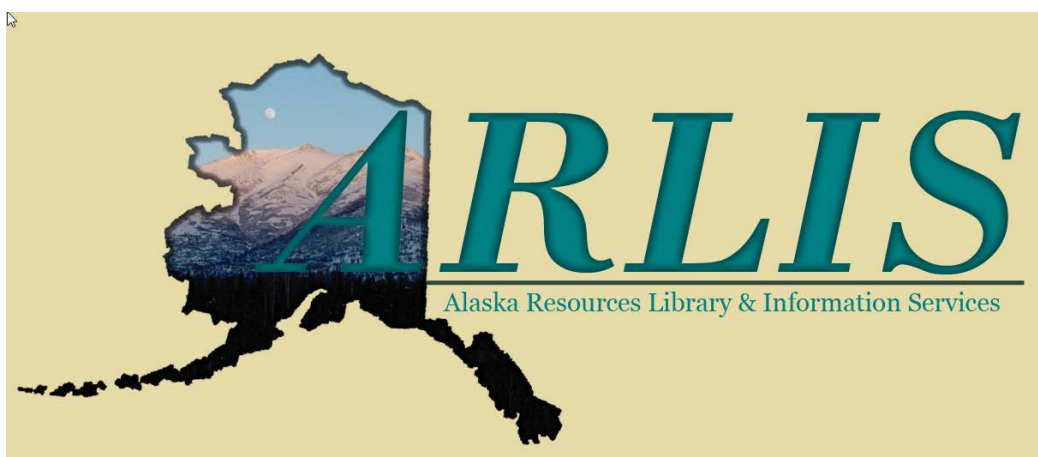


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Reproductive Ecology and Nest Attentiveness
of Piping Plovers (*Charadrius melodus*)
Breeding at Chaplin Lake, Saskatchewan

A Thesis
Submitted to the Faculty of Graduate Studies and Research
In Partial Fulfillment of the Requirements
for the Degree of
Master of Science
in Biology
University of Regina

by
Corie Lynn White
Regina, Saskatchewan
August, 2005

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UNIVERSITY OF REGINA

FACULTY OF GRADUATE STUDIES AND RESEARCH

SUPERVISORY AND EXAMINING COMMITTEE

Corie Lynn White, candidate for the degree of Master of Science, has presented a thesis titled, *Reproductive Ecology and Nest Attentiveness of Piping Plovers (Charadrius melodus) Breeding at Chaplin Lake, Saskatchewan*, in an oral examination held on August 12, 2005. The following committee members have found the thesis acceptable in form and content, and that the candidate demonstrated satisfactory knowledge of the subject material.

External Examiner: Dr. Cheri Lynn Gratto-Trevor,
Canadian Wildlife Service, Saskatoon, SK

Co-Supervisor: Dr. R. Mark Brigham, Department of Biology

Co-Supervisor: Dr. Stephen Davis, Environment Canada

Committee Member: Dr. Mary Vetter, Department of Biology

Chair of Defense: Dr. Kathryn Arbuthnott, Department of Psychology

Abstract

I examined piping plover (*Charadrius melodus circumcinctus*) reproductive success and nest attendance at Chaplin Lake, Saskatchewan (50° 26' N, 106° 40' W) from 2002-2004. Low reproductive success is considered the primary cause of the piping plover population decline across its breeding range. Reproductive success has been documented at relatively few alkali lakes, despite the fact that alkali lake habitat supports a large proportion of the Great Plains breeding population. I monitored 36, 41 and 75 nests in 2002, 2003 and 2004, respectively. Survival of the nests varied by year, but nest survival was most affected by date. Furthermore, nests that were monitored using video cameras had increased nest survival. Brood survival varied by year and date; however, brood survival was most influenced by age of the chicks. Fledging rates ranged from 0.86 to 0.69 chicks per pair, which is less than the 1.25 chicks per pair required to sustain the population.

Parental care strategies are a key life history characteristic and there are often differences in the relative contribution to incubation by each sex. I examined the contribution to incubation by male and female piping plovers. Behavioral data were recorded over continuous 24-hour periods at 10 nests, resulting in 1945.76 hours of observation. The results showed that males contributed more to incubation than females throughout the incubation period. Male and female piping plovers shared diurnal incubation duties equally, while males provided the majority of nocturnal incubation. Further investigation is required to gain a more complete understanding of the interactions among nest attendance and energy constraints.

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I would like to thank Dr. K. Arbuthnott for acting as the Chair of my defense.

Furthermore, I would also need to thank my external examiner Dr. C. L. Gratto-Trevor.

Dedication

I would like to thank Gladys and Bob Weppeler and the Staff at the Chaplin Nature Center, especially Bev Coates, for providing a home away from home and acceptance into the community. Trent Linford provided me with much needed laughter, support, and encouragement. Most importantly, I would like to thank my parents, Phyllis and Terry White, for their patience and many years of unconditional support and encouragement, and for believing in me when no one else did. Lastly, I would like to thank my Grandpa, Walter Smith, for instilling in me an appreciation, curiosity and wonder for the natural world that surrounds us.

