

**THE IMPACTS OF HUMAN RECREATIONAL ACTIVITIES, HABITAT
QUALITY AND WEATHER CONDITIONS ON THE FORAGING BEHAVIOUR
AND FLEDGING SUCCESS OF BREEDING PIPING PLOVERS (*CHARADRIUS
MELODUS*)**

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Supervisor: Dr. Colleen Barber

Supervisory Committee: Dr. Hugh Broders

Dr. Danika van Proosdij

Mr. Andrew Boyne



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THE IMPACTS OF HUMAN RECREATIONAL ACTIVITIES, HABITAT QUALITY AND WEATHER CONDITIONS ON THE FORAGING BEHAVIOUR AND FLEDGING SUCCESS OF BREEDING PIPING PLOVERS (*CHARADRIUS MELODUS*)

Kevin Murphy

April 2007

ABSTRACT

Many studies have found that shorebirds reduce the amount of time spent foraging in response to human recreational activity and have experienced lower reproductive success on beaches with human recreational activity. Nevertheless, a large part of these studies do not consider how other variables such as territory quality and meteorological conditions might also influence foraging and reproductive success. Therefore, the main objectives of this project were to investigate the influence of human recreational activity, habitat quality and meteorological conditions on piping plover (*Charadrius melodus*) foraging behaviour and fledging success. The proportion of time spent foraging was significantly positively correlated with overall invertebrate abundance (monthly mean of saturation zone and swash zone), air temperature and wind speed. In addition, invertebrate abundance and date were identified as significant predictors of piping plover foraging behaviour. Fledging success was negatively associated with hatching date and the proportion of open sand and was positively associated with the mean minimum daily temperature over the chick rearing period.

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TABLE OF CONTENTS

Abstract	ii
Acknowledgements	iii
Table of Contents	iv
List of Tables	v
List of Figures	vi
Chapter 1. Human recreational activity and piping plovers: general introduction	11
Chapter 2. The impacts of human recreational activities, habitat quality and weather conditions on the foraging behaviour of breeding piping plovers (<i>Charadrius melodus</i>).	20
Chapter 3. The effects of human disturbance, nest chronology, habitat quality and meteorological conditions on piping plover (<i>Charadrius melodus</i>) fledging success.	91

LIST OF TABLES

Chapter 2:

Table 2.1. Descriptive statistics for independent variables measured to predict piping plover foraging behaviour.

87

Table 2.2. Data output for GENMOD procedure in SAS for the proportion of time spent foraging by piping plovers. Parameters with $\alpha < 0.20$ were selected for inclusion within the multivariate GENMOD procedure.

88

Chapter 3:

Table 3.1. Descriptive statistics for independent variables measured to predict piping plover fledging success. Normality was determined using the D'Agostino and Pearson omnibus normality test and variables were considered normal if $p > 0.05$. Pearson correlations were used when independent variables were normal and Spearman correlations were used for non-normal variables. Correlations were significant at $\alpha < 0.05$.

134

Table 3.2. Results of the multiple linear regression with backward stepwise analysis of piping plover chick survival for pairs that hatch chicks on Prince Edward Island ($r = 0.49$, $r^2 = 0.350$, 1 df for each variable except constant).

135

Table 3.3. Results of the multiple linear regression with forward stepwise analysis of piping plover chick survival for pairs that hatch chicks on Prince Edward Island ($r = 0.479$, $r^2 = 0.229$, 1 df for each variable except constant).

136

LIST OF FIGURES

Chapter 2:

Figure 2.1.a. Map illustrating locations of piping plover breeding beaches studied on Prince Edward Island, Canada in 2005.

74

Figure 2.1.b. Map illustrating locations of piping plover breeding beaches where fledging success was monitored in 2006.

76

Figure 2.2.a. Box and whisker plot comparing the proportion of time spent foraging by male (range=0.17-0.75) and female (range=0.12-0.60) piping plovers. The proportion of time spent foraging did not differ significantly between sexes ($W=117.0$, $p=0.29$, $n=33$).

78

Figure 2.2.b. Histogram with standard error bars of the proportion of time spent foraging during pre-incubation (0.33 ± 0.044), incubation (0.33 ± 0.036), and pre-fledging (0.35 ± 0.046) reproductive stages. No significant differences were observed between reproductive stages ($F=0.075$, $p=0.9275$, $n=17$).

78

Figures 2.3.a. Comparison of the proportion of time spent foraging by piping plovers during periods when human activity occurred within 50 m ($t=1.17$, $p=0.27$, $n=11$) of the focal individual to periods with no human activity.

80

Figure 2.3.b. Comparison of the proportion of time spent foraging by piping plovers during periods when human activity occurred within 100 m ($t=0.31$, $n=13$, $p=0.76$) of the focal individual to periods with no human activity.

80

Figure 2.3.c. Comparison of the proportion of time spent foraging by piping plovers during periods when human activity occurred within 200 m ($W= -25.00$, $n=13$, $p=0.16$, $n=13$) of the focal individual to periods with no human activity.

80

Figures 2.4.a. Comparison of the proportion of time spent engaging in disturbance behaviour by piping plovers during periods when human activity occurred within 50 m ($W=56.0$, $n=11$, $p=0.0098$) of the focal individual to periods with no human activity.

82

Figure 2.4.b. Comparison of the proportion of time spent engaging in disturbance behaviour by piping plovers during periods when human activity occurred within 100 m ($W=28.00$, $n=13$, $p=0.016$) of the focal individual to periods with no human activity.

Figure 2.4.c. Comparison of the proportion of time spent engaging in disturbance behaviour by piping plovers during periods when human activity occurred within 200 m (W=12.00, n=13, p=0.38) of the focal individual to periods with no human activity.	82
	82
Figure 2.5.a. Histogram with standard errors of invertebrate abundance in the swash zone during the months of May, June and July of 2005 (F=2.97, p=0.19) and 2006 (F=5.19, p=0.06).	84
	84
Figure 2.5.b. Histogram with standard errors of invertebrate abundance in the saturation zone during the months of May, June and July of 2005 (F=1.45, p=0.57) and 2006 (F=0.93, p=0.63).	84
	84
Figure 2.5.c. Histogram with standard errors of overall invertebrate abundance during the months of May June and July of 2005 (F=0.42, p=0.81) and 2006 (F=7.091, p=0.027).	84
	84
Figures 2.6.a. Line graph of the components selected for inclusion within the best model, demonstrating the influence of invertebrate abundance on the percentage of time spent foraging by piping plovers.	86
	86
Figures 2.6.b. Line graph of the components selected for inclusion within the best model, demonstrating the influence of date on the percentage of time spent foraging by piping plovers.	86
	86
Figures 2.6.c. Line graph of the components selected for inclusion within the best model, the best model identified by GENMOD in SAS which includes invertebrate abundance/m ² and date.	86
	86
 Chapter 3:	
Figure 3.1.a. Map illustrating locations of piping plover breeding beaches where fledging success was monitored in 2005.	138
	138
Figure 3.1.a. Map illustrating locations of piping plover breeding beaches where fledging success was monitored in 2006.	140
	140
Figure 3.2.a. Chick mortalities as they relate to daily precipitation amounts at Environment Canada's weather monitoring stations in Stanhope, PEI from the period of June 1 to July 31.	

142

Figure 3.2.b. Chick mortalities as they relate to daily precipitation amounts at Environment Canada's weather monitoring stations in Saint Peter's, PEI from the period of June 1 to July 31, 2005.

142

Figure 3.2.c. Chick mortalities as they relate to daily precipitation amounts at Environment Canada's weather monitoring stations in Eastpoint, PEI from the period of July 1 to August 15, 2005.

142

Figure 3.3.a. Chick mortalities as they relate to daily precipitation amounts at Environment Canada's weather monitoring station in Stanhope, PEI from the period of July 1 to July 31, 2006.

144

Figure 3.3.b. Chick mortalities as they relate to daily precipitation amounts at Environment Canada's weather monitoring station in Saint Peter's, PEI from the period of July 1 to July 31, 2006.

144

Figure 3.3.c. Chick mortalities as they relate to daily precipitation amounts at Environment Canada's weather monitoring station in Eastpoint, PEI from the period of June 1 to June 30, 2006.

144

LIST OF APPENDICES

Chapter 3:

Appendix 1. Summary of fledging success for piping plovers on Prince Edward Island in 2005-2006. Only pairs having at least one hatched egg within a brood are included.

146

CHAPTER 1

Human Recreational Activity and Piping Plovers: General Introduction

The Earth is currently undergoing its sixth period of mass extinction. Due primarily to anthropogenic activities, it is expected that within the next 150 years as many as 50% of the Earth's species may succumb to extinction (Morrell 1999). Global biodiversity is steadily decreasing due mainly to anthropogenic activities. In fact, anthropogenic activities may be responsible for as much as 28 to 50% of population declines that lead to bird species becoming vulnerable to extinction (Kerr and Currie 1995). Currently, 11% of all bird species worldwide are at risk of extinction caused by anthropogenic threats such as territory fragmentation, loss of habitat, hunting, and failed nesting attempts due to predation or pesticides (Gill 1994).

Humans are viewed as predators by most animals, and in some cases animals have stronger responses to humans and pets than they do to natural predators (Flemming *et al.* 1988). Much as when exposed to natural predators, animals respond to non-lethal human activities by foregoing fitness-enhancing activities (e.g., foraging, parental care and mating displays) in order to increase vigilance, resulting in a trade-off between the two (Frid and Dill 2002, Mallord *et al.* 2006). As a result, Gill *et al.* (1996) suggest that human disturbance be quantified as resource uptake foregone as a result of human activity. Therefore, it is possible to determine the extent to which shorebirds are affected by human activity by measuring differences in foraging behaviour and vigilance and comparing them to periods with no human activity (Gill *et al.* 1996). When met with approaching pedestrians, the common gallinule (*Gallinula chloropus*), sora rail (*Porzana carolina*), glossy ibis (*Plegadis falcinellus*), little blue heron (*Egretta caerulea*) and Louisiana heron (*E. tricolor*) all decreased foraging and increased vigilance (Burger and Gochfield 1998). Similarly, African black oystercatchers (*Haematopus moquin*, Leseberg

et al. 2000), sanderlings (*Calidris alba*, Thomas *et al.* 2003) and blackbirds (*Turdus merula*, Fernández-Juricic and Telleria 2000) all reduced the amount of time spent foraging when human activity was taking place.

Human activities may also interfere with an individual's ability to care for their offspring, which can have obvious effects on reproductive success. Time spent incubating by European oystercatchers (*Haematopus ostralegus*, Verhulst *et al.* 2001) and northern New Zealand dotterels (*Charadrius obscurus aquilonius*, Lord *et al.* 2001) was lower during periods with high human activity than periods with no human activity. Less time engaging in activities such as foraging and thermoregulation of chicks during periods when human activity is taking place can also have considerable effects on productivity. Human recreational activities have been associated with reduced productivity in common loons (*Gavia immer*, Heimberger *et al.* 1983), African black oystercatchers (*Haematopus moquini*, Leseberg *et al.* 2000), kittiwakes (*Rissa tridactyla*), common murrelets (*Uria aalge*; Beale and Monaghan 2004) and snowy plovers (*Charadrius alexandrinus*, Ruhlen *et al.* 2003). Similar results have also been observed for piping plovers some of the time (*Charadrius melodus*; Cairns 1977, Flemming *et al.* 1988, Strauss 1990), but not always (Tull 1984, Hoopes 1993). The observed dichotomy between the results of the piping plover studies may suggest that piping plover productivity is negatively affected by human activity only beyond a certain threshold or when other variables are also acting to limit reproductive success.

Piping plovers are small socially monogamous shorebirds endemic to North America (Haig 1992). They are ground nesters and normally lay four eggs per clutch,

with incubation lasting approximately 28 days (Haig 1992). Once hatched, precocial chicks normally stay in the nest until they have dried off and until the remaining eggs in the clutch have hatched (Haig 1992). Chicks are able to forage independently but rely on their parents for thermoregulation and protection from predators (Haig 1992). Piping plover chicks become increasingly independent with age and rarely require thermoregulation beyond 21 days of age (Cairns 1977). Threatened primarily by depredation, loss or alteration of habitat, and changes in behaviour due to human activity (Haig 1992, Goossen *et al.* 2002), piping plovers have been listed as endangered in Canada (Goossen *et al.* 2002) and threatened or endangered throughout their U.S. range since 1985 (U.S. Fish and Wildlife Service 1985). Commonly located adjacent to sand dunes, the breeding territories of piping plovers along the Atlantic Coast typically have substrate composed mainly of open sand, gravel or cobble with very little vegetation (Haig 1992, Burger 1987). These range preferences often result in conflicts between breeding piping plovers and human recreational activities. In many cases, piping plovers establish territories before human activity becomes pronounced, thereby forcing them to either abandon their territories and eggs (if laid) or cope with the increased level of human activity later (June and July) in the breeding season (Strauss 1990). Piping plover chicks are thought to be especially sensitive to human recreational activity (Flemming *et al.* 1988). From hatching until the chicks fledge, chick mortality can occur when human recreational activities disrupt foraging or thermoregulation (Flemming *et al.* 1988). Piping plovers respond to human recreational activity by reducing the amount of time spent foraging in order to increase vigilance (Burger 1991, 1994, Flemming 1984,

Flemming *et al.* 1988). Human recreational activity may further influence piping plover survival by attracting potential predators (Strauss 1990).

Management goals established for imperiled species, such as the piping plover, most often focus on increasing population sizes to an acceptable level (Plissner and Haig 2000). The 2002 National Recovery Plan for the Canadian Atlantic Coast population of piping plovers sets a goal to reach and sustain a population of 670 adult piping plovers while maintaining productivity above 1.5 chicks per pair per year (Goossen *et al.* 2002). In order to protect this management-dependent species, it is important to understand the variables that influence the amount of time spent foraging by piping plovers because their fitness may be directly related to their ability to forage efficiently (Donnelly and Sullivan 1998). Furthermore, the majority of studies investigating the impact of human recreational activity on piping plover foraging behaviour and reproductive success have not considered the influence of potentially confounding variables. Variables that influence prey availability and energetic budgets, such as prey abundance, air temperature, and tide level, can all influence the amount of time an individual will spend foraging, which is directly related to fitness. For example, Yasué (2005) found that the response of least sandpipers (*Calidris minutilla*) to human recreational activity was dependent on invertebrate abundance. She found that only those foraging in areas with high invertebrate abundance spent less time foraging when faced with human recreational activity, presumably because they could afford to do so. Despite the influence of external variables on foraging decisions, the majority of studies investigated the effects of human activity in piping plovers without considering how external variables such as invertebrate abundance might influence foraging decisions (e.g. Burger 1991, 1994, Flemming 1984,

Flemming *et al.* 1988). Therefore, it is of the utmost importance to understand the impact of human activity on foraging behaviour and reproductive success of piping plovers while considering external variables such as, habitat quality and weather conditions. As a result, this thesis has been formulated with two primary objectives in place. They are as follows:

- 1.) To determine the impacts of human recreational activity, measures of habitat quality and meteorological conditions on the proportion of time spent foraging by piping plovers (Chapter 2).
- 2.) To determine the impacts of human recreational activity, measures of habitat quality and meteorological conditions on piping plover fledging success (Chapter 3).

This study was designed so that potentially confounding variables were measured and accounted for. Study sites and pairs observed were selected to minimize distance traveled between observations and to maximize sample sizes. In order to ensure clarity, this thesis has been prepared as two discrete manuscripts written for submission for publication in professional journals. Each chapter has been written to stand alone with an abstract and literature cited section. The knowledge gained by doing this thesis will hopefully help management officials determine the conditions under which piping plover adults and chicks are most vulnerable and allow effective allocation of conservation efforts for this management-dependent species.

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CHAPTER 2:

The effects of human recreational activity, habitat quality and weather conditions on the foraging behaviour of breeding piping plovers (*Charadrius melodus*)

Abstract: A number of studies have investigated the influence of human activity on the foraging behaviour of different shorebird species. In most cases, shorebirds reduce the time they spend foraging and increase the time they spend devoted to vigilance (watching for predators) when human activity is elevated. However, the majority of these studies have not accounted for variation in other important aspects of habitat quality (e.g. invertebrate abundance and beach width) and meteorological conditions (e.g., wind speed and air temperature) which may influence foraging decisions. These types of data are especially important to understand for endangered species, such as the piping plover (*Charadrius melodus*). I performed behavioural observations on piping plovers on breeding beaches located on Prince Edward Island, Canada during the 2005 and 2006 breeding seasons and documented their activity at 15-second intervals, over a half hour. Independent variables measured were the number of people within 50, 100 and 200 m of the focal bird, date, invertebrate abundance, beach width, the amount of wrack on the beach, and tide level during each behavioural observation. Human activity within 50 and 100 m, but not 200 m, resulted in an increase in their proportion of time spent engaged in disturbance behaviour. However, human activity at any of these distances did not affect the proportion of time spent foraging by piping plovers. Significant positive correlations were observed between the proportion of time spent foraging and overall invertebrate abundance (monthly mean of saturation zone and swash zone), air temperature and wind speed. Both invertebrate abundance and date were significant predictors of piping plover foraging behaviour. Piping plovers do not show disturbance behaviour in response to human activity beyond some distance between 100 and 200 m, therefore, conservation authorities should err on the side of caution and protect larger areas whenever possible.

Introduction

Fitness is directly related to foraging efficiency (Donnelly and Sullivan 1998). Nevertheless, an animal's ability to forage is dependent on a number of different variables. Factors such as perceived predatory threat (e.g. human activity), time of year, habitat quality (e.g. prey abundance) and weather conditions (e.g. air temperature) all have the potential to influence an individual's ability to gather food. Understanding how these factors influence foraging behaviour may help identify periods or conditions when management-dependent species, such as the endangered piping plover (*Charadrius melodus*), are most sensitive, thereby allowing those species to be best protected.

Piping plovers are small shorebirds endemic to North America (Haig 1992, Amirault 2005). Measuring approximately 17-18 cm in length, the piping plover can be distinguished by their stout bill, single black neck band (alternate plumage), pale upperparts and orange coloured legs (Haig 1992). Piping plover breeding populations are found in the Northern Great Plains, the Great Lakes and along the Atlantic Coast. They migrate to portions of the southern United States, Mexico and the Caribbean Islands for winter (Haig and Oring 1985a). Historically, it has been questioned whether piping plovers breeding along the Atlantic Coast and northern Great Plains had diverged into two subspecies; however, the lack of behavioural and genetic differentiation between the two populations suggest that classification into subspecies is not warranted (Haig and Oring 1985b).

Piping plovers begin arriving on Prince Edward Island (PEI) in late April (Cairns 1982). They form socially monogamous pairs and defend breeding territories from conspecifics (Goosen *et al.* 2002). Piping plover nests are shallow scrapes in the beach

substrate (Melvin *et al.* 1991). Nest characteristics are dependent on the underlying substrate type and are sometimes lined with broken seashells or pebbles if they are prominent on the beach (Cairns 1982, Canadian Wildlife Service 1995). There are typically four eggs per clutch, and it usually takes approximately 5 to 6 days for the female to lay the eggs (Cairns 1982, Canadian Wildlife Service 1995). The eggs, which are buff-colored with black speckles, blend in well with the beach substrate (Canadian Wildlife Service 1995). Incubation begins after the penultimate egg has been laid and typically lasts between 26 to 29 days (Cairns 1982, Canadian Wildlife Service 1995). Incubation duties are shared equally between the male and female (Cairns 1982), so eggs are incubated 100% of the time (Haig and Elliott-Smith 2004). Piping plovers normally raise only one brood per season, but will re-nest if a clutch is lost (Melvin *et al.* 1991). Chicks are precocial and are able to walk a few hours after hatching (Cairns 1977). Piping plover chicks take approximately 27 to 32 days to fledge (Cairns 1982; Canadian Wildlife Service 1995). Both parents care for the chicks, but females sometimes abandon their broods before they have fledged (Haig and Oring 1988).

Several factors have resulted in a dramatic decline in the number of piping plovers. During the 1870's and 1880's, piping plovers were heavily hunted for the millinery industry (Powell and Cuthbert 1993). Following the Second World War, development and human activity increased significantly along coastal areas, thereby causing disturbance to many shorebird communities. More recent threats to the success of piping plovers are flooding, poor water-level regulation, coastal development, predation, off-road vehicles, and human recreational activity (Melvin *et al.* 1991, Goossen 1990, Strauss 1990, Goosen *et al.* 2002). As a result, piping plovers have been listed as

endangered throughout their Canadian range since 1985 (Goossen *et al.* 2002), whereas within the United States they are listed as endangered within the Great Lakes population but threatened elsewhere (U.S. Fish and Wildlife Service 1985).

Most animals, shorebirds included, perceive humans as predators and face trade-offs between foraging and vigilance when human activity is high (Frid and Dill 2002, Mallord *et al.* 2006). Disturbance is defined as any deviation in behaviour resulting from human activity (Frid and Dill 2002, Amirault *et al.* 2004). Activities such as walking, unleashed pets, swimming, sunbathing, collecting driftwood/shells/wrack, horseback riding, fishing, flying kites, fireworks, and the use of all-terrain vehicles are identified as some of the activities that cause piping plovers to elicit disturbance behaviour. The response of many animals to human activity is often to reduce the amount of time spent engaging in activities such as foraging, caring for offspring, and participating in courtship displays, all of which influence an individual's fitness (Gill *et al.* 1996, Frid and Dill 2002). Animals experiencing elevated predation risk, whether perceived or real, may choose to forage in areas with fewer resources in order to reduce the likelihood of being depredated (Smith 1996, Krebs and Davies 1997). Shoal fish fed in areas with reduced predation risk unless food was unavailable (Pitcher *et al.* 1988). Similarly, willow tits (*Parus montanus*) and crested tits (*Parus cristatus*) chose to forage in lower quality habitats with fewer predators (Suhonen 1993). Nevertheless, shorebirds at Pachena Beach, British Columbia did not select sites based on the level of human activity within an area, but rather selected territories that were far from cover where natural predators could hide (Yasué 2006). In that study, the risk from actual predators must have outweighed the perceived threat from human activity. Nevertheless, this finding may also

reflect the fact that human activity could reduce an animal's risk of predation because predators also avoid people. A significant negative correlation was observed between the number of anglers and the abundance of common sandpipers (*Actitis hypoleucos*) in areas with no cover, but not in quieter areas with more cover (Yalden 1992) suggesting that sandpipers are able to tolerate human activity when they have cover from predators. Piping plovers in New Jersey responded to increased levels of human activity by foraging in areas or habitat types (e.g. beach, dune and back bay) with fewer humans (Burger 1994). Here, piping plovers were most commonly found in areas (dunes or back bays) where the number of people was low (Burger 1994). Therefore, animals may leave high-quality territories when faced with human recreational activity in order to minimize the perceived likelihood of depredation.

