THE IMPLICATIONS OF PREDATOR MANAGEMENT FOR AN ENDANGERED SHOREBIRD; DO NEST EXCLOSURES AFFECT THE BEHAVIOUR OF PIPING PLOVERS AND THEIR PREDATORS?

by

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The undersigned hereby certify that they have read and recommend to the Faculty of Graduate Studies for acceptance a thesis entitled "THE IMPLICATIONS OF PREDATOR MANAGEMENT FOR AN ENDANGERED SHOREBIRD; DO NEST EXCLOSURES AFFECT THE BEHAVIOUR OF PIPING PLOVERS AND THEIR PREDATORS?" by Gabrielle Beaulieu in partial fulfilment of the requirements for the degree of Master of Science.

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THESIS DEDICATION

I dedicate this thesis to my parents.
To my mother, for instilling in me the confidence and work ethic required for success.
À mon père, pour les voyages en canot qui m’ont inspiré à poursuivre ma passion.

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ABSTRACT

Predators are a threat to many ground-nesting shorebirds, although it remains largely unknown how they interact with passive predator management techniques such as nest exclosures. I examined the effects of nest exclosures on incubating Piping Plovers (*Charadrius melodus melodus*) and their predators on nesting beaches in Kouchibouguac and PEI National Parks. A combination of behavioural observations, video monitoring of nests and an artificial nest experiment was used to examine the effects of nest exclosures in this study system. The behaviour of Piping Plovers did not differ between exclosed and unexclosed nests, although different types of predators seemed to have an effect on plover nest attentiveness. Predators visited exclosed nests more often than unexclosed nests and spent more time in the vicinity of exclosed nests than unexclosed nests. Since increased adult mortality and nest abandonment have been documented at exclosed Piping Plover nests, as well as nests of other shorebirds, the results of this study provide evidence of a link between predator harassment and these negative effects.

LIST OF ABBREVIATIONS USED

KNP	Kouchibouguac National Park
PEINP	Prince Edward Island National Park
d	days
hrs	hours
min	minutes
s	seconds
Ex	Exclosure
Pred	Predator

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CHAPTER 1 INTRODUCTION

Predation shapes and maintains the functioning of ecosystems worldwide (Ritchie and Johnson 2009). When top predators are removed or reduced in number, the resulting trophic cascades can change the abundance of organisms at lower trophic levels. The loss of top predators from both terrestrial and marine ecosystems has had significant impacts on the composition of communities and also on the species interactions characterizing them (Elmhagen et al. 2010). The majority of these losses are typically due to human activities. For instance, in terrestrial systems, the habitat of large top predators has been removed or fragmented through intense forestry or agriculture (Elmhagen and Rushton 2007), forcing animals into smaller territories with insufficient prey and increased competition from conspecifics (Brashares et al. 2010). Similarly, the exploitation of top predators such as sharks and tuna in marine ecosystems has led to drastic population declines of those marine species. This has been linked to the localized collapse of inshore fisheries and changes in marine primary productivity due to large-scale range expansions of several smaller shark and pelagic fish species (Myers et al. 2007; Heithaus et al. 2008). Overall, the loss of top predators from ecosystems is a global phenomenon (Prugh et al. 2009), and the cascading effects can resonate throughout ecosystems (Ritchie and Johnson 2009).

Mesopredator release is a specific type of trophic cascade that occurs when the abundance of top predators is greatly reduced (Elmhagen and Rushton 2007). Mesopredators are usually one trophic level below top predators, and can quickly expand when a decrease in top predators releases them from competitive pressures (Ritchie and

Johnson 2009). These smaller predators (e.g., foxes, raccoons, crows, etc.) tend to have generalist diets, higher reproductive rates and easily adapt to changing landscapes (Brashares et al. 2010), thus making them highly successful at functionally replacing their top predator competitors (Elmhagen et al. 2010). Further, whereas top predators typically have specialized diets, the generalist diet of mesopredators allows them to affect several types of prey simultaneously (Ritchie and Johnson 2009). Consequently, abundant populations of mesopredators may inflict higher rates of predation on a broader range of prey populations (Elmhagen et al. 2010).

The loss of top predators in North America, including over 90% of large mammalian predators (Ritchie and Johnson 2009), and the resulting proliferation of mesopredators has led to the decline of many small prey species including birds (Crooks and Soulé 1999), rodents, reptiles and amphibians (Prugh et al. 2009). The concurrent habitat loss and degradation caused by humans presents an additional threat to these species. If prey populations are small or declining as a result of habitat loss, then an increase in the abundance of mesopredators could have particularly serious implications, potentially leading to localized extirpations or extinctions (Crooks and Soulé 1999; Ritchie and Johnson 2009). However, even where ecosystems remain reasonably intact (i.e., protected areas), some species vulnerable to habitat degradation are still in decline and the increased rates of predation by mesopredators experienced in these characteristically productive areas has been cited as a potential cause (Elmhagen and Rushton 2007). Controlling the effects of mesopredator release through predator management efforts tailored to diverse and abundant mesopredator populations could therefore be important for the conservation of species at risk.

A variety of predator management tools and strategies have been used in the protection and recovery of species at risk in North America. For critically endangered species, predator management is often the only effective solution to alleviate predation on recovering populations (Brashares et al. 2010). Options for predator management include relocation of individual predators (Neuman et al. 2004), the use of physical barriers around nests or critical habitat (Elmhagen et al. 2010) and lethal control (Prugh et al. 2009). Relocation is expensive and lethal control is often not tolerated by the public, so many species recovery efforts involve the use of predator barriers (Isaakson et al. 2007; Neuman et al. 2004).

Nest exclosures, for instance, are cage-like barriers that are placed over the nests of many ground-nesting bird species. These structures allow adults to pass back and forth to the nest, while preventing predators from accessing the eggs (Johnson and Oring 2002). Barrier fences also restrict the access of predators to vulnerable prey such as ground nesting birds or turtle nests and are usually erected around large areas of critical habitat. Despite the effectiveness of both these types of barriers (Schmelzeisen et al. 2004), nest exclosures are generally preferred in the protection of birds because barrier fences are expensive and difficult to maintain (Maslo and Lockwood 2009). Thus, nest exclosures have been widely used to protect the nests of ground-nesting birds and have been particularly effective at increasing the hatching success of shorebirds, many of which are considered threatened or endangered (Isaakson et al. 2007).

Despite their success in protecting eggs, nest exclosures may have negative effects on incubating adults (Vaske et al. 1994). Several studies investigating the effectiveness of nest exclosures in protecting shorebird nests have documented either increased adult mortality, nest abandonment or both (Murphy et al. 2003; Niehaus et al. 2004; Isaakson et al. 2007; Barber et al. 2010). Several explanations have been proposed for the increase in mortality associated with nest exclosures. For instance, exclosures may hinder exiting adults – this could be especially problematic for predators such as weasels or rodents that can get into the exclosure (Niehaus et al. 2004). The incubation behaviour of shorebirds may also exacerbate the negative effects of exclosures because many birds flush immediately before a predator reaches the nest thus increasing the risk of predation (Pauliny 2008).

The increased abandonment associated with exclosed shorebird nests (Maslo and Lockwood 2009) could be explained by increased predator harassment. Many so-called "smart" predators, namely raptors, canids and corvids (Niehaus et al. 2004), have been shown to use nest exclosures as cues to find nests, thereby increasing the rate of predator encounters at exclosed nests (Murphy et al. 2003). The frequent exposure of nesting birds to predators has been linked to chronic stress (Cockrem and Silverin 2002), which in turn, has been shown to inhibit behaviours such as parental care and foraging (Angelier and Chastel 2009). Therefore, if nest exclosures serve as an attractant to predators, and if prey just out of reach of the predator causes repeated nest visits, then associated increases in stress could cause adults to abandon their nests.

The examples above illustrate a potential trade-off between the protection of eggs and the increased loss of adults to predation and nests to abandonment in ground-nesting shorebirds. In fact, numerous studies on the effects of nest exclosure use in the recovery of the endangered Piping Plover (*Charadrius melodus* sp.) have suggested the existence of similar risk to adult plovers and their chicks (Mabee and Estelle 2000; Roche et al. 2010; Calvert and Taylor 2011).

The Piping Plover is a ground-nesting shorebird endemic to North America that has been the subject of intense recovery efforts throughout Canada since its listing as Endangered in 1985 (Plissner and Haig 2000; Ivan and Murphy 2005). Two subspecies of Piping Plover are geographically separated during the breeding season with *C. m. circumcinctus* breeding along the shores of lakes and rivers in North America's prairies and *C. m. melodus* breeding along the Atlantic coast. In late April to mid-May, male Piping Plovers establish nesting territories along stretches of beach ranging from 500 m^2 up to 8000 m^2 and will create several potential nest scrapes for the females to assess (Cairns 1982). Once a suitable nest site is selected, a clutch of four eggs is laid and both sexes share incubation duties over a period of approximately 26 days (Goossen et al. 2002). If the first nest attempt fails as a result of abandonment, flooding or nest predation, plovers will re-nest; three-egg clutches are typically laid if the first nest attempt failed to hatch (Stewart et al. 2008). Within the first few hours of hatching, the precocial chicks leave the nest and stay close to their parents, generally remaining within the established nesting territory (Gratto-Trevor and Abbott 2011; Goossen et al. 2002). In the Atlantic region of the plover's breeding range, chicks are considered fledged at 21 days (Stewart et al. 2008). Here, adults and fledglings will form small loose flocks as plovers prepare for fall migration (Cairns 1982), leaving as early as mid-July or as late as August 31st (G. Beaulieu personal observation) for wintering grounds in the United States, Mexico the Caribbean.

Predation has been identified as a major limiting factor in the recovery of the Piping Plover in Canada (Goossen et al. 2002; Stewart et al. 2008) and this threat has recently been the focus of research throughout Atlantic Canada where, as of 2011, approximately 10% of breeding pairs nested within Kejimkujik (NS), Kouchibouguac (NB), PEI and Gros Morne (NL) National Parks (Parks Canada, unpublished data). Nest predation in particular limits Piping Plover reproductive success and has been the primary target of plover recovery strategies. The Red Fox (*Vulpes vulpes*) and the American Crow (*Corvus brachyrhynchos*) are known mesopredators and are also the main plover nest predators in Atlantic Canada (Crooks and Soulé 1999; Linda Thomas pers. comm.). The most comprehensive dataset on Piping Plover nest predation exists within National Parks in the Atlantic Region, where the number of depredated plover nests has risen considerably over the last 20 years (Rock and Austin, *in prep.*). Thus, nest predator management tools have become an integral component of Piping Plover recovery efforts, especially within National Parks.

One of the main tools used in the management of Piping Plovers in Atlantic Canada is nest exclosures (Stewart et al. 2008), with 50% of the Atlantic Region's exclosure use occurring in National Parks (Rock and Austin, *in prep*). Nest exclosures have been used in the parks since the 1980's and following their application to nests, overall hatching success in National Parks increased by over 20% (Rock and Austin, *in prep*). However, despite this increase, Piping Plover numbers have continued to decline at a steady rate, with a 16% decline for the Atlantic Region population occurring in the last five years (Rock 2011). One potential explanation for the continued plover declines is the relatively high rates of adult mortality and nest abandonment associated with the long-term application of nest exclosures. Overall, 95 % of mortality and 27 % of abandonment in Atlantic Region National Parks occurred at exclosed nests compared to 5% and 11% respectively at unexclosed nests in the same 20 year time period (Rock and Austin, *in prep*; Parks Canada unpublished data). Although the reasons for these patterns are unknown, studies conducted on Piping Plovers in other parts of their breeding range suggest that an interaction between predators and nest exclosures may play a role in the greater rates of adult mortality and nest abandonment seen at exclosed nests (Mabee and Estelle 2000; Roche et al. 2010; Calvert and Taylor 2011). It is also worth noting that adult mortality may be underestimated because nest abandonment may in fact be due to adult mortality, in which the remaining mate is forced to desert the nest.