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CHAPTER 1: GENERAL INTRODUCTION

Reproduction is an essential and costly part of an organism's life history (Clutton Brock 1991; Alcock 1995). Reproductive decisions concerning initiation and cessation of breeding, breeding location, frequency of reproduction, and termination of parental care all influence the demography of a population and all have fitness consequences for the individuals involved (Walk et al. 2004). Successful reproduction is influenced by a number of variables ranging from environmental conditions to parental care. Life history theory explains the diversity of life cycles observed in nature (Stearns 1992; Reid et al. 2002) by providing a framework for interpretation of intra- and inter-specific variation in an organism's allocation of resources to growth, self maintenance, and reproduction (Reid et al. 2002). The central concept of life history theory is based on physiological tradeoffs due to finite resources at a given organism's disposal. Thus, the allocation of resources to one life history aspect will reduce the availability of resources to invest in others (Lessels 1991; Stearns 1992). Consequently, resources allocated to reproduction reduce the adult's capacity to invest elsewhere (Stearns 1992; Reid et al. 2002). Survival, growth rate, size at maturity, and dispersal of young are all life history traits that can only be increased at the expense of another (Stearns 1992; Lessels 1991). As a result, there is conflict pertaining to the allocation of resources, which translates into compromises that attempt to maximize the individual's reproductive output, and ultimately fitness (Stearns 1992; Reid et al. 2002). Many conflicts can potentially arise pertaining to a series of tradeoffs between the number and quality of offspring, adult reproductive effort, survival, and future reproduction (Houston & Davies 1985; Charnov & Krebs 1974; Lessels 1991; Stearns 1992; Wallander 2003). For these reasons, life history characteristics have

become a common component in the study of species ecology, particularly in studies of population and community structure (Lebreton et al. 1992).

Breeding Ecology:

Reproductive success is a measure of an organism's production of offspring (Drickmaer et al. 2002). Variations in survival and reproduction, and ultimately the transmission of an individual's heritable traits, provide the foundation for natural selection and evolution (Drickmare et al. 2002). Annual and seasonal variation in reproductive success has been documented in all organisms including insects, fish, mammals and birds (Clutton-Brock 1988, Siikamaki 1998). Reproductive success has been documented to vary among breeding seasons (Beintema & Muskens 1987; Hannon et al. 1988; Evans 1991; Rowely & Russel 1991; Berg et al. 1992; Nol et al. 1997; Grand & Flint 1997; Siikamaki 1998 Peak et al. 2004; Sheridan et al. 2004; Ramos 2004; Walk et al. 2004) in addition to spatial and temporal variation within a breeding season (Green 1988; Hannon et al. 1988; Berg et al. 1992; Ens et al. 1992; Westneat 1992; Verhulst et al. 1995 Burger et al. 1996; Nol et al. 1997; Kelly 1997; Sockmann 1997; Siikamaki 1998). This variation in reproductive success is influenced by a number of factors that affect the survival probability of the young, including predation, competition, and environmental conditions (Lebreton 1992; Smith 1996). Consequently, the survival of young during the various stages of development is critical to understanding the population dynamics of a species (Miller & Knopf 1993). Clearly, understanding factors influencing variation in reproductive success is important for gaining insight into the

evolution, ecology and conservation of a given species (Verhulst et al. 1995; Keyser et al. 2004).

The demographic makeup of a population is important to population dynamics (Colbert & Lebreton 1991, Stearns 1992, Underwood and Roth 2002). Demography is primarily focused on reproduction and survival (Prietz et al. 2004). Demographic parameters include fecundity, survival, population density, emigration and immigration (Colbert & Lebreton 1991). Consequently, reproductive strategies influence population growth and have fitness consequences (Walk et al. 2004). Nest success and fledging rates provide an important and often measured demographic parameter in avian studies (Armstrong et al. 2002; Peak et al. 2004; Underwood & Roth 2002). Understanding reproductive rates is essential to the study of a species population dynamics (Stearns 1992; Miller & Knopf 1993; Lukas et al. 2004) and to the development of sound management strategies (Sarno 1999).

Parental Care:

Parental care is a key component of life history and breeding systems, and is defined as any behaviour that increases the probability of offspring survival at a cost to the parent (Clutton-Brock 1991). In its broadest sense, parental care includes all parental activities during the development of offspring, from gamete production to care after nutritional independence (Trivers 1972). Care for offspring is a behaviour that has been observed in many animals in which one or both parents guard or incubate eggs or the brood and feed young (Webb et al. 2002). Parental care ranges from no care to extensive care (McNamara et al. 2000). A principle function of parental care in endothermic

organisms is to regulate the thermal environment for fertilized eggs, providing optimal conditions for embryo development (Clutton-Brock 1991). In addition, parental care provides protection for the eggs and young. Parental care strategies are of central importance because the striking differences in male and female reproductive strategies are associated with variations in their involvement in parental care (Trivers 1972; Lazarus 1990).