One method of quantifying the influence of human activity on wild populations is to compare behaviour during periods when human activity is taking place to periods without human activity. Gill *et al.* (1996) suggest that human disturbance be quantified as resource uptake foregone as a result of human activity. By quantifying the proportion of time spent foraging and time spent displaying vigilant behaviour at various levels of human activity, it is possible to determine the extent to which birds are affected by human activity. A multi-species study conducted on the common gallinule (*Gallinula chloropus*), sora rail (*Porzana carolina*), glossy ibis (*Plegadis falcinellus*), little blue heron (*Egretta caerulea*) and Louisiana heron (*E. tricolor*) found that as humans approached foraging birds, foraging decreased and vigilance increased in all five species (Burger and Gochfield 1998). In areas of high human activity, reduced foraging was observed in African black oystercatchers (*Haematopus moquin*, Leseberg *et al.* 2000),

sanderlings (*Calidris alba*, Thomas *et al.* 2003) and blackbirds (*Turdus merula*, Fernández-Juricic and Telleria 2000). In addition, human activity resulted in less time spent incubating by European oystercatchers (*Haematopus ostralegus*, Verhulst *et al.* 2001) and northern New Zealand dotterels (*Charadrius obscurus aquilonius*, Lord *et al.* 2001). Eastern oystercatchers (*Haematopus osculans*), curlews (*Nmenius arquata*) and redshanks (*Tringa totanus*) increased the time they devoted to vigilance as human activity increased, whereas the rate of prey capture did not significantly decrease but actually increased for oystercatchers and curlews perhaps because they were not foraging at their maximum possible rate during observations without human activity (Fitzpatrick and Bouchez 1998). However, there came a point when disturbance from human activity was enough for them to either walk or fly away (Fitzpatrick and Bouchez 1998).

Not all human activities elicit the same disturbance response in shorebirds (Burger 1981). Shorebirds appear to respond most to high-speed human activities (e.g. jogging) and activities in close proximity (Burger 1981). For example, the proportion of time spent foraging by sanderlings was significantly affected by the number of unleashed dogs, the number of people, and the activity type in which people were engaging. In all cases, sanderlings responded to human activity occurring within 30 m (Thomas *et al.* 2003). Northern New Zealand dotterels were most affected by dogs being walked (Lord *et al.* 2001). Therefore, the number of people, the activity type in which they are engaging and the proximity of the activity to the focal bird must be considered when investigating the impact of human activity on shorebirds.

Many shorebirds are thought to habituate to human activity. Nisbet (2000) argued that the most frequent use of the term habituation actually refers to variation in tolerance to human activity. He defined tolerance as “the intensity of disturbance that an individual bird tolerates without responding in a defined way” and suggests that observing differences in behaviour at disturbed sites and undisturbed sites can provide suggestive, but not conclusive, evidence of habituation. Increased tolerance of human activity may occur over time. Northern New Zealand dotterels that were observed on beaches with consistently high levels of human activity allowed humans to approach the nest closer than they did on beaches with little human activity (Lord *et al.* 2001). Common terns (*Sterna hirundo*) and roseate terns (*Sterna dougalli*) showed a marked increase in tolerance to intensive researcher handling over a 2-3 year period (Nisbet 2000). Similarly, magellanic penguins (*Spheniscus magellanicus*) in areas of consistently high human activity elicited less physiological stress when approached by humans than those exposed to moderate or low levels of human activity, suggesting that habituation to human activity may occur (Fowler 1999). Piping plovers on sites with consistently high levels of human recreational activity have demonstrated an ability to habituate to human recreational activity by allowing people to approach them without interrupting foraging (Hoopes 1993). Therefore, when measuring the impacts of human activity, it is important to distinguish between areas with persistent activity and areas with periodically elevated levels of human activity. The above results suggest that individuals inhabiting areas with periodic activity may elicit greater responses than those exposed to continuous activity.

Another factor influencing the manner in which piping plovers will respond to human activity is the physical condition of the individual being disturbed. Animals in

danger of starvation are likely more willing to risk predation while foraging than well-fed individuals (Krebs and Davies 1997). As a result, the fitness of individuals that respond sooner to human activities may be less affected because they are in better physical condition. Turnstones (*Arenaria interpres*) in better physical condition actually responded sooner to human activity than those that were not and did not represent the portion of the population whose fitness was most affected by human activity (Beale and Monaghan 2004). If animals are well fed or if they have adequate alternatives with low levels of human recreational activity (e.g. areas with low risk of predation where food resources are plentiful), they may be more willing and able to adjust their behaviour when faced with human activity (Beale and Monaghan 2004). Therefore, studies investigating the effects of human activity on avian foraging behaviour must also consider an individual's condition as well as its access to alternative foraging locations with low levels of human activity, which is not always possible. Individuals that forage more slowly or less efficiently may be more affected by human activity as they are unable to develop sufficient lipid reserves essential for successful migration and reproduction (Lafferty 2001, Skagen and Knopf 1993), a factor that is especially important to newly hatched or fledged individuals (Cairns 1982). A positive correlation has been observed between piping plover chick mass and foraging rate (Loegering and Fraser 1995). The importance of efficient undisturbed foraging for the piping plover chick is further demonstrated by the fact that chicks that fail to reach 60% of normal adult weight by 12 days of age are unlikely to survive (Cairns 1982), with the majority of chick deaths occurring during the first ten days following hatching (Patterson *et al.* 1991).

Although human activities are rarely lethal to plovers, it is the collective impact of reduced foraging and the lack of rest associated with human activity that can reduce productivity and survivorship of adult plovers and chicks (Flemming *et al.* 1988, Lafferty 2001). Piping plovers (*Charadrius melodus*) have highly specialized requirements for beaches (Plissner and Haig 2000). Therefore, when faced with increased levels of human activity on beaches, plovers are not always able to flee and will incur energetic costs from reduced foraging and increased vigilance (Burger 1991, 1994). Snowy plovers (*C. alexandrinus*), a threatened shorebird, reduced their feeding rate as human activity increased, and demonstrated the greatest amount of disturbance behaviour when people or pets were in close proximity (Lafferty 2001). Snowy plover chick mortality, attributed to decreased foraging caused by human activity, was also higher on busy beach days (i.e. weekends or holidays) than on days with less human activity (Ruhlen *et al.* 2003).

Piping plovers respond to potential predators by squatting, false brooding, high-tailed running, crouch running, injury feigning and by making “whirring” vocalizations when highly disturbed (Cairns 1982). This behaviour was displayed only when human activity occurred within 30 m of incubating plovers in another study (Strauss 1990). Nevertheless, the abovementioned response types may increase their likelihood of mortality by off-road vehicles because chicks may remain motionless, crouch or simply not move out of the way fast enough (Melvin *et al.* 1994). Piping plovers also appear to respond more intensively to humans than natural predators (Flemming *et al.* 1988).

The foraging behaviour of piping plovers is considerably reduced by human activity. When in close proximity to human activity they reduce the time they spend

foraging (Flemming *et al.* 1988, Burger 1991, Staine and Burger 1994, Strauss 1990). Piping plovers in New Jersey spent 30% less time foraging and decreased their pecking rate by 27% when human recreational activity took place (Staine and Burger 1994). The same study found that piping plovers exposed to human recreational activity at night reduced their pecking rate by as much as 61% (Staine and Burger 1994). Likewise, piping plovers in Massachusetts halted foraging in response to human activity 23 to 44% of the time (Hoopes 1993), and spent significantly less time foraging and more time standing alert when pedestrians were within 100 m when compared to periods with no human activity (Strauss 1990). Fencing surrounding foraging areas of multiple species of shorebirds has demonstrated some success in reducing the impacts of human activity on foraging behaviour, and as a result has been suggested as a means to limit human access to foraging areas and to provide refuge to shorebirds where they are able to forage without being disturbed (Ikuta and Blumstein 2003). Fencing has proven successful for piping plovers (Strauss 1990, Patterson *et al.* 1991, Melvin *et al.* 1992). The practice of surrounding nesting sites with symbolic fencing has been integrated into the management strategy for piping plovers on Prince Edward Island outside of the Prince Edward Island National Park (PEINP, Waddell 2004) which limits human activity to within a few meters of the water's edge. Within PEINP, large sections of beach where piping plovers nest are closed to human access.

Piping plovers may alter the proportion of time they spend foraging during different reproductive stages. During the breeding season the time budget of plovers may differ due to differing parental responsibilities and energetic requirements. However, Gautreau (1998) found that there was no significant difference between the average time

allotted to feeding, movement, intra-and interspecific interactions with intruders, preening, or flying during each of the reproductive stages for Prince Edward Island piping plovers. On the other hand, piping plovers in New Jersey lower their pecking rate during incubation and brood-rearing phases (Staine and Burger 1994). Considering the conflicting results of these two studies it is important to consider reproductive stage when attempting to understand foraging decisions of piping plovers.

Certain measures of habitat quality likely influence the proportion of time spent foraging by piping plovers. Perhaps one of the most obvious measures is prey abundance (Goss-Custard 1977). As prey abundance varies temporally and spatially (Gill 1994), individuals should select areas for foraging where prey abundance is reliable. In areas with low prey density, individuals must spend more time foraging and go farther distances in order to get the energy they require (Norberg 1977, McKnight 1998). Therefore, in areas with low prey abundance shorebirds must increase the proportion of time they spend foraging without necessarily increasing their pecking rate. As a result, it is energetically unprofitable for animals to forage in areas with low levels of prey (Smith 1996). Prey capture rates are commonly higher when prey abundance is higher (Brown 1993) or when there are a greater number of prey choices (Berkelman *et al.* 1999). A study involving brown-headed cowbirds (*Molothrus ater*) uncovered a positive correlation between invertebrate abundance and cowbird density, as well as between invertebrate abundance and the number of females present, suggesting cowbirds also select sites based on invertebrate abundance (Morris and Thompson 1998). Ovenbird territories and foraging sites had significantly higher prey biomass than randomly selected sites (Burke and Nol 1998, Zach and Falls 1979). Nevertheless, food abundance

failed to explain foraging performance in African black oystercatchers (*Haematopus moquini*, Leseberg *et al.* 2000), and did not influence the time spent foraging or pecking rate of brown-headed cowbirds (Morris and Thompson 1998).

The foraging techniques of piping plovers are well adapted to efficient foraging within the intertidal zone. Plovers rely entirely upon visual prey searching and rapid movements, often referred to as “stop-run-peck” (Cairns 1982), in order to locate and capture prey (Pienkowski 1981). Due to physical constraints associated with bill morphology, the foraging of piping plovers is confined to within the first one to two centimeters of the substrate surface (Nordstrum and Ryan 1996). However, it is believed that “foot-tapping”, a common foraging activity of plover species, is used to bring invertebrates to the surface of the substrate (Cairns 1977), or to elicit movement in prey to make them visible (Pienkowski 1981). Knowledge regarding the diet of piping plovers is sparse and varies regionally (Shaffer & Laporte 1994, Cuthbert *et al.* 1999). Insects (Shaffer & Laporte 1994, Cuthbert *et al.* 1999), worms, crustaceans and mollusks have all been identified as important components of piping plover diet (Staine and Burger 1994). Shaffer & Laporte (1994) gathered a total of 130 fecal droppings from piping plovers on the Magdalen Islands of Quebec. From these droppings, they identified specimens belonging to the Orders Gastropoda, Amphipoda, Coleoptera, Diptera and Hymenoptera (Shaffer & Laporte 1994). Marine worms were likely absent because they would be more easily digested (Shaffer & Laporte 1994). In fact, marine worms (ranging from 2.5 to 7.5 cm in length) are believed to be a major component of the piping plover’s diet. Piping plovers in Nova Scotia consume upwards of 58 worms per hour (Cairns 1977). The gizzard contents of dead chicks opportunistically collected in Grand Marais,

Michigan, were examined and Hymenoptera, Coleoptera and Diptera were the most abundant species identified (Cuthbert *et al.* 1999).

Piping plovers appear to evaluate invertebrate abundance prior to territory selection and establishment. Evidence of this is given by Stewart (2004) who found that the overall invertebrate abundance was significantly higher on current breeding beaches than beaches where piping plovers formerly bred. Invertebrate abundance within wrack and the intertidal zone was positively correlated with the amount of time spent foraging by piping plovers in Massachusetts; however, this relationship weakened later in the breeding season (Hoopes 1993). As a result, invertebrate abundance is especially important to address when attempting to draw conclusions regarding the impact of human activity on foraging rate (Yasué, 2005). Yasué (2005) discovered that reduced foraging was observed in least sandpipers (*Calidris minutilla*) only when human activity occurred on areas with high prey density. This is likely due to the fact that individuals foraging in areas with low invertebrate abundance must spend a greater proportion of time foraging in order to acquire their energy requirements and as a result are unable to give up foraging to respond to human activity. If similar trends are also observed for the piping plover there could be important conservation implications for this management-dependent species. The determination of piping plover diet and the availability of their prey at different sites will allow for better assessment and identification of potential breeding sites (Cuthbert *et al.* 1999). Piping plovers feed primarily within their own breeding territories (Cairns 1982), therefore understanding how variation in invertebrate abundance among sites influences the manner in which piping plovers respond to human activity may allow conservation efforts to be more effective. This is especially true for

piping plover chicks, as it has been suggested that differences in chick survival may be due to variation in invertebrate abundance (Patterson *et al.* 1991). Therefore, piping plover chicks on territories with low invertebrate abundance may be more vulnerable to human recreational activity. Piping plover chick survival on Assateague Island (Patterson *et al.* 1991) and along the Missouri River (Le Fer *et al.* 2004) was influenced by invertebrate abundance. As a result, it is not surprising that plover chicks in New York most often forage along ephemeral pools or tidal flats where arthropod abundance is high and that the foraging rate of piping plover broods is positively correlated with arthropod abundance (Elias *et al.* 2000). Therefore, plovers whose territories have higher invertebrate abundance would likely spend a greater proportion of time feeding and have increased chances of survival.

Another measure of habitat quality that may influence foraging decisions of piping plovers is the amount of wrack present on their territory. Wrack, which is “seaweed that has been washed up onshore” (Stewart 2004), contributes to biological richness of the intertidal zone (Dugan *et al.* 2003). A positive relationship has been observed between mean wrack cover and the abundance of macrofauna along California coastal beaches, as well as between wrack-associated macrofauna and the presence of black-bellied plovers (*Pluvialis squatarola*) and snowy plovers (*Charadrius alexandrinus nivosus*; Dugan *et al.* 2003). In South Africa, macrofaunal species richness was highest in the wrack line, of which Talitrid amphipods comprised 90% (Griffiths *et al.* 1983). Similarly, at Coal Oil Point, California as many as 87% of juvenile sand-beach amphipods (*Ochestoidea corniculata*) were found in sand directly beneath the wrack (Craig 1973). Therefore, it appears as though wrack is a crucial aspect of invertebrate

abundance and productivity on sandy beaches. In fact, wrack invertebrates are believed to be a key food source for piping plover chicks (Elias *et al.* 2000). Therefore, it is not surprising that piping plover chicks and adults demonstrated a significant preference for wrack habitat over other habitat types in Massachusetts .

Visibility on plover territories is another measure of habitat quality that may influence the proportion of time spent foraging by piping plovers. The majority of shorebirds do not take cover when confronted with a predator, but instead fly away (Amat and Masero 2004). Good visibility of the surrounding area has been identified as an important component of habitat quality for shorebirds because it allows them to detect approaching predators. As visibility at the nest sites of turnstones (*Arenaria interpres*) and purple sandpipers (*Calidris maritima*) decreases, the proportion of time spent vigilant increases, perhaps because the bird's ability to detect approaching predators is impeded (Metcalf 1984). Piping plovers that nest on wide beaches with either very little vegetation or clumped vegetation may benefit by blending in with their surroundings (Prindiville-Gaines and Ryan 1988) and by earlier predator detection (Metcalf 1984). Narrow beaches do not allow plovers and people to avoid one another, instead they are confined to small areas where interaction between plovers and people is more likely to occur (Hoopes 1993). Objects such as vegetation, logs or large rocks near the nest may hinder predator detection, thereby putting the incubating adult and eggs at risk of predation (Amat and Masero 2004). As a result, adults may spend more time scanning for predators and less time resting or foraging. Wide beaches are also advantageous to piping plovers faced with human recreational activity because it minimizes competition for different habitat types with humans (Burger 1994).

Piping plovers normally forage within 5 m of the water's edge within the intertidal zone and along the wrack line (Haig 1992, Gautreau 1998, Haig and Elliott-Smith 2004). Therefore, tide level would likely affect the proportion of time spent foraging by piping plovers because it determines the amount of area available for foraging. During high tide, less beach substrate would be available to piping plovers for foraging, perhaps even covering entire intertidal ranges of certain invertebrates (Connors *et al.* 1981), and spend less time foraging as a result (Puttick 1979). During low tide the amount of available feeding area increases (Puttick 1979) and so one might expect to find plovers spending a greater proportion of time foraging during low tide than high tide, as has been suggested by studies carried out along the Atlantic Coast (Cairns 1977, Staine and Burger 1994) and for plovers wintering in Alabama (Johnson and Baldassarre 1988). Not only were piping plovers in New Jersey most likely to forage during early flood and late ebb, but the rate at which they acquired food was also higher, with the amount of time spent foraging being negatively associated with tidal height (Staine and Burger 1994). Furthermore, the amount of time passed after high tide can also influence the ability of piping plovers to detect prey. As the substrate exposed by receding tides dries, intertidal invertebrates become less active and more difficult to detect (Pienkowski 1981). Although piping plovers in Massachusetts spent more time feeding during falling mid-tide and rising low-tide, these differences were not statistically significant (Hoopes 1993). Furthermore, Gautreau (1998) found that piping plovers on Prince Edward Island did not alter their foraging behaviour according to tide level. The observed dichotomy between the findings of Gautreau (1998) and that of the abovementioned research

suggests that further work is required in order to better understand the role of tide on foraging behaviour of piping plovers.

Another variable that has the capacity to alter foraging behaviour of piping plovers is weather. During cool conditions animals have greater energy requirements and may spend more time foraging to maintain daily fat reserves. Furthermore, the foraging techniques used by shorebirds are well adapted for efficient foraging within coastal habitats. Plovers rely entirely upon visual prey searching and rapid movements to locate prey and are successful upwards of 90% of the time during ideal foraging conditions (Pienkowski 1981). Nevertheless, weather conditions can influence the ease of detection and availability of intertidal invertebrates for uptake by piping plovers (Murphy 1987). Decreasing temperatures cause invertebrates to stay below the surface and remain inactive (Goss-Custard 1984), and wind, rain and time passed after high tide all reduce the ability of plovers to locate prey with visual cues (Pienkowski 1981). Nonetheless, a significant negative correlation has been observed between ambient air temperature and time spent foraging, as well as a positive correlation between wind speed and time spent foraging by piping plovers in Alabama (Johnson and Baldassarre 1988). Therefore, it appears as though prey availability due to weather conditions is less of a limiting factor in Alabama. Gautreau (1998), on the other hand found that the proportion of time spent foraging by piping plover adults on PEI, Canada was independent of environmental conditions. Nevertheless, she found that piping plover chicks spent more time being brooded and less time foraging when it was cool and raining, as was also found in Nova Scotia, Canada (Flemming *et al.* 1988). Sustained inclement weather may cause chicks to become weak and die (Flemming *et al.* 1988). Therefore, the influence of weather is

important to consider when understanding the factors affecting foraging behaviour of piping plovers.

Birds who spend more time foraging are likely in greater need, therefore, by identifying periods or locations where foraging is essential will allow us to better protect them. As a result, the primary objective of this study was to identify the predictors of the proportion of time spent foraging by piping plovers. By identifying the factors that have the greatest influence on piping plover foraging behaviour it may be possible to determine the level of protection required to enable undisturbed breeding of this management-dependent species. Previous studies on piping plovers have documented a decrease in foraging time and an increase in time spent vigilant as human activity on breeding territories increased (e.g. Flemming *et al.* 1988, Burger 1991, 1994). Piping plovers were expected to spend significantly less time foraging (Johnson and Baldassarre 1988) and significantly more time engaging in disturbance behaviour (the sum of squatting, false-brooding, high-tailed running, crouch running, injury feigning, distress calling, peeping, displaying head-up posture and being alert) when people were within 50, 100 and 200 m of the focal individual when compared to periods with no human activity. The most important predictor variables of the proportion of time spent foraging were expected to be 1) human activity, 2) invertebrate abundance, 3) air temperature, and 4) tide level. When faced with trade-offs between foraging and responding to potential predators (human activity), piping plovers should reduce the amount of time they spend foraging if they are physically able to do so. Thus, piping plover foraging behaviour was predicted to be negatively associated with human activity within 200 m of the focal individual. The proportion of time spent foraging was expected to be negatively

associated with invertebrate abundance because individuals on territories with low prey density must spend more time searching in order to get the prey required to meet their energetic requirements, whereas individuals on territories with high prey abundance would be able to meet their energetic requirements in less time (Norberg 1977). During cool conditions, the energy requirements of piping plovers are higher, therefore, it was predicted that the proportion of time spent foraging by piping plovers would be negatively associated with air temperature. Previous studies have found that piping plovers forage primarily within low or falling tides. Therefore, it was expected that the proportion of time spent foraging would be positively associated with the amount of substrate exposed at varying tide levels, with more time spent foraging during low tide.

Materials and Methods

Study Site

This study took place on piping plover breeding territories on Prince Edward Island, Canada in 2005 and 2006. Study sites were located both inside and outside of the PEI National Park (PEINP). As a result, piping plovers were protected within park boundaries by Parks Canada staff and outside of the park they were protected by Island Nature Trust staff and volunteers. Piping plover breeding sites within the park are closed to human activities (however human activity was occasionally present within the closed areas), whereas access to piping plover breeding beaches outside of PEINP may be controlled only through education, symbolic fencing and signage. PEINP extends 40 km from Dalway to Cavendish (Parks Canada 2005). The piping plovers that studied as part of this research breed in three main geographic clusters. These clusters are located in

PEINP (Lat: 46° 25' N, Long: 63° 15' W) and near the communities of Morell (Lat: 46° 25' N, Long: 62° 42' W) and Souris (Lat: 46° 21' N, Long: 62° 15' W), Prince Edward Island, Canada (Figures 1.1.a-c).

Field Observations

The behaviour of piping plovers was monitored visually over half-hour periods by three observers (Marie-Hélène Michaud, 2005; Rosalie Connolly, 2006; and Kevin Murphy 2005-2006). These half-hour observations took place between 07h00 and 15h00 daily for six days each week. The order of pairs observed was determined according to a randomized complete block design. Pairs were placed in clusters according to proximity between the sites in order to minimize travelling time. Observations took place on one cluster of sites per day, with the order of observations in each cluster being east to west. Each day that observations were performed, the first observation to be conducted was shifted one site east so that the same pairs were not observed consistently at the same time of the day. Upon arrival at each site, the following data were recorded daily: date, time of day, reproductive stage, number of chicks, and sex of the focal bird (Burger 1991).