The link between predators and Piping Plover mortality or nest abandonment should be examined in light of exclosure use as it may present a substantial risk to this Endangered species. As a novel object in a coastal landscape, a nest exclosure may attract predators to nests (see above; Neuman et al. 2004, Niehaus et al. 2004). Once the nest is located, predators may visit nests repeatedly in attempts to access eggs or adults inside the exclosure, further increasing the risk of adult predation or nest abandonment. Anecdotal evidence from Atlantic Canada showing tracks around exclosed nests that were ultimately abandoned suggests this might be the case (L. Thomas, pers. comm.). Although the circumstances leading to nest abandonment are not well-described for the Piping Plover, the greater occurrence of adult mortality at exclosed nests rather than unexclosed nests is suspected to play a role.

Perhaps the most compelling study linking adult Piping Plover mortalities to the abandonment of nests was conducted by Roche et al. (2010) in the Great Lakes Region.

The majority of Great Lakes Piping Plover nests are exclosed and the entire population is banded (Roche et al. 2010). In 70% of cases of abandonment, Roche et al. (2010) reported banded adults missing from the study population entirely while only 30% of abandonments had re-sightings of adults, suggesting that nest abandonment is indicative of adult mortality. Recent population modeling examining such negative effects of nest exclosures on the demographics of the Atlantic plover subpopulation found that the loss of adults to this subpopulation is a far more serious consequence than the simple loss of nests (Calvert and Taylor 2011). Indeed, population growth in birds relies mainly on adult survival (Roche et al. 2010), therefore it is of utmost importance that the link between predators and the negative effects of nest exclosures be examined.

The overall goal of my study is to evaluate the impact of nest exclosures on the behaviour of incubating Piping Plovers and their predators. Specifically, I use field observations and video recordings to compare the behaviour of adult plovers and predators at exclosed and unexclosed nests, and I use an artificial nest experiment to determine whether nest exclosures attract predators. If exclosures induce a stress response in plovers, it may be measurable by examining parental care which could be reduced at exclosed nests in comparison to unexclosed nests. By examining the behaviours of predators towards exclosures, I expect to find evidence of predator harassment at exclosed nests as has been suggested by so many previous studies (e.g. Mabee and Estelle 2000; Johnson and Oring 2002; Murphy et al. 2003; Maslo and Lockwood 2009; Roche et al. 2010). Furthermore, I expect that some predators may present different risks to nests and adults and that the behaviour of plovers will reflect this. Therefore my study also aims to identify Piping Plover nest predators and potential predators which elicit anti-predator behaviours in parent birds. Since Atlantic National Parks protect both the plovers as well as their various predators, Park beaches should offer the most natural predator-prey community in which to investigate the effects of nest exclosures.

CHAPTER 2 METHODS

2.1 STUDY SITE

My research took place from 1 May to 30 August 2010 and 2011 in Kouchibouguac and Prince Edward Island National Parks (see Figure 1). The beaches in Kouchibouguac National Park (KNP) span approximately 40km of coastline bordering the Northumberland Strait, from Pointe Sapin to the Richibucto Estuary. Similarly, the beaches of PEI National Park (PEINP) extend approximately 50km from Cavendish to Greenwich, bordering the Gulf of St. Lawrence. In both Parks, Piping Plover breeding habitat is characterized by long sand-cobble beaches delimited by mature dune systems and large estuaries. The plovers in both Parks are part of the Gulf of St. Lawrence breeding population of the species, and the National Park beaches have historically been important breeding grounds. From 1990 to 2011, KNP was host to an average of 14.5 nests per year (SE ± 0.92; range = 9 to 25 nests) and PEINP to 27.7 nests per year (SE ± 2.65; range = 7 to 56 nests). In recent years, the number of nest attempts in PEINP has been less than half of this 22-year average, whereas in KNP, the recent number of nest attempts remains close to the 22-year average (Parks Canada, unpublished data).

Red Foxes, American Crows and Common Ravens (*Corvus corax*) are predators of Piping Plover eggs and young, and breed at both sites; foxes may also depredate adult plovers (L. Thomas and E. Tremblay, pers. comm.). Additional potential predators that frequent the beaches at both sites include gulls (*Larus* spp.), Merlins (*Falco columbarius*), American Kestrels (*Falco sparverius*), Raccoons (*Procyon lotor*), Eastern

Coyotes (*Canis latrans*), Striped Skunks (*Mephitis mephitis*), Short-tailed Weasels (*Mustela erminea*) and American Mink (*Mustela vison;* Stewart et al. 2008).

Figure 1. Location of Kouchibouguac and PEI National Parks in Atlantic Canada depicted by darker green; courtesy of Parks Canada.

2.2 LOCATION OF NESTS AND ASSIGNMENT OF NEST EXCLOSURES

At least every three days, beginning 1 May and continuing until mid-August, I assisted Parks Canada staff in surveying 13 beaches where plovers had nested in the last five years. I considered beaches separate if a waterway of at least 5 m wide and 1m deep separated the two. The length of each beach was walked along the high tide line and every 100 m the area between the high tide line and the foredune was scanned for adult plovers. During each survey, the following information was collected: the number of breeding pairs, the number of unpaired adults, nest location, clutch initiation date, clutch size, hatching success and the number of fledglings/nest. Nests were classified as either successful (hatched: one or more eggs hatched), or unsuccessful (abandoned: one or more eggs left unattended for at least 48 hrs; flooded or depredated: one or more eggs are damaged or disappear before hatch date).

Nest exclosures were installed using protocols developed by the Atlantic Region Canadian Wildlife Service and Parks Canada (see Stewart et al. 2008 and Goodbrand et al. 2008 for details). I assigned the first nest having a complete clutch at each beach to either an exclosed (n = 17 nests/ 2 years) or unexclosed (n= 25 nests/ 2 years) treatment based on the toss of a coin, with each subsequent nest on that same beach receiving the opposite treatment.

The nest exclosures used in my study were circular structures, 2.5 m in diameter and 1.5 m high, and composed of 16 gauge galvanized grid fencing, topped with chicken coop nylon mesh (Figure 2). The size of the ‘gridding’ allowed adult plovers to move freely to and from the nest, while preventing access by most predators (see Schmelzeisen et al. 2004, Stewart et al. 2008 and Barber et al. 2010 for details). The fencing used to construct the exclosures was cut so that spikes of wire approximately 5cm tall would protrude from top of the exclosure walls. This was done in an effort to dissuade aerial predators from perching on the structures. Nest exclosures were generally installed within 10 min of an adult being flushed from a nest. Once an exclosure was installed, the nest was observed from a distance of 30-50 m. If an adult did not resume incubation within 45 min of installation, the exclosure was removed and the nest monitored for another 15 min to ensure the nest was not abandoned. If an adult had still not resumed incubation after that time, we left the area and attempted another exclosure installation in 24 hrs. If during this second attempt, a parent did not resume incubation after 45 min, the exclosure was removed and that nest received the 'unexclosed' treatment.

Figure 2. Image of a nest exclosure applied to real and artificial Piping Plover nests in Kouchibouguac and PEI National Parks from 2010-2011.

2.3 INFLUENCE OF EXCLOSURES ON PLOVER BEHAVIOUR (OBSERVATIONS)

In order to determine whether nest exclosures affect the behaviour of incubating Piping Plovers, I conducted a single, 30 min observation of incubating adults at 21 nests (n = 9 exclosed; n = 12 unexclosed) within the first ten days of incubation. I observed the incubating adult from a distance of 30-50 m between 10:00 and 14:00. Beginning 10 min after my arrival (after the birds had settled from any potential disturbance), I recorded the following behaviours : i) total number of scans by an incubating adult (VIGILANCE: converted to scans/min adult is incubating); defined as the number of horizontal head turns made by the incubating adult and returning to or passing through the start position (see Jones et al. 2007; Morrison 2011), ii) number of times an incubating adult moves on or within 5 m of the nest (MOVEMENT: number of movements/ 30 min observation); moving included feeding, preening, head-bobbing and walking, and nest switches involving both adults within 5 m of the nest (each of these would count as one movement), (iii) the number of times the focal adult moves > 5 m from the nest (DEPARTURE: number of departures/ 30 min observation), and iv) the occurrence of any other species within a 500 m radius of the nest (ANIMAL EVENTS).

To determine the influence of the nest environment (Exclosure, Park, Year and Number of ANIMAL EVENTS) on plover behaviour (VIGILANCE, MOVEMENT, DEPARTURES) during my 30 min observation periods, I used Generalized Linear Mixed Models (GLMMs) from the 'lme4' package found in R statistical software (Bates et al. 2011). In each model I included an offset for the amount of time adults were incubating because the time adults spent on the nest during my observations varied (29.23 min ± 0.36). I also included an observation-level random effect to account for data overdispersion (Bolker et al. 2009; range of dispersion from 1.17 to 2.25) with a Poisson error distribution. I applied backward stepwise selection to the full model (here, Behaviour ~ Exclosure + Park + Year + Animal Events + offset:Time + random:Overdisp) in which non-significant terms ($P > 0.05$) were removed from the model (Mundry and Nunn 2009). I used Akaike's Information Criterion (AICc) corrected for small sample sizes (Burnham and Anderson 1998) to select the model of best fit for each behaviour. Where several models had similar AIC values, I calculated delta AIC to determine which models were the most plausible (Δ AIC < 2) in explaining the influence of nest environment on plover behaviour. Finally, I used a Wald's test to examine the statistical significance of each model parameter within the best fitting models.

2.4 INFLUENCE OF PREDATOR VISITS AND EXCLOSURES ON PLOVER BEHAVIOUR (VIDEO)

To determine the identity of nest predators and the behaviours they elicit in incubating Piping Plovers, as well as differences in those behaviours between exclosed and unexclosed nests, video cameras were installed at 25 nests (n = 10 exclosed; n = 15 unexclosed). I selected nests for videotaping that were in areas with low human disturbance, were at least 5 m from the high tide mark and on beaches regularly accessible either by boat or on foot. In 2010-2011, cameras were deployed on nests randomly as nests were established by breeding birds and as camera equipment allowed. However, in 2008 and 2009, nests on beaches that had histories of nest predation or abandonment were preferentially selected.

Between days 3 and 5 of incubation, a Q-See Color IR Day/Night Camera was placed approximately 5 to 7 m from the nest cup and attached to a portable digital video recorder (DVR; PV-690s MPEG-4 Video Recorder) and three deep cycle 75A marine batteries, placed respectively in a large pelican case and cooler (Appendix 1) and buried in the sand approximately 40 m from the nest. Camera systems took up to 20 min to install and adults were generally off the nest for no more than 10 min following installation. If beaches were less accessible, a solar panel (Sharp 80W, 12V) may have been included in the set up to charge batteries and ensure a reliable source of power (see Appendix 1 for a list of equipment). Video camera systems were installed on days of favourable weather only and were removed if the incubating adults did not return to the nest within 45 min of installation.

The DVRs used 120 GB laptop hard drives to store video footage, which were replaced every few days, with minimal disturbance to incubating plovers. The contents of the hard drives were downloaded onto a 1 TB storage drive for transcription after the breeding season. The video cameras ran continuously until the nests had either hatched, were lost to predation, abandonment or flooding, or the equipment malfunctioned (see Beaulieu and Austin 2011 for more details on the cameras, set–up and nest suitability).

The equipment and protocols used in 2008 and 2009 (see Appendix 1 for differences in equipment between years) were as described above, with the following exceptions: i) distance from nest cup to camera varied from 1m to 3m depending on terrain, ii) cameras always faced North, iii) cameras were sometimes placed at nests that had signs of pending abandonment (missing adult), and iv) some equipment was left in the dune rather than buried out of sight.

Remote video recordings were transcribed by a team of observers (including volunteers, paid staff and me) who recorded the following information each time a potential predator was observed on a recording: i) the amount of time (s) the predator (corvid, fox, gull, other) spent in the field of view, which was within approximately 50 m of the nest cup (PRED TIME; when predators were seen on the footage this was called a 'Predator Event'), ii) the amount of time (s) an adult that was incubating spent more than 5 m from the nest cup (TIME AWAY), iii) the number of anti-predator displays (Table 1) given by an adult while a predator is in view (DISPLAY), iv) the amount of time (s) spent performing each display (DISPLAY TIME) and v) the amount of time (s) elapsed between a predator leaving the field of view and the plover resuming incubation (TIMESAFE). Observers (n=4) were given relatively little information on the goals of the study to reduce the chance of bias in the transcription of the behaviours. Inter-observer reliability tests (Pearson's correlation coefficients) using a 30-minute video clip ranged from 0.99 to 1.00, indicating little variability.

