in part be a consequence of the varied genetic backgrounds of individuals in the restored population. The detailed monitoring of nest sites in southern Ontario provides an opportunity to explore changes over time in the pedigree and population structure of a recovering population.

This manuscript is being submitted to the Journal of Raptor Research with co-authors D.M. Bird and T. Armstrong.

## **4 Origin, growth, and composition of the recovering Peregrine Falcon population in Ontario**

### **4.1 Abstract**

After an absence of over two decades, Peregrine Falcons (*Falco peregrinus*) resumed nesting regularly in Ontario in 1986. Between 1991 and 2006, at least 193 young in southern Ontario and 548 in northern Ontario are known to have fledged. The number of pairs, nesting attempts, successful nests, and young fledged have all steadily increased in both southern and northern Ontario. In southern Ontario, one quarter of adults have produced nearly half of all offspring, and 87% of young have been fledged from just eight sites. The age of breeding adults has increased over time, especially for females. Direction of dispersal has been variable, but females have consistently moved farther than males, and there has been frequent movement both to and from adjacent American states. The population recovery is the result of 592 captive-bred *F.p. anatum* juveniles hacked in Ontario between 1977 and 2005, and immigration from release efforts in adjacent regions of the United States, where at least five subspecies contributed to the gene pool of captive-bred birds. Recovery rates for both captive-bred and wild-fledged young in Ontario are low, but wild-raised young have been recruited to the breeding population almost twice as frequently. This in part accounts for the genetic composition of the southern Ontario population, where at most 21% of nesting attempts between 1995 and 2006 involved a pair of Canadian-released *anatum* adults, while in 59% of cases at least one adult was of American origin. Therefore, while the Ontario population now exceeds historical levels, it cannot be strictly considered an *anatum* population.

### **4.2 Introduction**

Historically, the Peregrine Falcon (*Falco peregrinus*; hereafter peregrine) was sparsely distributed across much of eastern North America, largely limited to remote cliffs (Hickey and Anderson 1969). This population was part of the *anatum* subspecies, but was sometimes considered a distinct form, known as the

Rock Peregrine or Appalachian Peregrine (Berry 2003). A rapid and drastic decline in peregrine numbers during the middle of the twentieth century was particularly dramatic in the east, causing this population to be declared extirpated (Fyfe *et al.* 1976). However, at least one nest site in southern Quebec remained active throughout the nadir of the population (Kiff 1988).

A large captive-breeding effort was initiated in the 1970s. The Canadian program used only *anatum* birds, mostly from near the northern limits of its range in the Yukon and Northwest Territories and Labrador (Fyfe *et al.* 2003). The American program used as many as seven subspecies from around the world, though the majority were from the three North American subspecies (*F.p. anatum*, *F.p. pealei*, and *F.p. tundrius*) and two European subspecies (*F.p. brookei* and *F.p. peregrinus*) (Temple 1988). Originally most releases were at cliffs, but the emphasis later shifted to cities or coastal towers due in part to high levels of predation by owls at cliff sites (Barclay 1988, Fyfe 1988).

Prior to the population decline, the eastern *anatum* peregrine was estimated to number 400 to 500 pairs, of which less than one-third were in Canada (Hickey 1942, Peakall 1990). The success of birds released from the captive-breeding program, and their progeny, has resulted in an eastern population which now rivals that historical number, and has prompted the removal of the species from the Endangered Species List in the United States (Mesta 1999) and a reduction in its status in Canada to threatened in 1999 (Johnstone 1999), then special concern in 2007 (COSEWIC 2007). The growth of the midwest population (ranging from North Dakota in the northwest to Kentucky in the southeast, and including southern Manitoba and the Lake Superior watershed of Ontario) has been documented in detail through annual reports produced by the University of Minnesota Raptor Center and partners since 1986 (e.g. Redig *et al.* 2007). While eastern states and provinces have also monitored population growth with various levels of consistency, no comparable publications exist for this region.

In eastern Canada, Ontario is the only province to have conducted full population surveys annually since 1990. The Ontario population is of particular interest, as it comprises two distinct components. In the northern part of the province, peregrines nest almost exclusively on cliffs, while in the southern part nearly all nests are in urban habitats. Cade and Fyfe (1970) considered only 29 historical nest sites in Ontario to be reliable, while Ratcliff and Armstrong (2002) identified 40 confirmed historical nest sites and an additional 8 suspected nest sites. All these estimates may somewhat under-represent the historical population, as observations from many remote parts of the province were limited. A nesting attempt in 1985 was the first documented since 1963 (Rowell *et al.* 2003). Nests producing young have been confirmed annually in northern Ontario since 1991, and in southern Ontario since 1995.

The objectives of our study were: 1) to document the growth of the southern Ontario population between 1995 and 2006; 2) to describe the geographic origin and pedigree of breeding adults, and changes in population structure over time; 3) to evaluate the success of the captive-breeding program in re-establishing an *anatum* population in southern Ontario, and 4) to compare these parameters with data available for northern Ontario between 1991 and 2006.

## **4.3 Methods**

### *4.3.1 Data sources*

We collected data for southern Ontario nesting attempts through direct observation, supplemented by databases maintained by the Canadian Peregrine Foundation (CPF) and the Ontario Ministry of Natural Resources (OMNR). Many nest sites were monitored daily or weekly throughout the year by local observers. Data for northern Ontario were for the Lake Superior basin, as reported in the annual Midwest Peregrine Falcon Restoration reports, based on OMNR helicopter surveys and banding efforts. Banding recovery data were obtained from the Bird Banding Office (Ottawa, Ontario) in 2007 for all peregrines banded or recovered in Ontario since the recovery effort began in 1975.

#### 4.3.2 *Data conventions*

We defined the dividing line between southern and northern Ontario to be 46.5°N, consistent with the Lake Superior basin representing northern Ontario in midwest reports (e.g. Redig *et al.* 2007). However, this differs from the terminology used by the Canadian peregrine surveys (e.g. Rowell *et al.* 2003) in which all known nest sites were considered to be in southern Ontario.

Definitions with respect to territories are consistent with those used in recent Canadian surveys (Murphy 1990, Holroyd and Banasch 1996, Rowell *et al.* 2003). An occupied site is defined as a location with a single adult or a pair of territorial adults. A territorial pair is one defending a nest site or persistently occupying it, a breeding pair is one that laid at least one egg, and a successful pair is one that raised at least one young to fledging. We additionally defined core nesting sites as those where breeding has occurred at least four times, and in a minimum of 90% of years since first occupied. Nesting success is defined as the production of at least one fledged juvenile.

In most cases, adults were considered to be recognizable individuals only if banded and of known origin. In southern Ontario, there were four exceptions to this rule, where birds unbanded or with bands that could not be fully read were virtually certain to be the same individuals from year to year due to a combination of band placement, distinct facial patterns, or consistent behaviour. Individuals produced through the Canadian captive-breeding program and their direct descendents were considered by definition to be of pure *anatum* heritage (Fyfe 1988). Unbanded birds were treated as being of unknown genetic heritage, and American birds were assumed to be of mixed heritage (Tordoff and Redig 2001), but the genealogy of individuals was not specifically traced.

#### 4.3.3 *Data analysis*

All statistical analyses were conducted using SPSS 9.0 (SPSS Inc, Chicago, Illinois) and techniques outlined by Zar (1999). Generalized linear models were

used to evaluate population trends over time. Sex ratios were evaluated using a binomial test. Directionality of dispersal was assessed using Rayleigh's test. Productivity was considered zero if no fledglings were observed, and one in the minority of cases where an unspecified number of fledglings were reported. Productivity and dispersal distances were both not normally distributed, therefore comparisons between groups were made using the Mann-Whitney test.

#### **4.4 Results**

Between 1977 and 2005, 592 captive-bred juvenile peregrines were released at hack sites across Ontario (Ratcliff and Armstrong 2008). The first nesting attempt in northern Ontario was recorded in 1986, while the first successful nest in southern Ontario was in 1995. Between 1991 and 2006, 193 wild young are known to have been produced in southern Ontario and 548 in northern Ontario.

##### *4.4.1 Population growth*

In southern Ontario, 93% of territorial pairs observed between 1995 and 2006 made nesting attempts, 74% of which were successful. In northern Ontario, the frequency of nesting attempts by territorial pairs between 1991 and 2006 was lower at 84%, but the success rate of 91% was higher. Both in southern and northern Ontario, the number of pairs, nesting attempts, and successful nests increased steadily during the study period (Figure 4-1). In southern Ontario, the average increase has been 0.6 nests per year ( $r^2 = 0.73$ ,  $P < 0.001$ ) since 1995, while in northern Ontario it has been 2.0 nests per year since 1991 ( $r^2 = 0.91$ ,  $P < 0.001$ ).

Trends in productivity (Figure 4-2) largely reflect the observed increases in successful nesting attempts. The southern Ontario output has increased at an average rate of 1.8 young per year ( $r^2 = 0.61$ ,  $P = 0.003$ ), peaking at 33 in 2005. In northern Ontario, the average increase has been 5.1 young per year ( $r^2 = 0.92$ ,  $P < 0.001$ ), peaking at 79 in 2005. Captive-bred young released at hack sites in northern and southern Ontario have over time contributed proportionately less to

the annual total of young fledged. The captive-bred young released in the north represent 11% of the total number fledged there since 1991; the corresponding value for captive bred young released in the south is 23%.

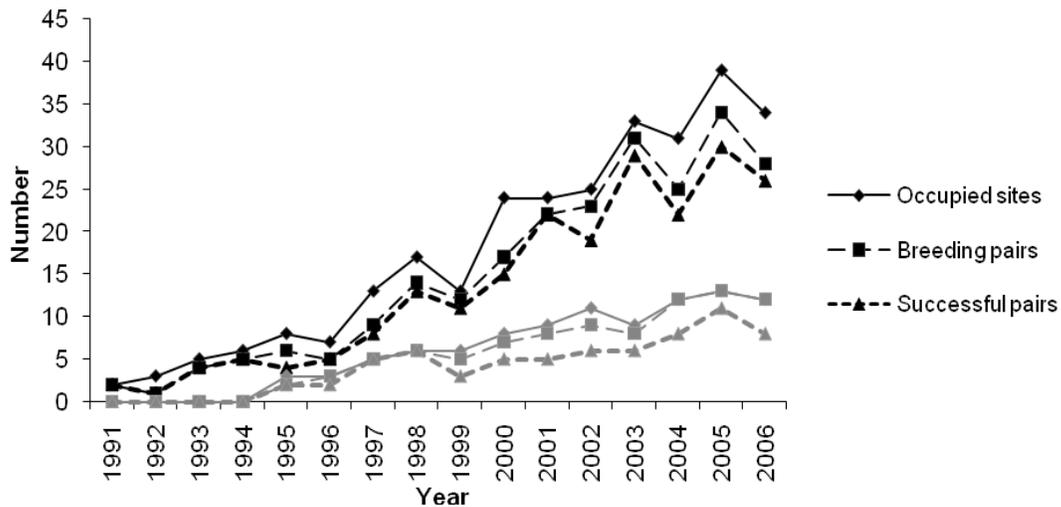


Figure 4-1. Increases in occupied sites, breeding pairs, and successful peregrine nests in southern (gray) and northern (black) Ontario, 1991-2006.

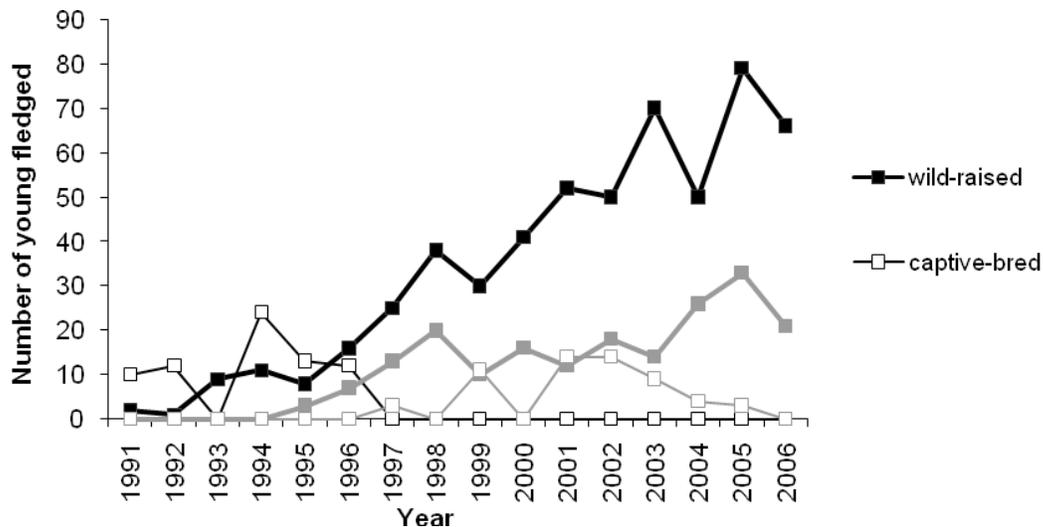


Figure 4-2. Number of wild-raised and captive-bred young peregrines successfully fledged in southern (gray) and northern (black) Ontario, 1991-2006.

Both in southern and northern Ontario, core locations represented a minority of nest locations but accounted for a majority of nesting attempts (Table 4-1). Nesting attempts were more frequently successful at core sites, and the number of young fledged per nesting attempt was greater at core sites than elsewhere in both southern ( $U = 393.0$ ,  $P = 0.001$ ) and northern Ontario ( $U = 5984.5$ ,  $P < 0.001$ ). Among successful nests, the number of young fledged per attempt was not significantly higher at core sites in southern Ontario ( $U = 217.0$ ,  $P > 0.1$ ), but was higher at core sites in northern Ontario ( $U = 3324.5$ ,  $P < 0.001$ ). In the early years of population recovery, activity was concentrated at core sites in both southern and northern Ontario, but over time the proportion of annual nesting attempts at core sites in both regions has declined to fewer than two-thirds of occupied sites in any given year, and fewer than half of all the sites that have been used (Figure 4-3).