Selection for parental care behaviours arises when the benefits of increased survival of offspring exceed the benefits to the parent if it were to desert and breed again (Smith 1977; Lazarus 1990; Reynolds & Székely 1997). In birds, social monogamy combined with bi-parental care occurs in approximately 90% of extant species (Clutton-Brock 1991, Alcock 1998), whereas it is uncommon in most other vertebrate taxa (Clutton-Brock 1991, Alcock 1998). Parental care is characteristic of most avian species because of the requirement to incubate and protect eggs before they hatch (Hauber 2002; Reid 2002; Deeming 2002); however patterns of parental care are highly variable and involve a series of tradeoffs (Székely 1999). Parental care is a costly behaviour (Clutton-Brock 1991) and the formation of a pair may not be to increase joint fitness, but rather individual fitness. Consequently, males and females can maximize fitness by using different strategies which commonly results in conflict between individuals over how much effort to put into parental care (Trivers 1972; Houston & Davies 1985; Davies 1991; Moller & Thornhill 1998; Parish & Coulson 1998).

Shorebirds (suborder Charadrii) have the greatest diversity of parental care within any suborder of birds (see Székely & Reynolds 1995). The diversity of parental care strategies found in shorebirds have made them an interesting group of organisms in

which to investigate reproductive behavior (Reynolds & Szekely 1997; Kosztolányi & Székely 2002; Deeming 2002). Within this suborder there are 203 species classified into 4 superfamilies (Scolopacoidea, Jacanoidea, Chionioidea and Charadriodea). Shorebirds display a variety of parental care strategies ranging from uni-parental to bi-parental care. Even within species with bi-parental care there is a wide range of disparities in the level of participation by each member of the pair during incubation and brooding rearing (Szekely & Reynolds 1995). Overall, parental care systems in shorebirds are diverse and the time devoted to parental care varies with species and sex (Thibault & McNeil 1995). Shorebirds provide an interesting taxa to work with because these birds tend to be relatively long lived, nests are accessible and they have a diversity of both mating and parental care systems, which make them amenable to comparative studies.

Study Species:

The piping plover (*C. melodus*) is a member of the plover family, *Charadriidae*. *Charadriidae* are small shorebirds found worldwide with the exception of the Antarctic. The piping plover (*C. melodus*) is one of 6 belted plover species in North America. Approximately half the species in this family have relatively small populations, restricted distributions and/or are listed as having vulnerable, threatened or endangered status (Johnson & Oring 2002).

Distribution

The Piping Plover is a small migratory shorebird, which inhabits sparsely vegetated beaches of alkali lakes, freshwater lakes/reservoirs and coastal areas of North America (Haig 1992). The species range encompasses three distinct areas, which include

Atlantic coastal areas, the Great Lakes and the Northern Great Plains (hereafter Great Plains; Haig 1997). Their range along the Atlantic coast extends from North Carolina in the United States to Prince Edward Island, Canada. Historically the piping plover had a wide distribution throughout the Great Lakes region, including beaches of Lake Superior, Lake Michigan and Lake Erie, throughout the states of Michigan, Wisconsin, Illinois in the United States and southern Ontario, Canada. However, the few breeding pairs remaining in this area (100 pairs) are currently restricted to areas along Lake Michigan, Lake Superior and Lake Huron (Haig & Elliot Smith 2004). Lastly, plovers occur in the Great Plains region from Nebraska to the Canadian prairies (Haig 1992). In 2001, the species was listed as two geographically and genetically distinct subspecies *C. m. melodus* (Eastern population) and *C. m. circumcinctus* (Great Plains population and Great Lake population; Haig & Elliot Smith 2004). Piping plovers have been recorded on wintering grounds along the southern Atlantic coast of North America, Gulf of Mexico, Bermuda, Bahamas, Virgin Islands, and the West Indies (Haig & Oring 1988).

Breeding ecology

Typically, adults arrive on the breeding grounds in late April or early May. During the 3-4 month breeding season, piping plovers are generally monogamous (Haig 1992) but will switch mates between breeding seasons (Weins & Cuthbert 1988). If a mate is retained from the previous breeding season it does not appear to be due to the outcome of previous breeding attempts (Weins & Cuthbert 1988). Piping plovers create small scrapes in the ground (1-2 cm in depth; 9-10 cm diameter; Haig 1992) which are used as nests. The female typically lays 4 eggs approximately 36 hours apart, resulting in a 7 day laying period. The eggs are incubated for approximately 28 days by both sexes

(Wilcox 1959; Haig 1992). However, the relative contribution to incubation by each member of the breeding pair has not been documented (Haig 1992). Typically, piping plovers raise only one brood per year, although Bottilla (1997) did document double brooding within in a season. As the breeding season comes to an end in late July and early August, plovers begin to flock in preparation for migration (Cairns 1982; Prindville-Gaines & Ryan 1988)