To determine whether plovers responded differently to known predators (e.g., foxes and crows) versus other animals (those typically not considered predators, e.g., grackles, rodents etc.), I compared the amount of time plovers spent away from the nest in the presence of each of those two groups using a Wilcox Rank Sum Test. The results of this test suggested that plovers spent significantly more time away from their nests in the presence of predators than in the presence of other animals (Wilcox = 56319.5, P = 0.003), therefore I restricted all subsequent analyses to plover responses in the presence of predators only. Since the risks posed to adults and nests were expected to vary by whether the predator was in the air or on the ground, with greater risk from predators that were on the ground versus flying over the nest, I also compared the time predators in the air and ground spent in the vicinity of the nest using a Wilcox rank sum test. I found that predators on the ground spent significantly more time at nests than those in the air (ground mean 129.76 sec ± 42.69, air mean 15.75 sec ± 6.08; Wilcox = 2864, $P < 0.01$), therefore, I restricted subsequent analyses to ground predator events only (Corvid Walking, Gull Walking or Fox).

I modeled the influence of nest environment (Exclosure, Park and Year) on predator (PRED TIME) and Piping Plover (TIME AWAY, DISPLAY, DISPLAY TIME, TIME SAFE) behaviours using GLMMs. In each model I included a random effect for nest to account for repeated measures and a random effect for overdispersion. I also weighted the nests according to the amount of footage collected from each. I applied backward stepwise selection to the full model (Behaviour~ Exclosure + Park + Year + random : Nest + random: Overdisp. + weights = footage), in which non-significant terms ($P > 0.05$) were removed from the model, and proceeded with model selection and examination of parameter significance as described for the observation data above.

Table 1. Piping Plover anti-predator behaviours recorded from video transcriptions of nest footage taken at Kouchibouguac and PEI National Parks in 2008-2011 (after Gochfeld 1984 and Byrkjedal 1987).

Anti-predator Display	**Description**
Crouching	adult sits motionless with its head down
Rodent Run	adult runs in a crouched position with feathers of neck and back raised
Stationary Distraction Display	adult flutters one or both wings on the ground while crouching or standing still
Mobile Distraction Display	adult drags and flutters both wings along the ground while walking or running and
Directed Aggression	adult plover hits a potential predator with its bill or wings during a Mobile Injury Feign

2.5 INFLUENCE OF EXCLOSURES ON PREDATOR BEHAVIOUR (EXPERIMENT)

An artificial nest experiment was conducted in 2011 to determine if nest exclosures attract predators to plover nests and increase the frequency of predator visits. I conducted an *a priori* power analysis using predator nest visitation data collected from 72 h of video footage from 10 Piping Plover nests to determine the minimum required sample size for this experiment. With a sample size of n=20 artificial nests per treatment, a large effect size would be detected with 65% statistical power at $\alpha = 0.05$. For a system involving an Endangered species and considerable logistic constraints, this was considered acceptable (Steidl et al, 1997). Therefore, 20 artificial nests (n = 10 each of exclosed and unexclosed) were placed at the mid-point between the high tide line and the foredune on each of Covehead Beach in PEINP and South Kouchibouguac Dune in KNP (see Appendix 2) from 24-26 June to 7-9 July, coinciding with the breeding season for

Piping Plovers. The beaches selected for the experiment had been used by plovers historically, but had no nesting Piping Plovers in the last five years. Artificial nests were randomly assigned to an exclosed or unexclosed treatment and set out in pairs that were separated from each other by 50 m and the next pair of nests by 100 m (Appendix 2). This density was similar to those recorded for Piping Plovers nesting in southern Nova Scotia (Cairns 1982). The distance between each nest and beach closure signs, where human activity ended on the beach, was measured, with the first nest positioned approximately 100 m from the signs and the last nest approximately 1500 m. Distance from the beach closure sign could have an effect on predator behaviour if predators are attracted to or avoid areas that humans use (Doherty and Heath 2011).

To ensure that artificial nests resembled natural nests, a nest cup was created using a tennis ball (to create uniform depressions in the sand), and a clay egg was placed in each nest cup. The clay eggs were designed to closely resemble Piping Plover eggs in both size (~30mm x ~12mm) and coloration. Each egg was placed in a bag containing the carcass of an adult plover (adult was found dead in Kejimkujik National Park, July 2011) for 24 hours before being placed in the nest. According to the experimental protocol, nests in the exclosed treatment were to be placed outside, but within 20 cm of the exclosure edge so that if tracks were not visible in the sand (indication of a predator visit), a missing, damaged or displaced egg could document a predator visit. Unfortunately in PEINP, the nest was mistakenly placed inside the exclosure instead of at the outside edge (see below for approach to analyses). To record the timing of predation attempts, each artificial nest was also randomly assigned either a motion-detection trail camera (n=10) or a weight-triggered timer (n=10). If one nest had a trail camera assigned to it, then its partner would also have a trail camera, and this was consistent for weight-triggered timers as well. In order for the weight-triggered timers to function, clay eggs each had a small piece of metal bonded to them and were balanced atop two screws in a block of wood. Therefore, in an effort to maintain a balanced experimental design, all eggs had metal bonded to them and were balanced atop two screws in a block of wood, regardless of how the timing of predation was recorded. We buried the blocks of wood under each nest cup so that only the screw tops were visible. We also buried the clocks and wires next to the artificial nests and positioned the motion-detection cameras 5m away from the artificial nests.

Artificial nests were visited daily between 09:00 and 11:00. At each nest, the identity of the tracks was recorded by predator type (corvid, gull, fox or other animal) observed within each of four quadrats of an approximately 5 m radius around each nest (see Appendix 2). The experimental area was divided into quadrats to determine whether an animal simply passed by the nest or encircled (visited) the nest, based on the continuation of tracks from one quadrat to the next (Appendix 2). Predators were considered to have walked past the nest if the egg was in the nest and if tracks occurred in only one quadrat, predators were considered to have visited the nest if the egg was missing or moved, or if tracks occurred in two or more quadrats. We considered the nest 'depredated' and did not replace the egg if the clay egg was moved or missing from the experimental area. We also noted the direction the animal was walking in relation to the artificial nest and its general proximity to the nest cup. When several tracks of the same species occurred within one experimental area, this was counted as one visit for that species to that particular nest. After each visit, all tracks were swept away.

Since nests were inside the exclosure at one park and outside the exclosure at the other, analyses were done separately for each park. I applied GLMMs to examine the influence of Exclosures and Distance from beach closure signs on predator behaviour (number of visits/ nest, over 14 d). Each model included nest and overdispersion as random effects and model selection was carried out in the same manner as described above. The full model for each Park (Number of Visits ~ Exclosure + Distance + random : Nest + random : Overdisp.) was also assessed for parameter significance as described above.

CHAPTER 3 RESULTS

3.1 GENERAL RESULTS

During my study (2010-2011), a total of 42 nests (sample unit) were initiated by Piping Plovers, with 17 nests receiving an exclosure and 25 remaining unexclosed. KNP was host to 25 nests (n = 12 exclosed; n = 13 unexclosed) and PEINP to 17 nests (n = 5 exclosed; n = 12 unexclosed). Overall, 19 nests (45.2%) hatched and 23 failed, with nest failures consisting of 12 incidences of nest predation (28.6%), six nest abandonments (14.3%) and five flooding events (11.9%). Nearly 65% (11/17) of exclosed nests hatched while 35.3% (6) were abandoned. Thirty-two percent (8/25) of unexclosed nests hatched while 48% (12) were lost to predators and 20% (5) to flooding. See Appendix 3 for a summary of Piping Plover nest outcomes during 2010-2011 in Kouchibouguac and PEI National Parks.

3.2 INFLUENCE OF EXCLOSURES ON PLOVER BEHAVIOUR (OBSERVATIONS)

After applying a GLMM to all three dependent variables (Vigilance, Movement and Departure), the best fitting models were those that did not include the treatments: Park, Year, Exclosure, or Animal Events (Table 2). The next best models for Vigilance and Departures included Animal Events and Exclosure as single predictors, respectively. However, Animal Events and Exclosure did not significantly explain variation in either of the dependent variables (Table 3), despite a categorical difference in the mean number of Departures between exclosed and unexclosed nests (Figure 3, Appendix 4).

Table 2. Candidate Generalized Linear Mixed Models for predicting Piping Plover behaviour as observed in Kouchibouguac and Prince Edward Island National Parks. ΔAIC values reflect the difference in score from the best fitting model.

Model Parameters		**Vigilance**		**Movements**		**Departures**	
	*K**	*AICc*	*ΔAIC*	*AICc*	*ΔAIC*	*AICc*	*ΔAIC*
Exclosure + Animal Events + Beach	11	12.91	38.30	124.84	38.13	70.01	31.87
Exlcosure + Animal Events	4	95.20	4.08	91.54	4.83	43.02	4.89
Exclosure + Beach	10	123.09	31.98	117.89	31.18	115.51	28.80
Animal Events + Beach	10	121.38	30.26	115.51	28.80	67.12	28.98
Exclosure	3	93.78	2.66	89.12	2.41	**39.94**	**1.80**
Animal Events	3	**92.15**	**1.03**	88.76	2.05	40.88	2.74
Beach	9	115.87	24.76	110.26	23.55	60.11	21.98
Intercept Model	2	**91.12**	**0.00**	**86.71**	**0.00**	**38.14**	**0.00**

* Number of model parameters; the random effects of nest and overdispersion each count as a parameter.

Bold indicates the best fitting model(s).

Table 3. Parameter estimates and significance tests for the best Generalized Linear Mixed Models describing the observed behaviour of plovers incubating their nests in both Kouchibouguac and PEI National Parks in 2010 and 2011.

Behaviour	**Observation Data**			
	Parameters	*Estimate*	*Wald's z-test*	*P-value*
Vigilance	**Intercept**	**-27.33**	**-70.31**	**< 0.01**
Vigilance	Animal Events	-0.10	-1.34	0.18
	Intercept	**-26.80**	**-49.50**	**< 0.01**
Movement	**Intercept**	**-28.10**	**-58.23**	**< 0.01**
Departure	**Intercept**	**-32.99**	**-27.73**	**< 0.01**
Departure	Exclosure	1.78	0.98	0.33
	Intercept	**-32.99**	**-23.80**	**< 0.01**

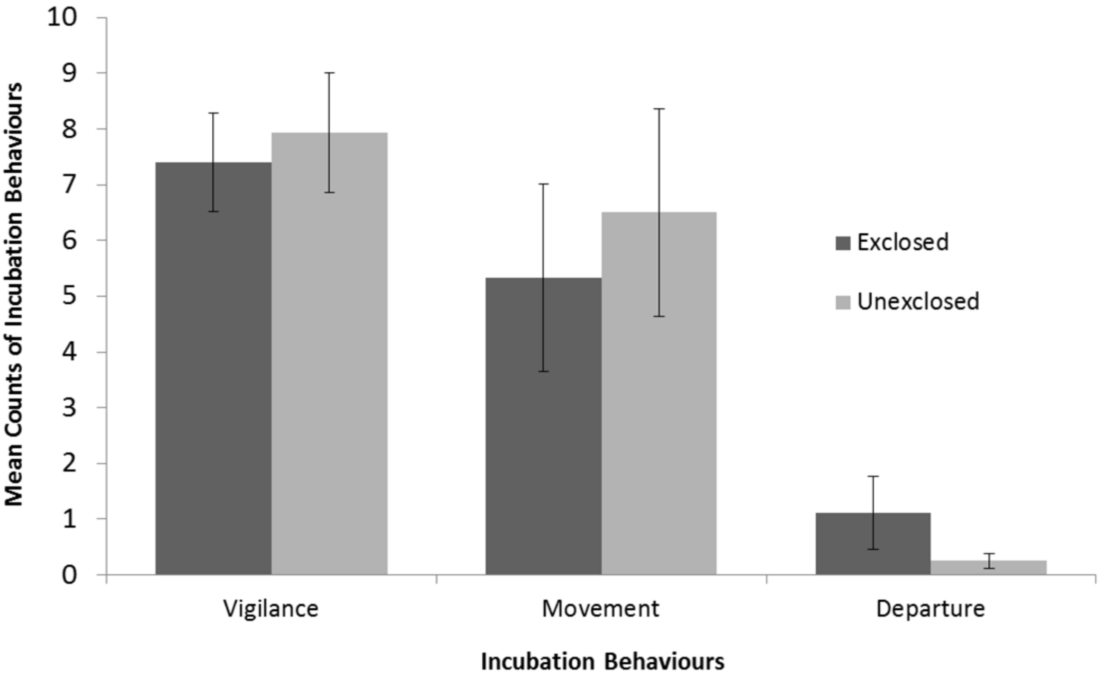

Figure 3. Means and standard errors of Piping Plover incubation behaviours observed at nests in KNP and PEINP from 2010-2011.