In order to increase confidence in these half-hour observations, multiple observations took place several times at different reproductive stages (pre-incubation, incubation, post-incubation/pre-fledge) for each adult pair and at different times of the day. Pre-incubation refers to the period following territory establishment until the time when adults begin incubating the eggs, which is normally after laying the penultimate egg. Incubation refers to the period of time when the eggs are being incubated by both the

male and female (normally lasts between 27 and 29 days). Post-incubation/pre-fledge refers to the period after the eggs have hatched until the chicks reach 20 days of age or die (Stewart 2004). Fledge is when chicks reach 20 days.

To minimize disturbance to the focal individual, we used spotting scopes and binoculars when conducting behavioural observations (Leseberg *et al.* 2000). Although the distance at which we observed the birds varied depending on the breeding territory where observations were taking place, generally piping plovers were observed at a distance of 100 to 150 m away. We were able to identify pairs based on the location in which they were observed foraging. On breeding beaches with more than one breeding pair, nesting and hatching chronology allowed us to distinguish between the pairs (Goldin and Regosin 1998). Some adults had United States Geological Survey (USGS) bands on one of their tarsi, and these bands were used to ensure that the same individuals were being observed. Adult males and females were differentiated based on physical characteristics (e.g. the black breast bands of males are darker and more complete, and the white eye-line and orange culmen of males are more pronounced than females during the breeding season; Haig and Elliott-Smith 2004, Vanner 2004). Observations were conducted alternately on males and females of each pair and observations where the sex of the focal individual was questionable were removed prior to analysis. If the target individual was disturbed upon our arrival at the site, the observation period was delayed 10 minutes (Gautreau 1998). The next individual within the breeding pair was selected if the target individual could not be located within 10 minutes of our arrival at the site, or we lost visual contact prior to completion of the entire half-hour observation period (Gautreau 1998). The activity of the focal individual was documented at 15-second

intervals and then placed in one of the following categories: foraging (the sum of feeding, running while searching for food, waiting, foot tapping, and feeding; Johnson and Baldassarre 1988), disturbance behaviour (the sum of squatting, false-brooding, high-tailed running, crouch running, injury feigning, distress calling, peeping, displaying head-up posture and being alert; Amirault *et al.* 2004), territorial behaviour, resting while vigilant (sitting or standing while looking around), resting while not vigilant (preening or sitting with the head tucked in the plumage), running (not for the purpose of foraging), tending to nest (scraping and sheltering the eggs from the sun), incubating (regulation of egg temperature outside of the body required to facilitate embryonic development; Gill 1994), brooding (which refers to parents sitting on newly hatched young to protect them from the cold, sun, rain and predators, Gill 1994), walking, flying, or courtship behaviour (tail-up, head-up tattoo, mounting and copulating; Cairns 1982).

The proportion of time spent in each activity type was determined by dividing the number of observations of each activity type by the total number of intervals within that observation (Gautreau 1998). The proportions of time spent engaging in certain activities were summed into more inclusive categories (e.g. foraging = sum of feeding, running while searching for food, waiting, and foot tapping). Multiple behavioural observations conducted on the same pairs and broods lack statistical independence (Goldin and Regosin 1998). As a result, the mean proportion of time spent in each activity type for each pair was taken as the unit of analysis when comparing observations with human activity to observations without (Goldin and Regosin 1998).

We documented the number of people and their activity type with or without accompanying animals within close proximity to the plovers (Lafferty 2001). In 2005, the

level of human activity was documented by counting the activity type (e.g., walking, sitting, running) of people within 50 m (Burger 1991), 100 m (Burger 1994) and 200 m of the focal piping plover at each 15-second interval while behavioural observations were conducted simultaneously. In 2006, the same information was documented along with the number and activity type of people within 150 m. Distance between the birds and a human was estimated by measuring the distance to natural landmarks in advance and using these locations as reference points.

Four modified dredge samples were collected from arbitrarily selected locations within both the saturation zone (area where a wave had just fallen back) and the swash zone (the intertidal area between the water line and the high tide line) at all of the sites where piping plovers were being observed. As piping plovers forage primarily in the top one to two centimetres of the substrate surface (Nordstrum and Ryan 1996), many of the invertebrates within this area are able to escape quickly, therefore, a modified dredge sampling technique was used. It was a 30 cm x 30 cm x 5cm box-shaped metal scoop with one open end which efficiently removed the top 2.5 cm of sediment. Upon arrival at the randomly selected sampling locations within the swash zone, the person gathering the sample would remain motionless for two minutes to allow invertebrates that may have been disturbed by vibrations from the approaching sampler to return to their normal location within the sediment.

Samples (2005, n = 280; 2006, n = 312) were collected from active breeding beaches (2005, n = 13; 2006, n = 14) during May, June and July of 2005 and 2006. Complete sampling rounds (samples collected once a month for three months) were not available for all sites because some pairs changed territories (2005, n=1) or settled on

their territory after the first or second sampling rounds had already taken place. However, invertebrate abundance was based on the following: three sampling rounds, 2005 n = 9, 2006 n = 10; two sampling rounds, 2005 n = 4, 2006 n = 2; one sampling round, 2006 n = 1.

Invertebrates were removed from dredge samples using 0.5 mm and 1.0 mm sieves, preserved in 80% ethanol and identified to Family (Eddy and Hodson 1961, Gosner 1978, Bromley and Bleakney 1984). In 2006, the wet weight of all specimens collected was determined using a precision balance accurate to 0.0001 g (samples were not weighed in 2005).

The number of invertebrates within each sample was determined as the mean number of invertebrates in samples collected within the swash zone and the saturation zone of each territory. For each territory, a monthly mean was taken of the invertebrate abundance within the swash zone and the saturation zone to provide a value for overall invertebrate abundance/territory. Invertebrate abundance within a given month was matched to observations performed in the same month for analysis purposes. For the 2006 field season we had the opportunity to adjust our methods slightly and perform behavioural observations immediately prior to collecting invertebrate samples. This allowed potential relationships between the proportion of time spent foraging and invertebrate abundance at that specific time and location to be investigated better. Nevertheless, because it was not always possible to locate the focal individual, collecting invertebrate samples and performing behavioural observations on the same day could not always be performed. Because data were available for more than one month for some

pairs but not others, the month chosen for statistical analysis (e.g. May, June or July) was randomly selected for each pair (n=19), in order to prevent pseudo-replication.

The amount of wrack on the beach between the waterline and the base of the foredune was estimated following each observation period at arbitrarily selected locations within the breeding territory. The amount of wrack on the beach was expressed as a quantitative variable (m). Similarly, beach width was measured at three arbitrarily selected locations extending from the waterline to the base of the foredune. These measurements were collected using a measuring wheel accurate to the nearest 2.5 cm.

Although Gautreau (1998) found that activities relating to foraging were not significantly influenced by tides on PEI, tide level was still considered as a possible variable. Tide level was expressed as a proportion by dividing the beach width immediately after an observation by the beach width during the lowest tide measured.

Ambient air temperature and wind speed were measured using a Kestrel 2000 handheld thermo wind gauge following each observation. The measurements were taken facing the direction of the wind with the meter held approximately 15 cm above the surface of the beach.

Data Analysis

A Wilcoxon matched pairs test was used to test for significant differences between the proportion of time spent foraging by male and female piping plovers. A one-way ANOVA was used to test for differences in the proportion of time spent foraging by piping plovers over the different reproductive stages.

The influence of human activity on piping plover behaviour was determined by comparing periods during an observation where human activity took place within 50,

100, and 200 m of the focal piping plover, to periods of similar length within that same observation period with no human activity. If the length of time with human activity could not be matched within that particular observation, the observation for that same individual with the closest date with no human activity was used for comparison.

Wilcoxon Signed Rank tests or paired t-tests were performed to determine whether piping plovers significantly adjusted the proportion of time spent engaging in disturbance behaviour and foraging when people were within 50 m, 100 m and 200 m. All tests were two-tailed and considered significant at $\alpha=0.05$.

Invertebrate abundance was determined by counting the number of individual specimens in each sample collected within each of the two zones ($n=4/\text{zone}$) and the mean invertebrate abundance was determined for each of the saturation zone and the swash zone at every site and converted to invertebrate abundance per m^2 . When sites had two piping plover pairs with adjacent territories and foraging areas that overlapped, the same data for invertebrate abundance were used for both pairs.

A three-step approach was used to evaluate the influence of human activity, date, invertebrate abundance, air temperature, wind speed, and tide on the proportion of time spent foraging by piping plovers. First, a correlation analysis was performed to test for relationships between the proportion of time spent foraging by piping plovers and the level of human activity, date, invertebrate abundance, air temperature, wind speed and tide. Averages of behavioural observations and independent variables were used for each pair to ensure pseudo-replication was not an issue because repeated observations on the same individuals lack statistical independence (averages were based on observations ranging from 10 to 30 min). Pearson correlations were used for normally-distributed

datasets and Spearman correlations for nonparametric datasets. Correlations were two-tailed and considered significant at $\alpha=0.05$. Bonferonni corrections were not used because they are unnecessarily conservative (Gotelli and Ellison 2004). Descriptive statistics, normality tests and correlations were performed using GraphPad Prism 4. Transformations (square root +1) were performed to improve normality of nonparametric variables as needed. Only observations where piping plovers fed at least once within the observation were included within the analysis.

GENMOD is a procedure that “fits a generalized linear model to the data by maximum likelihood estimation of the parameter vector β ” (Johnston 2006). GENMOD allows for repeated measures and takes into consideration unequal distribution of observations. GENMOD was performed in SAS to identify the best predictor equation of piping plover foraging behaviour. Variables were selected for inclusion within the multivariate GENMOD procedure using a cutoff level of $\alpha=0.20$ from a univariate GENMOD procedure performed in SAS. A less conservative significance level of 0.20 was used to ensure that variables that are important biologically and might provide insight on how better to manage piping plovers are not unnecessarily rejected. The level of human activity within 200 m of the focal individual was changed to a categorical variable (presence=1, absence=0) in order to account for non-normal distribution of the data. Variables were included within the final model based on $\alpha=0.05$.

Results

Piping plovers foraged at least once during a total of 142 out of 178 thirty-minute behavioural observations conducted on 18 pairs of piping plovers at 15 different breeding

sites between 2 May – 5 August, 2005 [$n = 7$ in Prince Edward Island National Park (PEINP), and $n = 11$ outside PEINP, Figure 2.1.a] and 205 out of 279 observations on 23 pairs of piping plovers at 15 different sites between 3 May - 23 July, 2006 [$n = 9$ in PEINP, and $n = 14$ outside of PEINP, Figure 2.1.b]. In 2005 and 2006, human activity occurred during 43 of these behavioural observations (variation in sample sizes for various tests are the result of missing variables for some observations).

The proportion of time spent foraging by males and females did not differ significantly ($W=117.00$, $n=33$, $p=0.29$, Figure 2.2.a). As a result, data for males and females were pooled. The proportion of time spent foraging also did not vary significantly as a result of reproductive stage ($F=0.075$, $n=17$, $p=0.93$, Figure 2.2.b) and therefore all three reproductive stages were pooled for analysis. Only pairs where data were available for all three reproductive stages were used when looking for differences in the proportions of time spent foraging according to reproductive stage, doing this allowed for repeated measures tests to be performed.

The mean number of people that came within 200 m of a focal piping plover over a thirty minute observation period, ranged from 0 to 2.86. The proportion of time spent foraging was not significantly affected by human activity within 50 m (Figure 2.3.a), 100 m (Figure 2.3.b) or 200 m (Figure 2.3.c). On the other hand, piping plovers spent significantly more time engaging in disturbance behaviour when human activity took place within 50 m (Figure 2.4.a) and 100 m (Figure 2.4.b), whereas there was no significant impact at 200m (Figure 2.4.c). There were too few observations with human activity within 150 m to perform statistical analyses ($n=6$).

Invertebrate abundance within the swash zone did not differ significantly between the months of May, June and July in either 2005 ($F=2.97$, $n=9$, $p=0.19$) or 2006 ($F=5.19$, $n=11$, $p=0.06$) but when all months were compared was significantly different ($K=11.67$, $p=0.04$, Figure 2.5.a). The observed difference was likely due to yearly differences in invertebrate abundance. Invertebrate abundance within the saturation zone did not differ significantly between the months of May, June and July in either 2005 ($F=1.45$, $n=9$, $p=0.57$) or 2006 ($F=0.93$, $n=11$, $p=0.63$) nor did it differ significantly between all months sampled ($K=5.289$, $p=0.3816$, Figure 2.5.b). The overall invertebrate abundance did not differ significantly between the months of May, June and July in 2005 ($F=2.97$, $p=0.19$) but did in 2006 ($F=5.19$, $p=0.06$) and between all months sampled ($K=11.63$, $p=0.04$, Figure 2.6.c). The overall invertebrate abundance ranged from 1.35 to 162.8 individuals per meter² and tended towards a significant positive correlation between the proportion of time spent foraging by piping plovers ($r_s=0.31$, $n=19$, $p=0.056$). There was also a tendency towards a significant and positive correlation between invertebrate abundance within the saturation zone and the proportion of time spent foraging by piping plovers measured immediately before invertebrate sampling in 2006 ($r_s=0.48$, $n=19$, $p=0.054$). The proportion of time spent foraging measured immediately before invertebrate sampling in 2006 was unrelated to the wet weight of invertebrate samples in both the swash zone ($r_s=0.16$, $n=19$, $p=0.53$) and saturation zone ($r_s=0.32$, $n=19$, $p=0.21$), as well as invertebrate abundance within the swash zone ($r_s=0.053$, $n=19$, $p=0.84$).

The mean beach width ranged from 2.17-137.4 m and the mean amount of wrack ranged from 0-19.5 meters. The proportion of time spent foraging by piping plovers was significantly higher during high tide than low tide ($W=-258.0$, $n=35$, $p=0.04$). Mean air

temperature was $16.91 \pm 0.56^{\circ}\text{C}$ (S.E.) and mean wind speed was 8.59 ± 0.38 km/h. The results of the correlation analysis identified significant positive correlations between the proportion of time spent foraging and the following independent variables: date, air temperature and wind speed (Table 2.1). A tendency towards a significant positive correlation was also observed between the proportion of time spent foraging and the overall invertebrate abundance within that month. The proportion of time spent foraging by piping plovers was not significantly correlated with total number of people within 200 m, invertebrate abundance within the swash zone, invertebrate abundance within the saturation zone, beach width, amount of wrack, or tidal level. Given the observed tendency towards a significant correlation, the overall invertebrate abundance was used in place of invertebrate abundance within each of the saturation and swash zones for the remainder of the analyses.

All independent variables except the presence of human activity within 200 m, air temperature, and wrack cover were selected for inclusion within the multivariate analysis ($\alpha=0.20$, Table 1.2). There were no intercorrelations between independent variables ($\rho=0.70$). The best model had date and overall invertebrate abundance within that month as the best predictors of piping plover foraging behaviour, giving an equation for the proportion of time spent foraging of: $y = 4.41 + 0.014 * \text{date} + 0.0063 * \text{invertebrate abundance}$ when $\alpha=0.05$ (Table 2.3 and Figures 2.6.a-c). If the cutoff level is increased to $\alpha=0.10$ the same model is selected. This equation then tells us that the proportion of time spent foraging by piping plovers increases later in the summer and increases with increasing invertebrate abundance. The only significant interaction was between beach width immediately following an observation and tide level. This finding may have

affected the ability to detect effects of tide level and beach width on piping plover foraging behaviour.

Discussion

Because the likelihood of attack is dependent on the distance from potential predators, the greater the distance from human recreational activity the less the perceived threat to animals will be (Beale and Monaghan 2004). As a result, the manner in which piping plovers responded to human recreational activity was dependent on proximity to the subject. Compared to periods with no human activity, piping plovers spent significantly more time engaged in disturbance behaviour when human activity took place within both 50 m and 100 m of the focal individual, but not 200 m. Disturbance behaviour such as injury feigning, peeping, and squatting were observed almost exclusively during periods when there was human activity or when natural predators were in close proximity, thereby suggesting that piping plovers, like many other animals, view humans as predators (Gill *et al.* 1996). Although piping plovers elicited behavioural responses to human activity within both 50 m and 100 m, their behaviour was unaffected by human activity that took place between 100 and 200 m. Other studies have also found that piping plovers respond to human activity but at different distances (Flemming *et al.* 1988, Burger 1994). Flemming *et al.* (1988) found that piping plover chicks altered their behaviour by spending less time foraging, brooding and sitting and spending more time being vigilant when people were within 160m. Similarly, the number of people within 100 m of piping plovers was negatively correlated with the amount of time spent foraging. Studies on other shorebirds have also found that avian response to human

activity is dependent on distance in snowy plovers (Ruhlen *et al.* 2003), western snowy plovers (Lafferty 2001), golden plovers (Yalden and Yalden 1990), and sanderlings (Thomas *et al.* 2003).

Despite increased elicitation of disturbance behaviour during periods when human activity took place within both 50 m and 100 m of the focal individual, human activity at any distance failed to influence the proportion of time piping plovers spent foraging when compared to periods with no human activity. Furthermore, the presence or absence of human activity within 200 m of the focal individual failed to predict the proportion of time spent foraging by piping plovers. These results are unlike those of Burger (1991, 1994), Staine and Burger (1994), and Flemming *et al.* (1988), who discovered that piping plovers spent less time foraging when in the presence of humans. Piping plovers breeding in New Jersey appear to minimize the influence of human activity by moving to areas within their territory with fewer humans nearby (Burger 1991). Shorebirds were less likely than ducks and terns to return to an area after fleeing from human activity (Burger 1981), perhaps suggesting that shorebirds are more sensitive to human activity. Therefore, based on the assumption that piping plovers view humans as potential predators, human activity was incorrectly expected to result in piping plovers reducing the amount of time they allocated to foraging.

The fact that piping plovers did not flee an area or alter the proportion of time spent foraging when human activity was within 200, 100 or 50 m does not indicate that piping plovers are unaffected by human activity. One potential explanation may be that piping plovers on PEI are unable to give up foraging because it is too costly for them to do so (Beale and Monaghan 2004). Because birds that respond to human activity are not

necessarily the ones most affected by it (Beale and Monaghan 2004), some researchers question the validity of behavioural observations as a method of investigating the level of stress caused by human activity. Instead, they suggest using measures of body condition and prey abundance when interpreting behavioural responses of animals to human activity (Beale and Monaghan 2004). However, pecking rate is positively correlated with piping plover chick mass (Cairns 1982). Therefore, piping plover pecking rate, although not measured within this study, could be considered an indirect measure of body condition. The introduction of potentially confounding variables into the equation (e.g. invertebrate abundance, size of defended territories and weather) allows for a better understanding of the complex interplay of costs and benefits that determine foraging decisions in piping plovers. When considered as a whole, human activity was not a significant predictor of piping plover foraging behaviour. This may have been due to habituation to human activity (Nisbet 2000). However, the number of observations where human activity took place within 200 m of the focal individual represented a small portion of the entire dataset (12% overall) and may explain its inability to significantly predict foraging behaviour. In addition, events involving human recreational activity were normally short lived and may not be enough to significantly alter the proportion of time spent foraging over a thirty minute observation period. Despite the limitations of research investigating the impact of human activity on shorebird behaviour, differences in response to human activity among subjects suggest that research of this nature is important. For example, previous research has uncovered site- and species-specific differences in behavioural responses to human activity in waterbirds (Madsen 1994).

Piping plovers within this study spent more time foraging later in the breeding season, maybe, because more time devoted to foraging was necessary to prepare for migration (Alerstam *et al.* 2003). Similar results were observed for curlew sandpipers (*Calidris ferruginea*) in southern Africa where the birds increased the amount of time they spent foraging later in the summer and actually increased their body weight by 40% (Puttick 1979). Nevertheless, the same argument could also be made had foraging rate been higher for females in the pre-incubation stage earlier in the breeding season. In addition to increasing energy requirements, the parental responsibilities of piping plover adults' decreases later in the summer as chicks hatch and become increasingly independent (Cairns 1982). Another potential explanation for the observed positive relationship between the proportion of time spent foraging and date is that the ability of plovers to detect prey, as well as the density of prey, increases later in the breeding season. As mentioned previously, air temperature, precipitation and wind are all capable of decreasing the ability of plovers to locate prey through visual cues (Pienkowski 1981). Air temperatures steadily increased from the beginning of May until the end of July on PEI, therefore, it appears logical that as temperatures increase piping plovers will be more able to locate and capture prey. Furthermore, prey items are increasingly difficult to locate during cool temperatures because intertidal invertebrates stay below the surface of the substrate (Goss-Custard 1984) which may further explain why the proportion of time foraging is greater late in the breeding season. Invertebrate density in the saturation zone of piping plover foraging sites was highest in July of 2005 and 2006, however, this difference was not statistically significant. Similarly, invertebrate density also appeared higher in the saturation zone of foraging sites in July of 2006 (although not statistically

significant) but not in 2005. Therefore, variation in piping plover foraging behaviour may be explained by a number of variables working in concert such as biological requirements for increased lipid consumption close to migration, shifting parental responsibilities, and differences in food abundance.

Invertebrate abundance within the two foraging zones had varying effects on the proportion of time spent foraging by piping plovers. The mean proportion of time spent foraging by piping plovers tended ($p=0.06$) toward a significant positive relationship with the overall mean invertebrate abundance within that month but not the invertebrate abundance within the swash zone or the saturation zone independently. Similarly, the proportion of time spent foraging immediately prior to invertebrate sampling was positively correlated with invertebrate abundance in the saturation zone in 2006 ($p=0.05$). This correlation is likely more able to identify actual relationships between the proportions of time spent foraging and invertebrate abundance because the samples were collected shortly after the behavioural observations had taken place. Therefore, piping plovers on PEI appear to increase the proportion of time spent foraging when invertebrate abundance within the saturation zone is higher, which is opposite to what had been expected. When foraging, piping plover adults are most often observed within 5 m of the water's edge (Haig 1992), as a result the proportion of time spent foraging would most likely be best predicted by invertebrate abundance within that zone measured shortly after having monitored the proportion of time spent foraging. However, it was not always possible to measure invertebrate abundance following each observation and as a result the overall invertebrate abundance (mean of saturation and swash zones) provides a more appropriate estimate of invertebrate abundance for making generalizations about

invertebrate abundance at a given sites. Justification for taking the mean of the saturation and swash zones comes from the fact that piping plover foraging is not restricted solely to either the saturation or the swash zone, instead plovers forage in both of these zones.