Table 4-1. Comparison of peregrine nesting attempts and nesting success at core nest sites and other nest sites in southern and northern Ontario

	Southern Ontario	Northern Ontario
<b>Core nest sites</b>		
Number (and percent) of locations	8 (42%)	20 (34%)
Number (and percent) of nesting attempts	68 (76%)	182 (59%)
Number (and percent) of successful nesting attempts	57 (84%)	151 (83%)
Mean $\pm$ SE fledged per nesting attempt	2.47 $\pm$ 0.18	2.34 $\pm$ 0.10
Mean $\pm$ SE fledged per successful nesting attempt	2.95 $\pm$ 0.15	2.77 $\pm$ 0.08
<b>Other nest sites</b>		
Number (and percent) of locations	11 (58%)	38 (66%)
Number (and percent) of nesting attempts	22 (24%)	124 (41%)
Number (and percent) of successful nesting attempts	10 (45%)	66 (53%)
Mean $\pm$ SE fledged per nesting attempt	1.14 $\pm$ 0.31	1.15 $\pm$ 0.12
Mean $\pm$ SE fledged per successful nesting attempt	2.50 $\pm$ 0.34	2.17 $\pm$ 0.12

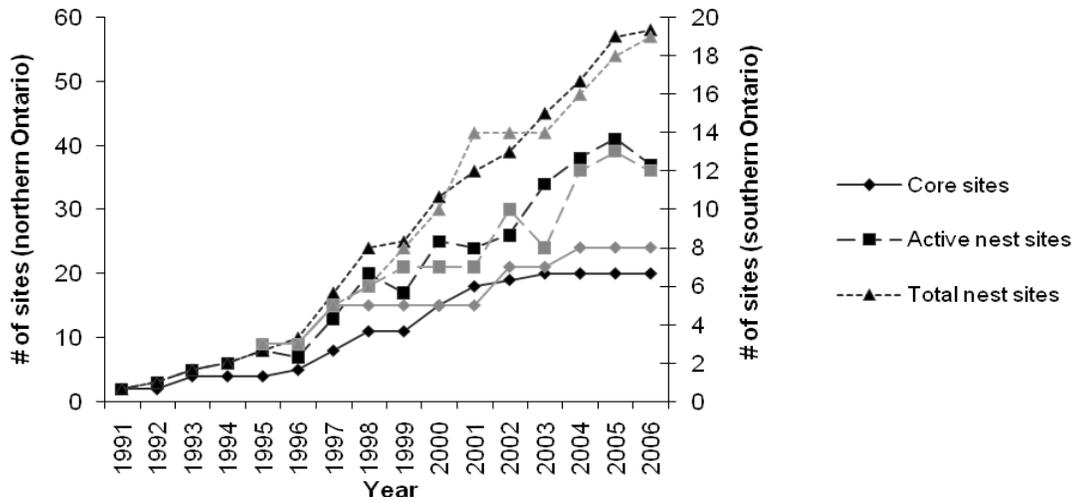


Figure 4-3. Growth in the number of core sites and active sites used annually by peregrines, and the cumulative total number of nest sites that have been used at least once in southern (gray) and northern (black) Ontario.

#### 4.4.2 Population structure

In southern Ontario, the age of breeding adults was known for 73% of nesting attempts by males and 62% by females. The mean age of breeding females increased significantly over time ( $r^2 = 0.80$ ,  $P < 0.001$ ), from an average of 1.8 years of age during the first four years (1995 - 1998) to 4.8 during the last four years (2003 - 2006) (Figure 4-4). Breeding males showed a minor non-significant increase in age over time ( $r^2 = 0.22$ ,  $P = 0.13$ ), from 3.2 during the first four years to 4.1 during the last four years. In northern Ontario, age of breeding adults was known in only 12% of cases, and as such, the mean age of those identified cannot necessarily be considered representative of the population. The gradual increase in the observed mean age of males is largely attributable to a single individual breeding at Lake Superior Provincial Park from 1993 through 2005 that skewed the mean upwards in later years. With that bird removed, neither sex shows any trend over time in northern Ontario (males  $r^2 = 0.001$ ,  $P = 0.92$ , females  $r^2 = 0.05$ ,  $P = 0.47$ ).

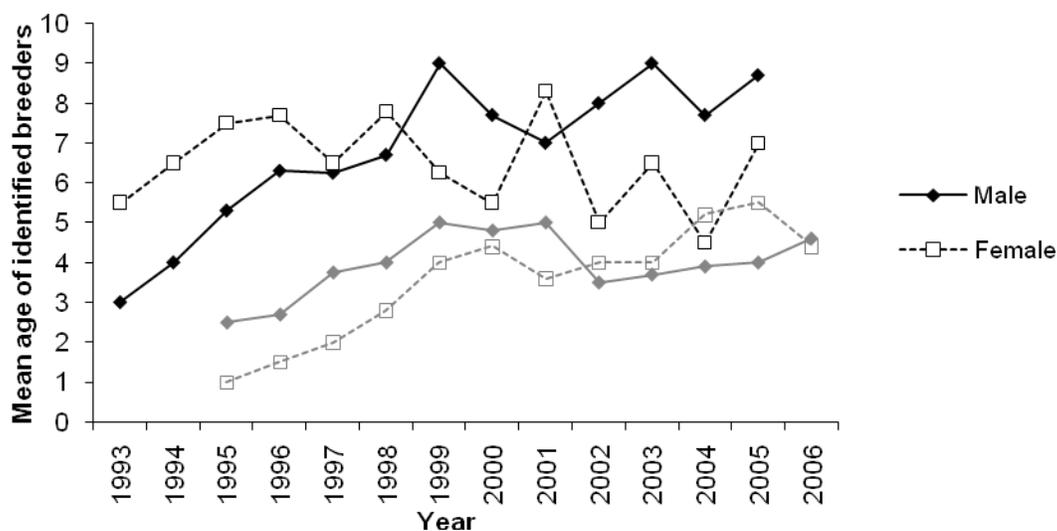


Figure 4-4. Mean age (in years) of identified breeding adult peregrines in southern (gray) and northern (black) Ontario.

Between 1995 and 2006, the sex of all but two of the 193 young fledged from nests in southern Ontario was determined. Overall, the sex ratio among fledglings did not differ significantly from the expected 1:1 ratio (47% males, 53% females; binomial test  $P = 0.39$ ). In northern Ontario, sex was determined only for the 336 (61%) nestlings that were banded. Within that sample, the pattern was the reverse of that in southern Ontario, with 54% males and 46% females, but was also not significantly different from 1:1 (binomial test  $P = 0.17$ ). Though the overall ratio is fairly even, in some years it was considerably skewed, most notably in 2006 when 81% of young produced in southern Ontario were female. Similarly, certain parents had a lifetime output skewed to one sex (Table 4-2). Of the 18 adults that have produced a minimum of 10 offspring in Ontario since 1991, six produced more than twice as many males as females, although the difference was significant only for one pair in Etobicoke.

Of 22 males breeding in southern Ontario since 1995, the six (27%) listed in Table 4-2 have accounted for 53% of all young fledged; the top six (25%) of 24

females have produced 49% of young. Four (18%) males and five (21%) females have nested but were unsuccessful in producing any offspring.

Table 4-2. Adult peregrines breeding in southern (S) and northern (N) Ontario known to have fledged at least 10 offspring. Individuals known to be pure *anatum* are marked with an asterisk (\*). P-values are highlighted in bold for individuals with a significantly skewed sex ratio among offspring.

Location	Years	Individual	Sex	# young produced			Total	Binomial test
				M	F	Unknown		
Devil's Warehouse (N)	1993-2005	816-81148*	M	9	5	18	32	p=0.424
Toronto (S)	1995-2002	1807-44110 ("Victoria")	F	10	19		29	p=0.137
Toronto (S)	1995-2002	2206-13765 ("Kingsley")	M	10	19		29	p=0.137
Devil's Warehouse (N)	1993-2001	877-42523 ("Poindexter")	F	8	3	16	27	p=0.227
Thunder Cape (N)	1993-2000	2206-13824	M	5	7	13	25	p=0.774
Toronto (S)	2003-2006	816-81882 ("Windwhistler")	M	12	9		21	p=0.664
Thunder Cape (N)	1993-1998	987-20758	F	4	3	13	20	p=1.000
Hamilton (S)	2001-2006	1807-44149 ("Madame X")	F	8	11		19	p=0.648
Ottawa (S)	1997-2006	unbanded ("Connor")	M	10	7		17	p=0.629
Ottawa (S)	1997-2005	727-03970 ("Horizon")	F	9	7		16	p=0.804
Hamilton (S)	1995-2001	816-33725* ("Dad")	M	8	7		15	p=1.000
Squaretop Mt (N)	1997-2000	987-86268*	F	5	2	5	12	p=0.453
Squaw Bay (N)	1998-2001	1807-53805 ("Rose")	F	5	7		12	p=0.774
Etobicoke (S)	1997-1999	1807-14062* ("Alberta")	F	7	3		10	p=0.344
Etobicoke (S)	1997-1999	2206-24602 ("Toby")	M	7	3		10	p=0.344
Etobicoke (S)	2000-2002	unbanded ("Angel")	F	9	1		10	<b>p=0.021</b>
Etobicoke (S)	2000-2002	816-81880 ("Marco")	M	9	1		10	<b>p=0.021</b>
Toronto (S)	2003-2005	2 D ("Mandy")	F	7	3		10	p=0.344

#### 4.4.3 Origin and dispersal

The origin is known for 21 males and 22 females that have bred in Ontario since 1991. Just under half of these breeders came from outside Ontario (12 of 24 in southern Ontario, 9 of 19 in northern Ontario). Males breeding in southern Ontario arrived from slightly closer natal sites ( $206 \pm 58$  km,  $n = 13$ ) than females

( $243 \pm 59$  km,  $n = 11$ ;  $U = 58.5$ ,  $P > 0.1$ ). The difference was more pronounced in northern Ontario, where males ( $261 \pm 193$  km,  $n = 8$ ) dispersed much shorter distances than females ( $446 \pm 127$  km,  $n = 11$ ;  $U = 16.0$ ,  $P = 0.020$ ). All movements were under 700 km, except for a female released from a hack box in Parc du Bic, Quebec, that nested 1540 km to the west at Sibley Peninsula, and a male from a hack release at Five Islands, Nova Scotia that nested 1600 km to the west at Devil's Warehouse in Lake Superior Provincial Park. At the opposite extreme, one female and two males nested where they were released or raised, while a third male moved only a few kilometres to a nearby cliff.

Since the beginning of the release program, 17 males and 26 females hacked or fledged in Ontario are known to have produced at least 344 offspring. Males from southern Ontario dispersed  $129 \pm 49$  km ( $n = 10$ ), much less than the  $379 \pm 58$  km by females ( $n = 16$ ;  $U = 29.5$ ,  $P = 0.016$ ). Results were similar for males from northern Ontario, which dispersed  $139 \pm 62$  km ( $n = 7$ ), compared to  $333 \pm 71$  km for females ( $n = 10$ ;  $U = 17.5$ ,  $P < 0.1$ ). The greatest distance traveled from Ontario was by a captive-bred female released in Toronto, found nesting 695 km to the east in Boston, Massachusetts. Mean dispersal distance decreased over time both for adults breeding in Ontario ( $r^2 = 0.50$ ,  $P = 0.002$ ) and those originally from Ontario ( $r^2 = 0.31$ ,  $P = 0.02$ ) (Figure 4-5).

The mean direction of dispersal of adults that bred in Ontario was nearly due north ( $357^\circ$ ) and significantly non-random (Rayleigh's test,  $Z = 2.65$ ,  $P = 0.009$ ). Both in southern and northern Ontario, identified breeding adults came more frequently from the southwest (i.e. headed northeast) than any other direction (7 of 22 in southern Ontario and 5 of 17 in northern Ontario). For adults originating in Ontario, the most common direction of dispersal was the opposite, as 7 of 16 from southern Ontario and 10 of 24 from northern Ontario headed southwest (Figure 7-6). Individuals from Ontario also often moved along an east-west axis, but rarely dispersed north or south; the mean direction of dispersal was southwest ( $237^\circ$ ) and was significantly non-random (Rayleigh's test,  $Z = 6.18$ ,  $P$

= 0.002). At least three instances are known where an individual returned to the city of origin of one of its parents: a female from Rochester returned 155 km NW to Toronto where her father had hatched, a female from Niagara Falls returned 175 km W to London where her mother had hatched, and a female from Hamilton returned 250 km SW to Cleveland where her father had hatched.

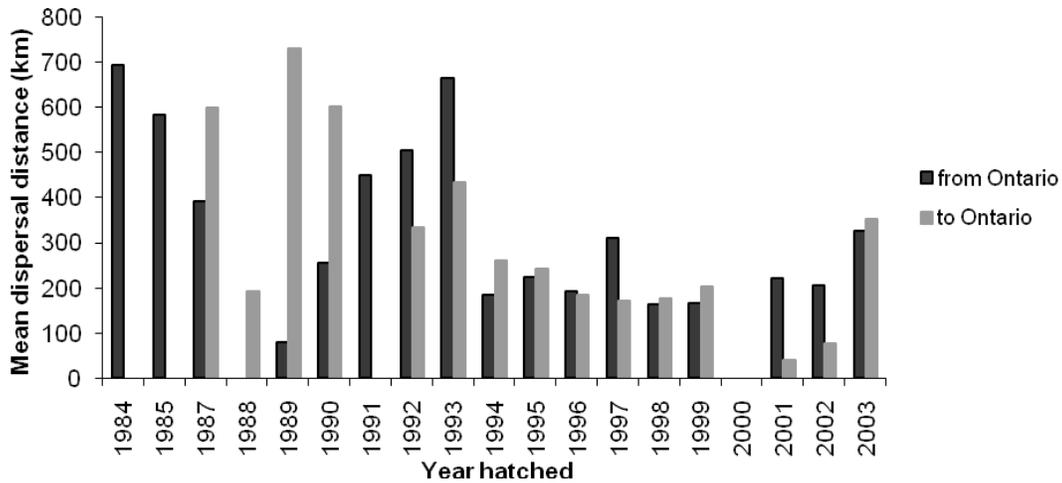


Figure 4-5. Mean distance of dispersal for adult peregrines breeding in Ontario, and adults originating in Ontario; note that the only breeding adult produced in 2000 subsequently nested at the location where it had hatched.

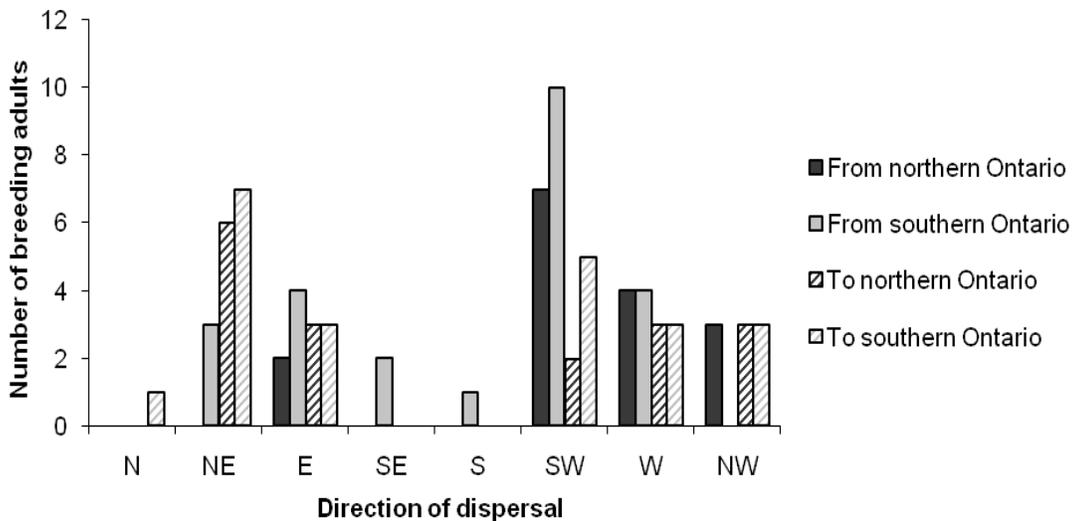


Figure 4-6. Direction of dispersal of breeding adult peregrines originally from Ontario, or nesting in Ontario.