3.3 INFLUENCE OF PREDATOR VISITS AND EXCLOSURES ON PLOVER BEHAVIOUR (VIDEO)

A total of 4377 hrs of video footage collected from 25 nests yielded 346 predator events overall with an average 20.5 ± 8.22 predator events per nest. Plovers interacted with a variety of animals, either through anti-predator displays or avoidance, including canids, raccoons, rodents, raptors, corvids, gulls, herons, some songbirds as well as conspecifics. Five nest predation events were observed (n=4 in PEINP) in which both Red Foxes and American Crows were recorded depredating Piping Plover nests (Appendix 6), and plovers vigorously performed distraction displays to both corvid and gull species (Appendix 5) only while they were on the ground. Nest abandonment happened gradually with adult plovers re-visiting nests periodically and less frequently as time progressed for up to 48 hrs, after which they didn't return. Nest exclosures were seen to impede the exit of plovers either by blocking their flight from the nest or by 'tripping' them up as they passed through (Appendix 6). Predators approaching nest exclosures were not successfully distracted by parents and would encircle the structures several times before leaving the camera's view.

The best predictor model for the time that predators spent (Predator Time) on the ground within 50 m of Piping Plover nests included Year as a predictor, although a model with Exclosure as a predictor and an additional model with Park and Year as predictors were also a good fit (see Table 4). Both Year and Exclosure had significant effects on Predator Time (Table 5), with predators spending more time at nests in 2008 (114.9 ± 40.99 seconds; Wald's = 2.41, $P = 0.02$) and spending less time at nests in 2009 (37.7 ± 18.19; Wald's = -2.51, $P = 0.01$). Subsequent years did not have a significant effect on the time predators spent at nests. Predators spent significantly more time in the vicinity of exclosed nests than unexclosed nests (Wald's = 2.29, $P = 0.02$; Figure 4, Appendix 4).

Table 4. Candidate Generalized Linear Mixed Models for predicting predator and plover behaviour from video data collected in Kouchibouguac and Prince Edward Island National Parks. ΔAIC values reflect the difference in score from the best fitting model.

Model Parameters		**Predator Time**		**Time Away**	
	*K**	*AICc*	*ΔAIC*	*AICc*	*ΔAIC*
Ex + Park + Year	8	1163.93	3.48	1077.57	2.35
Ex + Park	5	1162.44	2.00	$8.18x10^{11}$	$8.18x10^{11}$
Ex + Year	7	1162.46	3.01	$1.05x10^{5}$	$1.04x10^{5}$
Park + Year	7	**1161.98**	**1.54**	$1.11x10^{7}$	$1.11x10^{7}$
Exclosure	4	**1160.45**	**0.01**	1059.66	5.58
Park	4	1165.31	4.86	**1055.12**	**1.04**
Year	6	**1160.45**	**0.00**	**1054.08**	**0.00**
Intercept	3	1163.46	3.01	1061.40	7.32

* Number of model parameters; the random effects of nest and overdispersion each count as a parameter.

Bold indicates the best fitting model(s).

Table 5. Parameter estimates and significance tests for the best fitting Generalized Linear Mixed Models describing the time predators spent near nests and the time plovers spent away from nests in the presence of predators from video footage collected in Kouchibouguac and PEI National Parks 2008-2011.

Behaviour Modeled	**Parameter Estimates**			
	Parameters	*Estimate*	*Wald's z-test*	*P-value*
Predator Time	**Year1**	**3.59**	**2.41**	**0.02**
	Year2	**-2.34**	**-2.51**	**0.01**
	Year3	0.42	0.09	0.93
	Year4	0.43	-3.25	0.75
	Intercept	6.50	1.45	0.15
Predator Time	**Exclosure**	**1.85**	**2.29**	**0.02**
	Intercept	1.92	1.37	0.17
Time Away	Year1	4.37	1.16	0.25
	Year2	2.653	0.74	0.46
	Year3	**-10.09**	**-2.69**	**< 0.01**
	Year4	**-9.07**	**-2.66**	**< 0.01**
	Intercept	2.36	0.88	0.38
Time Away	**Park**	**-9.40**	**-3.23**	**< 0.01**
	Intercept	**12.77**	**2.67**	**< 0.01**

Bold indicates significance at $\alpha < 0.05$.

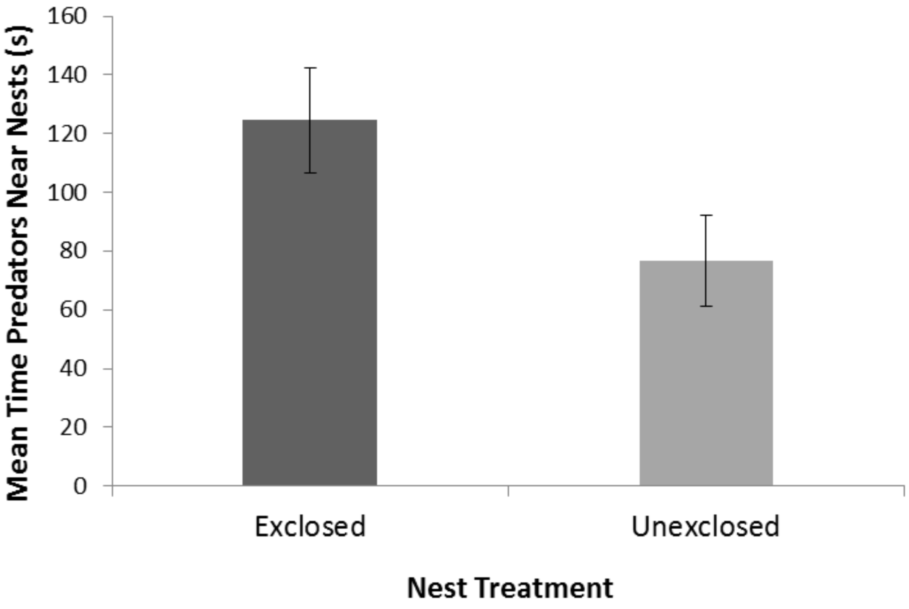

Figure 4. Mean and standard error of time predators spent near Piping Plover nests as recorded by remote video cameras in KNP and PEINP from 2008-2011.

The best predictor model for the amount of time that plovers spent away from their nests (Time Away) included Year as a predictor, although the next best model with Park as a predictor was also considered a good fit (Table 4). Both Year and Park had significant negative effects on the amount of time that plovers spent away from their nests, with plovers spending less time away from their nests in 2010 and 2011 than 2008 and 2009 (Wald's = -2.69, *P* = < 0.01; Wald's = -2.66, *P* = < 0.01; Figure 5) and less time away from their nests in PEINP than KNP (Wald's = -3.23, *P* = < 0.01) overall. None of the independent variables (Exclosure, Park and Year) were identified as predictors for the number of 'Displays' elicited by adults, the time spent displaying (Display Time), or the time within which plovers resumed incubation after a ground predator leaves the area (Time Safe; Appendix 5).

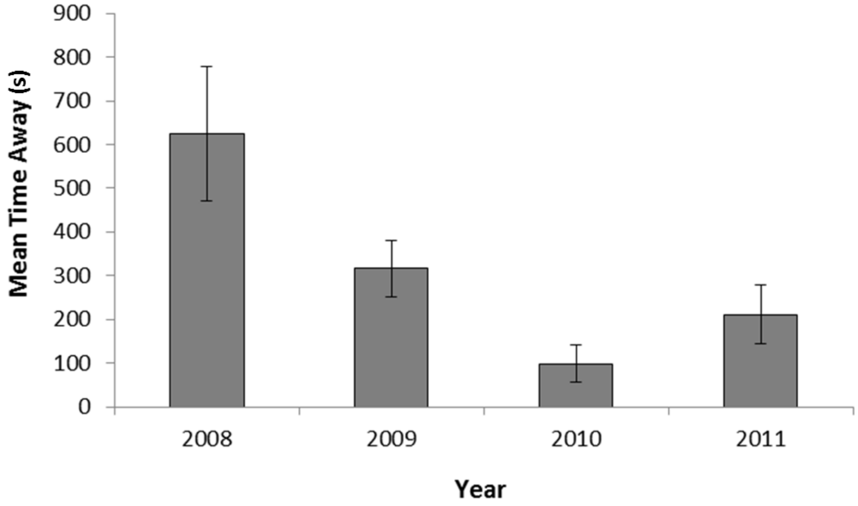

Figure 5. Means and standard errors for the time plovers spent away from their nests in the presence of predators on the ground as collected by remote video cameras in KNP and PEINP from 2008-2011.

3.4 INFLUENCE OF NEST EXCLOSURES ON PREDATOR BEHAVIOUR (EXPERIMENT)

Artificial nests were visited by potential predators 78 times in KNP with each nest receiving an average of 3.9 ± 0.59 visits during the experiment (4.6 ± 0.95 exclosed; 3.2 ± 0.73 unexclosed). In PEINP, artificial nests were visited 56 times by potential predators with each nest visited an average of 2.8 ± 0.65 times throughout the experiment (4.2 ± 1.04 exclosed; 1.4 ± 0.57 unexclosed). In both Parks, exclosed nests were visited more frequently than unexclosed nests (Figure 6). Artificial nests were visited mostly by foxes in both KNP and PEINP followed by corvids and then gulls (Appendix 4). Humans visited a total of 2 nests in KNP as well as in PEINP despite experimental areas being closed to public access. We were successful in identifying all but one set of tracks for the entire experiment. Nest 'predation' (n = 10 nests) occurred only at unexclosed nests with corvids being identified as the predator in all cases and 80% (n = 8) of predation events happening in PEINP. Unfortunately, the trail cameras proved ineffective at confirming the identity and timing of predation events, therefore predator tracks were used to identify the types of predator visits and predation events at artificial nests.

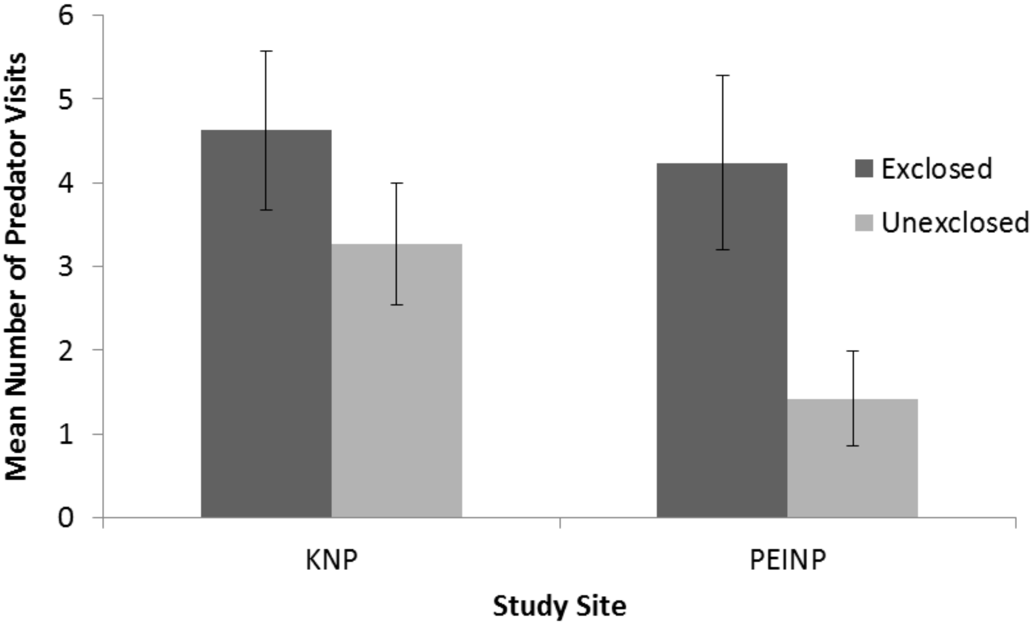

Figure 6. Means and standard errors of number of predator visits to artificial nests in KNP and PEINP during the artificial nest experiment in 2011.