The multivariate GENMOD procedure identified invertebrate abundance as a significant predictor of piping plover foraging behaviour, suggesting that piping plovers on sites with higher overall invertebrate abundance spend more time foraging than individuals on territories with fewer invertebrates. This finding refutes the hypothesis that piping plover prey density and the proportion of time spent foraging would be negatively associated. During the winter when American redstart (*Setophaga ruticilla*) prey availability is lower they spend more time foraging than during summer months when prey is more abundant (Lovette and Holmes 1995). This is likely done to compensate for lower rates of prey encounter during these periods (Lovette and Holmes 1995). Nevertheless, Hoopes (1993) found a significant positive correlation between invertebrate abundance within both the wrack and intertidal habitat and foraging rate of piping plovers in Massachusetts during the months of April and June. Capture rates are commonly higher when prey abundance is higher (Brown 1993) or when there are a greater number of prey choices (Berkelman *et al.* 1999). Norberg (1977) states that as prey abundance increases the search time required to find prey should decrease. Similarly, with decreasing prey density foraging individuals must cover larger areas and spend more time foraging in order to acquire the same energetic benefits (Norberg 1977, Lovette and Holmes 1995). An explanation for the observed trend may be that when there is more food available for uptake, piping plovers spend more time foraging because they are less limited by prey availability. Not only may piping plovers breeding on sites with higher

levels of invertebrates spend more time feeding, but the rate of prey capture is also likely higher. Higher prey capture rates in areas with more abundant prey has been observed in other species (Brown 1993). Piping plovers on sites with low invertebrate abundance on PEI did not spend more time foraging. Instead, pairs on territories with low prey density actually spent less time foraging than pairs feeding on territories with high invertebrate abundance, perhaps suggesting that piping plovers are foraging in relation to the amount of prey available or that prey abundance is not limiting at all.

Stewart (2004) found that piping plover breeding sites on PEI had higher overall invertebrate abundance than beaches where piping plovers formerly but no longer bred and suggested that piping plovers consider invertebrate abundance when evaluating and selecting breeding territories. Although it remains unknown whether piping plovers prefer certain prey items, the monthly overall invertebrate abundance provides an indication of the prey available for uptake. Least sandpipers (*Calidris minutilla*) at Pachena Beach, British Columbia reduced foraging in response to human recreational activity only when amphipod densities were high (Yasué 2005). Consequently, foraging rates of least sandpipers were highest when human densities and amphipod abundance were low. When in low density, intertidal invertebrates may be larger and easier prey than invertebrates in high density areas (Yasué 2005). Therefore, plovers on territories with low invertebrate abundance may spend less time foraging because the prey they were feeding on is larger and more profitable. There was, however, no evidence to suggest that piping plover foraging behaviour was related to the wet weight of invertebrates collected within their territory, which would have taken differences in prey size into consideration. These results are important because a number of studies that have

determined human activity does not have deleterious effects on foraging behaviour or reproductive success of piping plovers, have not considered invertebrate abundance within their analysis (Burger 1991, 1994, Flemming *et al.* 1988). One such example would be a study carried out on piping plovers in which a greater level of nest failure was observed for pairs near human activity during one year but not the next (Prindiville-Gaines and Ryan 1988). A potential explanation for the variation in survival between the two years may have been differences in invertebrate abundance and subsequently the proportion of time they spend foraging. If plovers foraging in areas with higher invertebrate abundance are also more fit, we may expect those individuals to respond sooner to human activity. This statement appears logical as the proportion of time spent foraging for piping plovers was higher on territories with high invertebrate abundance and would likely make these individuals more fit. Nevertheless, this study was limited by small sample sizes and variation in human activity, which prevented further investigation potential trends.

The proportion of time spent foraging by piping plovers was not significantly correlated with beach width, nor was it identified as a significant predictor of time spent foraging. It was predicted that plovers on wide beaches would spend more time foraging because they would be more able to see approaching predators and would therefore devote more time to foraging, but this was not the case. When visibility was impeded by rocks or logs, turnstones (*Arenaria interpres*) and purple sandpipers (*Calidris maritima*) both reduced the amount of time they spent being vigilant (Metcalf 1984), therefore, the same was expected to be true for piping plovers nesting on narrow beaches. Nevertheless,

no such relationship was identified, leading us to conclude that the proportion of time spent foraging by piping plovers is unaffected by beach width.

There was no significant relationship between the proportion of time spent foraging and the amount of wrack on the beach. The proportion of time spent foraging by piping plovers was expected to be negatively related with the amount of wrack on the beach because of the degree to which it contributes to the biological richness of the intertidal zone (Dugan *et al.* 2003). Mean wrack cover and the abundance of macrofauna were positively related along California coastal beaches, as well as between wrack-associated macrofauna and the presence of black-bellied plover (*Pluvialis squatarola*) and snowy plover (*Charadrius alexandrinus*, Dugan *et al.* 2003). Furthermore, invertebrates found in wrack are believed to be a key food source for piping plover chicks (Elias *et al.* 2000). However, the proportion of time spent foraging by piping plovers must have been driven by some variable other than wrack cover.

Piping plovers spent significantly more time foraging during high tide than low tide. This was opposite to what was expected and may have been due to individuals having to spend more time foraging during high tide in order to meet their energetic requirements. When considered along with other variables, tide was not identified as a significant predictor of piping plover foraging behaviour, nor was it significantly correlated. Gautreau (1998) found that the proportion of time spent foraging by piping plovers on PEI was unrelated to tide level. Piping plovers in other areas of the Atlantic Coast, specifically plovers in Nova Scotia foraged primarily during low or falling tides (Cairns 1977). Similarly, piping plovers in New Jersey were most likely to forage during late ebb and early flood tides, with the rate at which they acquired food also increasing

with decreasing tidal height (Staine and Burger 1994). The tidal range along Prince Edward Island coastlines are comparable to those of Atlantic City, however the tidal ranges of southern Nova Scotia are much higher and may explain the observed trend for piping plovers to forage more during low tide in this area. Furthermore, the difference in the effect of tide level on piping plover foraging behaviour within this study and others may be in the manner foraging behaviour was measured. Gautreau (1998) also used proportions to quantify the foraging behaviour of piping plovers. Piping plovers in this study did not vary the proportion of time they spent foraging according to tide, nor did the plovers within Gautreau's (1998) study. Instead, the proportion of time spent foraging may have remained unchanged, while pecking rate increased due to greater availability of food. In addition, these results suggest that the foraging behaviour of piping plovers on PEI is not significantly influenced by tides because they may be required to forage at all tide levels in order to acquire their energy requirements. Nevertheless, wrack on the beach on PEI beaches did not appear to be lacking (personal observation). Therefore, given the relative abundance of invertebrates within the wrack line, piping plovers on PEI may use wrack as an alternative source of food that is not restricted by tide level.

The proportion of time spent foraging by piping plovers was positively related to air temperature in the correlation analysis. These findings are unlike those of Gautreau (1998) or Johnson and Baldassarre (1988). Gautreau (1998) found that piping plover adults in PEI do not alter the proportion of time they spend foraging according to air temperature (Gautreau 1998). Piping plovers wintering in Alabama actually spent more time foraging during cool conditions, likely because of increased energy requirements. Although the energetic requirements of piping plovers are likely higher during periods of

cool weather conditions, the availability of prey is likely lower because intertidal invertebrates are more likely to remain below the surface and are generally less active (Goss-Custard 1984).

Cool temperatures may also result in a shift in the parental responsibilities of piping plovers. For example, during the pre-fledging period piping plover chicks exposed to cool conditions require longer and more frequent bouts of being brooded (Flemming *et al.* 1988). This finding in itself is important to chick survival; however, cooler temperatures result in piping plover adults facing trade offs between feeding and brooding thermally dependent chicks and may also contribute to the reduced foraging by piping plovers under cool conditions. Nevertheless, when considered within the multivariate analysis, air temperature was not identified as a significant predictor of piping plover foraging behaviour.

The proportion of time piping plovers spent foraging was positively correlated to wind speed. These findings are contrary to those of Johnson and Baldassarre (1988) who observed a significant negative correlation between time spent foraging and wind speed, and are contrary to what was expected. Pienkowski (1981) suggested that wind decreases a plover's ability to locate prey visually. Therefore, one would suspect that as wind speed increases piping plovers would reduce the proportion of time they spent foraging, which was not the case. Nevertheless, it might also be expected that piping plovers would spend a greater proportion of time foraging during windy conditions in order to get the amount of prey they would get during calm conditions. Blowing sand reduced visibility during periods when wind speed exceeded 32 km per hour. As a result, it was difficult to maintain visual contact with the focal individual, thereby prohibiting observations from

taking place. Although wind speed was positively correlated with the proportion of time spent foraging by piping plovers and was initially selected for inclusion within the full model, it was removed from the best model and therefore is not a reliable predictor of piping plover foraging behaviour.

The individual influences of several independent variables on the proportion of time spent foraging by piping plovers, and briefly how these variables interact in concert to identify the best predictor model of piping plover foraging behaviour, have been discussed. Using a multivariate approach allowed two independent variables to be identified as significant predictors of the proportion of time spent foraging by piping plovers; the date on which an observation was performed and the overall invertebrate density measured during the same month as the behavioural observation took place. What this model tells us is that piping plovers spend progressively more time foraging later in the breeding season and that piping plovers spend more time foraging when there is greater prey abundance. This information will provide conservation authorities with information regarding periods or conditions when piping plover foraging behaviour may be most sensitive to disturbance. An example of how this information might improve the ability of conservation authorities protect piping plovers would be to evaluate invertebrate abundance at potential breeding beaches and protect those with consistently high levels from coastal development.

Conclusions

An essential component of this study was to investigate the influence of human activity on piping plover foraging behaviour while considering external variables such as

invertebrate abundance, habitat quality and weather conditions; the importance of which is supported by the findings of Beale and Monaghan (2004) and Yasué (2006).

As we begin to realize the detrimental effects human activity may have on foraging and reproductive success of birds, there is an increased need to better understand the impacts on particular species (Hill *et al.* 1997). Specifically, the influence of human activity on sensitive species such as the management-dependent piping plover is of utmost importance. Many studies addressing the impact of human activity on birds have been primarily behavioural in nature and seldom have controls (reviewed by Hill *et al.* 1997). Therefore, my study fills a need for research regarding the impact of human activity, habitat quality, prey abundance, tide and weather on foraging decisions made by piping plovers. Although the impact of human activity on breeding piping plovers on PEI may be negligible, this is likely due to conservation efforts put in place by both the Island Nature Trust and Parks Canada aimed at minimizing the impact of human recreational activity. Within Parks Canada, large areas of piping plover breeding beaches are closed to human activity in order to minimize interactions between people and plovers. These areas receive relatively little human activity, however, pedestrians have been observed within closed areas and ATV tracks have also been observed. Outside PEINP, the Island Nature Trust erects symbolic fencing and signage around nesting sites. The area protected is centered on the nest location which normally allows for only a small passageway along the water's edge for pedestrians walking by. Stewart (2004) found significantly higher fledging success within PEINP boundaries than outside, suggesting that closing entire piping plover breeding beaches may be the most effective manner of protecting chicks when possible. However, this same trend was not observed for plovers part of this study

(Murphy 2007, unpublished data). Although human activity in this study did not predict the proportion of time spent foraging by piping plovers, the number of observations where human activity did in fact take place within 200 m of the focal individual was very small, and incidents involving human recreational activity were relatively short-lived. Nevertheless, piping plovers elicited significantly more disturbance behaviour when human activity took place within 100 m but not 200 m. Therefore, it is strongly recommended that the efforts being made by PEINP and INT to protect breeding piping plovers and their chicks be continued. Area closures should provide piping plovers with a minimum of 100 m of protection from human activity. To err on the side of caution, conservation groups should protect the largest allowable area from human activity until further research is able to pinpoint the distance between 100 and 200 m where piping plovers no longer respond to human activity. Nevertheless, because individuals which respond to human activity may not be the ones most affected by it (Beale and Monaghan 2004), large areas should remain protected.

The fitness of species is directly related to their ability to forage efficiently (Donnelly and Sullivan 1998). Prey abundance varies temporally and spatially, and it is energetically unprofitable for animals to forage in areas with low levels of prey (Smith 1996). As a result, it appears logical that when in areas with high prey abundance, piping plovers will spend more time foraging. Therefore, understanding how variation in prey abundance and date influence the proportion of time spent foraging will allow for sites where piping plovers may be at greater risk of disturbance from human activities to be better protected.

Piping plover territories with low prey density may be more sensitive to human activity. Shorebirds view humans as potential predators and as a result face trade-offs between foraging and vigilance when human activity is near (Frid and Dill 2002, Mallord *et al.* 2006). The results of my study suggest that piping plovers on sites with lower invertebrate abundance spend less time foraging. However, because it is the individuals who are most fit that are most likely to respond to human activity (Beale and Monaghan 2004), the impact of human activity on individuals on sites with fewer invertebrates may be underestimated. Therefore, invertebrate abundance should be considered when establishing the size of area closures for piping plovers, with larger areas being protected for piping plovers nesting on territories where invertebrate abundance is known to be low.

Since piping plover chick mass and foraging rate were positively related in another study (Loefering and Fraser 1995), ensuring undisturbed foraging for chicks and adults is essential to their survival and reproductive success. Furthermore, piping plovers in this study were more likely to forage later in the breeding season. This observed trend may reflect the need for piping plovers to develop lipid reserves in anticipation of migration (Skagen and Knopf 1993, Lafferty 2001). Nevertheless, if this were the case we would also expect piping plover females to increase foraging during pre-incubation in order to offset the costs of egg formation. As a result, efforts made to ensure compliance should be consistent throughout the breeding season.

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Figure 2.1.a. Map illustrating locations of piping plover breeding beaches studied on Prince Edward Island, Canada in 2005.

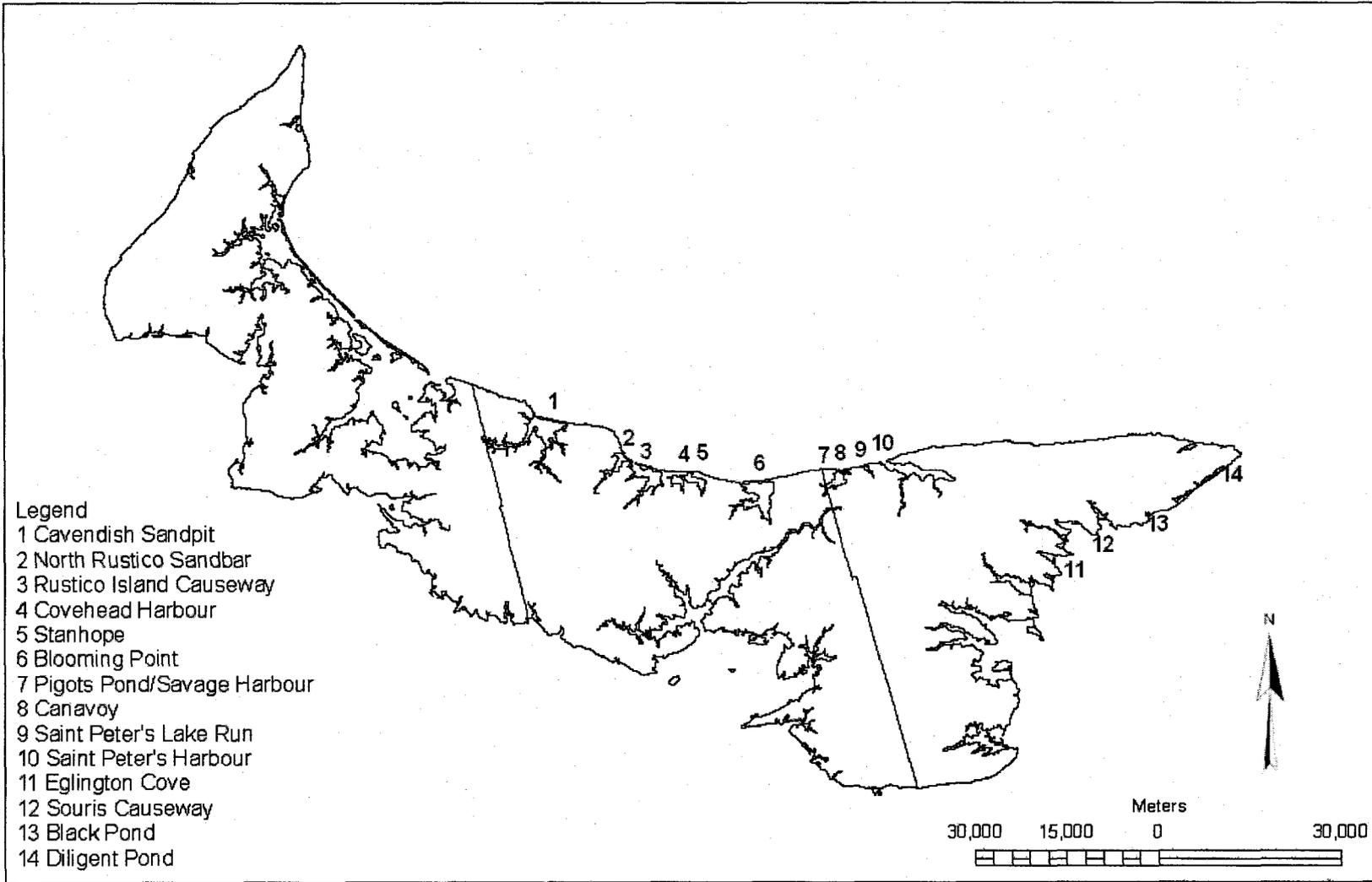
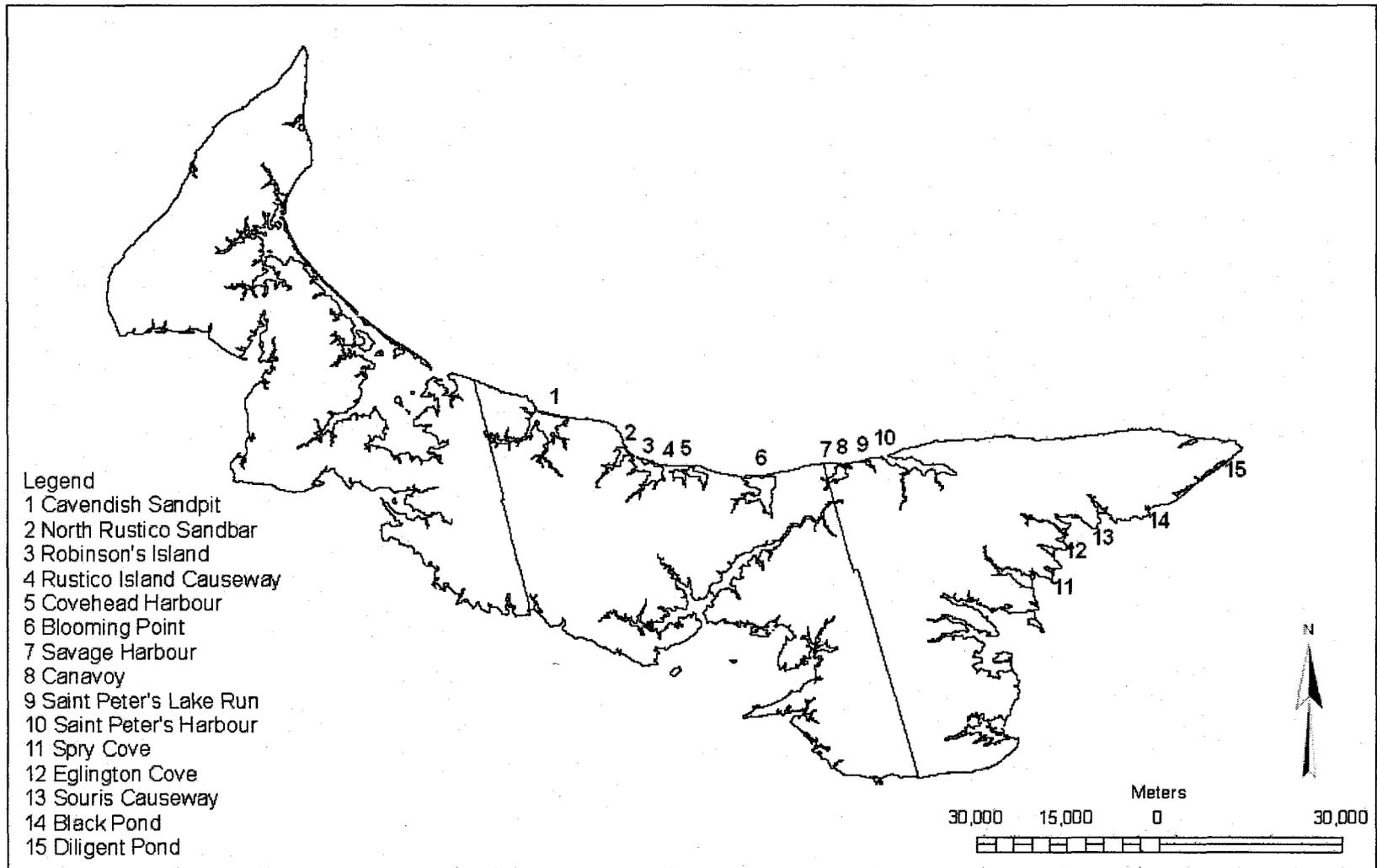
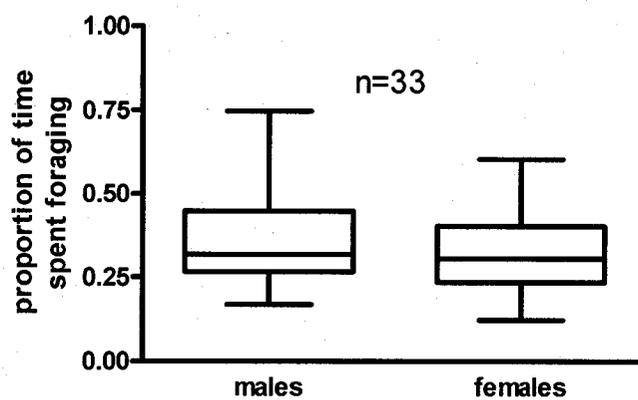


Figure 2.1.b. Map illustrating locations of piping plover breeding beaches studied on Prince Edward Island, Canada in 2006.

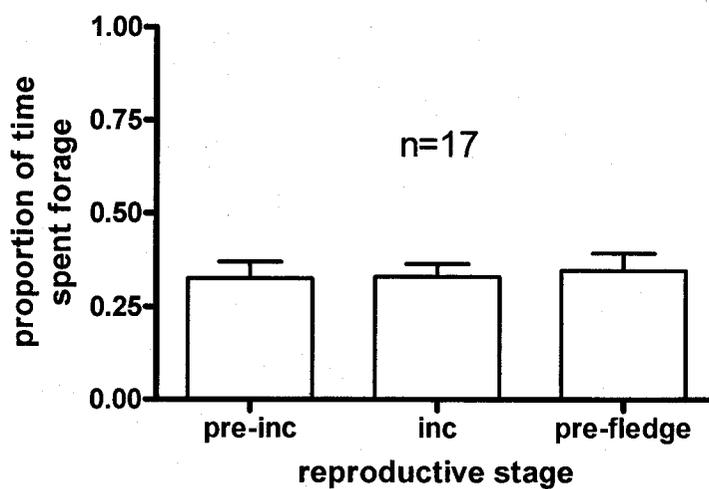


Figures 2.2.a-b. Box and whisker plots comparing the **a)** proportion of time spent foraging by male (range=0.17-0.75) and female (range=0.12-0.60) piping plovers. The proportion of time spent foraging did not differ significantly between sexes ($W=117.0$, $p=0.29$, $n=33$). **b)** Histogram with standard error bars of the proportion of time spent foraging during pre-incubation (pre-inc, 0.33 ± 0.044), incubation (inc, 0.33 ± 0.036), and pre-fledging (pre-fledge, 0.35 ± 0.046) reproductive stages. No significant differences were observed between reproductive stages ($F=0.075$, $p=0.9275$, $n=17$).