Across Ontario, just four of the 18 most productive breeders are known to be *anatum* (Table 4-2), and within southern Ontario, only seven of 46 breeders were known to be *anatum*. Only in one case did two such adults pair up, in London in 1996 and 1997, producing just four (2%) of the 193 young fledged in southern Ontario (Table 4-3). One of their offspring was the only southern Ontario adult known to nest on a cliff. Pairings between American immigrants were the most common, accounting for 21% of nesting attempts and 22% of young fledged, while at least one American parent was involved in 59% of nesting attempts and 58% of young fledged. Even if all unbanded young are assumed to be *anatum* (unlikely), *anatum* pairings would account for only 21% of nesting attempts and 20% of young fledged.

Table 4-3. Origin of breeding female (rows) and male (columns) peregrines in southern Ontario, 1995-2006 (number of pairs – number of nesting attempts – number of young fledged).

	<i>anatum</i>	American	American/ <i>anatum</i> <sup>a</sup>	unknown <sup>b</sup>
<i>anatum</i>	1 – 2 – 4	1 – 3 – 10	1 – 1 – 4	1 – 1 – 3
American	5 – 11 – 25	5 – 19 – 42	5 – 14 – 21	1 – 2 – 8
American/ <i>anatum</i> <sup>a</sup>	none	1 – 2 – 3	none	1 – 9 – 13
unknown <sup>b</sup>	1 – 4 – 9	2 – 2 – 2	2 – 8 – 26	5 – 12 – 23

a – represents the offspring of an American x *anatum* pair

b – indicates unbanded adults

Throughout Ontario, only seven male and seven female *anatum* adults are known to have bred, all of which were releases from the Canadian breeding program except one second-generation female produced by the pair of *anatum* adults in London in 1996. The mean dispersal of *anatum* adults breeding in Ontario was  $404 \pm 143$  km ( $n = 14$ ), considerably greater than for others ( $238 \pm 38$  km,  $n = 29$ ), but this was largely due to the two individuals that immigrated from eastern Canada, and even without discounting those outliers the difference between groups was not significant ( $U = 192$ ,  $P > 0.1$ ). For adults from Ontario,

mean dispersal distance was again non-significantly greater for *anatum* birds ( $319 \pm 55$  km,  $n = 17$ ) than others ( $247 \pm 43$  km,  $n = 26$ ;  $U = 174.5$ ,  $P > 0.1$ ).

All of the 592 juveniles hacked and 531 (72%) of the wild-produced fledglings in Ontario (94% of those in southern Ontario and 65% of those in northern Ontario) were banded. Of 159 peregrines from Ontario for which band recoveries exist, 80 (50%) were recorded in Ontario. Those 80 individuals represent 68% of the peregrine band recoveries that have been reported in Ontario. The discrepancy is largely due to the many individuals banded in Ontario that have been observed or recaptured during migration or on wintering grounds, with 11 records from Central/South America, and another 13 from the southeastern United States.

Overall, 7.6% of individuals are known to have survived at least one year, while 11.8% have eventually been recorded as dead, and 80.7% have never been reported at all. Wild birds have only been banded since 1995. Of those recovered within their first year, nearly two-thirds were dead, compared to slightly under half of hacked birds (Table 4-4). However, only 16 (2.7%) juveniles hacked in Ontario are known to have survived to breed, compared to 27 (5.1%) wild-raised juveniles.

Table 4-4. Summary of recoveries of peregrines banded in Ontario.

Origin	Period	# banded	Alive at 1 yr	Known fate at 1 yr	% survival	Dead
Captive	1975-1994	414	43 (10.4%)	80 (19.3%)	53.8	54 (13.0%)
	1995-2006	178	13 (7.3%)	29 (16.3%)	44.8	18 (10.1%)
	1975-2006	592	56 (9.5%)	109 (18.4%)	51.4	72 (12.2%)
Wild	1995-2006	531	29 (5.5%)	78 (14.7%)	37.2	60 (11.3%)

## **4.5 Discussion**

Since 1991 both southern and northern Ontario peregrine populations have grown significantly. Although productivity in 2006 was lower than in 2005, the overall trend remains positive, and there has not yet been any sign of population growth leveling off. While we believe that all nesting attempts in southern Ontario have been documented, we acknowledge that even in urban areas nesting activity may occasionally escape detection (Redig and Tordoff 1992a). The northern Ontario count likely underestimates the actual total due to the remoteness of many nest sites and less observation time per location. The higher rate of nesting success reported for northern Ontario may be an artifact of some cliff nests having failed early in the season and not even being documented as attempts. Meanwhile, productivity in northern Ontario was slightly lower, and may have even been overestimated since young three to four weeks old were assumed to subsequently fledge, but may not all have done so. The much higher population in northern Ontario reflects the larger area compared to southern Ontario, and greater availability of natural cliff nest sites. However, the carrying capacity of the new urban population in southern Ontario has yet to be determined, as it is continuing to expand both within the areas that have already been colonized, and to new cities and towns.

### *4.5.1 Nest site fidelity*

Whereas early in the Canadian recovery program many pairs nested only for one year before disappearing again (Holroyd and Banasch 1990), we documented many pairs in Ontario that returned over a period of several years, with at least 13 individuals recorded at the same location for four or more years. Occupancy of nest sites varies annually, but has historically been estimated at 80-90% of suitable locations in stable populations (Hickey and Anderson 1969, Ratcliffe 1993). In Ontario, the population has yet to plateau, therefore it is difficult to estimate the number of suitable nest sites, especially in southern Ontario where peregrines were historically limited to isolated cliffs, but now have a large and ever-increasing selection of tall buildings upon which to nest. Monitoring of the

Ontario population indicates that some nest sites are clearly preferred, with eight locations in the south and 19 in the north having been occupied annually since the first nesting attempt was made. From 2003 to 2006, only 57-75% of nest sites that have been used in the south since 1995 and 64-76% of those used in the north since 1991 were occupied each year, somewhat lower than the 84% occupancy between 1999 and 2002 at nest sites in the United States (USFWS 2003). The relatively low occupancy in Ontario suggests that some of the locations used only once or twice were of marginal quality, a conclusion also supported by the significantly greater productivity at core sites.

#### *4.5.2 Population structure*

Early in the midwest recovery, over 10% of breeding peregrines were second-year birds, but by 1998 they had dropped to under 1% (Tordoff *et al.* 1998). In southern Ontario we documented several second-year and third-year females breeding during the first few years of the population's recovery, but few in later years. For males the trend was different, with no records at all of second-year individuals attempting to breed. This is consistent with the observation by Wendt and Septon (1991) that among second-year peregrines in Wisconsin, males bred much more rarely than females. Grier and Barclay (1988) anticipated that the age of first breeding would increase along with rising population density, which appears to be the case in southern Ontario. More generally, competition for nesting sites is known to limit breeding by young raptors, which are typically less efficient hunters, have more difficulty defending territories, and tend to be limited to lesser quality territories (Hagar 1969, Newton and Mearns 1988). Overall, only a few second-year breeders were detected in Ontario. Perhaps this was in part because the population growth was not solely dependent on the release of captive-bred juveniles, as nearly half of the adults breeding in Ontario were immigrants from the US, where the population began to re-establish somewhat earlier. In northern Ontario, the mean breeding age for both sexes tended to be greater than in southern Ontario, but this may well be an artifact of the small percentage of northern birds for which age was known, biased by older

individuals that were recognized year after year. However, the greater availability of prey at urban territories in southern Ontario may facilitate nesting by younger birds (Wendt and Septon 1991).

Olsen and Cockburn (1991) reported that peregrines produce more female than male offspring, but Redig and Tordoff (1994b) noted a balanced sex ratio in the midwest population. We found that the overall sex ratio among individuals produced in Ontario since 1991 was also balanced, though at smaller temporal or spatial scales, some significantly skewed ratios were observed.

#### *4.5.3 Dispersal*

Tordoff and Redig (1997) reported the mean dispersal distance of females in the midwest to be nearly double that of males, Burnham *et al.* (1988) found a four-fold difference in the US Rockies, and Holroyd and Banasch (1990) documented an over five-fold difference in Canada, though the difference was not significant due to high variability. We found results in Ontario to be most similar to those from the midwest, in that females dispersing from Ontario traveled on average more than twice as far as males. While the pattern also held for adults dispersing to Ontario, the difference was smaller, and not even significant in southern Ontario. Female-biased dispersal is common for a variety of bird species (Greenwood 1980), and has been documented in several other peregrine populations (Newton 2003). Tordoff *et al.* (2003) proposed that for peregrines, female dispersal distance may be greater as they are restricted to finding unmated males, whereas males may settle at the nearest available suitable nest site. This may explain the greater similarity in southern Ontario, where nesting opportunities are largely clustered in cities. Thus, females may not have to travel as far to find an unmated male with a suitable nest site. Our observations in Ontario differed considerably from earlier assessments of the Canadian release program, in which the majority of individuals returned to their release sites (Holroyd and Banasch 1990). We noted returns for <1% of birds

(though more may have done so without being documented, especially if visits were only temporary).

Early in the American reintroduction program, dispersal was limited, raising concerns about the potential for inbreeding (Temple 1988). Tordoff and Redig (1999) postulated that the short dispersal distances were a function of the high availability of suitable territories nearby, while over time the saturation of these sites demanded that individuals travel farther to find unoccupied sites. The opposite pattern was observed in Ontario, with mean dispersal distance both in the north and south decreasing over time as the population increased. To some extent, peregrines attract other peregrines. Therefore, early settlers in Ontario may have skipped over potential territories where no other peregrines were present, whereas more recently, the existence of territorial pairs has attracted others to the area.

The midwest and southern Ontario populations differ considerably in terms of dispersal. Although Ontario is almost half as large in area as the 13 midwestern states, nearly half of breeders identified to date in Ontario came from outside the province. However, by 2002, only 5% of identified breeders in the midwest were from outside the region (Tordoff *et al.* 2002). The composition of the Ontario peregrine population is therefore influenced by the populations of adjacent states.

#### *4.5.4 Survivorship*

Redig and Tordoff (1994a) expected a first-year survival rate of 40%, but documented a rate of only 33% and suggested that the discrepancy could be accounted for by 10% of nesting pairs being missed. Enderson (1969b) estimated 30% first-year survival based on banding recoveries. Results were very different in Ontario, where fewer than 8% of young banded are known to have survived to at least one year. There may be some undiscovered nests in northern Ontario, as most of the annual helicopter surveying is concentrated

along the Lake Superior shoreline, despite some suitable habitat existing inland too. Moreover, it is likely that individuals are being identified in Ontario less frequently, as access to most of the northern Ontario sites is limited, and adults have been recognized in only 12% of breeding attempts despite a majority of them being banded. Similarly, whereas Tordoff and Redig (1999) reported that 21% of peregrines fledged in the midwest through 1998 were known to have become breeders, we documented this for only 2.5% of those fledged in Ontario. The discrepancy in success between Canadian and American release programs was noted previously by Peakall (1990), who observed that one possible explanation was a net emigration of peregrines from Canada. However, for Ontario, we found that among banded birds there were nearly identical rates of emigration and immigration over the past 25 years, and therefore underestimation due to survey limitations may be a better explanation.

A more realistic estimate of survival for the Ontario population may be calculated as the ratio of survivors to deaths among individuals with a known fate after one year. Over the 30 years since releases began in Ontario, this generates a first-year survival estimate of 45%. While it might seem more likely for deaths to go unreported, this may be offset by the difficulty in reading the bands of live birds, especially in remote areas where few people may have only brief opportunities to spot them. However, as 83% of individuals have not been reported at all by the end of their first year, any estimates derived from such statistics are likely subject to considerable error.

#### *4.5.5 Evaluation of hack releases*

As early as 1992, Redig and Tordoff (1992b) felt there was no need for additional releases of captive-bred peregrines in the midwest. As the Ontario population was slower to re-establish itself, OMNR supported releases until 1996, and a small number of additional releases continued as late as 2005. The last few, at a cliff site in eastern Ontario, were in part to promote the re-establishment of the population that occurred there historically. However, peregrines have proven to

be efficient at occupying suitable nest sites (Redig and Tordoff 1992b). The dispersal distances documented for Ontario peregrines suggest that they have had ample opportunity to recolonize this area, but have chosen not to, perhaps suggesting the habitat is of marginal quality (Armstrong 2007).

Hacked young in the midwest consistently had greater survival than those bred in the wild (Tordoff and Redig 1997). This is perhaps a function of human attendants being able to ensure an adequate source of prey more consistently, given that weight at fledging is positively correlated with first-year survival for many raptors (Newton 1979). It may also be that by virtue of being more closely monitored, hacked birds that encountered problems on their early flights were rescued more frequently. While hacked birds also had a higher first-year survival rate in Ontario, wild-raised individuals from the province have become successful breeders nearly twice as frequently. As Tordoff *et al.* (1996) noted, the quantity of young fledged is ultimately less significant than their quality, as measured by their future reproductive contribution to the population. In this respect, recovery data indicate the captive-bred birds in Ontario were inferior to those produced in the wild. While captive-bred birds were initially essential to the re-establishment of the eastern peregrine population, the very low recruitment rate of 2.7% to the breeding population from Ontario releases suggests that there is no value in continuing to devote resources to hack releases, especially since the population is increasing naturally from the production of wild-raised birds.

#### 4.5.6 Pedigree

In the midwest, captive-bred and wild birds alike have typically been of mixed pedigree. Of a sample of 398 peregrines hacked in the U.S. midwest by 2002, none were pure *anatum*, while 68 were pure *pealei*, 3 were pure *brookei*, and the remainder had a mixed pedigree comprising between two and four of the five subspecies widely used in the U.S. breeding program (*anatum*, *tundrius*, *pealei*, *peregrinus*, and *brookei*) (Tordoff *et al.* 2003). The genetic composition of midwest breeders in 2002 closely reflected that of the population released (48%

*anatum*, 28% *pealei*, 10% *peregrinus*, 8% *brookei*, and 7% *tundrius*), including only a few pure *anatum* and *pealei* adults (Tordoff *et al.* 2003). In the eastern states, *anatum* genes were even less prominent, contributing only 18% to the gene pool among the first 758 captive-bred birds released between 1975 and 1985, compared to 45% for *tundrius* (Temple 1988).

On the contrary, while a majority of young produced in Ontario are of mixed pedigree by virtue of the many American birds breeding in the province, all captive-bred peregrines hatched in Ontario were pure *anatum*. The lower recruitment of the Ontario-hatched birds into the breeding population may therefore suggest that the peregrines of mixed heritage are better adapted to breeding in the east. While this seems counter-intuitive, given that this was in the range of the *anatum* subspecies historically, most of the *anatum* stock for the Canadian breeding program originated instead from the northern limits of the historical *anatum* range, where individuals were on average considerably smaller, and adapted to a different habitat and climate (Tordoff and Redig 2001). It may be that the broader genetic variability of the American birds has better enabled them to adapt to breeding in Ontario, especially in urban areas (Peakall 1990), though among the American releases themselves, differences in fitness among the five subspecies have not been observed (Tordoff and Redig 2003).