Plover young leave the nest soon after they hatch. Both parents brood chicks until approximately 10 days after hatch (Haig 1992) and remain vigilant over chicks until they fledge. Female desertion of the young after the eggs hatch has been reported (Haig 1992). The estimated age of fledging (age at which young are capable of flight) is between 21 and 28 days (Prindville-Gaines & Ryan 1988; Haig 1992). Increased chick mortality has been observed to occur within the first 10 days after hatch (Patterson et al. 1991; Loegering & Fraser 1995; Jung et al. 1998; Murphy et al. 2000), however daily survival rates of chicks prior to fledge have only been reported in a few studies (Loegering & Fraser 1995; Prindville-Gaines & Ryan 1988; Patterson 1991). Survival to fledge and the age at which fledging occurs is influenced by habitat type and food availability (Murphy et al. 2000; Loegering & Fraser 1995).

Conservation Status

Over the past century, the piping plover population has fluctuated throughout its range (CWS 2002). Over-hunting in the early 1900s caused a decline; however evidence of recovery were reflected in a population increase during the 1920s (Haig 1992). In 1945, records indicated a decline in the North American piping plover population. In 1978, the species was listed by the Committee on the Status of Endangered Wildlife in

Canada (COSEWIC) as “Threatened”. In 1985, the species was re-classified as “Endangered” due to continued population declines (Haig 1985). The United States Fish and Wildlife Service lists the Great Lakes population as endangered and the remaining populations as threatened (Haig 1992). Current estimates suggest that the piping plover population consists of about 6,000 individuals. The International Piping Plover Breeding Pair Census results indicate that the piping plover population is declining at an annual rate of 1-3% (Haig & Plissner 1993, Plissner & Haig 2000). Additional estimates of an annual decline have been proposed based on the outcomes of population models (6.2%, Larson et al. 2002; 7.6%, Ryan et al. 1993)

Low reproductive success is thought to be the primary cause of the population decline in the Great Plains (Murphy et. al. 2000). Limiting factors are presumed to include predation, habitat alteration and destruction, water management, weather, and food availability and contamination (Haig 1992; Niver 2000). Population models based on current reproductive rates by birds nesting in the Great Plains suggest that the persistence of the population is low (Plissner & Haig 2000; Ryan et al. 1993). A number of productivity estimates for population stability have been proposed. Prindville-Gaines and Ryan (1988) estimated that a productivity rate of 1.15 - 1.44 chicks/pair/year is required to stabilize the Great Plains population. Ryan et al. (1993) constructed a demographic population model using an adult survival rate derived from a mark recapture study (Root et al. 1992). The results of this study suggest an annual fledging rate of 1.13 chicks/pair is required to stabilize the population. Furthermore, the results of a meta-population viability analysis suggest that 1.7 chicks/pair/year is required for a stable population (Plissner & Haig 2000). Larson et al. (2002) revised Ryan et al.’s (1993)

stochastic population simulation model by incorporating the most recent estimate of adult survival (0.737; Larson et al. 2000). This model accounted for differences in reproductive rates between alkali and freshwater habitats, resulting in an estimated productivity rate of 1.25 chicks/pair/year to stabilize the Great Plains population (Larson et al. 2002). This productivity estimate has been adopted as the goal for species recovery by the Canadian Piping Plover Recovery Plan (Goossen et al 2002).

The Great Plains breeding population is thought to provide the best opportunity for long-term conservation of the species due to the relatively small human population and large locally concentrated populations of piping plovers (Prindville-Gaines & Ryan 1988). However, inadequate information currently exists regarding productivity and breeding biology (Murphy et al. 2000). The Great Plains region provides habitat for 49.9-63.2% of the North American population (Skeel 1991, Skeel 1996, Dunlop 2001). Much of the recent work has concentrated on productivity of managed basin systems or freshwater lakes (Jung 1998, Goossen 1995; Niver 2000; Haig 1988 a, b). Reproductive success has been documented at relatively few alkali lakes, despite the fact that alkali lake habitat supported 62%-84% of piping plovers recorded during the previous International Breeding Piping Plover Censuses (Haig & Plissner 1993, Plissner & Haig 2000). Work on populations breeding on alkali lakes has been conducted at Big Quill Lake, Saskatchewan (Whyte 1985), Lostwood, North Dakota and Stateline, Montana (Murphy et al. 2000) and Williams Preserve, North Dakota (Pridville-Gaines & Ryan 1988; Mayer & Ryan 1991). Chaplin Lake is a large alkali lake in southern Saskatchewan and has supported up to 22% of the provincial population and 3.5% of the continental

population (Skeel, 1996). Despite the importance of Chaplin Lake, it has received little research attention (Dundas 1999).