2.2.a.

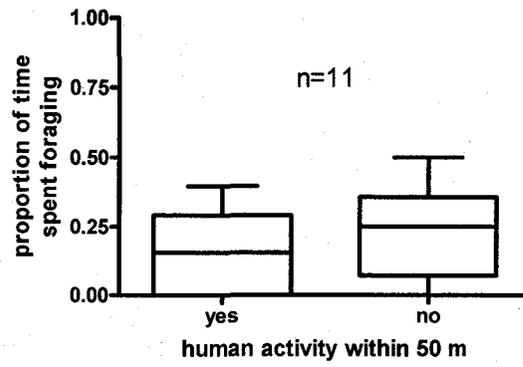


2.2.b.

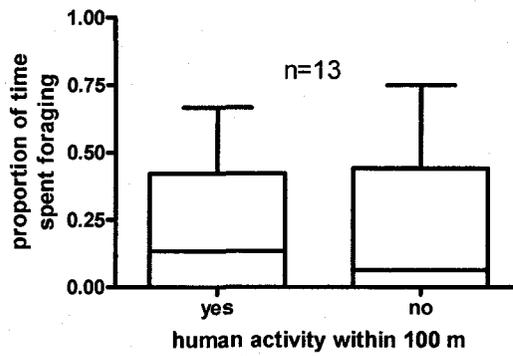


Figures 2.3.a-c. Comparison of the proportion of time spent foraging by piping plovers during periods when human activity occurred within **a)** 50 m ($t=1.17$, $p=0.27$, $n=11$), **b)** 100 m ($t=0.31$, $n=13$, $p=0.76$), and **c)** 200 m ($W= -25.00$, $n=13$, $p=0.16$, $n = 13$) of the focal individual to periods with no human activity.

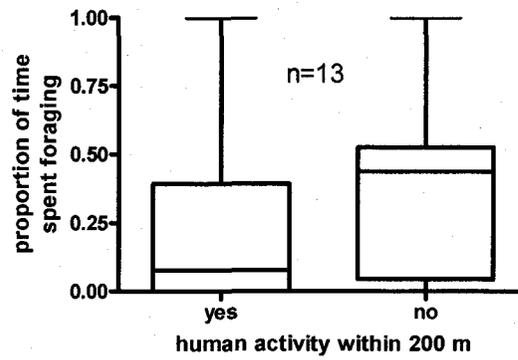
2.3.a)



2.3.b)

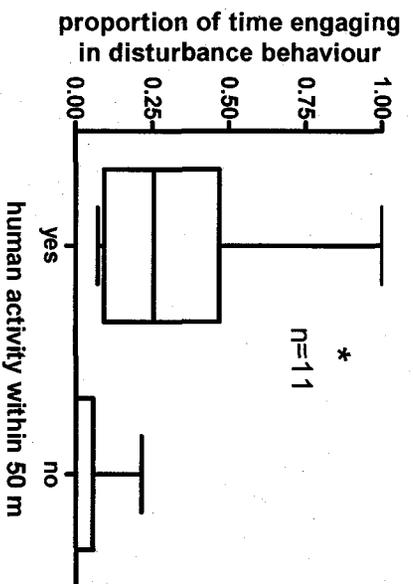


2.3.c)

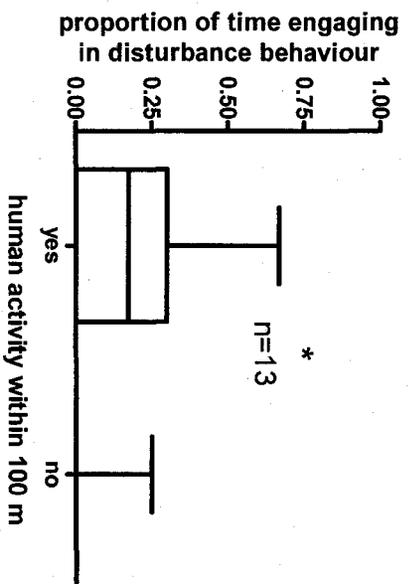


Figures 2.4.a-c. Comparison of the proportion of time spent engaging in disturbance behaviour by piping plovers during periods human activity occurred within **a)** 50 m ($W=56.0, n= 11, p = 0.0098,$), **b)** 100 m ($W= 28.00, n = 13, p = 0.016$), and **c)** 200 m ($W=12.00, n=13, p=0.38$) of the focal individual to periods with no human activity. .

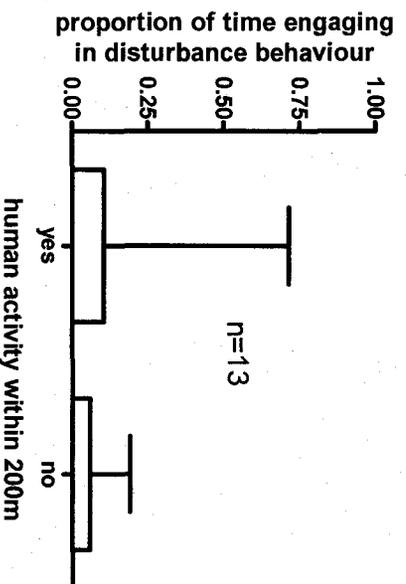
2.4.a)



2.4.b)

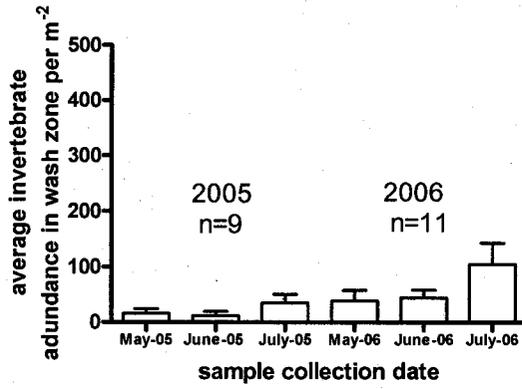


2.4.c)

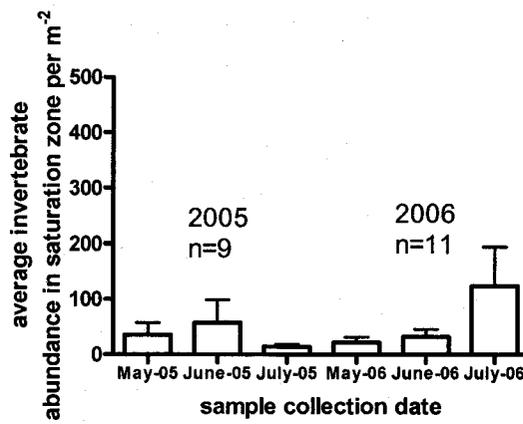


Figures 2.5.a-c. Histograms with standard errors of **a)** invertebrate abundance in the swash zone during the months of May, June and July of 2005 ($F=2.97$, $p=0.19$) and 2006 ($F=5.19$, $p=0.06$), **b)** invertebrate abundance in the saturation zone during the months of May, June and July of 2005 ($F=1.45$, $p=0.57$) and 2006 ($F=0.93$, $p=0.63$), and **c)** overall invertebrate abundance during the months of May June and July of 2005 ($F=0.42$, $p=0.81$) and 2006 ($F=7.091$, $p=0.03$).

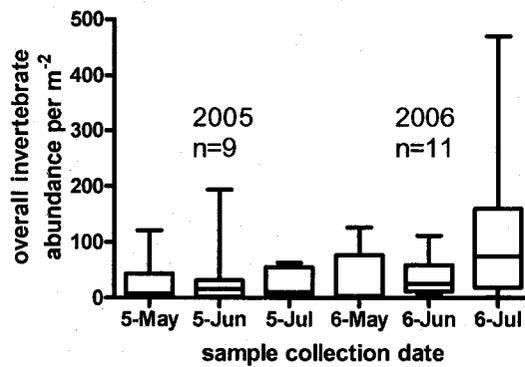
2.5.a.



2.5.b

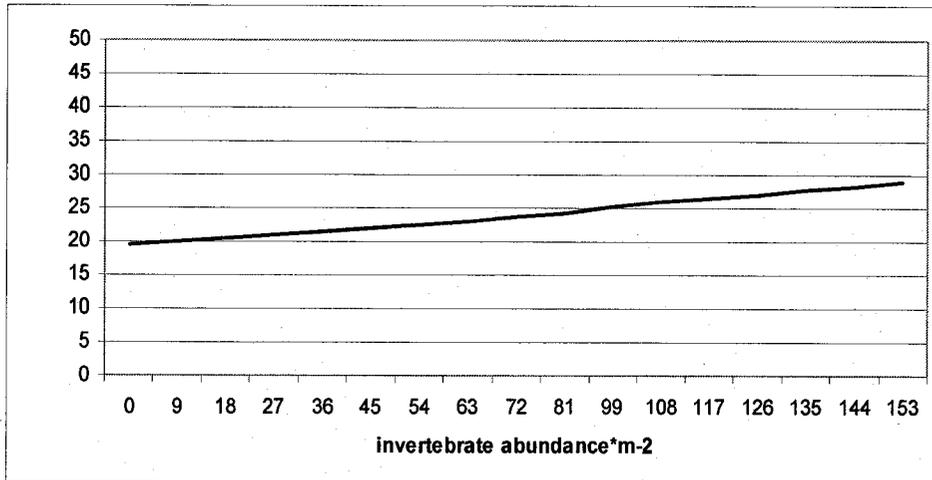


2.5.c

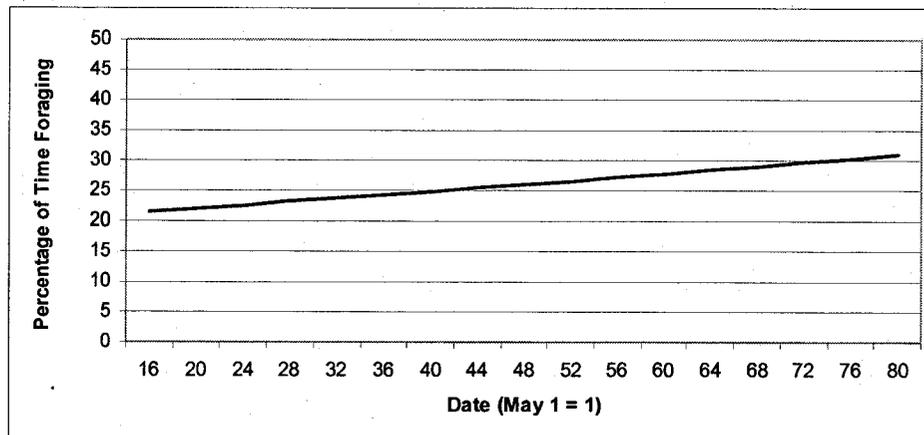


Figures 2.6.a-c. Line graphs of the components selected for inclusion within the best model, demonstrating **a.)** the influence of invertebrate abundance on the percentage of time spent foraging by piping plovers, **b.)** the influence of date on the percentage of time spent foraging by piping plovers, and **c.)** plot of the best model identified by GENMOD in SAS which includes invertebrate abundance/m² and date.

2.6.a.



2.6.b.



2.6.c.

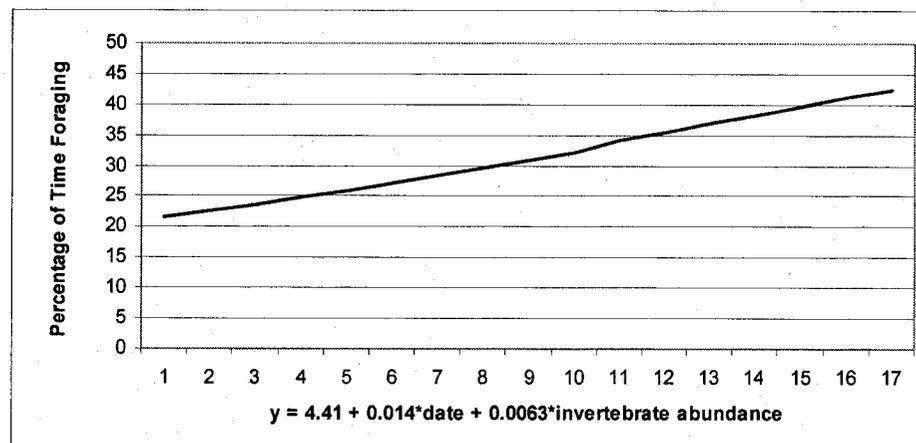


Table 2.1. Descriptive statistics for independent variables measured to predict piping plover foraging behaviour.

Independent Variable	Range	Mean (SE)	Normality p-value	Correlation coefficient (r)	p-value
Total disturbance ¹	0-2.86	0.480±0.11	<0.01	0.10	0.57
Date ²	15.2-75.3	41.34±2.13	0.64	0.32	0.048*
Invert abundance swash zone ³	0.30-153	39.19±6.41	<0.01	0.22	0.18
Invert abundance saturation zone ³	0.00-319	43.11±9.61	<0.01	0.25	0.12
Overall invert abundance ³	1.35-163	41.10±6.16	<0.01	0.31	0.06
Beach width ⁴	2.17-137	41.69±4.60	0.02	0.10	0.54
Wrack ⁵	0.00-19.1	2.260±0.52	<0.01	-0.04	0.79
Air temperature ⁶	9.83-26.1	16.91±0.56	0.64	0.34	0.03*
Wind speed ⁷	4.61-15.8	8.590±0.38	0.10	0.34	0.04*
Tide fraction ⁸	0.22-1.21	0.680±0.029	0.13	0.01	0.58

* denotes significant correlations

¹ The total number of people that came within 200 m of the focal piping plover during a given observation.

² Date (May 1=day 1).

³ Mean invertebrate abundance · m⁻².

⁴ Mean beach width on piping plover territories.

⁵ Amount of wrack on a piping plover breeding territory measured perpendicular to the waterline.

⁶ Ambient air temperature in degrees Celsius.

⁷ Wind speed measured in km per hour.

⁸ Beach width during a given observation divided by the beach width at low tide.

Table 2.2. Data output for GENMOD procedure in SAS for the proportion of time spent foraging by piping plovers. Parameters with $\alpha < 0.20$ were selected for inclusion within the multivariate GENMOD procedure.

Parameter	Estimate	(SE)	Chi ²	p-value
Presence of people within 200m ¹	0.016	0.17	0.00	0.98
Date ²	0.015	0.00	4.28	0.04*
Overall invert abundance ³	0.007	0.00	2.91	0.09*
Beach width ⁴	-0.004	0.00	1.70	0.19*
Wrack ⁵	0.013	0.02	0.47	0.49
Air temperature ⁶	0.022	0.02	1.04	0.31
Wind speed ⁷	0.057	0.03	2.91	0.09*
Tide fraction ⁸	-0.650	0.43	1.75	0.19*

* denotes parameters included within the multivariate analysis.

¹ The total number of people that came within 200 m of the focal piping plover during a given observation.

² Date when observation took place (May 1= day 1).

³ Mean invertebrate abundance $\cdot m^{-2}$ within the same month as the observation.

⁴ Mean beach width on piping plover territories.

⁵ Amount of wrack on a piping plover breeding territory measured perpendicular to the waterline.

⁶ Ambient air temperature in degrees Celsius.

⁷ Wind speed measured in km per hour.

⁸ Beach width during a given observation divided by the beach width at low tide.

Table 2.3. Data output for the multivariate GENMOD procedure in SAS for the proportion of time spent foraging by piping plovers. Parameters were selected for inclusion within the final model based on $\alpha=0.05$.

Parameter	Estimate	(SE)	Z	p-value (Z)	Chi ²	p-value (X ²)
Intercept	4.41	0.32	13.89	<0.0001		
Date ¹	0.014	0.006	2.38	0.017	4.06	0.044
Overall invert abundance ²	0.0063	0.0022	2.82	0.0049	2.95	0.086

¹ Date when observation took place (May 1=Julian day 1).

² Mean invertebrate abundance/m² within the same month as the observation.

CHAPTER 3:

The effects of human recreational activity, nest chronology, habitat quality and meteorological conditions on piping plover (*Charadrius melodus*) fledging success

Abstract: The reproductive success of piping plovers (*Charadrius melodus*), a small endangered shorebird, is highly variable. Some of the factors believed to have the greatest influence on piping plover reproductive success include human disturbance, flooding, ineffective regulation of dam water level, coastal development and predation. In this study, the impact of human activity, prey abundance, habitat quality and meteorological conditions on fledging success of piping plovers breeding in PEI, Canada (defined as the proportion of eggs hatched that survive to 20 days old) were specifically examined for 23 pairs of piping plovers on Prince Edward Island. Variables considered were a) disturbance level (based on number of observations where human activity occurred within 200 m), b) invertebrate abundance, c) substrate composition, d) vegetation density, e) beach width, f) minimum daily temperature, and g) total precipitation. Multiple linear regression with backward stepwise and forward stepwise analysis were used to select the best predictor equation of fledging success. The equation with the highest predictive value (35.1%) suggested that fledging success was negatively associated with hatching date and the proportion of open sand and was positively associated with the mean minimum daily temperature over the chick rearing period. As suggested within other studies, piping plovers who successfully fledge broods early in the breeding season achieve higher fledging success because they are less impacted by human disturbance and predation. These findings are important because the majority of research relating to human disturbance of piping plovers is univariate in its approach. Therefore, this study provides valuable information regarding periods and locations where piping plover chick survival may be most sensitive to disturbance from human activity.

Introduction

The reproductive success of many avian species is highly variable. With 11% of all bird species worldwide are at risk of extinction (Gill 1994), it is important to understand how different factors influence reproductive success. It is especially valuable to understand what factors influence the productivity of endangered species. One such species, the piping plover (*Charadrius melodus*) is a small migratory shorebird, endemic to North America (Haig 1992, Amirault 2005).

Piping plovers breed on open beaches, alkali flats, and sandflats in three separate populations located along the Atlantic Coast, Great Lakes and Northern Great Plains (Haig 1992). Piping plovers begin arriving on Prince Edward Island (PEI) in late April (Cairns 1982). They form monogamous pairs and defend breeding territories from conspecifics (Goosen *et al.* 2002). Piping plover nests are shallow scrapes in the sand, created by the male during courtship (Cairns 1982). Egg laying normally lasts five to six days for a typical four egg clutch (Cairns 1982). Incubation typically ranges from 27 to 29 days, and duties are shared equally between the male and female. Piping plover chicks are precocial and forage independently, nevertheless, they must rely on their parents for thermoregulation (rarely brooded after 21 days of age) and protection from predators (Cairns 1982). Chicks normally fledge within 28 to 32 days of hatching (Cairns 1982).

Historically, piping plovers were heavily hunted for their use in the millinery industry (Powell and Cuthbert 1993). Although hunting has since ceased, several threats still remain for piping plovers. Imperiled by predation, disturbance from human recreational activities (Melvin *et al.* 1991), flooding and coastal development (Goossen 1990, Goossen *et al.* 2002), piping plovers have been listed as endangered throughout

their Canadian range since 1985 (Goossen *et al.* 2002). Within the United States they are listed as endangered within the Great Lakes population but threatened elsewhere (U.S. Fish and Wildlife Service 1985).

During the 2001 International Piping Plover Census, 112 adult piping plovers were documented on PEI, representing 23% of the population estimate for Eastern Canada (Amirault 2005). A population viability analysis was done to determine the productivity level and population size required for the Atlantic Coast population of the piping plover to evade extinction within the next 100 years. It was found that a population size of 2000 breeding pairs with a mean productivity of 1.5 chicks per year would be adequate to maintain a stable population (Melvin and Gibbs 1994), whereas Plissner and Haig (2000) suggest that productivity of 1.25 chicks per pair per year would suffice. Nevertheless, the reproductive success of piping plovers is highly variable (Haig and Elliott-Smith 2004) and there are several factors believed to be affecting their productivity, a number of which are discussed herein.

Humans are perceived as potential predators by many animals (Gill *et al.* 1996, Frid and Dill 2002). Animals in close proximity to human activity may believe they are at risk of predation, resulting in a behavioural shift from foraging to vigilance (Krebs and Davies 1997). Predation risk also affects where an animal will choose to forage, with areas of high predation risk avoided in most cases (Suhonen 1993). Consequently, human disturbance can have considerable impacts on shorebird reproductive success. African black oystercatchers (*Haematopus moquini*) in areas protected from human activities have higher reproductive success than those who breed in unprotected areas (Leseberg *et al.* 2000). Similarly, common loons (nesting in areas with high amounts of cottage

development and human recreational activity had higher nest failure than loons nesting in completely undisturbed areas, however, fledging success was unaffected by human activity (Heimberger *et al.* 1983). The authors suggest that individuals in areas with high levels of human recreational activity and cottage development cope by moving to areas where the level of human activity and development is low (Heimberger *et al.* 1983). Nevertheless, not all species are able to avoid human recreational activity in order to ensure productivity is unaffected. For example, nest success of kittiwakes (*Rissa tridactyla*) was significantly negatively correlated with the people load, a measure of human disturbance that also takes distance from the focal bird to the disturbance into consideration (Beale and Monaghan 2004b). Snowy plovers (*Charadrius alexandrinus*) breeding on beaches in California have greater chick mortality on weekends and holidays (when the number of beachgoers was high), thereby suggesting that increased human activity on the beach had detrimental effects on chick survival (Ruhlen *et al.* 2003). The reproductive success of golden plovers (*Pluvialis fulva*) however, was not significantly influenced by human disturbance, despite intense behavioural responses to the disturbance (Yalden & Yalden 1990, Finney *et al.* 2005). A potential explanation for the reduced reproductive success observed in some species breeding in areas with increased levels of human activity comes from Flemming *et al.*'s (1988) study, where they attribute chick mortality to foregone foraging caused by human activity within the vicinity of piping plover chicks. Piping plover chicks spend approximately twice as much time engaging in disturbance behaviour as adults, suggesting they are more sensitive to disturbance from human recreational activity (Hoopes 1993). Chicks that forego foraging become weak and are less likely to survive during unfavorable conditions (e.g. poor

weather and high predation; Cairns 1982, Loegering and Fraser 1995). This hypothesis is supported by other studies that have found piping plovers reduce foraging and increase vigilance when disturbed by human activity (Flemming *et al.* 1988, Burger 1991 and 1994). Flemming *et al.* (1988) found that human recreational activity influenced the number of young surviving per pair per nest attempt and the number of young surviving per pair per successful nest attempt only when the number of chicks surviving to 17 days, but not 10 days of age, were considered. Nevertheless, piping plover chicks younger than 12 days old are particularly vulnerable to human disturbance because survival is directly related to body mass, with the majority of chick deaths occurring within 10 days of hatching (Cairns 1982, Patterson *et al.* 1991). This trend was also observed for piping plovers in this study, with 84% of chick mortalities occurring when chicks were less than or equal to eight days of age. This finding is important in that it reaffirms the fact that if piping plover chicks are able to survive passed 10 days of age they are unlikely to die

However, the cumulative impact of foregone foraging caused by human recreational activity is not the only way human activity can decrease piping plover chick survival. Chicks have been killed by all-terrain vehicles on Atlantic Coast beaches (Melvin *et al.* 1994). Human activity has also been suggested as an explanation for piping plovers utilizing alternative habitats. For example, piping plovers in Rhode Island with access to mudflats instead of beach and dunes alone had higher fledging success. Therefore, it has been suggested that piping plovers use mudflats to avoid human recreational activity and minimize the negative effects on chick survival (Goldin and Regossin 1998). Similarly, piping plover pairs in Nova Scotia nesting on beaches with relatively low levels of human disturbance had higher reproductive success than those

nesting on beaches with high anthropogenic use (Cairns 1977). The reproductive success of piping plover pairs was higher on beaches with signs and symbolic fencing aimed at minimizing disturbance to plovers in Cape Cod, Massachusetts (Strauss 1990). A two-year study carried out in North Dakota involving piping plovers found that those nesting on territories with evidence of disturbance (e.g. cattle or human tracks) had higher nest failure in one of two years (Prindiville-Gaines and Ryan 1988). However, Tull (1984) and Hoopes (1993) found that human disturbance did not significantly alter piping plover productivity in New Brunswick or Massachusetts respectively, suggesting that human disturbance might be a limiting factor only when some other factor limited reproductive success (e.g. invertebrate abundance and/or weather).