The growth of the Ontario population is reflected in the dramatic increase in the number of floaters. They quickly replace adults that are lost at existing sites, or with increasing frequency, battle them for territorial control. Several battles in the midwest have resulted in breeding adults being evicted from a territory or even killed (Tordoff *et al.* 1996). Redig and Tordoff (1994a) noted that in the new midwest population, migration might be maladaptive, as overwintering adults have an advantage in retaining control of territories. They further suggested that individuals descended from non-migratory races such as *pealei*, *peregrinus*, and *brookei* may be more likely to remain on territory year-round and have an advantage over those with a *tundrius* or *anatum* heritage. Lack (1954) noted that

selection should favour migration only if its benefits to survival and reproductive success are better than remaining on territory year-round. Therefore, if there is some genetic basis to migratory behaviour in peregrines, then those with such a tendency may be at a disadvantage in the current population. This has been documented for urban-nesting Merlins (*F. columbarius*) in Saskatchewan, where over-wintering adults tended to occupy better quality habitat than migrants (Warkentin *et al.* 1990). Historical records of peregrines overwintering in the midwest are scarce, and it is believed that the *anatum* population traditionally wintered farther south (Septon 2000), though some of the early urban sites in the east were occupied throughout the year (Hall 1955, Herbert and Herbert 1965).

The definition of subspecies has been a subject of much debate (e.g. Mayr 1982, Monroe Jr. 1982, O'Neill 1982, Phillips 1982). Peregrine subspecies have been particularly difficult to define, with considerable variation over time in the number accepted (White and Boyce Jr. 1988). The *tundrius* subspecies was only recognized in 1968 (White 1968), but recently microsatellite analysis has shown it to be indistinguishable from historical *anatum* samples, although it is distinct from the current eastern population (Brown *et al.* 2007). This supports Temple's (1988) contention that the recovering eastern population is genetically distinct from the original eastern *anatum* population and may in part account for the colonization of many new sites by the current population while some historically used cliffs remain vacant.

#### 4.5.7 Summary

The average of 46 territorial pairs recorded in Ontario between 2003 and 2006 is close to matching the total of 48 known and suspected territories prior to the population crash (Ratcliff and Armstrong 2002). In part this reflects the colonization of urban habitat in southern Ontario, where only a few cliff nests occurred historically, but the northern Ontario population alone is now almost comparable to the historical estimate. While documentation of nest sites was less comprehensive prior to the population crash, the current number of breeding

pairs nonetheless represents at a minimum a successful recovery, and may even be the largest total in the province's history. The Canadian recovery plan specified success as a minimum of 10 *anatum* pairs fledging a five-year average of at least 15 young annually by 1997 in five of six designated geographic zones, one of which includes both southern Ontario and the Lake Superior basin (Erickson *et al.* 1988). Although the number of peregrine pairs in this region met that target in 1997 (Ratcliff and Armstrong 2002) and now far exceeds it, our results suggest that at most 21% of pairings in southern Ontario have involved two *anatum* adults, even if all unbanded adults are assumed to be *anatum*. Since it is likely that some of those are also descended from American birds, the proportion is probably still lower. While there are likely at least some *anatum* pairs in northern Ontario, none have been confirmed since 1998, and in southern Ontario where our knowledge concerning the origin of peregrines is more extensive, the last known *anatum* pair bred in 1997. Therefore it seems unlikely that the goal of 10 *anatum* pairs breeding in Ontario has been met, nor that it ever will be, considering that over half the nesting attempts to date in southern Ontario have involved at least one American immigrant. However, this should not be construed as a failure. Rather, the growth of the Ontario population to record levels in the span of less than two decades since recovery began should be considered a great success, even if the population is genetically different from that which historically was present.

#### **Connecting statement 4: Defining characteristics of the emerging urban peregrine population**

In southern Ontario, growth in the peregrine population has occurred primarily in urban areas. A similar increase in urban-nesting peregrines has occurred throughout much of the former eastern range of the species. Assessing the recovery of the eastern population requires an understanding of the habitat preferences of urban peregrines, the risks they face, and their degree of dependence on human assistance.

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## **5 Productivity, mortality, and management of urban Peregrine Falcons in eastern North America**

### **5.1 Abstract**

The Peregrine Falcon (*Falco peregrinus*) population in eastern North America has grown significantly since the early 1980s, especially in urban areas. All documented nesting attempts from southern Quebec, southern Ontario, Pennsylvania, New Jersey, and Massachusetts from 1980 through 2006 were compiled and analyzed to evaluate factors affecting productivity. Of 801 nesting attempts, 663 were successful, producing a total of 1613 young. Mean productivity ranged from 1.7 young fledged per nesting attempt in New Jersey to 2.9 in Quebec. Peregrines nesting in quarries or on buildings had higher productivity than those using marsh towers or bridges, but productivity did not differ overall between urban and rural sites. Nests with overhead cover had higher productivity than those without, as did nests in trays or boxes compared to sites without any human-provided nesting aids. Peregrines favoured nest sites facing east to south, but productivity did not vary significantly with direction. Several adults have contributed disproportionately to the growth of the eastern population. Of over 350 identified breeders, just five females and males accounted for 8% and 9% of all young fledged, respectively; all of these were at urban locations. Mortality was recorded for 160 individuals during the period of study. Among the 118 for which cause of death was known, collisions with buildings (36%) were by far the most frequent, followed by collisions with vehicles (9%), aircraft (8%), and electrical wires (8%). In many urban areas, grounded fledglings are rescued and returned to higher perches. Of 85 individuals from southern Ontario known to have been rescued, at least 8 have gone on to breed, producing 65 known offspring. While peregrines have been thriving in eastern cities, continued management effort may be required for them to maintain their level of success.

## 5.2 Introduction

The Peregrine Falcon (*Falco peregrinus*; hereafter peregrine) has been a rare species historically in eastern North America, with a population of only 500 pairs believed to have existed east of the Rockies and south of the Arctic (Enderson *et al.* 1995). By the 1950s, a rapid and severe decline was underway, culminating in the eastern population being considered extirpated by 1964 (Berger *et al.* 1969, Bollengier 1979). While a few peregrines began breeding in cities as early as the 1930s, only six urban nest sites were known prior to 1949 (Groskin 1952). The growth of the urban population only became significant in the 1980s, following the release of many captive-bred juveniles in cities starting in 1974 (Fyfe 1988). Cities offer peregrines benefits in the form of abundant prey and potential nest sites, and scarce predators, but they also pose unique hazards such as buildings into which they may collide, a hazard that is especially great for juveniles learning to fly around towers with reflective glass walls.

Population regulation is a function of fecundity as well as mortality. Nest sites are a limiting factor for peregrines (Ratcliffe 1962) and reproductive success may be influenced by the microclimate at nest sites (e.g. Wiebe 2001, Ardia *et al.* 2006). In particular, temperature may affect both the viability of eggs (Webb 1987) and the survival of nestlings (Quinney *et al.* 1986). The choice of a nest site by peregrines is likely related to the presence/absence or quality of a combination of physical and ecological attributes. Hunt (1988) speculated that for peregrines, critical nest features may include protection from weather and predators, availability of a substrate in which a scrape for eggs can be excavated, and suitable directional exposure. Nest orientation has been shown to affect nest temperature for a variety of bird species (Conner 1975, Inouye 1976, Hartman and Oring 2003, Ardia *et al.* 2006). For some species though, reproductive success is unrelated to nest orientation (Rendell and Robertson 1994), suggesting that this topic must be assessed on a species by species basis.

Despite substantial recent growth in the eastern peregrine population, it remains a species of conservation interest in much of the region, therefore site managers and biologists are often called upon to encourage peregrines to nest in certain areas, or to lure them away from undesirable sites (Martell *et al.* 2000). However, little effort has been made in urban areas to identify the key features that attract peregrines and contribute most to nesting success. As peregrines show high fidelity to nest sites, and attractive locations are often used by a succession of adults, there is great value in understanding what can be done to maximize the suitability of these sites (Pagel 1989, Ratcliffe 1993). In the past, efforts have been made to improve cliff habitat in an attempt to attract peregrines (Boyce Jr. *et al.* 1982, Pagel 1989). In urban areas, human assistance has been provided in various forms, including hack releases, fosters, fledgling rescues, and nest site modifications, but their importance has not been evaluated.

Annual reports on the status of the midwest peregrine population have been produced since 1986, detailing activity at all known nests in the region, and summarizing emerging trends including the growth of a new urban population (e.g. Redig *et al.* 2007). However, the midwest results cannot necessarily be extrapolated to the eastern population. Analysis of the eastern population recovery has been limited to an overview of cliff-nesting peregrines in northern New York and New England (Corser *et al.* 1999), and assorted state wildlife reports with limited distribution.

We compiled data on nesting attempts from southern Ontario, Quebec, Pennsylvania, New Jersey, and Massachusetts to describe aspects of the nesting ecology of the eastern population, and provide recommendations for its effective management. Our overall objective was to evaluate the eastern urban population in terms of nesting success, mortality, and the degree to which active management is important to productivity and survival. Specifically we assessed 1) the relative importance of nest site attributes and their relationship to productivity, 2) causes of mortality, and 3) effects of human assistance on the

population. Where possible, we compared data between urban and cliff-nesting populations.

## **5.3 Methods**

### *5.3.1 Study area*

Our study area included several northeastern provinces and states that feature a concentration of urban-nesting peregrines: Ontario, Quebec, Massachusetts, New Jersey, and Pennsylvania. For Ontario, only data from the southern part of the province were used, as northern records have been previously reported as part of the midwest population (e.g. Redig *et al.* 2007).

All known nesting attempts in the study area were included, from the beginning of the population recovery in 1980 through 2006. In Quebec, monitoring effort was variable, with only urban sites and easily accessible cliff nests surveyed in most years, contrasting with extensive searches of historical and potentially suitable locations in 2002 and 2005. In the other provinces and states, surveying effort was fairly consistent, and the vast majority of nesting attempts are believed to have been documented. Data were collected by government agencies, non-profit organizations, and independent volunteer observers.

### *5.3.2 Characterization of site attributes:*

Eight nest site characteristics were identified (Table 5-1). While habitat and structure were known for all nest sites, all other attributes were missing data for some sites. We evaluated nest site selection in and around Toronto, Ontario, which represented the largest concentration of building-nesting peregrines in our study area. For each of seven nest sites used between 2002 and 2006, four unused but potential nest locations were randomly chosen within a 1 km radius, using a random number table to identify direction and distance from a nest site.

Based on nest occupancy data from throughout the study area, potential sites were restricted to structures at least 15 m in height and including a horizontal

surface on which nesting could occur. Additionally, to compare characteristics of used and available urban nest sites on a regional basis, another 28 buildings were randomly selected throughout Toronto, by using a random number table to select from a list of all buildings meeting the aforementioned criteria.

Table 5-1. Definition of attributes used to classify ecological and physical attributes of peregrine nest sites in the study area.

Attribute	Class	Description
Habitat	Urban (downtown)	Downtown core, characterized by a high density of skyscrapers
	Urban (other)	All other urban / suburban habitat, including quarries in an urban setting
	Rural ( cliff)	Areas away from urban and coastal habitat, including quarries in a rural setting
	Rural (marsh)	Coastal marshes
Structure	Building	Office towers, apartments, smokestacks
	Bridge	Bridges over water
	Quarry	Active or inactive rock quarries
	Cliff	Natural rock faces
	Tower	Nesting towers erected or adapted for peregrines
Cover	Full	Nest location with full overhead protection, exposed to snow or rain only when very windy
	Partial	Nest location with some overhead protection, but still exposed to most precipitation
	None	Nest location with no overhead cover
Substrate	Dirt / debris	Soil, accumulated dirt, pigeon droppings
	Gravel	Small, loose, movable pebbles
	Bare / metal	Smooth concrete or metal surface
Aid	Box	Nest box with sides and a full roof
	Tray	Nest tray without side walls or a roof
	None	Nothing provided for nesting
Orientation	E / SE / S / SW / W / NW / N / NE	Direction faced by the nest, to the nearest cardinal or intercardinal direction
Nest height	<50 m, 51-100 m, 101-150 m, >150 m	Height in metres, classified into four categories
Distance to water	<1 km, 1-4.9 km, 5-20 km	Distance in km to the nearest major water body (ocean, lake, or river >50 m in diameter)

### *5.3.3 Productivity*

The number of young fledged was documented for all nesting attempts. For some locations data on the number of eggs laid and hatched were also available, but hatching success was not evaluated as these data were not reliably collected at most sites. Fledging and nesting success, respectively, refer to the percentage of young that leave the nest successfully and the percentage of nests at which at least one juvenile fledges. We define mean nest productivity as the average number of young fledged per nesting attempt at each location. We ranked the total productivity of all nest sites and compared the top and bottom quartiles to identify differences in nest site attributes between locations that have made the greatest and least contributions to the eastern population.

### *5.3.4 Mortality and human assistance*

Data on mortality were available only for southern Ontario, Massachusetts, and Pennsylvania. All records included age and location of death, while sex and cause of death were also available for most.

Indirect human influence on peregrine productivity was assessed with respect to the provision of nest boxes or trays (Table 5-1). Additionally, direct assistance was occasionally provided by rescuing fledglings that came to the ground in urban areas. Fledgling rescues were systematically recorded only for southern Ontario, and were therefore assessed only for that region.

### *5.3.5 Statistical analyses*

As the size of the recovering population was relatively small, and some attributes were not consistently recorded at all sites, the data were inadequate for reliable multivariate analyses. Rather, univariate analyses of each nest site attribute were performed using Mann-Whitney U or Kruskal-Wallis tests, as mean nest productivity was in most cases not normally distributed. Chi-square goodness-of-fit tests were used to compare the frequency of use of categorical nest site attributes. Random orientation of nest sites was evaluated using the Rayleigh

test, while the Watson-Williams test was used to compare orientation of used and available nest sites (Zar 1999). All statistical analyses were performed using SPSS 9.0 (SPSS Inc., Chicago, Illinois).

## 5.4 Results

From 1980 through 2006, 1613 young were documented from 801 known nesting attempts at 152 nest sites in southern Ontario, Quebec, Massachusetts, New Jersey, and Pennsylvania (Table 5-2). The number of nesting attempts increased over time, from a mean of 9 per year in the 1980s to a mean of 67 per year between 2002 and 2006.

Table 5-2. Summary of nesting attempts and productivity by peregrines in five regions between 1980 and 2006.

Region	# nest sites	# nesting attempts	# young fledged	# young fledged / nesting attempt	mean nest productivity ( $\pm$ SE)
Southern Ontario	21	90	193	2.14	1.70 $\pm$ 0.31
Quebec	61	225	518	2.30	2.16 $\pm$ 0.09
Massachusetts	20	85	191	2.25	2.24 $\pm$ 0.22
New Jersey	31	290	489	1.69	1.32 $\pm$ 0.17
Pennsylvania	19	111	222	2.00	2.16 $\pm$ 0.22
TOTAL	152	801	1613	2.01	1.92 $\pm$ 0.08

### 5.4.1 Nest site characteristics and productivity

Urban nests ( $n = 87$ ) outnumbered rural nests ( $n = 65$ ). The mean number of young fledged per nesting attempt was similar between urban ( $2.03 \pm 0.07$ ,  $n = 416$ ) and rural ( $1.99 \pm 0.06$ ,  $n = 385$ ) nesting attempts (Mann-Whitney  $U = 79229$ ,  $Z = 0.268$ ,  $P = 0.790$ ).