Objectives:

The objectives of my study were to 1) document reproductive success and 2) determine the relative contribution to incubation by male and female breeding piping plovers at Chaplin Lake. The data come from three consecutive breeding seasons 2002, 2003 and 2004. The specific objectives of my research were to:

1. Investigate the general reproductive ecology of piping plovers breeding at Chaplin Lake. I report nest initiation dates, clutch sizes, hatching success, and nest and brood survival.
2. Quantify the relative contribution of males and females to incubation. I tested the null hypothesis that parental care is shared equally among males and females.

By coupling measures of reproductive success and parental care, I expected to provide insight into the selection pressures placed on the breeding biology of piping plovers.

The two chapters of my thesis address the two objectives in turn. The thesis is organized in a manuscript style as 2 stand-alone chapters plus a general Introduction and Conclusion section. Thus, some material is repeated among chapters in terms of introductory material, methods, and references.

1.1 LITERATURE CITED

Alcock J. 1998. *Animal Behavior: an evolutionary approach*, 6th edition. Sinauer Associates, Massachusetts.

- Armstrong D. P., E. H. Raeburn, R. G. Powelsland, H. H., B. Christensen & J. G. Ewen. 2002. *New Zealand Journal of Ecology* 26, 1-13.
- Berg, A., T. Kubberg & K. G. Kallebrink. 1992. Hatching success of lapwings on farmland: differences between habitat types and colonies of different sizes. *The Journal of Animal Ecology* 61, 469-476.
- Burger J., I. C. T. Nisbet, C. Safia & M. Gochfeld. 1996. Temporal patterns in reproductive success in endangered roseate tern (*Sterna dougallii*) nesting on Long Island, New York and Bird Island, Massachusetts. *Auk* 113, 131-142.
- Beintema, A.J. & G. J. D. M. Muskens. 1987. Nesting success of birds breeding in dutch agricultural grasslands. *The Journal of Applied Ecology* 24, 743-758.
- Bottilla, G.E. 1997. Piping Plovers produce two broods. *Wilson Bulletin* 109, 337-339.
- Brunton, D.H. 1988. Sexual differences in reproductive effort: time activity budgets of monogamous killdeer, *Charadrius vociferus*. *Animal Behaviour* 36, 705-717.
- Cairns, W.E. 1982. Biology and behaviour of breeding Piping Plovers. *The Wilson Bulletin* 94, 531-545.
- Canadian Wildlife Service. 2002. Piping Plover Conservation Plan for Lake Diefenbaker. Unpublished Report. 43pp + Appendices.
- Charnov E. L. & J. R. Krebs. 1974. On clutch size and fitness. *Ibis* 116, 217-219.
- Clutton-Brock, T.H. 1988. *Reproductive Success. Studies of individual variation in contrasting breeding systems*. (Eds T, H. Clutton Brock). University of Chicago Press, Chicago, USA. Pp 1-10.
- Clutton-Brock, T.H. 1991a. *The evolution of parental care*. Princeton University Press.
- Clutton-Brock, T.H. 1991b. Parental Investment. in *Behavioural Ecology* Eds J.R. Krebs and N.B. Davies. Blackwell Scientific Publications, Oxford.
- Deeming, D.C. 2002. Importance and evolution of incubation in avian reproduction. Eds D. C. Deeming. In: *Avian Incubation* pp. 1-7.
- Drietz V. J., W. M. Kitchens & D. L. DeAngelis. 2004. Effects of natal departure and water level on survival of juvenile snail kites (*Rostrhamus sociabilis*) in Florida. *Auk* 121, 894-903.
- Dundas, H.A. 1995. Breeding habitat selection by Piping Plovers in southern Saskatchewan. MSc. Thesis. University of Saskatchewan, Saskatoon, SK.
- Dunlop, L. 2001. The 2001 International Piping Plover Breeding Census – Saskatchewan.

Saskatchewan. Unpublished report for Saskatchewan Environment and Resource Management. 22pp. + appendices