Within the Great Plains population, piping plovers that nested early in the breeding season were more likely to fledge at least one chick than pairs that nested later (Knetter *et al.* 2002). Three explanations are provided in an attempt to explain the effect of hatch date on piping plover chick survival. They are as follows: 1) parental quality may decrease as the breeding season goes on, 2) environmental factors may vary enough seasonally to reduce chick survival, and 3) food availability may decrease later in the breeding season. The authors point to three studies carried out on great tits (*Parus major*, Verhulst *et al.* 1995), snow geese (*Anser caerulescens*; Lepage *et al.* 1999), and pied flycatchers (*Ficedula hypoleuca*; Siikamaki 1998) respectively to provide evidence for these hypotheses. All of these explanations appear plausible; however, many populations of piping plover experience temporal variability in the amount of human recreational activity they experience. Piping plover chicks that hatch earlier in the breeding season may experience higher survivorship because they are able to forage undisturbed (Burger

1987). Chicks in the presence of human activity forego foraging in order to minimize the likelihood of predation. As mentioned earlier, piping plover chick survival is dependent upon body weight, and responding to human activity at the expense of foregone foraging may result in chick mortality over time (Cairns 1982; Flemming *et al.* 1988). As a result, increased human activity as the breeding season progresses (when it gets warmer) should also be considered as a possibility where chick survival is low.

Prey abundance is another factor which can greatly influence reproductive success. Bicknell's thrush (*Catharus bicknelli*) had higher fledging success when invertebrate abundance was high (Strong *et al.* 2004). Research on roseate (*Sterna dougallii*) and sandwich terns (*Sterna sandvicensis*) in the Caribbean discovered similar benefits for pairs nesting in areas with higher prey abundance (Shealer 1995). That study found that reproductive success in a given year was positively correlated with prey abundance. Similarly, the abundance of amphipods in the Gulf of Saint-Lawrence was positively correlated with fat intake of semipalmated sandpipers (Mawhinney-Gilliland 1992). Evidence that invertebrate abundance affects piping plover chick survival has been observed on Assateague Island (Patterson *et al.* 1991) and along the Missouri River (Le Fer *et al.* 2004). Therefore, it is not surprising that plover chicks in New York forage most often along ephemeral pools or tidal flats where arthropod abundance is high (Patterson *et al.* 1991). Piping plover chick foraging rate is positively correlated with chick mass (Loegering and Fraser 1995) and chick weight is an important determinant of chick survival. In fact, chicks that fail to reach 60% of their adult weight by the time they reach 12 days old are unlikely to survive (Cairns 1982). This is further illustrated by the

fact that the majority of piping plover chick deaths occur within ten days of hatching (Patterson *et al.* 1991). For this reason, studies examining the effects of human disturbance on reproductive success should also quantify prey abundance.

Substrate composition is another measure of habitat quality that is important to consider when drawing conclusions regarding the potential factors influencing reproductive success of ground-nesting birds. Reduced reproductive success has been observed in Heerman's gulls (*Larus heermanni*) nesting on rocky substrates where large rocks would impede the bird's ability to detect approaching predators (Vellarde 1999). Turnstones (*Arenaria interpres*) and purple sandpipers (*Calidris maritima*) nesting in areas where visibility is impeded by rocks and other objects spend more time scanning for predators than in areas with better visibility (Metcalf 1984). The cryptic coloration of piping plovers and their eggs make the choice of a nest site extremely important. Piping plovers are ground nesters, and those along the Atlantic Coast nest on shorelines with substrates composed mainly of sand, mixed sand-cobble, mudflats or gravel (Plissner and Haig 2000). Characteristics of their nesting sites vary considerably and because piping plovers are ground nesters, substrate composition within a breeding territory may influence reproductive success. Heterogeneity of substrate types within a breeding territory allows for adults, chicks and nests to remain inconspicuous by means of disruptive camouflage, whereas territories devoid of substrate diversity may increase their conspicuousness (Prindiville Gaines and Ryan 1988, Flemming *et al.* 1992, Stewart 2004). Interestingly, beaches where piping plovers formerly bred have fewer substrate-type changes than do current breeding sites on PEI (Stewart 2004). Prindiville Gaines and Ryan (1988) found that piping plover territories in North Dakota were wider with more

abundant and evenly distributed gravel than were random sites. They also found that nest success was higher on open territories with very little vegetation or having clumped vegetation (Prindiville Gaines and Ryan 1988). Nest success (a nest with at least one egg hatching) in North Dakota was higher on nest sites with gravel than alkali substrates, whereas the reproductive success of piping plovers in the Great Plains (Knetter *et al.* 2002) and Prince Edward Island (Stewart 2004) were unaffected by substrate composition.

Beach width is another component of habitat quality believed to influence piping plover reproductive success. Wide beaches allow shorebirds to recognize predators sooner, whereas pairs on narrow beaches may be less able to see approaching predators, increasing the likelihood of surprise attack (Beale and Monaghan 2004a). This may explain why shorebirds nesting on wide beaches sometimes experience higher nesting success. For example, the high reproductive success of piping plovers on Big Quill Lake, Saskatchewan is believed to be attributed to wide beaches (200-1000 m), which are thought to make detection of piping plover chicks by predators less likely because chicks are able to see approaching predators and seek cover or protection (Harris *et al.* 2005). Wide beaches are also thought to allow for better nest placement such that the likelihood of flooding, predation and disturbance from human recreational activity is minimized (Burger 1987, Espie *et al.* 1996). Nevertheless, reproductive success of piping plovers in North Dakota did not differ as a result of beach width (Prindiville-Gaines and Ryan 1988). Previous studies have compared the width of beaches where piping plover used to breed to occupied beaches and found that occupied beaches were wider (Prindiville-Gaines and Ryan 1988, Boyne and Amirault in prep, Stewart 2004). However, another

study found no significant difference in beach width when comparing sites where piping plovers used to but no longer breed to current breeding sites (Espie *et al.* 1996).

Nevertheless, the reproductive success of piping plovers in North Dakota was unaffected by beach width (Prindiville Gaines and Ryan 1988).

Another variable that appears to play an important role in piping plover reproductive success is vegetation. In areas where the main predators are mammalian, vegetation is believed to decrease reproductive success by providing mammalian predators with cover when hunting (Burger 1987). Nevertheless, chicks with access to vegetation may be at an advantage because it allows them to take cover from predators and the elements (Burger 1987). The vegetative cover of piping plover breeding sites in North Dakota did not differ significantly from sites unoccupied by piping plovers (Prindiville Gaines and Ryan 1988). Nevertheless, this same study found that piping plover nest success was higher on territories with less vegetative cover in one year but was unaffected by vegetation cover in the other year (Prindiville Gaines and Ryan 1988). Conversely, piping plover nest sites in northern and southern Nova Scotia, but not northern New Brunswick, had significantly more vegetation shoots than random locations (Flemming *et al.* 1992). Flemming *et al.* (1992) seldom observed avian predators searching in dune vegetation, whereas gulls and crows were commonly observed scanning the beach and edge of the dune vegetation. In fact, broods in New York spent more than 40% of their time in vegetation (Elias *et al.* 2000). With 76 % of chick mortalities in southern Nova Scotia being the result of avian predation, it is not surprising that nest sites in this area had significantly more vegetation than random sites (Flemming *et al.* 1992). Finally, although piping plover nest site characteristics vary among regions,

plovers may be selecting the best nest sites from what is available. Different populations of piping plovers may also have different selective pressures acting upon them that are reflected in territory selection (Flemming *et al.* 1992). Therefore, birds in regions with primarily avian predators may select territories with more vegetation, whereas those in regions affected primarily by mammalian predators may select territories with less vegetation (Flemming *et al.* 1992).

Temperature and rainfall during incubation and chick-rearing phases can also influence nesting and fledging success of many bird species. The reproductive success of snowy plovers (*Charadrius alexandrinus*) is affected by meteorological conditions such as temperature and precipitation during chick rearing (Grover and Knopf 1982). In fact, weather may be the most important factor determining nest success of snowy plovers. That study also proposed severe inclement weather (e.g. hail) also caused adults to die (e.g. hail, Grover and Knopf 1982). Weather is also believed to affect the survival of piping plover chicks, and time spent foraging by both chicks and adults. Piping plovers nesting along Big Quill Lake, Saskatchewan experienced high chick mortality in 1993 during a week-long bout of extreme rainfall and generally cold and windy conditions (Harris *et al.* 2005). A significant negative correlation has been observed between temperature and time spent foraging by wintering piping plovers (Johnson and Baldassarre 1988). Similarly, results from a study conducted on piping plovers in Nova Scotia suggest that inclement weather (e.g. rain) may result in higher chick mortality because piping plover chicks would be required to spend more time being brooded to maintain their body temperature, resulting in less time foraging (Flemming *et al.* 1988). Similarly, Gautreau (1998) found that piping plover chicks on PEI, Canada spend significantly less

time foraging during rainy conditions and significantly more time being brooded when it is cool and raining, which further supports Flemming *et al.*'s theory. Piping plover chicks are not completely thermally independent until three weeks of age, after which they are seldomly brooded (Cairns 1977). In the Great Plains, meteorological conditions did not reduced piping plover chick survival (Knetter *et al.* 2002). Nevertheless, weather can also influence chick survival by limiting both the availability and the ability of plovers to detect prey. Plovers search for prey visually and use a sequence of short high speed runs and pecks at the ground (Cairns 1977) during which time they are successful at catching invertebrates 90% of the time (Pienkowski 1981). Inclement weather such as rain and/or cool temperatures cause invertebrates to stay below the surface (Goss-Custard 1984), making them less available. Since plovers locate prey visually, their ability to detect prey can be significantly reduced by high wind speeds, rain and tide level (Pienkowski 1981). Therefore, when examining the influence of human recreational activities on piping plover fledging success there are a number of different variables which must be considered ximulganeously.

Nisbet (2000) found that the majority of research published on the impact of disturbance on birds is "of low scientific value" and further pointed out that demonstrating cause and effect relationships between human disturbance and reproductive success is difficult to achieve because a number of other variables also act to limit productivity. He specifically identifies predation, weather, food availability and flooding as variables influencing reproductive success of waterbirds. Therefore, the objective of this study was to consider the impact of human activity, as well as hatching date, habitat characteristics, invertebrate abundance and weather on the fledging success

of the endangered shorebird, the piping plover. Another objective was to determine which of a) human disturbance, b) hatch date, c) invertebrate abundance, d) substrate composition, e) vegetation density, f) beach width, g) mean minimum daily temperature and h) mean daily precipitation best explain variation in piping plover fledging success, as well as to provide an indication of how these variables together influence overall fledging success.

Materials and Methods

Study Site and Subject Selection

This study took place on Prince Edward Island, Canada between 2 May and 5 August, 2005 and between 1 May and 1 August, 2006. The total number of piping plover pairs on PEI was 37 in 2005 and 60 (although fledging rate was known only for 53 pairs) in 2006. The fledging success of the 37 and 53 pairs in 2005/2006 were 1.70 and 1.65 respectively. A total of 23 pairs (12 pairs in 2005 and 11 pairs in 2006) were included for analysis. Subjects were selected based on four criteria: 1) nest success (only pairs that had at least one egg hatch were included), 2) location and accessibility of breeding territory (only pairs breeding on sites accessible by foot were included), 3) availability of data regarding the level of human activity, hatching date, invertebrate abundance, habitat quality and weather conditions experienced by the adults and chicks (pairs with missing variables were removed from the analysis), and 4) knowledge of reproductive outcome (in this case fledging success).

The piping plovers that I studied breed in three main geographic clusters (Figures 3.1.a-b.). These clusters are located in and around Prince Edward Island National Park

(PEINP) (Lat: 46° 25' N, Long: -63° 15' W; 2005 n=4 pairs, 2006 n=3 pairs), and near the communities of Morell (Lat: 46° 25' N, Long: 62° 42' W; 2005 n=5 pairs, 2006 n=4 pairs) and Souris (Lat: 46° 21' N, Long: 62° 15' W; 2005 n=3 pairs, 2006 n=4 pairs), Prince Edward Island. PEINP extends 40 km from Dalvay to Cavendish (Parks Canada 2005). Piping plover nesting sites within the park are closed to the public during the breeding season. Thus, pairs nesting inside of PEINP should be less affected by human recreational activity. Outside of the park, the Island Nature Trust (INT) employs education, symbolic fencing and signage to encourage the public to respect established conservation efforts, but beachgoers are permitted along the water's edge.

Measurement of Reproductive Success

Information on fledging success was supplemented by information provided by Parks Canada as well as INT employees and volunteers who monitored nest success and fledging success of piping plovers on PEI. Data collected by local piping plover conservation groups are considered accurate due to the extensive training of the staff. Values for piping plover reproductive success within this study are based on fledging success data collected in conjunction with these two groups. Fledging success refers to the number of chicks fledged per pair per year (Stewart 2004) and is expressed as the number of chicks surviving to fledge (20 days) out of the total number of hatched eggs within a clutch (Amirault *et al.* 2004).

Measurement of Human Disturbance

The level of human disturbance at each piping plover territory was classified based on the proportion of total observation periods conducted as part of an adjacent study (Chapter 2) where human activity occurred within 200 m of the focal piping plover.

Hatch Date

The dates when eggs hatched for each pair were expressed as a number representing the date. For both 2005 and 2006, May 1st was documented as day 1.

Measurement of Invertebrate Abundance

To provide an indication of invertebrate abundance, four modified dredge samples were collected from arbitrarily selected random locations within both the saturation zone (area where a wave had just fallen back) and the swash zone (the intertidal area between the water line and the high tide line) at all of the sites where piping plovers were being observed and known to forage. Samples were collected between the hours of 7h00 and 15h00 mid-way through the months of May, June and July in both 2005 and 2006. Piping plovers forage primarily within the top one to two centimetres of the substrate surface (Nordstrum and Ryan 1996), and many of the invertebrates within this area are able to escape quickly, therefore a modified dredge sampling technique was employed. This involved using a 30 cm x 30 cm x 5 cm box-shaped scoop with one open end which quickly and efficiently removed the top inch of sediment. Within the swash zone, the individual gathering the sample remained motionless for a period of two minutes to allow

invertebrates that may have been disturbed by vibrations from the approaching sampler to return to their normal location.

Invertebrates were collected from dredge samples using 0.5 mm and 1.0 mm sieves, were preserved in 80% ethanol (Bromley and Bleakney 1984, Eddy and Hodson 1961, Gosner 1978). The number of invertebrates within each sample was determined as the mean number of invertebrates for samples collected within the swash zone and the saturation zone for each site.

Measurement of Substrate Composition, Vegetation Density and Beach Width

Substrate composition was measured along five transects of randomly selected distances from the nest ranging from 0 to 250 m of each side of the nest (total=10 transects/nest) using a measuring wheel accurate to the nearest inch (later converted to meters). Beach transects extended perpendicular from the mean high water mark to the base of the foredune (Boyne and Amirault, in prep). A foredune is “a dune ridge built up behind a coastline” (Grimes 1995). On territories with a backbay (bay separated from the ocean by a peninsula of land) but lacking a foredune, transects extended from the mean high water mark on the ocean side to the mean high water mark on the bay side of the beach. Substrate composition was classified as open sand, buried wrack, wrack, water, vegetation, light cobble and cobble (Boyne and Amirault, in prep). When birds moved newly hatched chicks to different territories to forage and care for their chicks (n=1), the randomly selected transects were measured from the center of the area closed to human recreational activity by either Parks Canada or INT. On beaches where transects ended at the base of a vegetated foredune, the number of vegetation shoots within a 1 x 1 m

quadrat was counted to determine vegetation density (Boyne and Amirault, in prep). The distance of the transect from the nest or center of the area closed to human activity were selected using a random number generator between 0 and 250 m. These measurements were collected between August 1 and August 7, 2005 and between July 23 and July 28, 2006 after chicks had fledged (or were close to fledging), or after the nest or brood had been lost. This was done in order to minimize disturbance to piping plover chicks and adults (Powell and Cuthbert 1992).

Monitoring Meteorological Conditions

Daily minimum air temperatures and daily cumulative precipitation for the duration of this study were provided by Environment Canada Weather Stations. These weather stations were located in Stanhope (Lat: 46° 25' N, Long: 63° 4' W), Saint Peters (Lat: 46° 27' N, Long: 62° 34' W) and East Point (Lat: 46° 27' N, Long: 61° 59' W), which were close to the three geographic clusters. The minimum daily temperature (degrees celcius) and daily precipitation (mm) from chick hatching until the chicks reached 20 days of age or until they died were summed daily and averaged according to the number of chicks within a brood. The mean minimum temperature, and mean daily temperature were then determined for all live chick days in each brood. For example, if chick A lived for 8 days, chick B lived for 10 days, and chicks C and D fledged at 20 days, then the value for mean daily precipitation for this brood would be:

Mean daily precipitation = [(sum of rainfall for days 1 to 8) + (sum of rainfall for days 1 to 10) + (sum of rainfall for days 1 to 20) + (sum of rainfall for days 1 to 20)]/total number of live chick days (e.g. 58).

Mean minimum daily temperature was calculated in the same way.

Data analysis

Fledging success was expressed as a proportion and was measured as the number of chicks surviving to 20 days out of the total number of eggs that hatched for each pair. This was done in order to account for variation in brood size. Only pairs with eggs that hatched were included within the analysis.

The level of human activity at piping plover breeding beaches was expressed as the proportion of observations conducted as part of an adjacent study (Chapter 2) where human activity occurred within 200 m of the focal individual. Measures of habitat quality such as invertebrate abundance, beach width, substrate composition (e.g. proportion of beach transect covered in open sand, light cobble, cobble, buried wrack, and the number of substrate transitions), the number of different substrate type changes, and vegetation stem density were used to assess the influence of piping plover territory quality on fledging success. Similarly, meteorological conditions during the chick rearing period (from the hatching date until the chicks were 20 days old or died) were considered as potential predictors of piping plover foraging behaviour.

Invertebrate abundance was determined using the mean total number of individual specimens found in each sample collected within that zone (n=4 samples). Mean invertebrate abundance was determined for both the saturation zone and the swash zone at each site and the values were converted to abundance per m². When two pairs had adjacent territories and foraging areas that overlapped, the same data for invertebrate abundance were used for both pairs. Overall invertebrate abundance was calculated by

taking the mean samples collected within the swash zone and the saturation zone of each territory for each month to provide one mean for monthly invertebrate abundance.

The proportions of open sand, buried wrack, wrack, water, vegetation, light cobble and cobble at each transect were determined and the mean was taken for each breeding site. This was done by taking the sum of the distances of a given substrate type and dividing it by the beach width to give the proportion of the beach covered in that substrate. Beach width was determined by taking the sum of all substrate types within a transect and taking the mean all transects. The mean number of vegetation shoots was also determined for each breeding territory using similar methods.

A three step approach was used to statistically evaluate potential relationships between fledging success and anthropogenic, temporal, environmental and meteorological conditions. A univariate correlation analysis was performed followed by multiple linear regressions with backward and forward stepwise analyses. Means \pm SE are presented.

As part of the univariate correlation analysis, Pearson correlations were used when data were normal and Spearman correlations were used for nonparametric datasets. All correlations were two-tailed and considered significant at $p < 0.05$.

Multiple linear regressions allow for the influence of multiple variables to be considered together (Bronikowski and Altman 1996). Two types of multiple linear regression were performed: forward stepwise analysis and backward stepwise analysis. Multiple linear regression with backward stepwise analysis involves initially including all variables and systematically removing the variable contributing the least to explaining fledging success with a p-to-remove criterion of $\alpha = 0.20$ (Legendre and Legendre 1998).

Alternatively, multiple linear regression with forward stepwise analysis involves starting with no variables in the model and systematically adding terms that contribute to the greatest increase in the multiple regression correlation coefficient R^2 . Again, terms were added to the regression equation based on a p-to-enter criterion of $\alpha=0.20$. Forward selection may often contain variables that actually contribute little to the model due to the way forward selection keeps previously added variables. To test whether my data met the assumption of normality, D'Agostino and Pearson omnibus normality tests were used and the data considered normal if $p>0.05$. Transformations ($\log+1$) were performed whenever necessary to improve normality. The dependent variable in this study was the number of chicks surviving to fledge per brood (or fledging success), expressed as a proportion (e.g. number of fledged chicks per brood \div total number of eggs hatched per clutch). The independent variables that were considered for inclusion were: a) the level of human disturbance (expressed as the proportion of observations where human activity took place within 200 m of the subject), b) hatch date c) invertebrate abundance, d) the proportion of open sand, e) the proportion of light cobble, f) mean minimum daily temperature, and g) mean daily rainfall during the chick rearing stage. Descriptive statistics, normality tests and correlations were all performed on GraphPad Prism 4 and multiple linear regressions were performed using SYSTAT 9. Pairs with missing variables were not included within the analyses.