The best predictor model for predator visits to artificial nests in KNP included Distance along the beach as a single predictor. The next best models included the intercept model and the model including both nest Exclosure and Distance along the beach as predictors (Table 6). Distance along the beach was the only statistically significant term explaining predator visits to artificial nests in KNP (Table 7), with more predator visits to artificial nests occurring further from the beach closure signs (Wald's = 2.05, *P* = 0.04). When split according to predator type, distance along the beach was still the best single-predictor model (Tables 8 and 9). Distance along the beach was not, however, a statistically significant predictor for corvids (Wald's = 1.49, *P* = 0.14; Table 10) in KNP whereas it was for foxes (Wald's = 2.83, *P* = <0.01; Table 10), with more fox visits occurring further from the beach closure signs. For both corvids and foxes in KNP, the next best models did not include either of the independent variables (Exclosure and Beach Distance) as predictors (Tables 9 and 10).

Table 6. Candidate Generalized Linear Mixed Models for predicting predator behaviour towards nest exclosures in Kouchibouguac and Prince Edward Island National Parks. ΔAIC values reflect the difference in score from the best fitting model.

Model Parameters		**KNP**		**PEINP**	
	*K**	*AICc*	*ΔAIC*	*AICc*	*ΔAIC*
Exclosure **:** Beach Distance	6	41.32	5.14	47.53	2.15
Exclosure + Beach Distance	5	**38.02**	**1.83**	**45.38**	**0.00**
Exclosure	4	38.40	2.21	**45.49**	**0.10**
Beach Distance	4	**36.18**	**0.00**	50.50	5.12
Intercept Model	**3**	**36.91**	**0.73**	**49.63**	4.25

* Number of model parameters; the random effects of nest and overdispersion each count as a parameter.
Bold indicates best fitting model(s).

Table 7. Parameter estimates and significance tests for the best Generalized Linear Mixed Models describing the visits of plover predators to artificial nests in Kouchibouguac and PEI National Parks.

Best Models (ΔAIC< 2)	**Parameter Estimates**			
	Parameters	*Estimate*	*Wald's z-test*	*P-value*
Visits (KNP) ~ Beach Distance + Int.	**Beach Dist.**	**0.05**	**2.04**	**0.04**
	Intercept	**0.80**	**2.68**	**< 0.01**
Visits (KNP) ~ Intercept	**Intercept**	**1.29**	**9.08**	**< 0.01**
Visits (KNP) ~ Exclosure + Beach Dist. + Int.	Exclosure	0.34	1.34	0.18
	Beach Dist.	**0.05**	**2.05**	**0.04**

Best Models (ΔAIC< 2)	**Parameter Estimates**			
	Parameters	*Estimate*	*Wald's z-test*	*P-value*
	Intercept	0.64	1.99	0.05
Visits (PEINP) ~ Exclosure + Beach Dist. + Int.	**Exclosure**	**1.09**	**3.15**	**< 0.01**
	Beach Dist.	**-0.06**	**-2.21**	**0.03**
	Intercept	**0.88**	**2.31**	**0.02**
Visits (PEINP) ~ Exclosure + Int.	**Exclosure**	**1.12**	**2.77**	**< 0.01**
	Intercept	0.17	0.53	0.59

Bold indicates significance at $\alpha < 0.05$.

The best predictor model for the number of Predator Visits to artificial nests in PEINP included nest Exclosures and Distance along the beach as predictors (Table 7), and the next best model with Exclosure as a single predictor was also considered a good fit. Both nest Exclosures as well as Distance along the beach were statistically significant in explaining predator visits to artificial nests in PEINP (Wald's = 3.15, P = <0.01; Wald's = -2.21, P = 0.03), with exclosed artificial nests receiving significantly more predator visits (Figure 6) and nests closest to the beach closure signs also being visited more (Figure 7). When examined by predator type, the best predictor model for corvid visits to artificial nests in PEINP included Exclosure and Distance along the beach as predictors with the next best model including Exclosure as a single predictor (Table 8). Exclosed artificial nests were visited significantly more by corvids (Wald's = 2.57, P = 0.01) than unexclosed nests (Table 10). The best predictor model for fox visits in PEINP did not include either Exclosure nor Distance along the beach as predictors, and although the next best models had them each as a single predictor (Table 9), neither of these predictors were significant in explaining fox visits to artificial nests in PEINP (Table 10).

Table 8. Candidate Generalized Linear Mixed Models for predicting number of corvid visits to nest exclosures in Kouchibouguac and Prince Edward Island National Parks. ΔAIC values reflect the difference in score from the best fitting model.

Model Parameters		**KNP** - Corvid		**PEINP** - Corvid	
	*K**	*AICc*	*ΔAIC*	*AICc*	*ΔAIC*
Exclosure **:** Beach Distance	6	41.32	5.14	47.53	2.15
Exlcosure + Beach Distance	5	38.02	1.83	**45.38**	**0.00**
Exclosure	4	38.40	2.21	**45.49**	**0.10**
Beach Distance	4	**36.18**	**0.00**	50.50	5.12
Intercept Model	**3**	**36.91**	**0.73**	49.63	4.25

* Number of model parameters; the random effects of nest and overdispersion each count as a parameter.

Bold indicates best fitting model(s).

Table 9. Candidate Generalized Linear Mixed Models for predicting number of fox visits to nest exclosures in Kouchibouguac and Prince Edward Island National Parks. ΔAIC values reflect the difference in score from the best fitting model.

Model Parameters		**KNP** - Fox		**PEINP** - Fox	
	*K**	*AICc*	*ΔAIC*	*AICc*	*ΔAIC*
Exclosure **:** Beach Distance	6	40.50	7.11	48.95	5.13
Exlcosure + Beach Distance	5	36.45	3.06	45.91	2.08
Exclosure	4	39.89	6.50	**45.52**	**1.70**
Beach Distance	4	**33.39**	**0.00**	**43.95**	**0.13**
Intercept Model	**3**	37.26	3.87	**43.82**	**0.00**

* Number of model parameters; the random effects of nest and overdispersion each count as a parameter.

Bold indicates best fitting model(s).

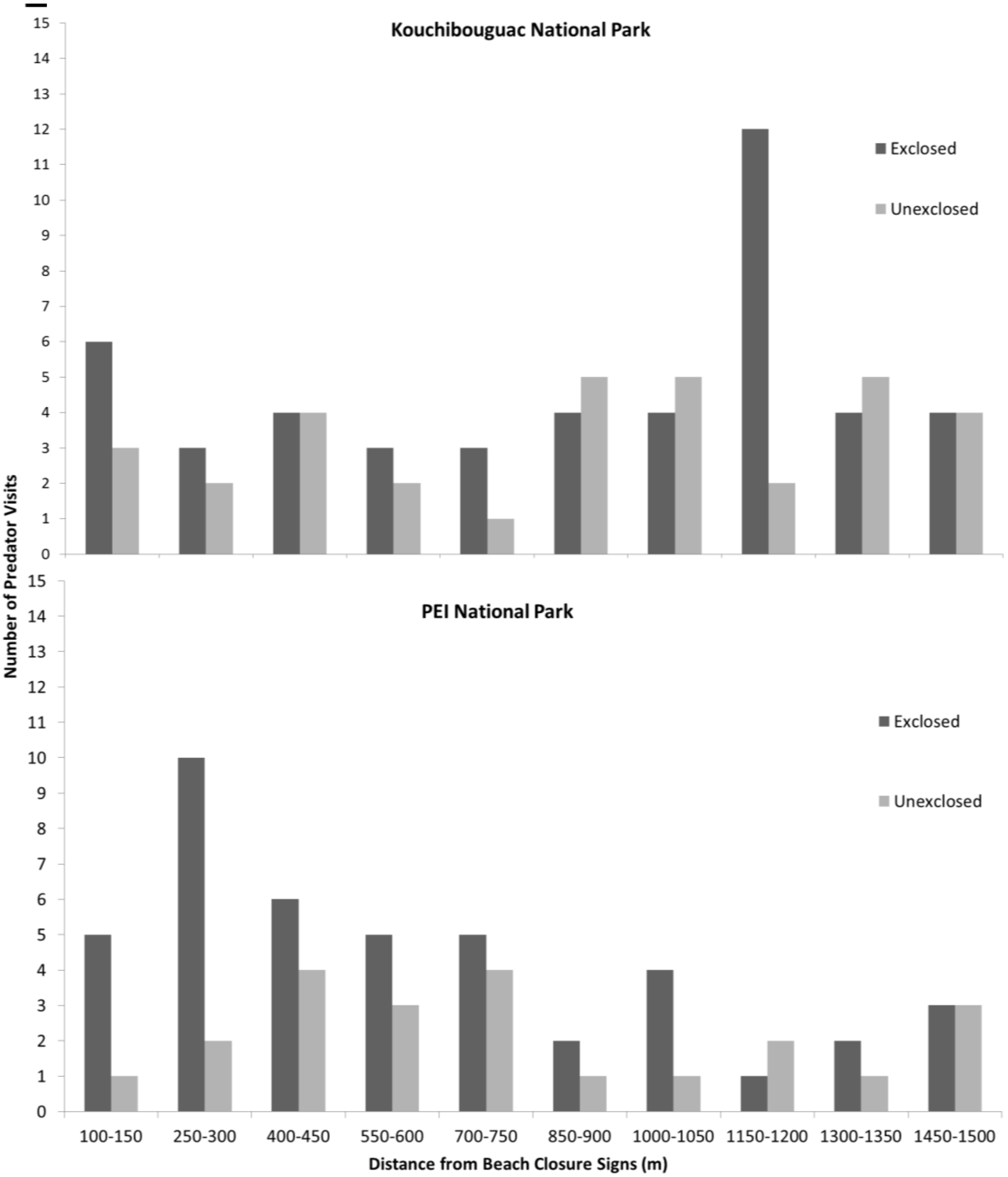

Figure 7. Predator visits to artificial nests according to distance from area closure signs in Kouchibouguac and PEI National Parks.

Table 10. Parameter estimates and significance tests for the best Generalized Linear Mixed Models describing the visits of corvids and foxes to artificial nests in Kouchibouguac and PEI National Parks.

Best Models (ΔAIC< 2)	**Parameter Estimates**			
	Parameters	*Estimate*	*Wald's z-test*	*p-value*
Visits (KNP corvids) ~ Intercept	Intercept	-0.43	-1.55	0.12
Visits (KNP foxes) ~ Beach Distance + Int.	**Beach Dist.**	**0.08**	**2.83**	**< 0.01**
	Intercept	0.003	0.008	0.99
Visits (PEINP corvids)~ Exclosure + Beach Distance + Int.	**Exclosure**	**1.95**	**2.57**	**0.01**
	Beach Dist.	-0.004	-0.10	0.92
	Intercept	-1.57	-1.87	0.06
Visits (PEINP corvids) ~ Exclosure + Int.	**Exclosure**	**1.95**	**2.57**	**0.01**
	Intercept	**-1.61**	**-2.28**	**0.02**
Visits (PEINP fox) ~ Intercept	Intercept	0.17	0.53	0.59
Visits (PEINP fox) ~ Beach Distance + Int.	Beach Dist.	-0.09	-1.78	0.07
	Intercept	0.93	1.84	0.07
Visits (PEINP fox) ~ Exclosure + Int.	Exclosure	0.71	1.21	0.23
	Intercept	-0.35	-0.78	0.43

Bold indicates significance at $\alpha < 0.05$.