- Ens, B. J., M. Kersten, M., A. Brenninkmeijer, & J. B. Hulscher. 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* 61, 703-716.
- Evans P.R. 1991. Seasonal and annual patterns of mortality in migratory shorebirds: some conservation implications. In: *Bird Population Studies: Relevance to Conservation and Management* (Eds. C.M. Perrins, J.D. Lebreton & G .J. M. Hirons), Oxford, Oxford University Press. pp. 346-359.
- Goossen, J.P., D.L. Amirault, J. Arndt, R. Borge, S. Boates, J. Brazil, S. Brechtel, R. Chaisson, G.N. Corbett, R. Curley, M. Elderskin, S.P. Flemming, W. Harris, L. Heyens, D. Hjertass, M. Hout, B. Johnson, R. Jones, W. Koonz, P. Laporte, D. McAskill, R.I.G. Morrison, S. Richard, R. Schaffer, C. Stewart, L. Swanson, and E. Wiltse. 2002. National recovery plan for the Piping Plover (*Charadrius melodus*). National Recovery Plan No. 22. Recovery of Nationally Endangered Wildlife. Ottawa. 47pp.
- Grand J. B. & P. L. Flint 1997. Productivity of nesting spectacled eiders on the lower Kashunuk River, Alaska. *The Condor* 99, 926-932.
- Green, R.E. 1988. Effects of environmental factors on the timing and success of breeding of common snipe gallinago (Aves: scolopacidae). *The Journal of Applied Ecology* 25, 79-93.
- Grzybowski, J. A. & C. M. Pease. 2005. Re-nesting determines seasonal fecundity in songbirds: what do we know? *Auk* 122, 280-291.
- Haig S. M. & L.W.Oring. 1985.Distribution and status of the piping plover throughout the annual cycle. *Journal of Field Ecology* 56, 334-345.
- Haig, S. M. & L. W. Oring 1988. Mate, site, and territory fidelity in Piping Plovers. *Auk* 105, 268-277.
- Haig, S. M. 1992. Piping Plover. In *The Birds of North America*, No. 2 (A. Poole, P. Stettenheim and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences: Washington, DC: The American Ornithologist Union.
- Haig, S. M., and E. Elliott-Smith. 2004. Piping Plover. *The Birds of North America Online*. (A. Poole, Ed.) Ithaca: Cornell Laboratory of Ornithology.
- Hannon, S. J., K. Martin & J. O. Schieck 1988. Timing of reproduction in two populations of willow ptarmigan in northern Canada. *The Auk* 105, 330-338.
- Hauber, M. E. 2002. Is reduced clutch size a cost of parental care in Eastern phoebes (*Sayornis phoebe*)? *Behavioral Ecology & Sociobiology*. 51:503-509.

- Houston, A. I. & N. B. Davies. 1985. The evolution of cooperation and life history in the dunnock *Prunella modularis*., In: *Behavioural Ecology*. Oxford, Blackwell Scientific Publications. pp. 471-487.
- Johnson, M. & L.W. Oring. 2002. Are nest exclosures an effective tool in plover conservation? *Waterbirds* 25, 184-190.
- Kosztolányi, A. & T. Székely 2002. Using a transponder system to monitor incubation routines of Snowy Plovers. *Journal of Field Ornithology* 73, 199-205.
- Kelly, J.F. & B. Van Horne. 1997. Effects of food supplementation on timing of nest initiation in belted kingfishers. *Ecology* 78, 2504-2511.
- Keyser A. J., M. T. Keyser & D. E. L. Promislow. 2004. Life-history variation and demography in western bluebirds (*Sialia mexicana*) in Oregon. *Auk* 121, 118-133.
- Larson, M.A., M.R. Ryan & R. K. Murphy. 2002. Population viability of piping plovers: effects of predator exclosures. *Journal of Wildlife Management* 66, 361-371.
- Lazarus, J. 1990. The logic of mate desertion. *Animal Behaviour* 39, 672-684.
- Lebreton, J. D., Burnham, K. P., J. Colbert, & Anderson, D. R. 1992. Modeling survival and testing biological hypothesis using marked animals. A unified approach with case studies. *Ecological Monographs* 62, 67-118.
- Lessels, C. M. 1991. The evolution of life histories. In, J. R. Krebs, and N. B. Davies (eds.), *Behavioural ecology: an evolutionary approach* (3rd edition). Blackwell Scientific Publications, pp. 32-65.
- Loefering, J. P. & J. D. Fraser 1995. Factors affecting piping plover chick survival in different brood rearing habitats. *Journal of Wildlife Management* 59, 646-655.
- Lukacs P. M., Dreitz V. J., Knopf F. L. & Burnham K. P. 2004. Estimating survival probabilities of unmarked dependent young when detection is imperfect. *Condor* 106, 926-931.
- McNamara, J. M., T. Székely, J. Webb & A. I. Houston. 2000. A Dynamic Game-theoretic model of parental care. *Journal of Theoretical Biology* 205, 605-623.
- Moller, A. P. & R. Thornhill, 1998. Male parental care, differential parental investment by females and sexual selection. *Animal Behaviour* 55, 1507-1515.
- Murphy, R. K., M. J. Rabenberg, M. L. Sondreal, B. R. Casler & D. A. Guenther. 2000. Reproductive success of Piping Plovers on alkali lakes in North Dakota and Montana. *The Prairie Naturalist* 32, 233-241.
- Niver, R. A. 2000. An Evaluation of captive rearing as a management tool for piping