Results

There was no significant difference between 2005 (0.69 ± 0.10 , $n=12$) and 2006 (0.62 ± 0.12 , $n = 11$) ($t = 0.45$, $p = 0.66$, $df = 21$, Appendix 1). When the fledging success of

plover pairs monitored with successful nests was pooled over both years, there was no significant difference between within PEINP (0.75 ± 0.09 , $n = 7$) and outside PEINP (0.62 ± 0.10 , $n=16$) ($U = 51.0$, $p = 0.76$).

Fledging success was significantly negatively correlated with beach width (Table 3.1) but not with the level of human activity, invertebrate abundance or any measure of substrate composition or vegetation stem density. Similarly, neither mean minimum daily temperature nor mean daily precipitation were significantly correlated with fledging success (Table 3.1). To further understand interactions between piping plover chick survival and precipitation events, chick mortality was plotted against the amount of daily precipitation recorded at the nearest weather station (see figures 3.2.a-c and 3.3.a-c). Of the 27 chick mortalities that occurred, 41% of them occurred the day of or after a precipitation event, defined as any day with ≥ 1 mm of rain. Therefore, although precipitation was not significantly correlated with piping plover fledging success, precipitation appeared to decrease chick survival. Nevertheless, many of the precipitation events were small in size and therefore may have actually contributed very little to increased thermoregulation and chick mortality.

Of these variables, all but hatch date, mean minimum temperature and the proportion of open sand were removed to provide an equation for fledging success with a predictive ability of 35.0% (see Table 3.2). The predictor equation, from the multiple linear regression with backward stepwise analysis removed variables to create an equation as follows:

$$\text{Fledging success} = 0.710 - 0.015*(\text{Hatch date}) + 0.103*(\text{mean minimum daily temp}) - 1.011*(\text{proportion of open sand}).$$

Multiple linear regression with forward stepwise analysis resulted in the following equation having a predictive ability of 22.9%.

$$\text{Fledging success} = 1.669 - 0.628 * (\log \text{ beach width} + 1)$$

Significant intercorrelations among independent variables were also investigated. Hatch date and air temperature were significantly intercorrelated which could have reduced the ability to identify trends in piping plover chick survival.

Discussion

The influence of human activity on piping plover fledging success

Piping plover fledging success on PEI was not related to our measure of human disturbance (based on the proportion of observations where human activity came within 200 m of the subject). These findings are contrary to what had been predicted, however, the percent of observations where human activity occurred within 200 m of the focal plover was low (from 0 to 38% of total observations). Human recreational activity failed to reduce reproductive success of golden plovers (Yalden & Yalden 1990, Finney *et al.* 2005) and piping plovers (Tull 1984) in other studies. Therefore, human disturbance may be problematic only during periods when other factors are also acting to limit reproductive success (Tull 1984), which might explain why human activity did not influence piping plover fledging success on PEI. Nevertheless, Cairns (1977), Flemming *et al.* (1988), Strauss (1990), and Prindiville Gaines and Ryan (1988) all observed lower reproductive success of piping plovers on beaches with more human activity. With disturbance, individuals may be unable to forage efficiently and therefore may lack the lipid reserves necessary for reproduction (Lafferty 2001, Skagen and Knopf 1993), chick

survival (Cairns 1982, Loegering and Fraser 1995), and migration. This is particularly true for piping plover chicks less than 12 days old because their likelihood of survival is directly related to body mass; the majority of chick mortalities occur within 10 days of hatching (Cairns 1982, Patterson *et al.* 1991). The majority of chick mortalities (84%) in this study occurred when chicks were ≤ 8 days old.

In order to maintain a stable population of piping plovers the minimum number of chicks each pair needs to fledge is 1.5 or 1.25 (Melvin and Gibbs 1994, Plissner and Haig 2000). The stable productivity values for 2005 and 2006 (1.70 and 1.65 chicks per pair respectively; MacDonald 2006 pers. comm. and Thomas 2006 pers. comm.) suggest that piping plovers on PEI may be selecting high quality territories in order to offset the negative impact of human activity, in turn allowing fledging success to remain high. Given the option of selecting two territories of equal quality, piping plovers would likely select the territory with less human disturbance. Nevertheless, the level of human recreational activity increases later in the breeding season and therefore may not allow piping plovers to assess the level of disturbance that will be encountered prior to territory selection.

Human activity may not have significantly influenced piping plover fledging success in the direction predicted if the measure of human disturbance used within this study did not reflect actual levels the plovers would have been exposed to on a daily basis. Observations for this study took place between 7h00 and 16h00, and although human activity did on occasion take place within 200 m of the focal individual, it is expected that higher intensity and more frequent disturbance events would take place

during the evening. Throughout the evening, beachgoers may be more likely to engage in “risky behaviour” (e.g. ATV use or entering closed areas) because there are fewer resources available to ensure compliance of area closures. Alternatively, human activity may not have influenced fledging success because conservation efforts put in place by the INT and Parks Canada are successful in minimizing disturbance caused by human activities. These findings are supported by those of Patterson *et al.* (1991) and Melvin *et al.* (1992) who found that erecting symbolic fencing was an effective manner of minimizing the impact of human recreational activity to breeding piping plovers. Although the measure of human activity used within this study may have underestimated the level of human activity encountered by piping plovers, it is expected that the actual daily level would be directly proportional to the level documented. Therefore, beaches with high daytime use where also expected to receive high night time use.

Human recreational activity may not have significantly influenced the reproductive success of piping plovers in my study because they may have habituated to human activity. Another study found that individuals on sites with consistently high levels of human recreational activity allow people to approach more closely without interrupting foraging (Hoopes 1993). Although it is possible that the piping plovers studied became habituated to human recreational activity, it is unlikely because the level of human recreational activity encountered on PEI was kept artificially low through education and area closures. Furthermore, piping plover chicks in another study spent twice as much time in disturbance behaviour when met with human recreational activity than did adults, suggesting chicks are more sensitive to human recreational activity than adults (Hoopes 1993). Therefore, considering the relatively young age at which

monitoring of survival was stopped (20 days), it is unlikely that chicks would have had time to habituate to human recreational activity.

The influence of hatching chronology on fledging success

Hatch date was identified as a significant predictor of fledging success within the backward stepwise multiple linear regression, and tended to be negatively correlated with fledging success ($p=0.085$). Piping plovers able to hatch a clutch early in the breeding season have higher fledging success than those nesting later. Reproductive success was also found to be negatively correlated with hatching date in golden plovers (Finney *et al.* 2005) and piping plovers in New Brunswick (Tull 1984) and the Great Plains (Knetter *et al.* 2002). In their study, Knetter *et al.* (2002) proposed three potential explanations for this apparent trend. First they suggest that parental quality decreases progressively throughout the breeding season. Although this may have been the case within the current study it was impossible for me to measure parental quality. Second, they suggest that differences in environmental variables over time, and finally changes in food availability, may explain higher fledging success of pairs that hatch a clutch early in the breeding season. These variables were measured and considered as potential predictors of fledging success but they were not found to influence fledging success significantly. Pairs that hatch a clutch early in the breeding season may benefit by experiencing lower levels of human activity. Although not observed within this study (Chapter 2), piping plovers have been known to decrease foraging and increase vigilance in the presence of human activity (Flemming *et al.* 1988, Burger 1991) and use different habitat types to avoid interaction with human recreational activities (Burger 1994). Many shorebirds, such as piping

plovers, may be unable to leave a site where human activity is taking place due to biological limitations associated with breeding and foraging (Plissner and Haig 2000). Given the relatively long incubation (27-29 days, Cairns 1982) and pre-fledging periods (20 days, Flemming *et al.* 1992) of piping plovers in comparison to the PEI tourist season, the level of human activity at a specific location can change considerably over the breeding season. Therefore, if a pair is able to successfully fledge chicks prior to increasing beach use they may be able to curtail the negative impacts of human activity on chick survival.

Another variable that might also explain hatch date as a significant predictor of piping plover fledging success is predation pressure. Predators may be attracted to refuse left on the beach from human activities (Burger 1987). Therefore, predation pressure may be higher later in the breeding season because the potential source of refuse (human activity on the beach) would be higher, thus reducing fledging success. Even when considered in the absence of human activity, predation pressure would likely increase throughout the summer due to increasing energy requirements for young predators also born in that year. Although predation pressure on piping plover breeding territories was assumed equal, my findings may suggest that predation pressure is neither temporally nor spatially uniform.

The influence of prey abundance on piping plover fledging success

When invertebrate abundance was considered together with other independent variables, it failed to be identified as an important predictor of piping plover fledging success. According to my study, survival of piping plover chicks does not appear to

depend on invertebrate abundance. These findings are contrary to what would be expected. Amphipod abundance and fat intake of semipalmated sandpipers in the Bay of Fundy were positively correlated (Mawhinney-Gilliland 1992). Therefore, it is not surprising that piping plover chick growth and survival along the Missouri River increases with increasing invertebrate abundance (Le Fer *et al.* 2004). If prey are sparse, birds foraging on sites with low invertebrate abundance are forced to go longer distances in order to find the food they require (Norberg 1977, McKnight 1998). Although they spend a greater proportion of time foraging, birds foraging in areas with low invertebrate abundance would likely have lower pecking rates, which may have direct implications for chick survival. Nevertheless, pecking rate of redshanks along the Ythan estuary in Aberdeenshire was independent of invertebrate density (Goss-Custard 1970), suggesting that relationships between invertebrate abundance and pecking rate are not always apparent.

Invertebrate abundance within this study did not vary significantly among months or between years sampled. Therefore, the variability in invertebrate abundance observed between sites may have been too narrow to identify significant relationships with fledging success. Invertebrate abundance was estimated on a monthly basis but it likely varies considerably both temporally and spatially. More comprehensive invertebrate sampling may be required in order to better understand the extent to which invertebrate abundance influences fledging success. Nevertheless, it does provide us with an overall indication of prey availability on piping plover breeding sites and suggests that invertebrate abundance does not play as large a role as might have been expected.

Nevertheless, invertebrate abundance remains an important variable to consider when investigating the impact of human activity on piping plover chick survival and should be taken into consideration in future studies. Yasué (2006) found that response to human activity in least sandpipers (*Calidris minutilla*) was dependent upon invertebrate abundance, with birds in areas of high invertebrate abundance responding to human activity sooner. Therefore, it would be valuable to monitor invertebrate abundance and determine prey availability in areas where coastal development is being proposed to evaluate the relative importance of a given site to shorebirds, and more specifically to piping plovers.

The influence of substrate composition, vegetation density and beach width on piping plover fledging success

Piping plover fledging success was not significantly correlated with any measure of substrate composition or the mean number of substrate type changes. When considered in concert with other variables, the multiple linear regression with backward analysis (but not forward) identified the proportion of open sand on a breeding site as a significant predictor of piping plover fledging success. Fledging success of piping plovers on PEI was lower on breeding territories with more open sand, but was not influenced by the proportion of light cobble, or the mean number of substrate type changes along a beach profile. This may be due in part to the fact that disruptive camouflage is not facilitated on territories with homogenous substrate composition. Chicks raised on territories with a large amount of open sand might be more visible to predators than on territories with mixed substrate types, which may result in lower fledging success. Piping plover chicks

respond to parental alarm calls by quickly lying flat on the ground to remain as inconspicuous as possible (Haig 1992). Certain substrate types might provide better camouflage to cryptically coloured downy chicks (Burger 1987, Flemming *et al.* 1992), thereby making detection by predators less likely and the chances of survival higher. The heterogeneity of mixed substrates, unlike open sand, provides piping plover chicks with additional protection from predators by decreasing conspicuousness. Open sand beaches are visually homogenous, allowing chicks to be spotted easier than mixed substrates. Previous studies suggest that piping plovers generally select habitats that are wider, have more substrate type changes, have more mixed substrate and less open sand. Considering these trends, and that open sand was the most abundant substrate type observed, it would appear as though territory selection is based more on hatching success than fledging success for piping plovers on PEI.

Stewart (2004) also investigated relationships between substrate composition and measures of productivity such as hatching success and fledging success for piping plovers on PEI. She found that piping plover productivity was not significantly influenced by substrate composition; however, she did note that current piping plover breeding sites had significantly more substrate type changes than did former breeding sites (Stewart 2004). She suggested that piping plovers select breeding territories with more substrate type changes because habitat quality is dependent upon the use (i.e. foraging, nesting, chick rearing). The preferred substrate composition differs for piping plovers depending on if they are nesting, foraging or chick rearing; as a result, pairs which select territories in locations with more diverse substrate types are selecting territories that better meet the requirements of all uses. Stewart (2004) proposed that habitats with more substrate type

changes allow adults, chicks and nests to remain as inconspicuous as possible, suggesting that birds which select territories with uniform substrate types would be more conspicuous.

Boyne and Amirault (in prep) found that sites along the Atlantic Coast where use by piping plovers had declined in recent years had significantly less sand and more cobble than stable sites or sites no longer used by piping plovers. They also found that former piping plover breeding sites that had been abandoned had more sand and less mixed substrate than sites where use by piping plovers had declined or remained stable. In fact, they found that along the Gulf of Saint Lawrence the variable which best predicted whether a site was still in use by piping plovers was the percent mixed substrate.

Piping plover fledging success was not affected by vegetation stem density in this study. As mentioned earlier, there are two general hypotheses regarding the importance of vegetation to piping plover chicks. Some believe that vegetation provides chicks with shelter from the elements and avian predators, whereas others believe that vegetation provides a vantage point whereby mammalian predators can conceal themselves and learn to search for plover chicks (Burger 1987). Given this information, we might deduce that different types of predators (mammalian vs. avian) are affecting plovers at different sites and therefore may influence whether vegetation improves or reduces the likelihood of survival.

Fledging success of piping plovers on PEI was significantly negatively correlated with mean beach width within a breeding territory. With forward stepwise analysis, the multiple linear regression identified beach width alone as an important predictor of piping

plover fledging success. Piping plovers on narrow beaches had higher fledging success than pairs on wide beaches, which is opposite to what was expected. Piping plovers are thought to benefit by breeding on wide beaches because it allows for the nest to be placed in a location that minimizes the likelihood of flooding, predation and human disturbance (Burger 1987, Espie *et al.* 1996). Previous studies have compared the width of unoccupied piping plover breeding beaches to occupied beaches and found that occupied beaches were wider (Prindiville-Gaines and Ryan 1988, Boyne and Amirault in prep, Stewart 2004), whereas others found no significant difference in beach width (Espie *et al.* 1996). Nesting on wide beaches is believed to be advantageous to shorebirds because they are able to identify approaching predators well in advance, whereas pairs nesting on narrow beaches are more likely to receive surprise attacks by predators (Beale and Monaghan 2004a). Although piping plovers select wide as well as narrow territories, the survival of chicks reared on wide beaches was not higher. In fact, the results of this study suggest that piping plover chick survival is actually higher on narrower beaches than wide beaches. Plover chicks reared on narrow beaches may experience higher survival rates because they are closer to foredune vegetation. Foredune vegetation provides piping plover chicks with protection from the elements and perceived predators (both actual and human, Burger 1987). Plover chicks on narrow beaches would be closer to cover should a disturbance event occur, potentially increasing their likelihood of evading predation. Alternatively, the risk of depredation may be higher for pairs on narrow beaches because mammalian predators learn to search in and are able to hide in nearby vegetation (Burger 1987). As a result, piping plover territory selection may be based on requirements for nest success rather than chick survival. Nevertheless, caution should be used when

interpreting these results because beach width was identified as an important predictor variable within the multiple linear regression only with forward stepwise analysis (and not backwards), which is the weaker of the two analyses (Legendre and Legendre 1998).

The influence of weather conditions on piping plover fledging success

Fledging success of piping plovers was not significantly correlated with either mean minimum daily temperature or mean daily precipitation over the chick rearing period (from hatching until 20 days old). Nevertheless, the multiple linear regression with forward analysis identified the mean minimum daily temperature over the pre-fledging period as a significant predictor of piping plover fledging success. Chick survival was positively influenced by mean minimum daily temperature. Furthermore, 41% of piping plover chick mortalities documented in this study occurred either the day of or the day after a precipitation event. These results are consistent with Flemming *et al.*'s (1988) assertion that piping plovers experiencing cool and wet weather conditions during the pre-fledging period must spend more time being brooded, consequently resulting in less time foraging, which may in turn result in low chick survival. High winds, cool temperatures and heavy rain have all been associated with piping plover chick loss in Saskatchewan (Harris *et al.* 2005). Because piping plover chick mass and pecking rate are positively correlated, and chick survival is related to chick mass (Cairns 1982), chicks unable to forage efficiently would be less likely to survive. Nevertheless, it should also be noted that 59% of chick mortalities occurred when precipitation did not occur within the same day or the day before. Many of the precipitation events were small

in size and therefore may have actually contributed very little to increased thermoregulation and chick mortality.

Piping plover prey (intertidal invertebrates) also respond to cool weather conditions in a way that would affect the ability of chicks to forage. Because plovers are not tactile feeders, they rely upon visual prey searching and rapid movements to locate prey (Pienkowski 1981). When feeding, piping plovers are successful at catching prey 90% of the time during good conditions (Pienkowski 1981), however, decreasing temperatures cause invertebrates to stay below the surface (Goss-Custard 1984). Intensity of wind, precipitation and time passed after high tide are all believed to impact the ability of plovers to locate prey with visual cues (Pienkowski 1981). As a result, the effects of weather on chick survival may be direct (e.g. starvation) or indirect (e.g. weaken chicks so they become easier prey).

Summary - Cumulative influence of human activity, habitat quality and weather on piping plover fledging success

Multiple linear regressions with forward and backward stepwise analyses were performed to determine the extent to which piping plover fledging success was influenced by human activity, hatch date, prey abundance, substrate composition, vegetation density, beach width, air temperature and precipitation together. The forward stepwise analysis identified only beach width as an important predictor of piping plover fledging success, with beach width and piping plover fledging success on PEI being negatively associated. This model, although parsimonious, conflicts with other studies on

piping plovers that have found piping plovers to actually benefit from nesting on wide beaches.

The backward stepwise analysis identified hatch date, the proportion of open sand and the mean minimum daily temperature as significant predictors of piping plover fledging success. This model had the highest predictive ability while maintaining parsimony and the results appear to agree with the available literature. Piping plovers therefore benefit by breeding early in the season, on beaches with low proportions of open sand and during periods when minimum daily temperatures are higher. As a result, it appears as though piping plovers face trade-offs between hatching chicks early in the breeding season (perhaps to minimize interactions with human recreational activity or predators) and hatching chicks when the minimum daily temperature is higher (later in the breeding season). Hatching date was identified as the best predictor of piping plover fledging success, therefore, the benefits of early nesting appear to outweigh those of warm weather.

All of the variables selected for inclusion within this analysis vary temporally and whenever possible multiple measurements were taken throughout the breeding season and the course of a day to account for temporal differences. Nevertheless, one variable that was not accounted for within this study was predation pressure. Predation pressure, as well as human disturbance, invertebrate abundance and weather conditions vary over the piping plover breeding season. While guarding chicks, adults respond to predators by alarm calling, feigning injury and luring predators away from the chicks (Haig 1992). Chicks respond to potential predators by quickly dropping to the ground and remaining motionless (Haig 1992). Piping plovers react to predators in the same way they do to

human recreational activity, by reducing the amount of time they spend foraging and increasing the time they spend scanning for predators. This would have implications for chick survival because chicks unable to forage efficiently may develop starvation-induced weakness (Stewart 2004), making them easier prey.

Conclusions

The findings of this study are novel in that it is the first study of its kind to consider the influence of human activity, hatching date, prey abundance, substrate composition, beach width, minimum daily temperature and mean daily precipitation on piping plover fledging success all together. Human disturbance did not appear to be a factor limiting fledging success of piping plovers on PEI. However, the ability of this study to detect an effect of human recreational activity on chick survival was kept artificially low because disturbance was limited by conservation efforts.

In the second chapter, the proportion of time piping plovers spent engaging in disturbance behaviour was determined to be significantly higher when human activity took place within 100 m and 50 m of the focal individual, but was unaffected by human activity within 200 m. The distance where piping plovers no longer responded to human disturbance was therefore between 100 m and 200 m. As a result, area closures established for the purpose of minimizing disturbance to piping plovers should be no less than 200 m from human recreational activity until further research can more definitively pinpoint the distance at which piping plovers no longer respond to human activity. The frequency and intensity (primarily walking) of human activity observed within this study was relatively low, therefore, when establishing area closures around territories that

might receive higher more intense levels of human activity, it may be necessary to further limit access.

Pairs with clutches hatching later in the breeding season, on territories with a higher proportion of open sand and during cool conditions were most likely to have lower reproductive success. Therefore, it might be advantageous to monitor these variables and increase the level of protection for pairs nesting in areas where chicks may be at greater risk. A potential confounding variable within this study may have been the variability of predation pressure among sites. Predation pressure was assumed to be equal from site to site within this study, which more than likely was not the case. This variability would have had obvious influences on chick survival and the information that could be drawn from this research. Nevertheless, the findings are relevant because nearly all of the variables quantified would somehow influence the ability of both chicks and adults to remain vigilant and avoid predators. Depredation of nests and chicks are believed to be some of the most important variables influencing productivity of piping plovers (Amirault 2005) and measures taken to minimize predation should continue.

All of the variables considered as potential predictors of piping plover fledging success have the ability to influence a chick's condition and therefore their ability to respond to variation in predation pressure. Despite the fact that it was not possible to decipher whether mortality was caused by predation or some other external variable, all of the variables considered would influence an individual's condition and ability to avoid predation.

Finally, this research will provide much needed insight into the factors affecting piping plover fledging success on PEI. Identifying the variables that contribute the most

to changes in fledging success will provide management officials with an indication of where best to direct conservation efforts. This information may be used to determine areas and periods where piping plovers may be most vulnerable, allowing for the most efficient distribution of conservation efforts.

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Table 3.1. Descriptive statistics for independent variables measured to predict piping plover fledging success. Normality was determined using the D'Agostino and Pearson omnibus normality test and variables were considered normal if $p > 0.05$. Pearson correlations were used when independent variables were normal and Spearman correlations were used for non-normal variables. Correlations were significant at $\alpha < 0.05$.

Independent Variable	Range	Mean (SE)	Correlation coefficient (r)	p-value
Hatch date ¹	44.0-90.0	65.9±2.74	-0.4	0.09
Proportion of human activity ²	0-0.4	0.13±0.024	0.1	0.61
Minimum temperature ³	11.2-17.5	14.90±0.36	0.1	0.79
Mean daily precipitation ⁴	0-6.3	2.72±0.37	0.1	0.52
Beach width ⁵	10.7-17.2	48.44±7.46	-0.6	0.04*
Buried wrack ⁵	0.0-0.5	0.13±0.02	0.1	0.79
Buried wrack light cobble ⁵	0.0-0.03	0.0070±0.0020	-0.2	0.42
Light cobble ⁵	0.0-0.6	0.25±0.030	0.2	0.39
Vegetation ⁵	0.0-0.1	0.0061±0.0023	0.1	0.82
Open sand ⁵	0.1-0.8	0.56±0.036	-0.3	0.14
Wrack ⁵	0.0-0.1	0.029±0.0084	0.1	0.82
Cobble ⁵	0.0-0.4	0.030±0.018	0.4	0.10
Vegetation stem density ⁶	0-435.7	45.00±18.97	0.0	0.96
Number of substrate type changes ⁷	3.4-15.4	8.85±0.58	-0.2	0.40
Invertebrate abundance ⁸	0-470.9	58.09±20.78	0.1	0.82

* denotes significant correlations

¹ Nest hatching hatch date (May 1=Hatch day 1).