CHAPTER 4 DISCUSSION

My work helps to explain the results of previous studies suggesting a link between predators and the negative effects of nest exclosures. Overall, the community of potential Piping Plover predators is diverse and they spend more time near exclosed nests than unexclosed nests and visit exclosed nests more often in PEINP. The increased presence of predators at exclosed nests did not, however, appear to affect the behaviour of incubating adults. My field observations showed no difference in behaviour between plovers nesting in exclosed and unexclosed nests. Similarly, the video monitoring results showed no difference in behaviour between plovers in exclosed and unexclosed nests while in the presence of predators. The results of my artificial nest experiment also showed that proximity to areas of human activity could have an effect on the frequency of predator visits to nests. Overall, my results suggest that nest exclosures could have an effect on the behaviour of predators. This result may be important to consider for the management of Piping Plovers and other ground-nesting species where exclosures are used to reduce nest predation.

Both the video monitoring of nests and the artificial nest experiment confirmed that the main predators at both sites were the Red Fox and American Crow. Of the five predation events caught on video, two were caused by foxes and two by crows (one predator was unidentifiable), and the majority of tracks recorded in the artificial nest experiment were also made by these predators. Other studies have also identified foxes and American Crows as predators of Piping Plovers (Johnson and Oring 2002; Murphy et al. 2003), although this is the first time it has been captured by video in Canada.

A variety of other potential predators were also identified by video including, raccoons, gulls, rodents, grackles, herons and Osprey, although in small numbers. For each of these, the behavioural response of plovers ranged from fleeing the nest entirely to mobile distraction displays. Along the U.S. Eastern seaboard, food-subsidized raccoons are considered a major predator of plover nests (Engeman et al. 2010). However, only a single raccoon was recorded in my study and it was in KNP. Here, the plover flushed from the nest shortly before the raccoon appeared and returned several minutes after it left. Both deer mice and grackles are known egg predators in other ecosystems (Miller and Hobbs 2000; Johnson and Oring 2002). The reaction by the plovers elicited by these animals included standing over the nest with wings raised and slowed rodent run (walking) for mice and grackles, respectively. In contrast to these encounters, an Osprey spent 30 minutes preening within 2 m of a plover nest. This elcited mobile distraction displays for an initial 17 minutes, followed by the plover resuming incubation in the presence of the Osprey for the remaining 13 minutes. The few encounters of these potential predators with plovers, as captured on video, suggest that the chances of Piping Plover nests in Atlantic Canada being depredated by these other animals are slim since they rarely seem to encounter them. Overall, I found that Piping Plovers encountered a variety of known predators and potential predators during incubation and that the behavioural response of plovers seemed to vary with predator type, potentially due to the different levels of risk each type presented.

During both field observations and video monitoring, I found that Piping Plover behaviour did not differ between exclosed and unexclosed nests, either in the absence or presence of predators. The results of my field observations showed no difference between exclosed and unexclosed nests in terms of vigilance, movement or departures in the absence of predators, suggesting that the presence of the exclosure, *per se*, does not affect behaviour during incubation. More importantly, however, while approximately 350 predator events were observed in the video footage, the behaviour of incubating adults at exclosed and unexclosed nests did not differ. I expected that plovers might have difficulties leaving the exclosures when flushed from the nest by predators (Murphy et al. 2003; Niehaus et al. 2004) and that this would translate into behavioural differences between nest treatments. I based this assumption on accounts of Piping Plover entanglements in the top netting of exclosures (Murphy et al. 2003) and of Western Sandpipers (*Calidris mauri*) flying into the tops or sides of exclosures when flushed by predators (Niehaus et al. 2004). Although a few cases of adults being hindered by exclosures were caught on video (see below), predators were not visible within the camera's view at those points, and these difficulties did not manifest themselves as differences in behaviour between birds at exclosed and unexclosed nests.

The behaviour of plovers during incubation was, however, influenced by season and study site. More specifically, video data showed that plovers spent more time away from their nests during predator events in 2008 and 2009 than in the following years. This difference might be the result of differences in predation risk across years and the ability of birds to assess this risk and adjust incubation behaviour accordingly (Fontaine and Martin 2006). In my study, there were fewer predator events captured on video in 2008 and 2009 than in 2010 and 2011**.** If this reflects differences in predator abundance across years, then predation risk may have been lower in 2008 and 2009 than subsequent years. Fontaine et al. (2007) demonstrated that incubating passerines decreased their nest attentiveness when nest predators were removed. They suggested that birds may leave nests more or for longer periods when the risk to nests is low, presumably in response to lowered risks of nest predation. Although in this study plover behaviour was measured in the presence of predators, the lower seasonal predation risk may be more influential than daily predation risks for nests. Therefore differences in plover behaviour between years seems to support the findings of similar studies that report reduced nest attentiveness in times of low nest predator abundance.

I also found that plovers in KNP spent more time away from their nests during a predator event than plovers in PEINP. This variation in response may be a result of differences in predator types between parks and the inherent risks they pose to incubating adults as opposed to nests. In KNP, the number of fox events seen on video was five times greater than in PEINP, and twice as many corvids were recorded from the footage in PEINP than in KNP. Foxes prey not only on eggs and chicks, but also adults (Liebezeit et al. 2009) and could therefore present a greater risk to incubating adults. In fact, the presence of Red Fox on breeding beaches has been linked to the probability of Piping Plover nest abandonment (Doherty and Heath 2011). Furthermore, plovers would flush from the nest well before foxes appeared and did not engage in anti-predator displays, suggesting that doing so would have been too risky (G. Beaulieu pers. obs.). Therefore, the potentially greater risk to adults presented by a higher fox presence in KNP could offer an explanation for these site-dependent differences in plover behaviour.

Overall, predators spent more time near exclosed nests than unexclosed nests, which may explain the increase in adult mortality and nest abandonment observed at exclosed nests in previous studies (e.g., Murphy et al. 2003; Maslo and Lockwood 2009;

Barber et al. 2010). Predation risk should increase with increasing time spent by predators in the proximity of the nest. This risk may be further increased by the fact that adults could have difficulties exiting exclosures potentially increasing the time it takes to leave. Although anecdotal, I did observe four occasions when plovers either flew up into the netting covering the tops of exclosures or 'tripped' over the bottom rung of the structures (Appendix 6). Other shorebirds have also been observed having difficulties exiting nest exclosures (Niehaus et al. 2004), and some raptors appear to use these difficulties to capture incubating adults (Murphy et al. 2003). Thus, predators spending more time at nests might increase the direct risks to incubating adults.

In addition, the increased presence of predators at exclosed nests, may also explain why nest abandonment occurs more frequently at exclosed nests than unexclosed nests (Maslo and Lockwood 2009). There are several ways in which the presence of the predator may increase the risk of abandonment. First, if a predator removes one adult, the energetic demands of continued incubation and subsequent brood-rearing may be too great for the remaining parent, which could lead to nest abandonment. This is supported by the results of a study on banded Piping Plovers in the Great Lakes Region, showing that nests were abandoned by the remaining bird following the mortality of its mate (Roche et al. 2010). Second, the continued presence of a predator in the vicinity of the nest may increase stress levels for incubating birds, potentially resulting in abandonment. Frequent predator encounters have been shown to induce a state of chronic stress in birds (Scheuerlein et al. 2001), which has been linked to reduced parental care and subsequent nest abandonment (Angelier and Chastel 2009). Although no studies have described the physiological response of Piping Plovers to stress, it seems very likely that increased predation risk could elevate stress levels, potentially leading to greater rates of abandonment at exclosed nests.

Using artificial nests, I also found that predators visited exclosed nests more often than unexclosed nests, and significantly so in PEINP. Previous studies on the effect of nest exclosures on Piping Plovers and other shorebirds also report increased predator visits to exclosed nests (Murphy et al. 2003; Neuman et al. 2004). This suggests that predators might be attracted to exclosures. Perhaps because Piping Plovers rely on camouflage as their primary defense against predation, exclosures may act as markers for predators, essentially eliminating the challenge of finding plover nests. This seems like a reasonable assumption because unlike the well-camouflaged adult, nest exclosures would be highly visible objects in open landscapes and may attract predators to nests. Research on Western Sandpipers showed that predators located exclosed nests but failed to notice unexclosed nests nearby (Niehaus et al. 2004). Similarly, results from this study may indicate that predators could use exclosures as a visual cue to find adults or nests.

The results of the artificial nest experiment also suggest that the frequency of predator visits to exclosed nests may be affected by the distance of exclosures to human activities. Specifically, I found that the probability of a predator nest visit in PEINP decreased with the distance from beach closure signs (Figure 7). That is, the greater the distance from the signs, the further the nest was from human activities. This result suggests that the main predators in PEINP (i.e., corvids) may not stray too far from areas with human activity. Therefore, not only are exclosed nests at greater risk of adult mortality and abandonment, but exclosed nests near human-disturbed areas may be particularly vulnerable, at least where corvids are the main threat. Indeed, nesting shorebirds in the Arctic suffered greater rates of nest predation near oilfields where garbage and human subsidized food sources attracted predators (Liebezeit et al. 2009). In contrast, in KNP the probability of predator visits increased with distance. However, predators, such as foxes, which were more common at KNP than PEINP, have been shown to avoid humans (Berger 2007; Doherty and Heath 2011) and this may explain the patterns seen in KNP, where more predator visits occurred at nests furthest from the beach closure signs.

Within KNP and PEINP, undisturbed natural areas coexist alongside areas with seasonably variable levels of human activity. Proximity to human activity, as measured in the artificial nest experiment, was shown to affect predator behaviour although this effect differed between Parks. Differences in geography may explain some of the differences observed between Parks. PEINP protects a very narrow strip of land along the northern coast of PEI, which according to habitat edge theory, suggests that predators are likely habituated to human activity (Miller and Hobbs 2000). Thus it comes as no surprise that predators in PEINP visited nests located nearby human recreational areas more than nests further from these areas. In KNP, plover nesting beaches are located much further from designated human recreational areas in the Park (many having boat access only) and the greater number of predator visits to nests furthest from human activity suggests that predators there still avoid humans. Outside of National Parks, human activity on plover nesting beaches is not as controlled and the suite of predators visiting nests may differ in response to a higher presence of humans. The combination of both natural, undisturbed areas as well as human recreational areas within Parks may exacerbate the effect of predation on Piping Plovers seen here since both human-habituated and wild predators can be supported.

Interestingly, our findings relating distance to the number of predator visits received by artificial nests are in contrast to those of Cossitt (2012) for PEINP, in which she used historical nesting locations to determine the effects of proximity to human activities on nest success. This study ran in parallel to my video monitoring of nests in PEI, and contrary to my results, Cossitt (2012) found that proximity to human activities increased the probability of nest success, suggesting fewer predator visits to nests closer to human activity. However, Cossitt (2012) did not discriminate between exclosed and unexclosed nests. If nests closest to human activity were exclosed and thus had higher success, it could explain the differences between our findings. The data regarding which types of nests were closest to areas of human recreation is not available for discussion in this study. Yet, hatch success was 40% greater at exclosed nests in PEINP than unexclosed nests for the historical years that Cossitt (2012) examined (Parks Canada unpublished data).

The results of the artificial nest experiment should, however, be treated with some caution. First, only two beaches were included in the experiment. Therefore the predator visits recorded may be due to only a few or even individual predators that repeatedly approached artificial nests, rather than multiple predators independently locating nest exclosures. Second, the location of the artificial nest in relation to the exclosure edge in PEINP and KNP makes the isolation of a potential attraction effect of the exclosures from the possible effect of egg location difficult. Specifically, eggs located outside of exclosures in KNP may have attracted predators, and not the exclosure itself. If this were the case, a stronger attraction effect (i.e., more visits to artificial nests) would be expected in KNP; however, statistical comparisons between Parks were not made because of the differences in nest placement. Nevertheless, the artificial nest experiment provides Piping Plover managers with a snapshot of how exclosures could affect predators and presents a potentially robust method in which to assess nest exclosures or additional predator management techniques in the future.