- plovers in the Great Plains. MSc. Thesis. University of Wisconsin. Madison Wisconsin, 66pp + appendices.
- Nol, E., M. S. Blanken & L. Flynn. 1997. Sources of variation in clutch size, egg size, and clutch completion dates of semipalmated plovers in Churchill, Manitoba. *Condor* 99, 289-296.
- Parish, D. M. B. & Coulson, J. C. 1998. Parental investment, reproductive success and polygyny in the lapwing, *Vanellus vanellus*. *Animal Behaviour* 56, 1161-1167.
- Patterson, M.E., J. D. Fraser & J. W. Roggenbuck. 1991. Factors affecting piping plover productivity on Assateague Island. *Journal of Wildlife Management* 55, 525-531.
- Peak R. C., Thompson III F.R. & Shaffer, T.L. 2004. Factors affecting songbird nest survival in riparian forests in a Midwestern agricultural landscape. *Auk* 121, 726-737.
- Plissner, J. H. & S. M. Haig. 2000. Viability of Piping Plover *Charadrius melodus* metapopulations. *Biological Conservation* 93, 163-173.
- Prindville-Gaines, E. & M. R. Ryan. 1988. Piping Plover habitat use and reproductive success in North Dakota. *Journal of Wildlife Management* 52, 266-273.
- Ramos, J. A. 2003. Intraspecific aggression by Roseate Tern adults on chicks in a tropical colony. *Waterbirds* 26, 160-165.
- Reid, J.M., P. Monaghan & Nager 2002c. Incubation and the cost of reproduction. In: *Avian Incubation*. (Eds D.C. Deeming) Oxford University Press, Oxford. Pages 314-326
- Reid, J., P. Monaghan, & G. D. Ruxton. 2002. Males matter: the occurrence and consequences of male incubation in starling. *Behavioral Ecology & Sociobiology*. 51, 255-261.
- Reynolds J. D. & T. Székely, 1997. The evolution of parental care in shorebirds: life histories, ecology and sexual selection. *Behavioral Ecology* 8, 126-134.
- Root, B.G., M. R. Ryan & P.M. Mayer 1992. Piping Plover survival in the Great Plains. *Journal of Field Ornithology* 63, 10-15.
- Ryan, M. R., B. G. Root & P. M. Mayer. 1993. Status of Piping Plovers in the Great Plains of North America: A Demographic Simulation Model. *Conservation Biology* 7, 581-585.
- Sarno, R. J., Clark, W.R., Bank, M. S., Prexl, W. S., Behl, M.J., Johnson, W. E. & Franklin, W.L. 1999. Juvenile guanaco survival: Management and conservation implications. *Journal of Applied Ecology* 36, 937-945

- Sheridan J. A., S. R. Beissinger & Hughes C.R. 2004. Weak associations between measures of health and reproductive success in green rumped parrotlets (*Forpus passerinus*) in Venezuela. *Auk* 121, 717-725.
- Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. *Ecology* 79, 1789-1796.
- Skeel, M. A., D. C. Duncan, and E. R. Wiltse. 1996. The 1996 International piping plover breeding census – Saskatchewan. Unpublished report for Saskatchewan Wetland Conservation Corporation and Saskatchewan Environment and Resource Management. 22pp. + appendices
- Smith, M. 1977. Parental investment: a prospective analysis. *Animal Behaviour* 25, 1-9.
- Smith R.L. 1996. *Ecology and Field Biology*, 5th edition. Harper Collins Publishing New York, USA.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Sockmann, K. W. 1997. Variation in life-history traits and nest-site selection affects risk of nest predation in the California gnatcatcher. *The Auk* 114, 324-332.
- Szekely, T. & J. D. Reynolds. 1995. Evolutionary transitions in parental care in shorebirds. *Proceedings of the Royal Society of London: Series B* 262 (1363), 57-64.
- Székely, T. & J. C. Cuthill. 1999. Brood desertion in Kentish plover: the value of parental care. *Behavioral Ecology* 10, 191-197.
- Thibault, M. & R. McNeil, 1995. Day- and night-time parental investment by incubating Wilson's Plovers in a tropical environment. *Canadian Journal of Zoology* 73, 879-886.
- Trivers, R.L. 1972. Parental investment and sexual selection. In: Sexual selection and the descent of man (Ed B. Campbell) Aldine publishing company, Chicago. pp 136-179.
- Underwood, T. J. & R. R. Roth. 2002. Demographic variables are poor indicators of wood thrush productivity. *Condor* 104, 92-102.
- Verhulst, S., J. H. Van Balen & J. M. Tinbergen. 1995. Seasonal decline in reproductive success of the great tit: variation in time or quality? *Ecology* 76, 2392-2403.
- Walk J. W., K. Wentworth, E. L. Kershner, E. K. Bollinger & R. E. Warner 2004. Renesting decisions and annual fecundity of female dickcissels (*Spiza americana*) in Illinois. *Auk* 121, 1250-1261.
- Warnock, N. & L.W. Oring, 1996. Nocturnal nest attendance of killdeer: more than

meets the eye. *Auk* 113, 502-504.

Webb, J. N., T. Szekely, A. I. Houston & J. M. McNamara .2002. A theoretical analysis of energetic costs and consequences of parental care decisions. *Proceedings of the Royal Society of London, Series B* 357, 331-340.

Westneat, D. F. 1992. Nesting synchrony by female red-wing black bird: effects of predation on nest success. *Ecology* 73, 2284-2294.