² Mean proportion/pair of total observations for which human activity occurred within 200 m of the focal individual.

³ Mean minimum daily temperature in degrees Celsius for all chicks within a brood from hatching until fledging or depredation.

⁴ Mean daily precipitation in mm for all chicks within a brood from hatching until fledging or depredation.

⁵ Proportion of piping plover breeding beaches covered in this substrate type.

⁶ Mean vegetation stem density per m^{-2}

⁷ Mean number of substrate type changes within a given breeding territory.

⁸ Mean invertebrate abundance within the saturation zone and the swash zone within the month of chick rearing (number of invertebrates/ m^2)

Table 3.2. Results of the multiple linear regression with backward stepwise analysis of piping plover chick survival for pairs that hatch chicks on Prince Edward Island ($r=0.49$, $r^2=0.350$, 1 df for each variable except constant).

Effect	Coefficient	Std. Error	F	p-value
In				
▪ Constant				
1. hatch date	-0.015	0.01	6.42	0.02
2. mean minimum temperature	0.103	0.48	4.47	0.05
3. proportion of open sand	-1.011	0.42	5.81	0.03
Out				
4. proportion of light cobble	-0.041		0.03	0.86
5. proportion of observations with human activity within 200 m	-0.067		0.08	0.78
6. mean precipitation (mm) per chick day	0.126		0.29	0.60
7. log(beach width+1)	-0.222		0.93	0.35
8. mean number of substrate transitions	0.109		0.22	0.65
9. log(invertebrate abundance+1)	-0.062		0.07	0.80

Fledging success = $0.710 - 0.015*(\text{hatch date}) + 0.103*(\text{mean minimum daily temp}) - 1.011*(\text{proportion of open sand})$

1. Nest hatching date (May 1=Hatch day 1).
2. Mean minimum daily temperature for all chicks within a brood from hatching until fledging or depredation.
3. Proportion of piping plover breeding beaches covered in open sand.
4. Proportion of piping plover breeding beaches covered in light cobble.
5. Mean proportion/pair of total observations for which human activity occurred within 200 m of the focal individual.
6. Mean daily precipitation for all chicks within a brood from hatching until fledging or depredation.
7. Log (+1) of the mean beach width along beach profiles on piping plover breeding territories.
8. Mean number of substrate type changes within a given breeding territory.
9. Log (+1) of the mean invertebrate abundance within the saturation zone and the swash zone within the month of chick rearing

Table 3.3. Results of the multiple linear regression with forward stepwise analysis of piping plover chick survival for pairs that hatch chicks on Prince Edward Island ($r=0.479$, $r^2=0.229$, 1 df for each variable except constant).

Effect	Coefficient	Std. Error	F	p-value
In				
▪ Constant				
1. log(beach width+1)	-0.628	0.251	6.242	0.02
Out				
2. Hatch date	-0.063		0.081	0.78
3. proportion of observations with human activity within 200 m	0.050		0.049	0.83
4. mean daily minimum temperature	0.254		1.374	0.26
5. mean daily precipitation (mm) per chick day	0.200		0.832	0.37
6. proportion of light cobble	0.114		0.262	0.61
7. proportion of open sand	-0.140		0.399	0.54
8. mean number of substrate transitions	0.150		0.461	0.51
9. log(invertebrate abundance+1)	0.019		0.007	0.934

$$\text{Fledging success} = 1.669 - 0.628 * (\log \text{ beach width} + 1)$$

1. Log (+1) of the mean beach width along beach profiles on piping plover breeding territories.
 2. Nest hatching date (May 1=Hatch day 1).
 3. Mean proportions of total observations conducted where human activity occurred within 200 m of the focal individual (chapter 2).
 4. Mean minimum daily temperature for all chicks within a brood from hatching until fledging or depredation.
 5. Mean daily precipitation for all chicks within a brood from hatching until fledging or depredation.
 6. Proportion of piping plover breeding beaches covered in light cobble.
 7. Proportion of piping plover breeding beaches covered in open sand.
 8. Mean number of substrate type changes within a given breeding territory.
- Log (+1) of the mean invertebrate abundance within the saturation zone and the swash zone within the month of chick rearing

Figure 3.1.a. Map illustrating locations of piping plover breeding beaches where fledging success was monitored in 2005.

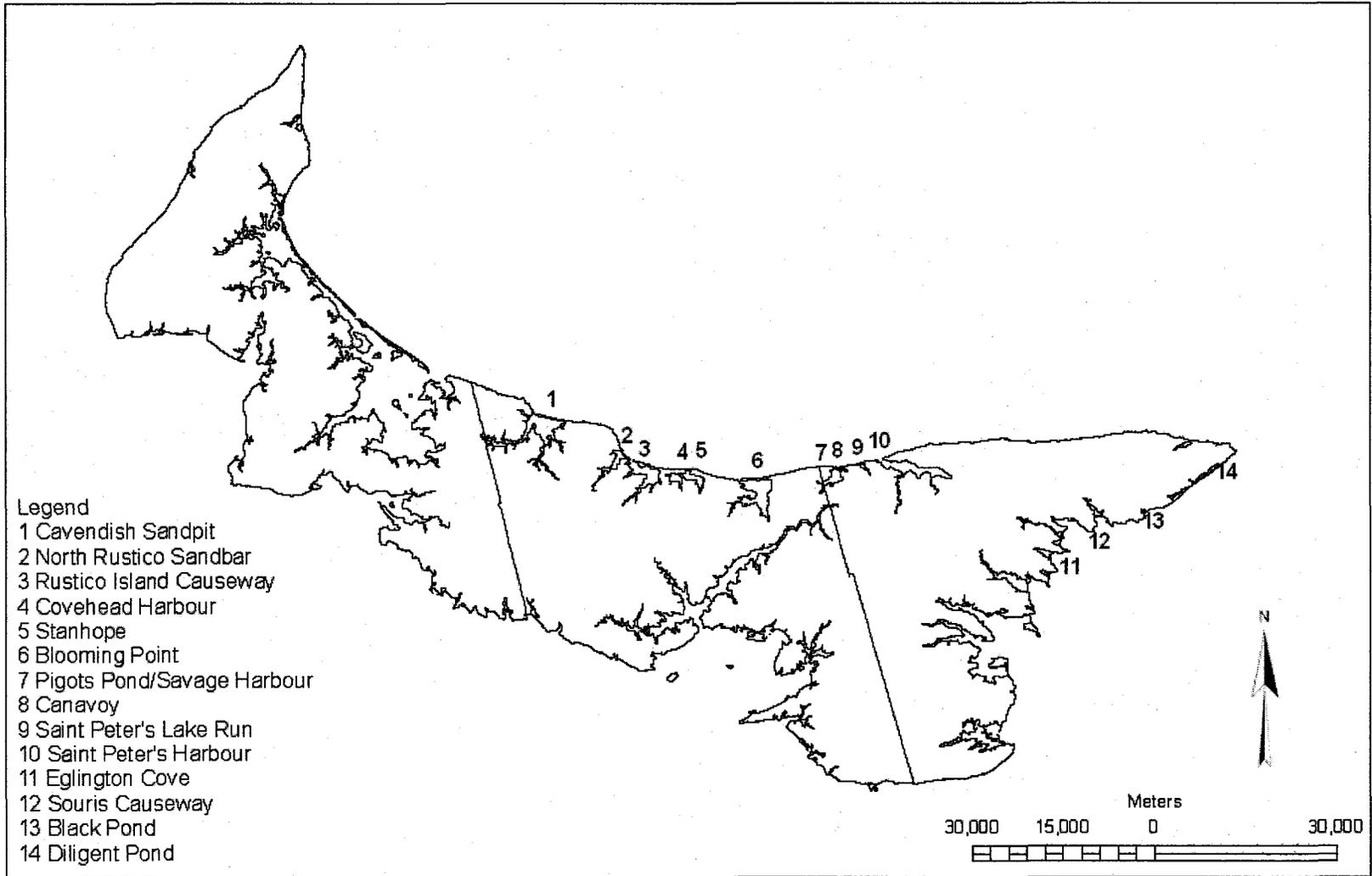
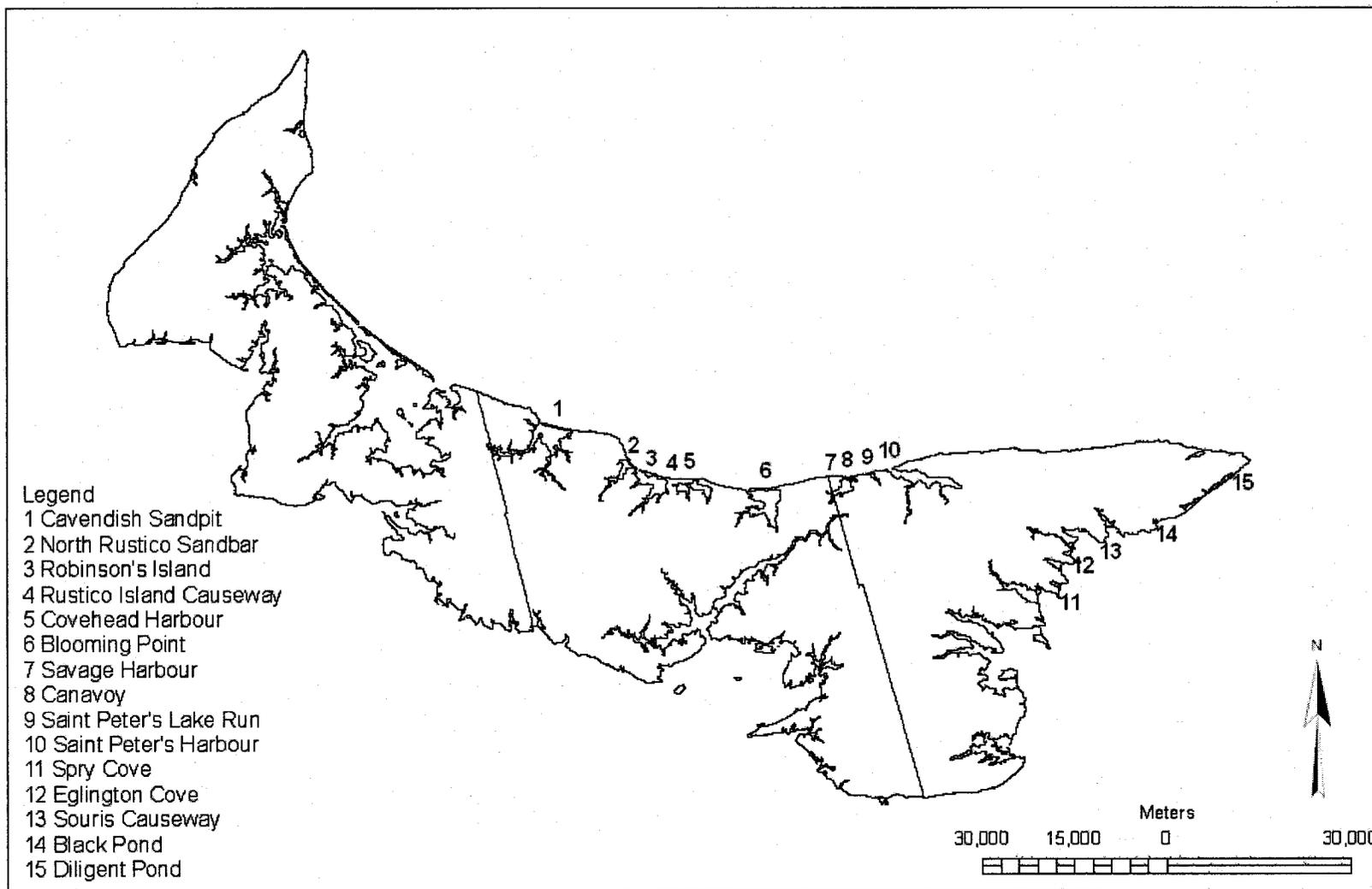
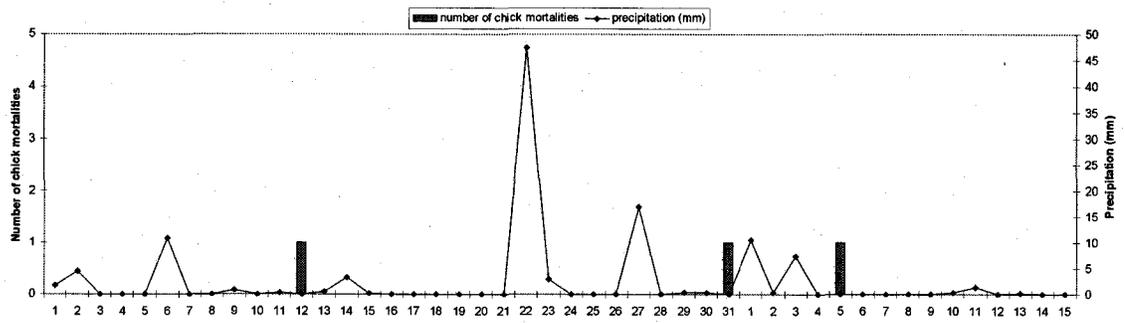


Figure 3.1.b. Map illustrating locations of piping plover breeding beaches where fledging success was monitored in 2006.

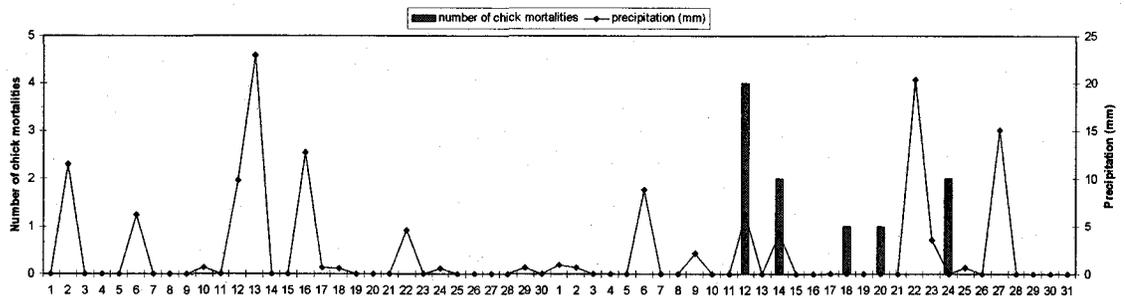


Figures 3.2.a-c. Chick mortalities as they related to daily precipitation amounts at Environment Canada's weather monitoring stations in a.) Stanhope, PEI from the period of June 1 to July 31, 2005 [all mortalities were from two broods out of a total of four broods; brood 1=1 chick (out of 4) died at 17 days, brood 2= 1 chick (out of 3) died at 3 days and another died at 8 days], and in b.) Saint Peter's, PEI from the period of June 1 to July 31, 2005 [all mortalities occurred within four broods out of a total 5 broods; brood 1=4 chicks (out of 4) died at 1 day, brood 2=2 chicks (out of 4) died at 3 days old, brood 3=1 chick (out of 2) died at 4 days old, and brood 4=1 chick (out of 4) died at 1 day old and another at 5 days old], and in c.) Eastpoint, PEI from the period of July 1 to August 15, 2005 [all mortalities occurred in one brood out of a total of 4 broods; brood 1=1 chick (out of 4) died at 3 days old and another at 5 days old].

3.2.a.)



3.2.b.)



3.2.c.)

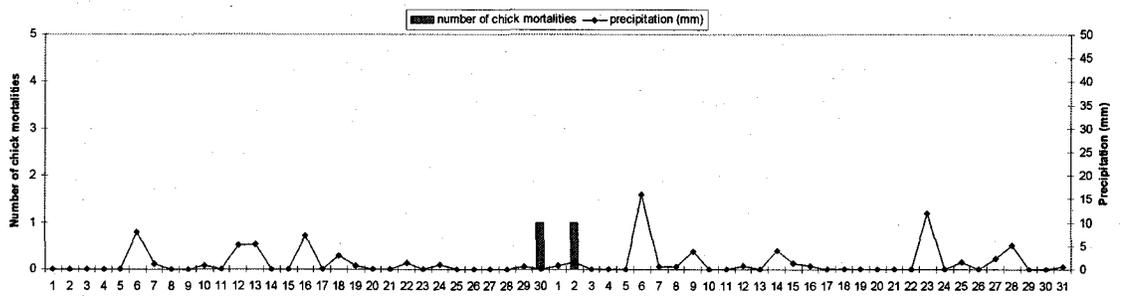
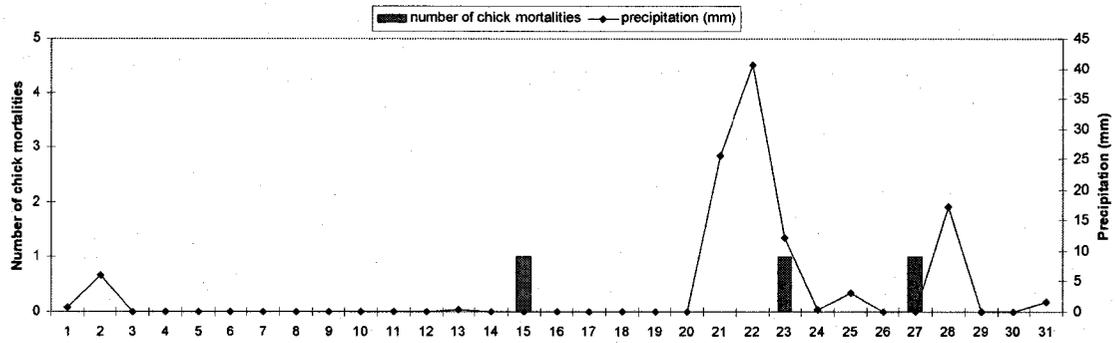
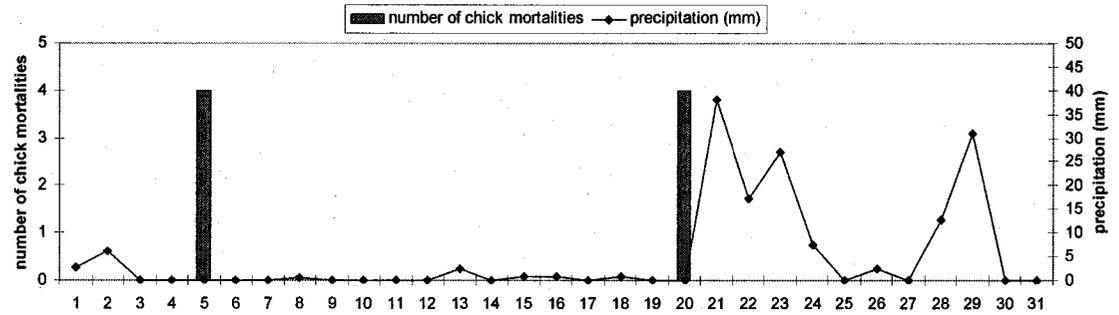


Figure 3.3.a-c. Chick mortalities as they related to daily precipitation amounts at Environment Canada's weather monitoring stations in a.) Stanhope, PEI from the period of July 1 to July 31, 2006 [all mortalities were from three broods out of a total of three broods; brood 1=1 chick (out of 3) died at 15 days, brood 2= 1 chick (out of 4) died at 6 days, and brood 3=1 chick (out of 4) died at 16 days], and in b.) Saint Peter's, PEI from the period of July 1 to July 31, 2006 [all mortalities occurred within three broods out of a total three broods; brood 1=1 chick (out of 2) died at 2 days and another chick died at 5 days, brood 2=2 chicks (out of 2) died at 1 day old, brood 3=4 chicks (out of 5) died at 8 days old, and in c.) Eastpoint, PEI from the period of June 1 to June 30, 2006 [all mortalities occurred in one brood out of a total 4 broods; brood 1=1 chick (out of 4) died at 15 days old].

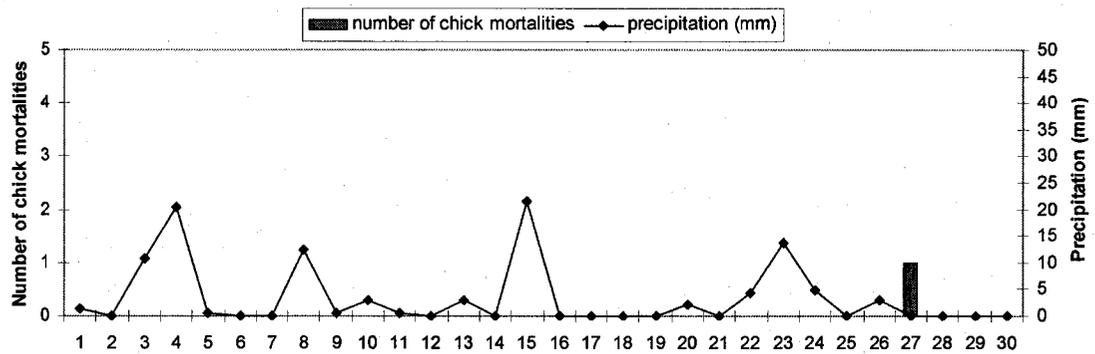
3.3.a.)



3.3.b.)



3.3.c.)



Appendix 1. Summary of fledging success for piping plovers on Prince Edward Island in 2005-2006. Only pairs having at least one hatched egg within a brood are included.

Pair Identity	Year	No. fledged	Fledging Success
Souris Causeway	2005	4	1.00
Diligent Pond	2005	4	1.00
Saint Peter's Lake Run	2005	2	0.50
St. Peter's Harbour, Pair 1	2005	4	1.00
Canavoy	2005	0	0.00
St. Peter's Harbour, Pair 2	2005	1	0.50
Eglinton Cove	2005	4	1.00
Canavoy (Pigots pair)	2005	1	0.25
Cavendish, Pair 1	2005	4	1.00
Blooming Point, Pair 2	2005	1	0.33
Covehead Harbour	2005	4	1.00
Stanhope	2005	3	0.75
Black Pond	2006	4	1.00
Canavoy	2006	0	0.00
Diligent Pond	2006	4	1.00
Eglinton Cove, Pair 1	2006	3	0.75
Saint Peter's Harbour, Pair 3	2006	1	0.20
Saint Peter's Harbour, Pair 1	2006	3	0.75
Saint Peter's Harbour, Pair 4	2006	0	0.00
Cavendish Sandspit, Pair 2	2006	3	0.75
Cavendish Sandspit, Pair 3	2006	3	0.75
Blooming Point, Pair 2	2006	2	0.67
Spry Cove	2006	4	1.00