The results of my study must also be viewed in the context of where it was conducted, i.e., National Parks, where certain unique aspects of protected areas may be particularly relevant. Both the Piping Plover and their predators are protected in National Parks and predator abundance is likely higher as a result. Furthermore, the generally higher ecosystem productivity of protected areas can also result in greater abundances of small-sized predators in comparison to the surrounding human-disturbed landscapes since the prey and suitable habitat exists to support larger populations (DeCesare et al. 2009; Ritchie and Johnson 2009). If the abundance of predators in KNP and PEINP is indeed higher than in surrounding areas, then the encounter rate of predators with plover nests might be higher in Parks. Coupled with the possible attraction effect of nest exclosures, this may explain why predators were found to visit exclosed nests more. If I had conducted this study outside of National Parks, an exclosure effect on the behaviour of predators may not have been found, particularly if predator abundance was lower due to less productive ecosystems and the lack of protection from hunting and trapping. However, the relative abundance of mid-sized predators within and outside of these National Parks was not assessed in this study, and may be worth examining in future.

Essentially, the results of my study suggest that predators spend more time at exclosed nests and visit exclosures more often in PEINP, which may explain previous trends showing increased adult mortality and abandonment at exclosed nests. Although nest exclosures increase Piping Plover hatching success, the potential loss of breeding adults, along with greater risk of nest abandonment would have a far greater impact on the population recovery of this Endangered species than simply the loss of eggs (e.g., Roche et al. 2010; Barber et al. 2010; Calvert and Taylor 2011). Based on this, I would recommend that nest exclosures be used with great caution, if at all, and alternative predator management tools, such as taste aversion techniques or the use of corvid effigies be explored. However, if new management tools are applied to this population they should be used on a shorter time-scale than exclosures to reduce the chances of predators habituating. Further, I recommend that the population of plovers breeding in Atlantic Canada be considered for an adult banding program. Individually identified plovers would help determine whether nest abandonment is a result of adult mortality and would enable managers to tailor any future predator management strategies, both of which would further increase our capacity to recover the species.

Nest exclosures have been applied to the nests of Piping Plovers in Atlantic Canada since the late 1980's, largely without any evaluation of their effectiveness. Studies such as this are essential in providing the information necessary to examine the effects of management techniques and adapt accordingly. Therefore, any new predator management tools should be regularly assessed both from the perspective of predator response, but perhaps even more importantly, in terms of contributions towards increasing Piping Plover productivity and population abundance. Adaptive management techniques (i.e., population viability analyses) that use monitoring data and measures of management effects in population modelling (Bakker and Doak 2011) would be useful for this, and should be considered as the next best step in effectively addressing the threats to breeding Piping Plovers (e.g. Calvert and Taylor 2011). Adaptive management is designed to respond to short-term population fluctuations and may be better suited to identifying whether management efforts positively affect species at risk recovery. In a landscape of changing predator communities, developing adaptive predator management strategies will be especially crucial for the recovery of species at risk such as the Piping Plover.

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APPENDIX 1

Remote Video Monitoring Equipment and Set Up used at Piping Plover Nests

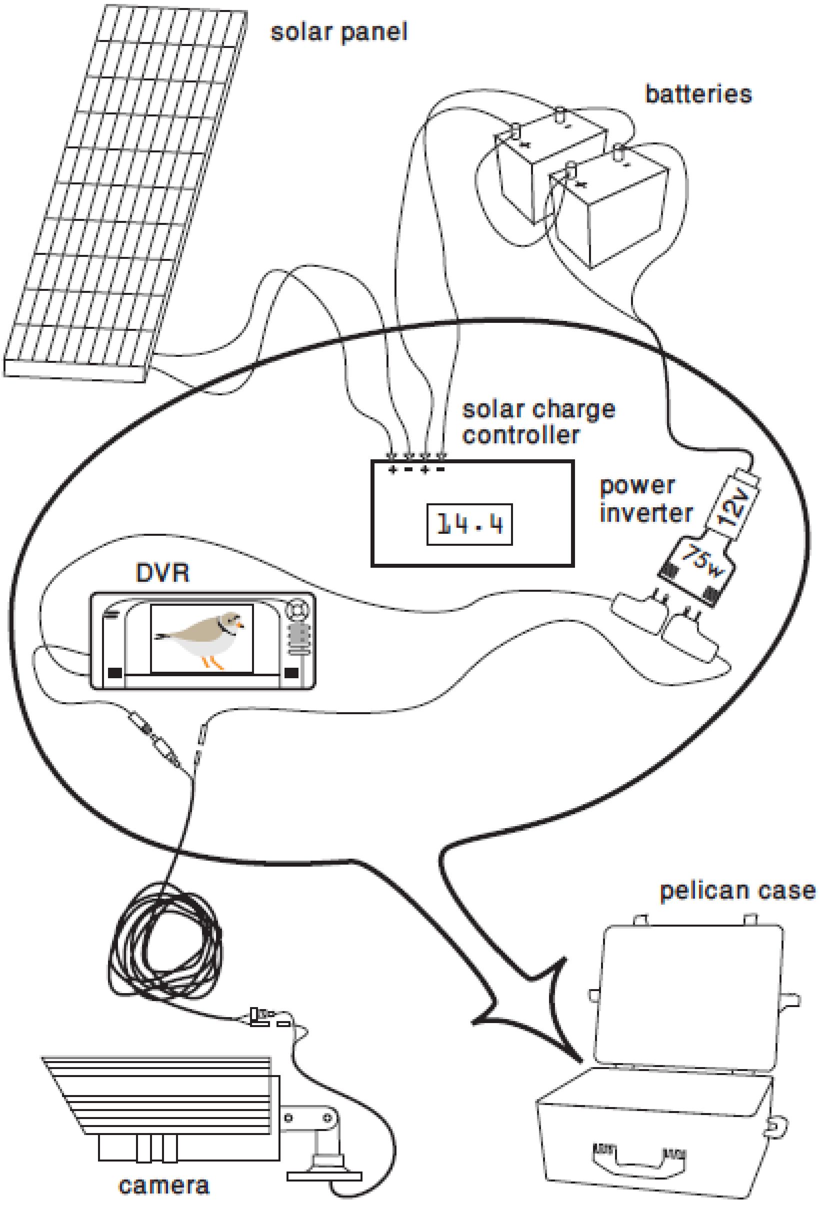
Equipment used in 2010-2011 research

1 Q-See Color IR Day/Night Camera
1 PV-690s MPEG-4 Video Recorder
1 Western Digital 320GB Hard Drive
2-3 75Ah Deep Cycle Battery
(1) Sharp Solar Panel
(1) Solar Controller
(1) Solar Panel Voltage Tester
1 Pelican Case
1 70 Qt Cooler
1 Wooden box
1 50ft White Co-Axial Cable
1 Camera Power Cord (square; green light)
1 Video Recorder Power Cord (rounded)
1 Video Recorder AV Cable
Series Connector Wires
1 Solderless BNC (golden) Connector
1 BNC Video Adaptor (plastic encased)
1 Mobile Power Inverter (cigarette plug)
1 3-Outlet Plug
Indoor/ Outdoor Thermometer
AAA batteries
1 TB Storage Hard Drive
Rings for Battery Terminals (+/ -)
Soldering Kit
Wire Cutters
Set of Small Screwdrivers
Compressed Air to clean out sand
2-3 Shovels
Stopwatch

Equipment used in 2008-2009 Pilot Study

National Electronics Bullet IR Camera
Speco Technologies Multiple Channel DVR
DVR Unit DC Wire (Red/Black)
DVR Unit AC Adapter
Motomaster 75 Ah Deep Cycle Battery
Motomaster Solar Controller
Multimeter
Sharp Solar Panel
Video Adaptor (Yellow)
100ft Co-Axial Cable (Black)
Short Co-Axial Cable (Black)
Electrical wire, 14 gauge
Venturer Video Monitor
Motomaster 12V Battery Charger
Pelican Case
Cooler

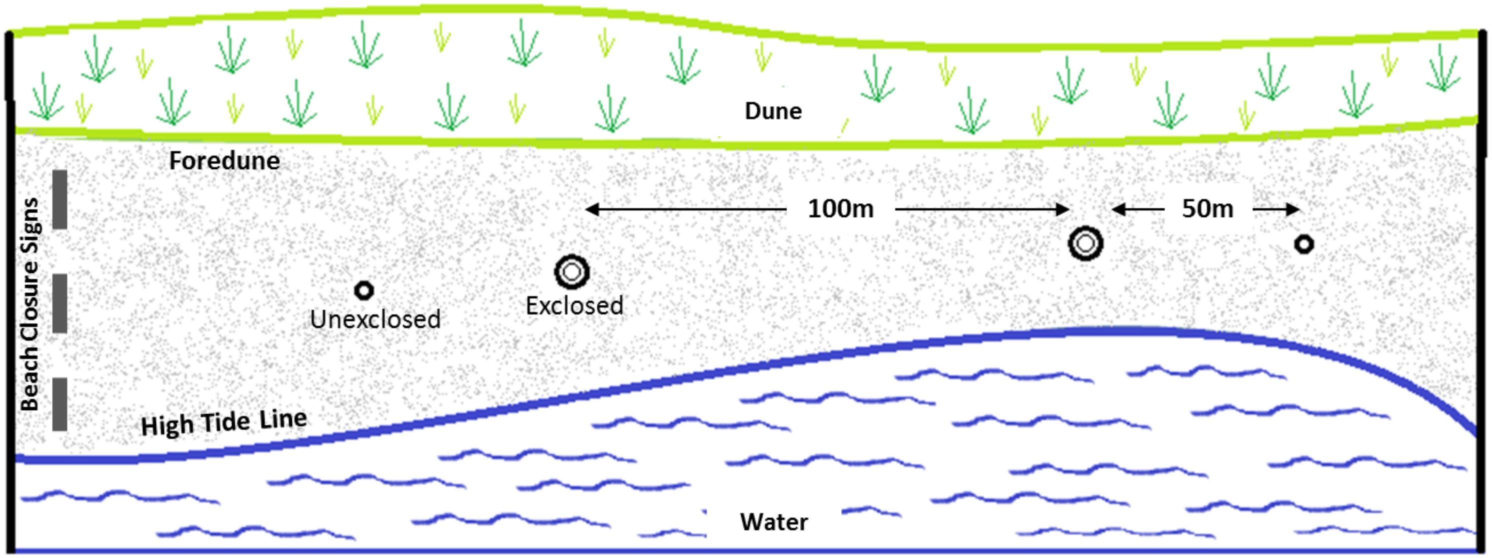
APPENDIX 1 cont'd



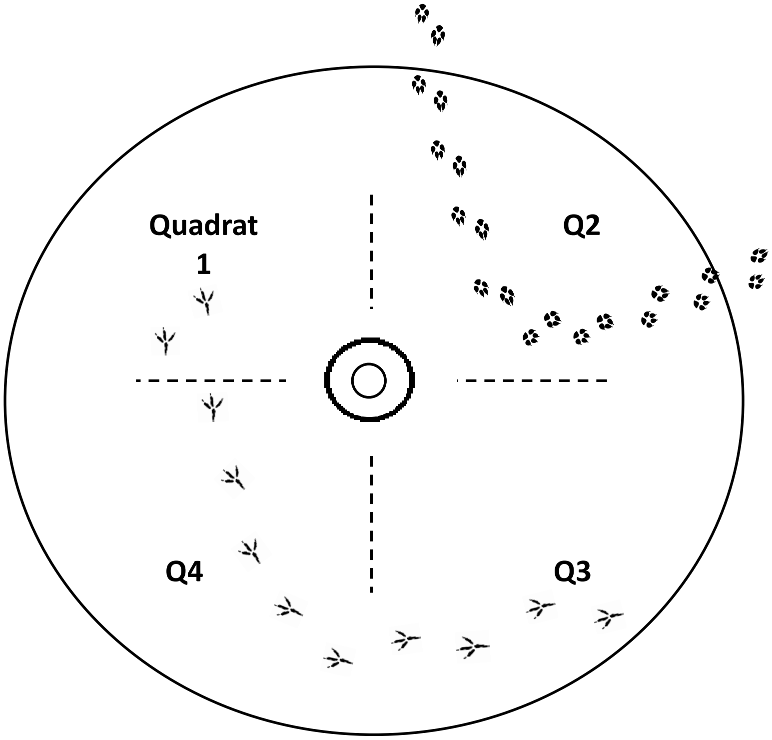
Remote video camera equipment set up (courtesy of Doug Smith, Parks Canada).