Within urban areas, fledging success varied significantly by nesting structure (Table 5-3; K-W  $\chi^2 = 7.71$ ,  $df = 2$ ,  $P = 0.021$ ), with nest sites in quarries having a mean productivity almost twice as great as those on bridges, while productivity at building nests was intermediate. There was no difference in productivity

between nests on downtown buildings ( $2.10 \pm 0.20$ ,  $n = 22$ ) and those on buildings in less intensively developed urban habitat ( $2.09 \pm 0.28$ ,  $n = 26$ ; Mann-Whitney  $U = 270.0$ ,  $Z = 0.332$ ,  $P = 0.740$ ).

The extent of overhead cover was known for 42 of 48 building nest sites. Sites with full overhead cover had higher mean productivity ( $2.34 \pm 0.20$ ,  $n = 30$ ) than those with only partial cover or no cover at all ( $1.69 \pm 0.40$ ,  $n = 12$ ), but the difference was not significant (Mann-Whitney  $U = 129.5$ ,  $Z = 1.41$ ,  $P = 0.158$ ).

Table 5-3. Comparison of productivity of peregrines among nest structures in urban habitat in southern Ontario, Quebec, Massachusetts, New Jersey, and Pennsylvania, between 1980 and 2006

Structure	# nest sites	# nesting attempts	# young fledged	# young fledged / nesting attempt	mean nest productivity ( $\pm$ SE)
Bridge	35	160	235	1.47	$1.53 \pm 0.19$
Building	48	246	575	2.35	$2.10 \pm 0.17$
Quarry	4	10	32	3.20	$2.83 \pm 0.44$

Nesting substrate was identified for 60 of the urban nests. Productivity was greatest at nests with dirt or debris ( $2.72 \pm 0.46$ ,  $n = 6$ ), intermediate at nests with gravel ( $1.93 \pm 0.16$ ,  $n = 48$ ), and lowest at nest on bare concrete or metal ledges ( $1.32 \pm 0.44$ ,  $n = 6$ ). However, the difference among substrate types only approached marginal significance (K-W  $\chi^2 = 4.12$ ,  $df = 2$ ,  $P = 0.127$ ).

On bridges, fledging success was similarly low regardless of whether or not aid was provided in the form of a nest tray or box (Table 5-4; K-W  $\chi^2 = 0.37$ ,  $df = 2$ ,  $P = 0.832$ ). On buildings, fledging success was higher at sites with trays or boxes than those without, though the differences were only approaching weak statistical significance (K-W  $\chi^2 = 4.01$ ,  $df = 2$ ,  $P = 0.135$ ). However, on buildings mean productivity at nests with boxes was greater than at all other sites (Mann-Whitney  $U = 74.5$ ,  $Z = 1.84$ ,  $P = 0.066$ ).

Table 5-4. Comparison of peregrine productivity on bridges and buildings in relation to the presence or absence of nest trays or boxes

Structure	Nest aid	# nest sites	# nesting attempts	# young fledged	# young fledged / nesting attempt	mean nest productivity ( $\pm$ SE)
Bridge	none	12	42	65	1.55	1.93 $\pm$ 0.33
	tray	3	41	64	1.56	1.50 $\pm$ 0.20
	box	6	33	50	1.52	1.54 $\pm$ 0.40
Building	none	24	86	168	1.95	1.87 $\pm$ 0.25
	tray	14	120	300	2.50	2.14 $\pm$ 0.34
	box	7	34	100	2.94	2.83 $\pm$ 0.11

While 57% of nest sites on buildings faced east to south (Table 5-5), overall nest orientation was statistically random (Rayleigh test,  $Z = 1.41$ ,  $n = 42$ ,  $P < 0.2$ ). Productivity differed considerably by orientation, being highest at nests facing southeast and lowest at those facing northwest. However, variability was high and the difference among directions was only approaching marginal statistical significance (K-W  $\chi^2 = 11.31$ ,  $df = 7$ ,  $P = 0.126$ ).

Table 5-5. Distribution and productivity of building nest sites and nesting attempts by orientation

Region	# nest sites	# nesting attempts	# young fledged	# young fledged / nesting attempt	mean nest productivity ( $\pm$ SE)
East	12	66	163	2.47	1.92 $\pm$ 0.40
Southeast	4	27	93	3.44	3.41 $\pm$ 0.13
South	8	37	82	2.22	2.21 $\pm$ 0.29
Southwest	3	17	42	2.47	2.22 $\pm$ 0.22
West	6	27	44	1.63	1.99 $\pm$ 0.58
Northwest	2	19	26	1.37	0.72 $\pm$ 0.72
North	6	35	99	2.83	2.04 $\pm$ 0.49
Northeast	1	1	4	4.00	4.00

Nest height was known for 54 urban sites (Table 5-6). Fledging success was positively correlated with nest height, though the difference among classes only approached marginal significance (K-W  $\chi^2 = 5.77$ ,  $df = 3$ ,  $P = 0.123$ ).

Table 5-6. Distribution and productivity of nest sites and nesting attempts by nest height

Height	# nest sites	# nesting attempts	# young fledged	# young fledged / nesting attempt	mean nest productivity ( $\pm$ SE)
15 – 50 m	22	91	144	1.58	1.67 $\pm$ 0.24
51 – 100 m	21	156	341	2.19	2.02 $\pm$ 0.27
101 – 150 m	8	60	158	2.63	2.42 $\pm$ 0.45
151 – 200 m	3	17	53	3.12	3.07 $\pm$ 0.16

All bridge nests were over water, while all other nest sites were set back at least a short distance from water bodies. Distance to water was calculated for all 52 urban quarry and building nest sites (Table 5-7). While fledging success was greatest at nests an intermediate distance from water, there was no significant difference among distance classes ( $F_{2,49} = 0.085$ ,  $P = 0.919$  / K-W  $\chi^2 = 0.27$ ,  $df = 2$ ,  $P = 0.874$ )

Table 5-7. Distribution and productivity of nest sites and nesting attempts by distance to the nearest major body of water

Height	# nest sites	# nesting attempts	# young fledged	# young fledged / nesting attempt	mean nest productivity ( $\pm$ SE)
< 1 km	30	169	387	2.29	2.06 $\pm$ 0.18
1 - 4.9 km	18	74	199	2.69	2.74 $\pm$ 0.35
5 – 20 km	4	12	21	1.75	2.05 $\pm$ 0.73

#### 5.4.2 Nest site selection

Among breeding adults that were hatched and/or bred in southern Ontario, 36 of 37 from urban nests also chose cities for nesting, while the only two adults produced at cliff sites both moved to urban habitat.

Nest site selection within an urban environment was examined in the Toronto area (Table 5-8). Used sites did not differ significantly from either adjacent or regionally available potential nesting locations in terms of building height or nest height. Used sites were on average almost twice as close to water as randomly selected potential sites within the region, though the difference was not significant. Peregrines appeared to select strongly for the presence of ledges with overhead cover. All used nest sites in the Toronto area faced east, southeast, or south, while both adjacent and regionally available sites were distributed relatively evenly in all directions.

Table 5-8. Comparison of attributes of used and potential urban nest sites for peregrines in the Toronto area (mean  $\pm$  SE). Adjacent sites were randomly selected from within a 1 km radius of used nest sites, while regional sites were randomly selected from all buildings of at least 15 m height in the Toronto area.

	Used (n = 7)	Adjacent (n = 28)	Regional (n = 28)	Used vs. adjacent	Used vs. regional
Mean building height (m)	96.4 $\pm$ 9.8	107.0 $\pm$ 9.9	85.4 $\pm$ 7.5	M-W U = 94.5, Z = 0.145, P = 0.885	M-W U = 65.0, Z = 1.363, P = 0.173
Mean nest height <sup>1</sup> (m)	89.3 $\pm$ 9.8	95.5 $\pm$ 8.8	75.0 $\pm$ 6.2	M-W U = 97.0, Z = 0.041, P = 0.967	M-W U = 60.0, Z = 1.57, P = 0.116
Ledges present?	7 of 7 (100%)	14 of 28 (50%)	18 of 28 (64%)	$\chi^2 = 5.93$ , df=1, P < 0.02	$\chi^2 = 3.50$ , df=1, P < 0.1
Full overhead cover?	6 of 7 (85%)	8 of 28 (29%)	11 of 28 (39%)	$\chi^2 = 7.62$ , df=1, P < 0.01	$\chi^2 = 4.83$ , df=1, P < 0.05
Orientation	4 E, 2 SE, 1 S	2 E, 1 SE, 2 S, 1 SW, 4W, 1 NW, 2 N, 1 NE, 14 n/a	3 E, 1 SE, 3 S, 3 SW, 2 W, 1 NW, 3 N, 10 n/a	Watson-Williams test: F <sub>1,33</sub> = 3.05, P < 0.1	Watson-Williams test: F <sub>1,33</sub> = 1.71, P > 0.1
Mean distance to water (km)	3.9 $\pm$ 0.9	3.5 $\pm$ 0.4	7.1 $\pm$ 1.0	M-W U = 83.5, Z = 0.60, P = 0.549	M-W U = 69.5, Z = 1.18, P = 0.240

<sup>1</sup>randomly selected from available ledge heights for adjacent and regional sites, or equivalent to building height in cases where the roof provides the only nesting opportunities

#### 5.4.3 Characteristics of preferred nest sites

In terms of total productivity between 1980 and 2006, the top quartile ( $n = 21$ ) of urban nest sites accounted for 70% of all young fledged, while the bottom quartile contributed only 2% (Table 5-9). Nest sites in the top quartile were located higher on buildings than those in the bottom quartile, but the two groups did not differ significantly with respect to distance from water, substrate, or overhead cover. Nest boxes or trays were used significantly more frequently at nest sites in the top quartile of total productivity.

Table 5-9. Comparison of productivity and nest site attributes between top and bottom quartiles of total productivity at urban nest sites in the study area from 1980 - 2006

	top quartile	bottom quartile	statistical comparison
Total # young fledged	592	15	
# Nesting attempts	242	36	
Young fledged/attempt	2.45	0.42	
Mean productivity	2.64 $\pm$ 0.17	0.55 $\pm$ 0.16	M-W U = 22.0, Z = 5.31, $P < 0.001$
Nest height (m)	96.2 $\pm$ 9.9	63.6 $\pm$ 9.8	M-W U = 60.5, Z = 1.90, $P = 0.058$
Distance to water (km)	1.1 $\pm$ 0.4	1.4 $\pm$ 0.5	M-W U = 206.0, Z = 1.10, $P = 0.272$
Substrate	0 dirt/debris 18 gravel 1 bare/metal	1 dirt/debris 9 gravel 2 bare/metal	$\chi^2 = 2.32$ , df = 2, $P > 0.2$
Cover	16 full 2 part 2 none	6 full 1 part 4 none	$\chi^2 = 3.20$ , df = 2, $P > 0.2$
Aid	4 box 12 tray 5 none	2 box 3 tray 17 none	$\chi^2 = 12.58$ , df = 2, $P < 0.002$

The colonization of new urban nest sites has become increasingly rapid as the eastern population has expanded, with half of the known locations occupied for the first time only since 2001 (Table 5-10). Over time, the mean height of newly occupied nest sites has declined significantly, while the mean distance of nests from water has consistently increased, although the trend is only weakly significant. There was no difference over time in selection of sites with respect to

overhead cover, as full cover has been preferred consistently. However, there was a significant difference over time in substrate selection, with nesting in dirt/debris being a relatively new phenomenon. Early colonizers showed a much greater tendency to use nest boxes or trays.

Table 5-10. Comparison of productivity and nest site attributes for peregrines among temporal quartiles representing the colonization of urban nest sites from 1980 - 2006

	first quartile	second quartile	third quartile	last quartile	statistical comparison
First year of occupation	1983 - 1994	1995 - 2000	2001 - 2003	2004 - 2006	
Total # young fledged	361	306	125	53	
Number of nesting attempts	198	128	62	28	
Young fledged / attempt	1.82	2.39	2.02	1.89	
Mean productivity	1.52	2.45	1.82	2.04	K-W $\chi^2 = 5.77$ , df = 3, $P = 0.316$
Nest height	93.6 ± 11.1	82.4 ± 9.9	56.4 ± 8.6	57.5 ± 11.5	K-W $\chi^2 = 7.54$ , df = 3, $P = 0.057$
Distance to water	0.3 ± 0.1	1.0 ± 0.3	1.3 ± 0.5	2.1 ± 1.0	K-W $\chi^2 = 6.30$ , df = 3, $P = 0.098$
Substrate	0 dirt/debris 13 gravel 0 bare/metal	1 dirt/debris 16 gravel 3 bare/metal	1 dirt/debris 13 gravel 1 bare/metal	4 dirt/debris 6 gravel 2 bare/metal	$\chi^2 = 13.08$ df = 6 $P < 0.05$
Cover	10 full 1 part 2 none	15 full 1 part 4 none	11 full 1 part 2 none	9 full 0 part 3 none	$\chi^2 = 1.34$ df = 6 $P > 0.1$
Aid	4 box 8 tray 4 none	1 box 6 tray 13 none	5 box 3 tray 9 none	3 box 0 tray 14 none	$\chi^2 = 22.88$ df = 6 $P < 0.001$

Some individual adults contributed disproportionately to the growth of the eastern population. Of over 350 identified breeders, just five (<3%) females and males accounted for 8% and 9% of all young fledged, respectively (Table 5-11). All of these individuals nested at urban sites with a gravel substrate. Just one site lacked overhead cover, and all individuals except the pair in Toronto used a nest

tray or box. Five of eight sites used by these 10 adults faced either east or southeast. Nest height was variable, but distance to water was short (1.1 km or less) for all but one site.

Table 5-11. Top five female and male peregrines in the study area in terms of total number of young fledged, and characteristics of associated nest sites

Band number and location	Years breeding	# (mean) young fledged	Cover	Substrate	Aid	Orientation	Height (m)	Distance to water (km)
<i>Females</i>								
987-63743 Boston MA	1996-2006 (11)	35 (3.2)	Full	gravel	tray	N	100	0.8
1807-44110 Toronto ON	1995-2002 (8)	29 (3.6)	Full	gravel	none	E	75	1.1
1807-00284 Boston MA	1994-2003 (10)	27 (2.7)	Full	gravel	box	E	120	0.3
617-22675 Atlantic City NJ	1987-2001 (15)	26 (1.7)	Full	gravel	tray	NW	95	0.1
band unknown Harrisburg PA	2000-2005 (6)	22 (3.7)	Part	gravel	tray	SE	55	0.6
<i>Males</i>								
816-75370 Boston MA	1988-2003 (16)	46 (2.9)	Full	gravel	box	E	120	0.3
2206-24655 Pittsburgh PA	1991-2002 (12)	36 (3.0)	Full	gravel	tray	N	150	0.5
2206-13765 Toronto ON	1995-2002 (8)	29 (3.6)	Full	gravel	none	E	75	1.1
816-93507 Springfield MA	1989-1998 (10)	22 (2.2)	None	gravel	tray	E	85	0.4
1807-13328 Mississauga ON	2002-2006 (5)	16 (3.2)	Full	gravel	box	SE	75	7.2

#### 5.4.4 Mortality

In total, 160 mortalities were reported from Ontario, Massachusetts, and Pennsylvania. Eleven of these involved young that died in the nest prior to fledging. Mortality was greatest for young birds, with half of all recorded deaths

occurring within the first month of flight, including 24 (15.0%) on the first day of flight, and another 20 (12.5%) in the first week. In southern Ontario, fewer females (23 of 102, 22.5%) than males (32 of 89, 36.0%) died within their first month of flight ( $\chi^2 = 4.17$ ,  $df = 1$ ,  $P < 0.05$ ).

The key causes of mortality differed by age group (Table 5-12). Collisions with buildings were overwhelmingly the leading cause of mortality for fledglings, but much less common for older birds. Collectively, collisions represented the greatest source of mortality for juveniles, but stationary objects such as buildings and electrical wires accounted for fewer deaths than aircraft and other vehicles. Territorial battles were the most frequent cause of death for adults, but were not an issue for younger birds. However, predation or attacks by other raptors were a minor cause of mortality for juveniles and fledglings, while not reported at all for adults. In New Jersey, mortality of nestlings due to trichomoniasis has been such a serious problem at some urban nests that young at three locations are routinely administered medication at one and three weeks of age.

Table 5-12. Causes of death reported for peregrines in southern Ontario, Massachusetts, and Pennsylvania, 1988-2006 (percentage of known causes of mortality within each age group shown in parentheses)

	Adult (>1 year)	Juvenile (>1 month)	Fledgling (<1 month)
Collision – building	3 (16%)	2 (8%)	38 (61%)
Collision – vehicle	2 (11%)	5 (19%)	4 (6%)
Collision – aircraft	1 (5%)	8 (31%)	1 (2%)
Collision – electrical wires	1 (5%)	4 (15%)	4 (6%)
Territorial battle	7 (39%)	--	--
Other raptor / predation	--	1 (4%)	5 (8%)
Drowning	--	--	4 (6%)
Other	5 (26%)	6 (23%)	6 (10%)
Unknown	12	12	18
Total	31	38	80

#### 5.4.5 Human assistance

Human assistance in the form of nest trays or boxes was provided at 30 of 152 nest sites. In urban habitat, the mean total number of young fledged was significantly higher at nest sites with trays or boxes ( $17.1 \pm 2.7$ ,  $n = 30$ ) than those without ( $5.9 \pm 0.9$ ,  $n = 57$ ; Mann-Whitney  $U = 474.0$ ,  $Z = 3.41$ ,  $P = 0.001$ ).

A more direct form of assistance is the rescue of fledglings that have come to the ground on one of their early flights, where they are at risk due to traffic or other urban hazards. Statistics on the frequency of fledgling rescues were available only for southern Ontario. Of the 193 young fledged in southern Ontario between 1995 and 2006, 85 (44%) were rescued a total of 109 times. Eight (9.4%) of these individuals are known to have subsequently survived and bred successfully, producing a total of 65 young. In comparison, 10 of 108 (9.3%) individuals that were not rescued as fledglings are known to have bred successfully, producing 63 offspring.

### 5.5 Discussion

Our survey of over 150 eastern nest sites revealed no difference in mean productivity between urban and rural habitat, nor between downtown areas and less intensively developed parts of cities. Most urban nests were on buildings or bridges, with productivity on average over one-third higher on buildings. Among urban nests, productivity tended to be higher at those with overhead cover, dirt or gravel substrate, and nest boxes. Although a majority of nests faced east, southeast, or south, there was no consistent relationship between orientation and productivity. Productivity was also unrelated to distance to water, but it was positively correlated with nest height. In addition to providing nest boxes and trays, human assistance extends to rescuing fledglings from hazardous ground conditions in cities, and individuals assisted in this manner accounted for half of the next generation offspring produced by Ontario peregrines. Despite this assistance, there is high mortality for young peregrines in cities, with building

collisions taking the biggest toll on fledglings, and other hazards such as vehicles and electrical wires becoming greater concerns after the first few weeks of flight.

#### *5.5.1 Nest site selection and productivity*

The use of nest structures we documented in the east differs somewhat from that in the midwest, as summarized by Tordoff *et al.* (2003) for the period 1998-2002. Buildings represented a smaller proportion of nest sites in the east (32%) than the midwest (44%), while bridge use was more frequent in the east (23% vs. 10%). Cliff use was similar in both areas, accounting for 33% of eastern sites and 27% of midwestern sites. The biggest differences were with respect to smokestacks, i.e. used at just two eastern locations but at 19% of midwestern nests, and two habitat types used only in the east, i.e. coastal marshes (7%) and quarries (5%). Nesting on smokestacks has been encouraged in the midwest through the provision of nest boxes, while this has been rarely done in the east. All quarry nests in our study were in Quebec, but their use has previously been documented in Britain (Ratcliffe 1993), Ireland (Moore *et al.* 1997), Australia (White *et al.* 1988), and Alaska (Ritchie *et al.* 1998). White *et al.* (1988) postulated that these were secondary quality nests, primarily used by inexperienced individuals unable to compete for superior territories. In our study the mean productivity at quarry nests was 2.79 young fledged per nesting attempt, far higher than on any other structure.

In southern Ontario, we found that 97% of peregrines hatched in urban habitat also bred in cities, consistent with earlier results showing that 91% of individuals from eastern Canadian releases returned to habitat similar to that in which they were raised or released (Holroyd and Banasch 1990). Only two cliff-hatched peregrines nested in southern Ontario during our study, but both did so at urban locations. Although the sample size is too small to draw any conclusions, the result is consistent with the net movement of eastern peregrines into urban habitat reported by Cade and Bird (1990) and the dispersal of coastally-hatched peregrines in California to nearby cities (Kauffman *et al.* 2003). The growth of

the urban population therefore appears to be more than just a consequence of habitat imprinting on young released in cities, as had been proposed by Temple (1988).

Tordoff *et al.* (1998) suggested that the best nest sites are colonized first, and as the population grows, secondary quality sites are eventually settled. To an extent this was evident in the east, as productivity was positively correlated with nest height, and the mean height of newly colonized nests declined significantly over time. Distance to water also increased over time, suggesting that prime closer sites may have been occupied first. Similar changes are evident in Alaska, where peregrines formerly nested only along rivers, but have expanded to more landlocked cliffs as well as to urban areas (White 2006). However, peregrines appear to not always assess sites accurately, as over one-quarter of the first 22 urban nest sites colonized were abandoned after four or fewer nesting attempts.

In a review of the early years of urban colonization by peregrines in the east, Cade and Bird (1990) found that 78% of the 19 known nest sites were on buildings that were among the tallest in their respective cities, averaging 30 stories, or approximately 120 m. Redig and Tordoff (1994a) likewise noted that peregrines are attracted to the tallest structures on the landscape, and will tend to settle if suitable nest sites are available, a pattern similar to that traditionally observed with cliffs (Tordoff *et al.* 1999). In comparison, we found urban peregrine nests to have an average height of 79 m, and using the Toronto population as an example, concluded that peregrines did not select exceptionally tall buildings on either a local or a regional basis. Other nest site attributes may therefore be of greater importance to peregrines than height.

Cade and Bird (1990) also reported that 84% of the first 19 urban nest sites following recovery were within 800 m of water. This tendency has remained fairly consistent over time, with 79% of the 152 sites in our review falling in the

same range. Peregrines in the midwest also show a distribution strongly linked to the shorelines of large lakes (Tordoff *et al.* 1996). However, we found no evidence to suggest that productivity was correlated with proximity to water for eastern peregrines. While cliff-nesting peregrines may benefit from greater concentrations of prey in association with water bodies, this may be of lesser importance to urban-nesters as their prey base is more terrestrial.

Quick re-occupancy of vacated territories has long been observed (Hickey 1942), suggesting that certain sites are particularly attractive. Our comparison of used and available sites in the Toronto area indicated that the only features strongly selected by peregrines are the presence of recessed ledges and overhead cover. The preference for ledges over rooftops is likely motivated mostly by an effort to seek shelter from the elements, but also reduces the probability of disturbance from routine maintenance activities (Cade and Bird 1990).

Site suitability can also be assessed with respect to productivity. In terms of habitat, we found mean productivity to be 2.0 young per nesting attempt at both rural and urban nests, consistent with the lack of difference in the success rate of rural and urban releases during the early part of the Canadian recovery program (Fyfe 1988). However, it reflects an improvement in the relative success of urban sites compared to the 1.7 young per nesting attempt at urban sites and 1.9 at rural sites reported by Cade and Bird (1990). Within urban areas, we documented significantly greater productivity on buildings than bridges. Tordoff *et al.* (1998) reported that as of 1998, productivity in the midwest was higher on smokestacks and buildings than on cliffs and bridges, but not to a significant degree.

Cold weather, especially accompanied by rain, reduces nesting success for some birds (e.g. Kostrzewa and Kostrzewa 1990, Boal *et al.* 2005), and has specifically been implicated in nest failure of peregrines (Redig and Tordoff 1992a). Conversely, peregrines may also be at risk of nest failure from very hot

weather in early summer at exposed nests (Redig and Tordoff 1996). As such, it is not surprising that we found productivity to be higher at nest sites with full overhead cover.

While shelter from above offers the best protection from the elements, nest orientation can also have an impact on temperature regulation. Sullivan *et al.* (2003) reported a significant preference for southeast facing nests among a cliff-nesting population of American Kestrels (*F. sparverius*). Hooge *et al.* (1999) found that woodpecker nests facing east warmed up more quickly each morning and had greater reproductive success. Similarly, Tree Swallows (*Tachycineta bicolor*) favour nest boxes facing east or southeast (Lumsden 1986, Rendell and Robertson 1994), though Ardia *et al.* (2006) reported similar results only in the first half of the breeding season, suggesting that orientation toward the morning sun may hold a significant advantage only to early nesters. As peregrines typically begin nesting in early spring, they would be expected to benefit from having nests exposed to the morning sun. Among the first 19 urban nests in the east, 42% faced east (Cade and Bird 1990). This has remained the preferred orientation, though the frequency has dropped to 29%; southeast and south are the next most frequented orientations, and also likely to benefit from warmer mornings. However, local factors such as the direction of prevailing winds may cause other orientations to be optimal at some nest sites. To some degree, the results may reflect the disproportionate placement of nest trays and boxes on east/southeast facing ledges, making it impossible to differentiate whether peregrines are picking a site due to orientation or nesting aids.

We found productivity at eastern urban nests to be positively correlated with nest height. At cliff nests, the opportunity to hunt prey directly from high nests has been associated with greater hunting success (Jenkins 2000). This may hold true to an even greater extent in cities, as visibility from lower ledges could be limited by taller adjacent buildings.

As in the midwest (Tordoff *et al.* 1997), the adults in the east with the greatest total lifetime production also tended to have higher than average annual productivity. Most of these eastern birds nested at sites that had attributes associated with high productivity. However, the degree to which their success is associated with the features of the nest site or the birds themselves is impossible to determine. This reflects the challenge of attempting to assess productivity in relation to nest site features, without being able to account for the variation in the fertility and parenting abilities of the adults using them. Relatively few of the contrasts we documented were statistically significant due to the high level of variability in data, much of which may be related to the biology and behaviour of the individuals involved.

#### *5.5.2 Urban advantages and disadvantages*

Although we found no difference in productivity between rural and urban nests, the urban population has grown to account for the majority of the eastern population, indicating an attraction of peregrines to such habitat. Given that peregrine populations are generally considered to be limited by the availability of nest sites (Ratcliffe 1962, Tordoff *et al.* 1998), this may simply reflect peregrines taking advantage of the substantial increase in the availability of nest sites compared to the historically limited options on eastern cliffs. For example, peregrines have in recent decades expanded into areas such as Ohio where there were no historical breeding records due to a lack of suitable natural habitat for nesting (Redig and Tordoff 1996).

It seems probable that peregrines are also attracted to cities by the scarcity of predators, abundance of prey throughout the year, and variety of high perches and potential nest ledges that fit the role of natural cliffs, albeit often providing superior shelter from weather (Cade and Bird 1990, Redig and Tordoff 1996). Not only is the prey base in cities typically more abundant and accessible than in rural areas, but lights in cities permit peregrines to hunt at night if necessary (Wendt *et al.* 1991, DeCandido and Allen 2006). Though rare, polygyny has

been documented at least a few times at urban sites in the midwest (Redig and Tordoff 1994a) and for at least one male in Ontario, a behaviour perhaps enabled by the denser food resources in cities.

Collisions with buildings, vehicles, and utility lines are the most obvious additional sources of mortality present in urban areas compared to rural habitat, and account for a majority of deaths by urban-hatched peregrines in the east, as in the midwest (Sweeney *et al.* 1997; Tordoff *et al.* 2000). But as common as such collisions are, only 20% of urban-hatched peregrines in southern Ontario, Massachusetts, and Pennsylvania are known to have died in their first year. In New Jersey, trichomoniasis has also been an important cause of mortality among nestlings, but it appears to be much less prevalent through the rest of the study area. High first-year mortality is typical among raptors (Newton 1979), with estimates of 57% (Brown and Amadon 1968), 60% (Tordoff and Redig 1999), and 70% (Enderson 1969b) for peregrines. No doubt many additional mortalities were sustained by urban-hatched peregrines that were not documented, but the reported frequency of collisions alone does not provide evidence of a higher mortality rate in cities.

There are various other hazards unique to the urban environment, including open chimneys and narrow courtyards with high vertical walls that may trap young birds with weak flight skills. Peregrines are also at risk of indirect poisoning through the ingestion of pigeons contaminated with toxins intended to control their population (Cade and Bird 1990). But conversely, there are other risks faced primarily by rural peregrines. Predation by other raptors, especially Great Horned Owls (*Bubo virginianus*) can be a considerable threat at cliffs (Herbert and Herbert 1965). The risk of starvation is also greater for young that do not learn to hunt quickly, as prey are often scarcer than in cities, and may decrease more rapidly as prey species flock for migration. Weighing these factors against the distinct benefits offered by urban habitat, Tordoff *et al.* (1999) argued that perhaps cliffs have become second-class nest sites. If this is the

case, then over time the strongest adults may be expected to concentrate in cities, perhaps leading to mean productivity in urban habitat exceeding that in rural areas.

### 5.5.3 *Human assistance*

Tordoff *et al.* (1996) noted that in the midwest, nest failure is so high at urban nests lacking nest boxes (largely due to heavy rain) that peregrines would likely be unable to persist in cities without the provision of sheltered nest sites. Our results suggest that nest boxes are not equally critical in the east, as boxes were present at only a minority of buildings, yet overall urban productivity was high. Nonetheless, eastern data agree that boxes on buildings provide a significant advantage, whereas nest trays alone do not, likely due to the additional protection from the elements provided by boxes. Unlike in the midwest, where boxes also improved nesting success on bridges (Tordoff *et al.* 2003), boxes conferred no advantage to bridge-nesting peregrines in the east, suggesting that their low rate of success may be related to factors other than shelter, such as disturbance or low height over water, which increases the risk of drowning by fledglings. Only a small minority of new nest sites in recent years have been at boxes, but this may be more a reflection of most such existing sites already being occupied than a reduced interest in them.