APPENDIX 2

Experimental Design Diagrams for Artificial Nest Experiment



APPENDIX 2 cont'd



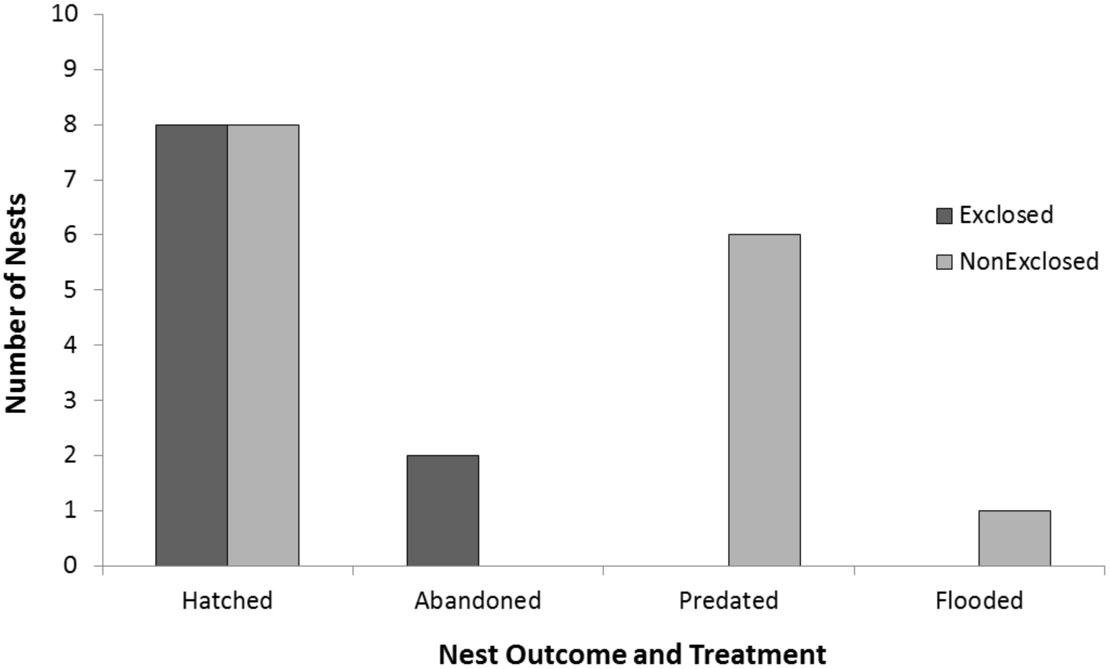
Experimental area defined around an exclosed artificial nest. Fox tracks are seen in quadrat 2 only and would not be counted as a predator visit, whereas the corvid tracks go from quadrat 3 to quadrat 1, therefore this would count as a predator visit.

APPENDIX 3

Piping Plover Nest Success in Kouchibouguac and PEI National Parks 2010-2011

Overall Nest Success for n = 42 Piping Plover Nests.

	Kouchibouguac National Park		**PEI National Park**		**Total**
	2010	*2011*	*2010*	*2011*	
Exclosures	*5*	*7*	*4*	*1*	*17*
Hatched	8	4	5	3	20
Predated	1	6	1	3	11
Abandoned	1	4 (all exclosed)	1 (exclosed)	0	6
Flooded	1	0	3	1	5
Total	**11**	**14**	**10**	**7**	**42**



A total of 25 nests (n=10 exclosed; n=15 unexclosed) were video monitored from 2008-2011 in KNP and PEINP. Approximately 2015 h of footage was collected from exclosed nests and 2362 h was collected from unexclosed nests. Nests were depredated by Red Fox and American Crow, and all nests that hatched fledged at least one chick.

APPENDIX 4

Means and Standard Errors of Behavioural Measurements

Means and standard errors of behavioural measurements taken during observations of incubating Piping Plovers in Kouchibouguac and PEI National Parks from 2010-2011.

Behaviour	**Overall Mean (± SE)**	**Mean Exclosed (± SE)**	**Mean Unexclosed (± SE)**
Animal Events	5.43 ± 1.18	5.89 ± 2.40	5.08 ± 1.23
Vigilance	7.71 ± 0.69	7.43 ± 0.88	7.91 ± 1.07
Movement	6.00 ± 1.2	5.37 ± 1.7	6.50 ± 1.9
Departure	0.62 ± 0.29	1.16 ± 0.65	0.25 ± 0.14

Means and standard errors of behavioural measurements taken from video footage of incubating Piping Plovers and predators positioned on the ground in Kouchibouguac and PEI National Parks from 2008-2011.

Behaviour	**Overall Mean (± SE)**	**Mean Exclosed (± SE)**	**Mean Unexclosed (± SE)**
Pred Time	122.15 ± 40.39	79.10 ± 17.91	165.20 ± 79.37
Time Away	296.02 ± 46.39	366.23 ± 63.77	225.80 ± 67.00
Display	0.38 ± 0.06	0.47 ± 0.09	0.3 ± 0.09
Display Time	35.5 ± 9.72	41.43 ± 13.89	29.56 ± 13.98
Time Safe	92.85 ± 20.60	112.93 ± 32.58	72.76 ± 25.81

Means and standard errors for predator visits recorded at artificial nests in Kouchibouguac and PEI National Parks during the artificial nest experiment.

Predator Visits	**Overall Mean (± SE)**	**Mean Exclosed (± SE)**	**Mean Unexclosed (± SE)**
KNP Corvid	0.7 ± 0.17	0.7 ± 0.27	0.6 ± 0.23
KNP Fox	2.6 ± 0.49	2.9 ± 0.84	2.2 ± 0.56
*KNP Gull	0.7 ± 0.18	0.9 ± 0.29	0.5 ± 0.24
PEINP Corvid	0.8 ± 0.18	1.4 ± 0.17	0.2 ± 0.14
PEINP Fox	1.6 ± 0.49	2.1 ± 0.90	1.0 ± 0.44

* Only one visit to artificial nests was made by a gull in PEINP

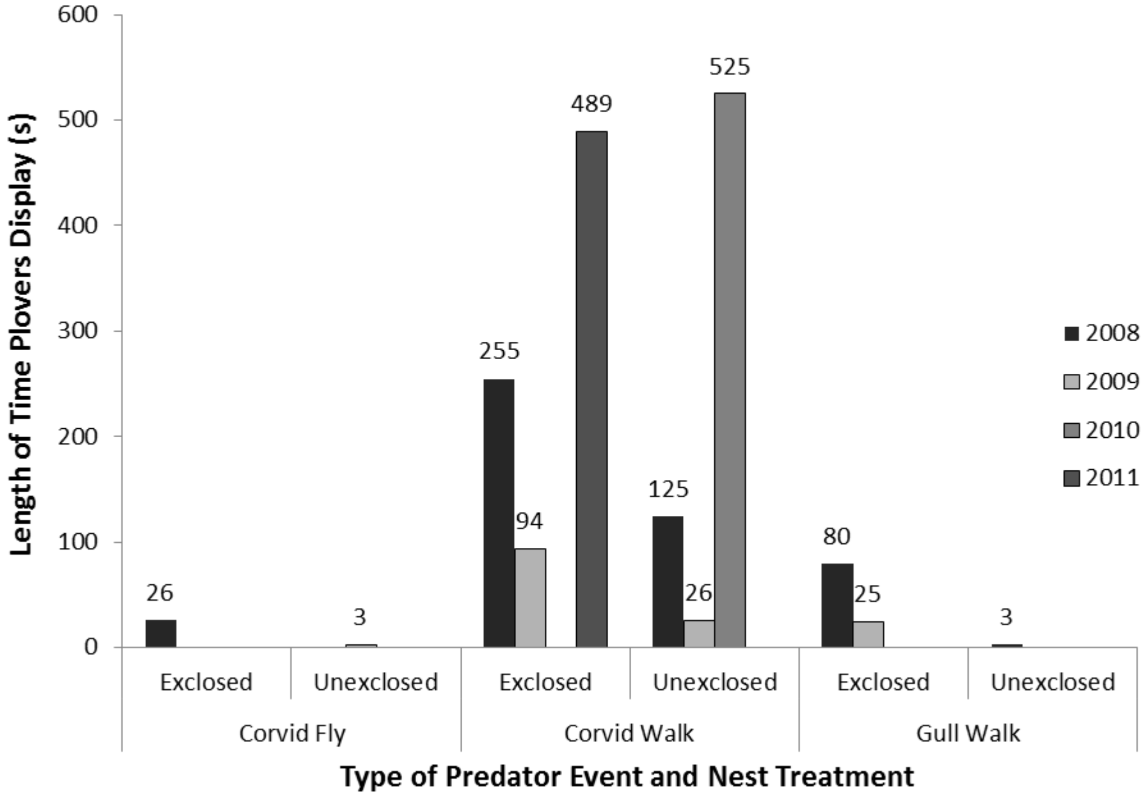
APPENDIX 5

Piping Plover Anti-Predator Displays from Video Footage in KNP and PEINP

Candidate GLMMs Applied to Video Data of Piping Plover Nests 2008-2009.

Model Parameters		**Display**		**Display Time**		**Time Safe**	
	*K**	*AICc*	*ΔAIC*	*AICc*	*ΔAIC*	*AICc*	*ΔAIC*
Ex + Park + Year	8	547.45	25.48	694.43	4.88	874.85	49.30
Ex + Park	5	537.79	15.82	$1.41x10^{11}$	$1.41x10^{11}$	846.48	20.92
Ex + Year	7	$2.16x10^{8}$	$2.16x10^{8}$	$1.99x10^{6}$	$1.99x10^{6}$	$2.60x10^{29}$	$2.60x10^{29}$
Park + Year	7	546.42	24.45	$3.37x10^{6}$	$3.37x10^{6}$	863.16	37.60
Exclosure	4	524.83	2.86	654.33	8.71	82.86	3.10
Park	4	535.07	13.09	$1.41x^{11}$	$1.41x10^{11}$	$1.78x10^{11}$	$1.78x10^{11}$
Year	6	533.90	11.92	$6.36x10^{5}$	$6.35x10^{5}$	840.71	15.16
Intercept	3	**521.97**	**0.00**	**645.62**	**0.00**	**82.56**	**0.00**

* Number of model parameters; random effects of nest and overdispersion are each a parameter. **Bold** indicates best fitting model(s).



APPENDIX 6

Events Recorded at Video Monitored Piping Plover Nests

Nest and Site	Year	Exclosed	Predator Event	Plover Response
BP4-PEINP	2008	N	Nest depredated by fox	Flies off nest 14 s before fox appears; nest in heavy vegetation
CS1-PEINP	2008	N	Nest depredated by crow	Mobile distraction display
RC1-PEINP	2009	N	Nest depredated, predator unknown	Video camera obstructed by vegetation
CP1-PEINP	2010	N	Nest depredated by crow over period of an hour	Mobile distraction display and directed aggression; estimated hatch day
CP1-PEINP	2010	N	Osprey loafing within 2m of nest	Mobile distraction display for 37min; incubates in presence of osprey for 9min
GR3-PEINP	2010	N	Mouse within 50cm of nest	Stands and raises wings, mouse flees
KN7-KNP	2010	N	Grackle lands within 1m of nest	Rodent run towards grackle
KN7-KNP	2010	N	Raccoon sniffing within 50cm of nest	Sneaks from nest and returns after 22min of raccoon departure
KN7-KNP	2010	N	Mouse within 50cm of nest	Stands and raises wings, mouse flees
KN9-KNP	2011	N	Nest depredated by fox	Flies off nest; returns sporadically for up to 5 hrs

APPENDIX 6 cont'd

Nest and Site	Year	Exclosed	Predator Event	Plover Response
KS1-KNP	2008	Y	Gull encircles exclosure	Mobile distraction display
KN6-KNP	2010	Y	n/a	Flies into top of exclosure
GR1-PEINP	2010	Y	n/a	Flies into top of exclosure; trips over exclosure during subsequent exit
CS1-PEINP	2010	Y	n/a	Flies into top of exclosure
PS2-KNP	2011	Y	n/a	Flies into top of exclosure following a lightning strike