Many young peregrines are unable to maintain altitude well when they first take flight, and in an urban environment, perching options at lower levels may be limited, leading some to come to the ground (Cade and Bird 1990). Only on one occasion in Ontario did we observe an adult descend to provide food to a grounded youngster; more typically they circle above, encouraging the fledgling to fly back up, but the lack of 'stepping stone' perches on skyscrapers makes that nearly impossible for those that have only begun developing their flight skills. The majority of grounded fledglings would likely die of starvation (or else collisions) if not rescued and returned to higher perches. In southern Ontario, almost half of fledglings were rescued, and these individuals have in turn

accounted for half of the known next-generation offspring. While similar statistics were not available for other regions, if the Ontario data are at all typical, it is evident that rescues have a significant impact not only on survival of urban offspring, but also on the continued growth of the population. Similarly in New Jersey, the provision of medication to protect nestlings at three key urban sites against trichomoniasis likely improves survival significantly.

#### *5.5.4 Implications and recommendations*

Urban growth has created an abundance of new potential nest sites for peregrines, thereby increasing the potential carrying capacity of the eastern population. Both the rural and urban populations have increased steadily over the past two decades, suggesting that neither should be considered a source or sink population. As the urban peregrine population continues to expand, individuals will increasingly attempt to nest at sites of secondary quality. Their potential for nesting successfully is likely to be improved if they are provided nest boxes. Local considerations may take precedence, but as general guidelines we recommend they be placed on recessed ledges of tall buildings facing east or southeast, as these are the conditions that have been most favoured by eastern peregrines. Considering that productivity was similar between downtown and suburban areas, but the concentration of hazards to peregrines is typically far greater in the city core, it may be advisable to focus box placement on suitable buildings in moderately developed areas with less traffic and fewer building collision hazards. We also encourage the continued documentation of both urban mortalities and rescues, to allow for assessment of their importance to the urban population over greater temporal and geographic scales.

## **6 General discussion and synthesis**

### **6.1 Summary**

The peregrine has been widely studied around the world, and especially extensively in North America, but to date relatively little research has focused on the rapidly emerging urban population. This study demonstrates that while the growth in urban numbers has been substantial in eastern North America over the past couple of decades, it has not come at the expense of the cliff-nesting population, which has also increased significantly during that period. Moreover, it shows that while mean productivity is similar between the two habitat types, there are a number of factors related to urban nesting options that may influence productivity. Both the study of urban nesting and the tracking of migrant juveniles show that there is considerable variability in the behaviour of peregrines, at least some of which may reflect the infusion of genetic variability through the use of multiple subspecies in the captive-breeding effort used to initiate population recovery. Previously undocumented, the migratory tendencies of urban peregrines appear to be influenced by a number of factors, including sex, captive/wild origin, and age, but the results of this research have also raised a number of questions for further research.

#### *6.1.1 Accuracy of small satellite transmitters*

Using satellite telemetry to study the movements of animals will always involve some degree of error, as there are factors beyond a researcher's control such as weather, physical interference from surroundings, and satellite access that are unpredictable sources of variability. It is therefore important to minimize other sources of error where possible, and to recognize that there are limits to accuracy beyond that. While the Argos Location Class index provides a generally reliable indication of the accuracy of each data point, the stated errors represent statistical probabilities, and any individual point may differ from the true location by a much greater distance than expected. Therefore selection of data points strictly according to Location Class is discouraged; rather, data points

should be individually evaluated for biological plausibility and eliminated when unrealistic. For studies where highly accurate data are not critical, such as long-distance migration, use of Argos class 0 and A data is encouraged, as the errors associated with them are generally trivial at that scale, and they can more than triple the sample size of points available for analysis. For future studies on peregrines, use of solar-powered transmitters is highly recommended, as they have been shown to last longer and provide more accurate data throughout their lifetime, whereas the accuracy of battery-powered transmitters declines over time and is lower in winter. However, solar-powered PTTs may not be advisable for all species, as those that spend less time perching in exposed locations may not receive enough sunlight to recharge the batteries regularly.

Assessment of the factors influencing satellite transmitter accuracy was somewhat compromised by virtue of the study being an incidental by-product of an active research program. As such, the high degree of temporal and spatial variation in the deployment of PTTs added considerable variability that could not easily be accounted for. Also, while correlation among latitude, date, and transmitter age was low, it, in combination with the relatively small number of PTTs, may have obscured patterns to some degree. The full significance of these factors could be better assessed in a study where all transmitters are deployed close together and around the same time.

### *6.1.2 Peregrine dispersal and migration*

Using satellite telemetry, juvenile peregrines were revealed to have widely varying strategies, ranging from remaining at release sites to migrating many thousands of kilometres. Some plasticity in behaviour was observed, in that there were considerable differences in migratory strategies even among siblings, and one male shifted from migratory to resident after establishing a nesting territory as an adult. These results indicate that while a variety of studies have suggested a genetic basis to migration, other factors may strongly influence individual patterns of movement, and these may change over time.

Despite the high amount of variability among birds, some patterns did emerge. Satellite-tracked juvenile males consistently migrated farther than females, yet analysis of banding recoveries indicated that females tend to disperse much greater distances than males. This suggests that while movement away from the natal territory is important for both sexes, they tend to pursue it through different strategies. Dispersal strategies also appear to vary over time and in different areas, as the tendency of Ontario peregrines to disperse shorter distances in recent years contrasts with the opposite pattern in the adjacent US midwest. Another phenomenon that deserves further exploration is the evidence for multiple cases of back-and-forth dispersal across generations between some pairs of cities.

Among juveniles, rural birds departed their natal territory earlier than urban birds, likely reflecting the pressure to follow migratory prey. Wild-raised birds also departed earlier than captive-raised birds, perhaps suggesting that provision of food should be cut off earlier at hack releases. While adults migrated significantly farther than juveniles, this may simply reflect one of the limitations of the telemetry study, namely imbalances in the sampling distribution. Most notably, all Alberta birds were adults, while all eastern birds were juveniles, making it impossible to separate effects of age and geography. Rural juveniles were also greatly under-represented in the study, as an unfortunate but largely inevitable consequence of the concentration of fundraising opportunities in urban centres. The resolution of some movements was also less than optimal due to long gaps in some of the duty cycles, a problem which has largely been eliminated through the advent of reliable solar-powered transmitters.

### *6.1.3 Peregrine population growth*

The Ontario peregrine population provides a good case study of the eastern recovery program. Population growth has been rapid both in the urban environment of southern Ontario and on the cliffs of northern Ontario, reflecting the general increase in eastern North America, where overall one-quarter of

known nest sites were first occupied between 2004 and 2006. While the potential always exists for nests to remain undiscovered, the Ontario search effort has been consistent and thorough since the early 1990s. The only notable limiting factor in the study of this population is restricted access to many of the northern Ontario sites, which prevents some young from being banded, and greatly reduces the number of adults that can be identified by their leg bands. All the same, it was possible to demonstrate a high rate of reuse of favoured nest sites, and an increasing number of marginal quality sites used just once or twice as the population grew larger.

#### *6.1.4 Peregrine genetics*

Despite an extensive captive-breeding program that involved the release of only *anatum* peregrines in Ontario, these birds represent a small minority of the individuals that have bred in the province since 1991. This is a result of the considerable influx of American peregrines with mixed pedigrees, and reflects the substantial degree of medium-distance dispersal shown by peregrines in all directions. While the current population does not strictly meet the objective of restoring an *anatum* population to southern Ontario, it has already exceeded the size of the province's historical peregrine population and continues to grow, and should therefore be viewed as a great success. In fact, considering that the few *anatum* peregrines in southern Ontario appear to have had less than average productivity, it may be that the new mixed breed is actually better suited to eastern North America, especially with respect to colonization of urban areas. Unfortunately, aside from the *anatum* birds released in Ontario and their direct descendents, the precise pedigree is known for very few other eastern peregrines, therefore this is difficult to evaluate. While the outcome of the American cross-breeding of multiple subspecies appears to have been favourable in the case of peregrines, the evolution of the composition of the Ontario population highlights the potential risk of such a strategy, and serves as a reminder of the need for international agreement and cooperation on future conservation ventures of such a nature.

### *6.1.5 Peregrine nest site characteristics*

Peregrines historically showed a strong preference for particular cliffs, and this tendency appears to have transferred to the urban population, where certain buildings are occupied perennially. While the attractiveness of these sites may be obvious to peregrines, not all their characteristics are easily defined. Analysis of the sequence of occupation of urban nest sites across the northeast indicated that peregrines first chose taller buildings close to large bodies of water, and with gravel substrates – all preferences consistent with peregrine ecology. Over time, these characteristics at newly occupied sites have changed significantly, suggesting that peregrines may have exhausted the supply of ideal urban nest sites fairly quickly.

Other factors appear to be important for peregrines too. In Toronto, several nest sites have been used by a succession of two or more pairs, yet they differ little from other available buildings in terms of height, distance to water, and orientation. Of the building characteristics assessed, only the presence of covered ledges provided a significant contrast to unused sites. While there must also be factors used by peregrines to select from among covered ledges, these remain difficult to identify.

Results of the nest site selection analysis were somewhat limited by differences in data collection protocols among regions. Probably of greater significance, there is likely considerable variability among individual peregrines with respect to nest site preferences, which may be influenced by a combination of previous experience and genetics.

Despite the possibility that the best nest sites were occupied long ago, the urban peregrine population continues to grow across the northeast. Peregrines showed flexibility in their rapid and successful adaptation to city life in the first place, and have recently also thrived in expanding to quarries in Quebec.

Perhaps as the population continues to grow, peregrines will again find another niche in urban habitat to occupy that previously seemed unsuitable.

#### *6.1.6 Factors influencing peregrine nest site productivity*

It was difficult to determine which factors have the greatest influence on productivity in eastern North America, even though over 800 nesting attempts were examined. In part, this stemmed from the different approaches taken to collect data across the regions included in the study, which precluded multivariate analyses. However, it is likely that even the most thorough records failed to include all relevant predictors of productivity. Most notably, intrinsic biological differences among individuals (e.g. fertility) have a great bearing on reproductive output, but in a wild population are impossible to quantify in isolation from environmental factors.

Despite these limitations, some interesting results emerged. Although very few nesting attempts were made in quarries, their mean productivity was higher than on any other structure type, in contrast to limited reports of marginal quarry nesting success by peregrines elsewhere in the world. Within urban areas, productivity was much greater on buildings than on bridges, and nest boxes on buildings conferred a significant advantage. South- and east-facing nests tended to have greater productivity, though one excellent north-facing nest showed how easily statistics can be skewed by a single location that may be favourable for entirely unrelated reasons. While local influences and the condition of breeding adults may have a substantial impact on productivity, results suggest that as a default approach, the best management policy is to encourage nesting on high, covered ledges facing south to east, by placing nest boxes in such locations.

#### *6.1.7 Sources of peregrine mortality*

Peregrine mortality was a common theme through the various aspects of this research. Analysis of urban mortalities showed that building collisions take a significant toll on fledglings, while those that survive their first week of flight still

are at considerable risk of vehicle collisions. Those that make it to adulthood appear to be at greater risk of interspecific and intraspecific battles for territory, having by that time adapted to urban hazards. However, for the most part mortality statistics are biased by sampling effort. Only a small fraction of banded peregrines are ever reported dead, but not surprisingly a great majority of these are in urban areas, where there is a much higher chance of them being discovered – or in the case of disaster-prone fledglings, observed as they meet their fate. Therefore, while the statistics make urban life look especially risky for peregrines, it may simply be that there are few opportunities for predation, disease, and starvation in rural areas to get documented. Satellite telemetry offered some insight into mortalities that occurred after tracked birds left urban areas, but was in itself limited in that cause of death was often difficult to identify conclusively. However, it did reveal that the post-independence period can be a hazardous phase for juveniles, and that severe storms can doom juveniles and adults alike.

## **6.2 Recommendations for management and future research**

### *6.2.1 Management recommendations*

Adaptive management of the recovering eastern peregrine population has contributed greatly to its success, especially through hack releases, rescues of grounded fledglings, and provision of nest boxes. Much of it is also costly and labour-intensive, therefore such actions need to be critically evaluated in light of the limited availability of conservation funds.

While the captive-breeding and release program launching the recovery of the eastern peregrine population, data from Ontario show that recent releases have had only a negligible impact. Additional hack releases may well be relatively easy to fund because of the peregrine's high profile and appeal to the public, but those factors should hold little weight in determining conservation priorities. The considerable resources demanded by hack releases can be more productively directed toward other species at risk, or at least toward other aspects of

peregrine management that are more likely to make a difference at this point in the population's recovery. In particular, efforts to improve nesting success and survival of fledgling peregrines appear to have greater value, and can be continued at minimal expense through the provision of additional nest boxes and the maintenance of existing volunteer programs. Territorial battles between urban peregrines have become increasingly frequent and severe, suggesting that desirable nest sites have become a limiting factor for that population. Since peregrines have already been shown to benefit significantly from the provision of nest boxes, adding to the supply available could reduce the probability of such conflicts. To maximize their usefulness, boxes should be placed in areas already known to be frequented by peregrines, and in specific locations that are most likely to favour nesting success (i.e. in most cases high covered ledges facing between east and south).

Considering how quickly the peregrine population declined in the mid-twentieth century, it is worthwhile to continue monitoring annual nesting success as thoroughly as possible, especially as this can be done with relatively little cost in most areas through the assistance of well-established volunteer networks. It is also valuable for these volunteers to continue rescuing grounded fledglings, both for the potential benefit to the population, and for the educational opportunities their efforts provide in urban centres. Further pooling of data to summarize regional trends on an ongoing basis would ensure that any future population declines are identified quickly and accurately to allow for rapid investigation and intervention if necessary.

### *6.2.2 Research recommendations*

The satellite telemetry findings in this thesis showed considerable variability, largely reflecting the diverse backgrounds of the individuals studied. While some trends related to sex and captive/wild origin were evident, these and other contrasts could likely be more clearly demonstrated if other sources of variation were minimized. Ideally, entire families of peregrines should be tracked

simultaneously, over several years, to permit age and sex differences with respect to migration and dispersal to be teased apart without confounding factors of origin. Any future satellite telemetry research on peregrines should use solar-powered transmitters to maximize the duration of study and quality of data, and data should be collected daily to adequately capture details of movement. PTTs with GPS capacity have continued to decrease in size, and have just recently become light enough to be deployed on peregrines, allowing for precise home range definition and the potential to determine habitat associations throughout the year.

Despite these remaining gaps in knowledge, the peregrine has become a very well-studied species, and much more is known about it than many species of conservation concern that are currently in much greater jeopardy. With growth of the peregrine population remaining strong in eastern North America, it would be inappropriate to continue recommending the peregrine for conservation funding support over others that should rightly be considered higher priorities now. Rather, efforts should be made to consider how lessons learned from the peregrine population recovery may be applied to other species. For example, effective use of satellite telemetry could provide critical insights into the movements and associated conservation needs of Short-eared Owl (*Asio flammeus*) and Ivory Gull (*Pagophila eburnea*). Detailed research on urban nesting preferences and requirements could help identify solutions to arrest the alarming declines of Common Nighthawk (*Chordeiles minor*) and Chimney Swift (*Chaetura pelagica*). The eastern Loggerhead Shrike (*Lanius ludovicianus*) could have the potential to thrive through urban releases much like the peregrine. These and other species present emerging challenges in avian conservation. The peregrine has already been a remarkable success story, but if any of the research and management techniques applied to its recovery can be effectively adapted to other species, the effort invested will have been all the more worthwhile.

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## Appendix A: List of all peregrines and transmitters in the telemetry study

PTT	Name	A g e	S e x	Date active	Deployment	Origin	Habitat	Pedigree	Coverage	End
5735	--	A d	F	Jul 97 - Jun 98	Peace Point AB	Wild	Rural	Anatum	Fall to spring	Transmitter removed
5735	--	A d	F	Jul 98 - Nov 98	Fort Chipewyan AB	Wild	Rural	Anatum	Fall	Bird died (hurricane)
24422	--	A d	M	Jul 99 - Sep 99	Edmonton AB	Wild	Urban	Anatum	Fall (part)	Transmitter failed
24424	--	A d	F	Jul 99 - Dec 00	Fort Chipewyan AB	Wild	Rural	Anatum	Fall to second fall	Transmitter failed
24427	--	A d	F	Jul 99 - Jul 00	Edmonton AB	Wild	Urban	Anatum	Fall to summer	Transmitter removed
24868	--	A d	M	Jul 99 - Nov 99	Fort Chipewyan AB	Wild	Rural	Anatum	Fall	Transmitter failed
20892	Rouge	J u v	M	Aug 99 - Dec 99	Richmond Hill ON	Hack	Urban	Anatum	Fall	Transmitter removed
20898	Lincoln	J u v	M	Aug 99 - Oct 99	Guelph ON	Hack	Urban	Anatum	Fall	Bird died (storm?)
24862	Eco	J u v	M	Sep 99 - Oct 99	Richmond Hill ON	Hack	Urban	Anatum	Fall	Bird died (storm?)
24863	Nate	J u v	M	Sep 99 - Jun 00	Richmond Hill ON	Hack	Urban	Anatum	Fall to summer	Transmitter removed
05256	Nate	A	M	Oct 00 - Jun 01	Richmond Hill ON	Hack	Urban	Anatum	Fall to summer	Transmitter

19277	Nate	d A d J	M	Jul 01 - May 02	Mississauga ON	Hack	Urban	Anatum	Fall to spring	removed Transmitter failed
5258	Maryann	u v J	F	Jun 00 - Aug 00	Rochester NY	Wild	Urban	Unknown	Post-fledging only	Bird died (unknown)
5259	Adelaide	u v J	F	Jun 00 - Dec 00	Toronto ON	Wild	Urban	Unknown	Fall	Transmitter removed
5260	Pinnacle	u v J	F	Jul 00 - Oct 00	Lac Lyster QC	Wild	Urban	Unknown	Post-fledging only	Bird died (unknown)
15114	Magellan	u v J	M	Jun 00 - Feb 01	Etobicoke ON	Wild	Urban	Unknown	Fall to winter	Bird died (collision)
5256	Lionheart	u v J	M	Aug 01 - Jun 02	Richmond Hill ON	Hack	Urban	Anatum	Fall to spring	Transmitter failed
5257	Lightning	u v J	M	Aug 01 - Jul 02	Richmond Hill ON	Hack	Urban	Anatum	Fall to spring	Transmitter failed
5259	Ruby	u v J	F	Aug 01 - Apr 02	Charleston Lake ON	Hack	Rural	Anatum	Fall to spring	Transmitter removed
5261	Sarah	u v J	F	Aug 01 - Sep 01	Kitchener ON	Hack	Urban	Anatum	Post-fledging only	Bird died (collision)
15113	Trillium	u v J	M	Jul 01 - Aug 01	Toronto ON	Wild	Urban	Unknown	Post-fledging only	Bird died (unknown)
15114	Dieppe	J	M	Aug 01 - Sep 01	St-Hilaire QC	Wild	Rural	Unknown	Post-fledging only	Bird died (collision)

		u									
		v									
		J									
5258	--	u	F	Jun 02 - Jul 03	Harrisburg PA	Wild	Urban	Unknown	Fall to summer	Transmitter failed	
		v									
		J									
5260	--	u	F	Jun 02 - Jun 03	Harrisburg PA	Wild	Urban	Unknown	Fall to summer	Transmitter failed	
		v									
		J									
15114	--	u	F	May 02 - Jul 03	Pittsburgh PA	Wild	Urban	Unknown	Fall to summer	Transmitter failed	
		v									
		J									
15115	--	u	F	Jun 02 - Jul 03	Pittsburgh PA	Wild	Urban	Unknown	Fall to summer	Transmitter failed	
		v									
		J									
15113	Horus	u	M	Jul 02	Charleston Lake ON	Hack	Rural	Anatum	Post-fledging only	Bird died (predation)	
		v									
		J									
15116	--	u	M	Aug 02 - Feb 03	Drumheller AB	Wild	Rural	Unknown	Fall to winter (part)	Transmitter failed	
		v									
		J									
15117	Destiny	u	F	Aug 02 - Sep 03	Kitchener ON	Hack	Urban	Anatum	Post-fledging only	Bird died (unknown)	
		v									
		J									
24863	Hope	u	F	Jul 02 - Aug 03	Richmond Hill ON	Wild	Urban	Unknown	Post-fledging only	Bird died (unknown)	
		v									
		J									
5256	Teedee	u	F	Aug 03 - Dec 03	Kitchener ON	Hack	Urban	Unknown	Fall	Transmitter failed	
		v									
		J									
5259	--	u	F	Jun 03 - Nov 03	Pittsburgh PA	Wild	Urban	Unknown	Fall (part)	Bird died	



	<b>McGill University</b> <b>Animal Use Protocol – Research</b>	Protocol #: <u>4282</u> Investigator #: <u>391</u> Approval End Date: <u>June 30, 2003</u> Facility Committee: <u>AGK</u>
<b>Title: Satellite Tracking of Peregrine Falcons</b> <i>(must match the title of the funding source application)</i>		
<input type="checkbox"/> New Application <input checked="" type="checkbox"/> Renewal of Protocol # <u>4282</u> <input type="checkbox"/> Pilot                     Category (see section 11): <u>B</u>		
<b>1. Investigator Data:</b>		
Principal Investigator: <u>David M. Bird</u>		Phone #: <u>398-7760</u>
Department: <u>Avian Science and Conservation Centre</u>		Fax #: <u>398-7990</u>
Address: <u>Macdonald Campus</u>		Email: <u>bird@nrs.mcgill.ca</u>

<b>2. Emergency Contacts: Two people must be designated to handle emergencies.</b>		
Name: <u>David Bird</u>	Work #: <u>398-7760</u>	Emergency #: <u>457-6800</u>
Name: <u>Ian Ritchie</u>	Work #: <u>398-7932</u>	Emergency #: <u>457-9051</u>

<b>3. Funding Source:</b> External <input checked="" type="checkbox"/> Internal <input type="checkbox"/> Source (s): <u>Canadian Peregrine Foundation</u> Source (s): _____ Peer Reviewed: <input checked="" type="checkbox"/> YES <input type="checkbox"/> NO**     Peer Reviewed: <input type="checkbox"/> YES <input type="checkbox"/> NO** Status: <input checked="" type="checkbox"/> Awarded <input type="checkbox"/> Pending     Status: <input type="checkbox"/> Awarded <input type="checkbox"/> Pending Funding period: <u>June 1/02 to May 31/03</u> Funding period: _____	For Office Use Only: <table border="1" style="width: 100%; border-collapse: collapse;"> <tr> <td style="text-align: center;">ACTION</td> <td style="text-align: center;">✓</td> <td style="text-align: center;">DATE</td> </tr> <tr> <td style="text-align: center;">CCs</td> <td style="text-align: center;">✓</td> <td style="text-align: center;"><u>June 3, 03</u></td> </tr> <tr> <td style="text-align: center;">DB</td> <td></td> <td></td> </tr> <tr> <td colspan="3" style="text-align: center;">APPROVED</td> </tr> </table>	ACTION	✓	DATE	CCs	✓	<u>June 3, 03</u>	DB			APPROVED		
ACTION	✓	DATE											
CCs	✓	<u>June 3, 03</u>											
DB													
APPROVED													

**\*\* All projects that have not been peer reviewed for scientific merit by the funding source require 2 Peer Review Forms to be completed e.g. Projects funded from industrial sources. Peer Review Forms are available at [www.mcgill.ca/rgo/animal](http://www.mcgill.ca/rgo/animal)**

Proposed Start Date of Animal Use (d/m/y): <u>June 1, 2002</u>	or ongoing <input type="checkbox"/>
Expected Date of Completion of Animal Use (d/m/y): <u>May 31, 2003</u>	or ongoing <input type="checkbox"/>

**Investigator's Statement:** The information in this application is exact and complete. I assure that all care and use of animals in this proposal will be in accordance with the guidelines and policies of the Canadian Council on Animal Care and those of McGill University. I shall request the Animal Care Committee's approval prior to any deviations from this protocol as approved. I understand that this approval is valid for one year and must be approved on an annual basis.

Principal Investigator's signature: [Signature]     Date: June 15/03

Approved by:

Chair, Facility Animal Care Committee:	<u>[Signature]</u>	Date: <u>22/1/03</u>
University Veterinarian:	<u>[Signature]</u>	Date: <u>June 22, 2003</u>



**McGill University**  
**Animal Use Protocol – Research**

Protocol #: 4282  
Investigator #: 391  
Approval End Date: June 30, 2004  
Facility Committee: AGR

**Title: Satellite Tracking of Peregrine Falcons**  
*(must match the title of the funding source application)*

New Application    
  Renewal of Protocol # 4282    
  Pilot    
 Category (see section 11): B

**1. Investigator Data:**

Principal Investigator: David M. Bird Phone #: 398-7760  
 Department: Avian Science and Conservation Centre Fax#: 398-7990  
 Address: Macdonald Campus Email: bird@nrs.mcgill.ca

**2. Emergency Contacts:** Two people must be designated to handle emergencies.

Name: David Bird Work #: 398-7760 Emergency #: 457-6800  
 Name: Ian Ritchie Work #: 398-7932 Emergency #: 457-9051

**3. Funding Source:**

External  Internal

Source (s): Migration Research Foundation Source (s): \_\_\_\_\_

Peer Reviewed:  YES  NO\*\* Peer Reviewed:  YES  NO\*\*

Status:  Awarded  Pending Status:  Awarded  Pending

Funding period: Jan 1/03 - Dec 31/03 Funding period: \_\_\_\_\_

For Office Use Only:

ACTION	✓	DATE
CCs	✓	<u>March 11/03</u>
DB		
APPROVED		

**\*\* All projects that have not been peer reviewed for scientific merit by the funding source require 2 Peer Review Forms to be completed e.g. Projects funded from industrial sources. Peer Review Forms are available at [www.mcgill.ca/rgo/animal](http://www.mcgill.ca/rgo/animal)**

Proposed Start Date of Animal Use (d/m/y): 01/04/03 or ongoing

Expected Date of Completion of Animal Use (d/m/y): 31/10/03 or ongoing

**Investigator's Statement:** The information in this application is exact and complete. I assure that all care and use of animals in this proposal will be in accordance with the guidelines and policies of the Canadian Council on Animal Care and those of McGill University. I shall request the Animal Care Committee's approval prior to any deviations from this protocol as approved. I understand that this approval is valid for one year and must be approved on an annual basis.

Principal Investigator's signature: [Signature] Date: Feb 6/03

Approved by:

Chair, Faculty Animal Care Committee: [Signature] Date: 2/13/03

## Appendix C: Scientific permit to capture and band migratory birds

 Environment Canada / Environnement Canada Environmental Conservation Service / Service de la conservation de l'environnement		<b>SCIENTIFIC PERMIT TO CAPTURE AND BAND MIGRATORY BIRDS</b> <b>PERMIS DE CAPTURE ET DE BAGUAGE D'OISEAUX MIGRATEURS</b>	
In the Province(s) - Dans la (les) province(s) <b>Ontario, Québec</b>		Permit No. / N° de permis <b>10309 AN</b>	
Name and Address - Nom et adresse <b>GAHBAUER MARCEL</b> <b># 913 2470 SOUTHWALE CRESCENT</b> <b>OTTAWA, ON K1B 4L9</b>		Issued under Migratory Bird Regulations / Émis en vertu du règlement concernant les oiseaux migrateurs: Section / Article <b>4 and 19</b>	
		Issue Date / Date d'émission <b>2001/07/04</b>	
		Expiry Date / Date d'expiration <b>2001/12/31</b>	
Signature of Holder - Signature du détenteur 		For the Minister - Pour le Ministre Name (Print) - Nom (Lettres moulées) <b>A. Demers</b>	
		Signature 	
PERMIT CONDITIONS ON REVERSE SIDE - CONDITIONS DU PERMIS AU VERSO			

**Authorized to:**

- Band raptors (IF IN POSSESSION OF A CURRENT & VALID PROVINCIAL/TERRITORIAL PERMIT).
- Band restricted species Peregrine Falcon (PEFA) (3560)
- Use baited traps (BAL-CHATRI AND BOWNET TRAPS).
- Mark Peregrine Falcon (PEFA) (3560) with Colored Leg Bands BLK WITH VERT CODE NUM-ALPHA SIL (IN COORDINATION WITH PERMIT # 10665). in Ontario, Québec
- Use Satellite Transmitter on Peregrine Falcon (PEFA) (3560) (5 BIRDS). (SATELLITE TRANSMITTER USE MAY REQUIRE CERTIFICATION OF THE DEVICE BY INDUSTRY CANADA) (IF IN POSSESSION OF A CURRENT ANIMAL CARE COMMITTEE APPROVAL) in Ontario, Québec

## **Appendix D: Waivers from co-authors**

To confirm our earlier agreement, I approve your use of my Alberta peregrine satellite telemetry data in your thesis.

Geoff Holroyd  
Research Scientist  
Canadian Wildlife Service, Environment Canada  
Room 200, 4999-98 Ave., Edmonton, AB, T6B 2X3  
phone 780-951-8689; cell 780-717-9678; FAX 780-495-2615  
Email: geoffrey.holroyd@ec.gc.ca

By way of this email message, you are authorized to use the Peregrine Falcon data that I provided from Massachusetts in any publications that I am aware of and have approved. Any versions of the manuscript that I have just reviewed are hereby approved.

Thomas W. French, Ph.D  
Assistant Director  
Massachusetts Division of Fisheries and Wildlife  
One Rabbit Hill Road  
Westboro, MA 01581  
508-389-6355

I am glad to provide authorization for full use of the data provided by the Pennsylvania Game Commission (via Dr. Art McMorris or Dan Brauning) for use in your thesis and in any resulting publication. We appreciate the opportunity to collaborate with you.

Dan Brauning

Wildlife Diversity Program Chief  
Pennsylvania Game Commission  
2001 Elmerton Ave,  
Harrisburg, PA 17710  
570-547-6938

You have my permission to include the information I supplied on peregrine falcons in your thesis. I am very pleased to be able to contribute to your interesting and important studies.

Art

F. Arthur McMorris  
mcmorris@mac.com

Looks good! Congratulations. I think your paper is very good, very thorough. Re: Acknowledgments, please note that NJ funding was provided by the New Jersey Tax Check-off for Wildlife. My phone, fax and other info are below.

Kathy

Kathleen E. Clark  
Supervising Zoologist  
Endangered & Nongame Species Program  
NJ Division of Fish and Wildlife  
2201 Route 631  
Woodbine, NJ 08270

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Fax: 609.628.2734  
kathy.clark@hughes.net