Wiens, T. P. & F. J. Cuthbert. 1988. Nest site tenacity and mate retention of the Piping Plover. *Wilson Bulletin* 100, 545-553.

Wilcox, L. 1959. A twenty year banding study of the Piping Plover. *Auk* 76, 129-152.

CHAPTER 2: REPRODUCTIVE ECOLOGY OF PIPING PLOVERS (*Charadrius melodus*) AT CHAPLIN LAKE SASKATCHEWAN

2.1 INTRODUCTION

Individual variation in reproductive success is common to all organisms (Clutton-Brock 1988; Siikamäki 1998). In birds, this variation in reproductive success has been attributed to predation (Beintema & Muskens 1987), environmental conditions (Hannon et al. 1988), disease (Sheridan et al. 2004), and anthropogenic disturbance and management (Green 1988). Environmental conditions can influence reproductive success through their effects on food availability and abundance (Ramos 2003) and initiation of the breeding period (Kelly & Van Horne 1997). Seasonal declines in reproductive success have also been well documented in a range of bird species. Seasonal declines related to date have been attributed to date of clutch initiation (Verhulst et al. 1995), parental quality (Ens et al. 1992), seasonal predation pressure (Sackmann 1997; Burger et al. 1996), livestock management (Green 1988) and seasonal food abundance (Siikamäki 1998). Much of the seasonal variation is driven by environmental (Westneat 1992) or physiological conditions (Kelly & Van Horne 1997). Understanding the underlying causes of variation in reproductive success is important in the context of the evolution, ecology and ultimately conservation of a species (Verhulst et al. 1995; Grant 2004).

Information about basic population parameters such as productivity, survival and dispersal is important to our understanding of avian population dynamics (Underwood & Roth 2002). Nest success and fledging rates are important demographic parameters in

avian studies (Armstrong et al. 2002) and are critical for predicting and understanding population declines (Miller & Knopf 1994; Lukacs et al. 2004) and the development of management strategies (Sarno 1999). Reliable estimates of productivity are generated through intensive nest searching and monitoring rather than using non-reproductive indicators, such as abundance (Underwood & Roth 2002; Vickery et al. 1992). Survival to fledging or independence is often used as an estimate of reproductive success (Armstrong et al. 2002; Dzus & Clark 1998). Fecundity is an important demographic parameter (Walk et al. 2004) and is key for assessing fitness and population viability (Grzybowski et al. 2005). Seasonal fecundity is defined as the number of offspring produced by a female in a breeding season (Grzybowksi 2005; Kershner et al. 2004). More frequently fecundity is inferred from a measure of nest productivity, such as the number of young fledged per pair, due to the difficulties in ascertaining all the reproductive activities of a female (Grzybowski 2005; Kershner et al. 2004). It is important to keep in mind however that seasonal fecundity may not equal recruitment into the breeding population (Ricklefs 1973), but in species in which young disperse from the natal territory it provides the most practical estimate of recruitment (Hoekmann et al. 2002; Clutton-Brock 1988). Overall, knowledge of a species' demographic characteristics is important for understanding factors that influence population dynamics (Stearns 1980).

For birds it is frequently of interest to estimate the daily survival rate to estimate nest success (Stanley 2000). In the past, apparent rates of nest success (ratio of successful nests to total nests found) were frequently used to determine nest success. However, this estimator of nest success has an upward bias due to the increased probability of finding nests that survive to later nesting stages (Mayfield 1961). Mayfield (1961) developed an

estimator of nest success to correct for this upward bias by basing overall nest success estimates on daily survival rates, which incorporates the amount of time a nest has been under observation. Daily survival rate is often used to determine the effects of management or as a measure of productivity (Stanley 2004). Mayfield's estimate uses data averaged within time-specific categories based on biological divisions such as nesting stage (laying, incubating, and brood rearing) or arbitrary categories (early, middle and late incubation; Grant et al. 2004). Mayfield's estimate assumes that survival is constant within the nest stage or category. Many past studies that have documented changes in survival rates as a function of nest stage have done so by comparing constant survival rates between nesting stages. Recent advances in analytical techniques (Shaffer 2004) allow for powerful analysis of explanatory variables including continuous temporal variables such as nest age or Julian date (Grant et al. 2004). Shaffer's (2004) logistic exposure method accounts for the bias previously noted by Mayfield (1961) but also provides the additional advantage of investigating explanatory variables via a logistic regression model. Past piping plover studies have employed either an apparent (Haig 1987; Whyte 1985) or Mayfield's estimate to determine nest success (Prindville-Gaines & Ryan 1988; Jung 1998; Murphy 2000) and have assumed that constant survival during the incubation period. Survival estimates that account for temporal effects, however, may provide insight into the patterns of survival over the breeding period and allow for more effective conservation efforts.

For piping plovers, reproductive success is thought to be the primary cause of population decline across the species range (Murphy et al. 2000). These declines resulted in the eventual listing of the piping plover as endangered by the Committee on the Status

of Endangered Wildlife in Canada (COSEWIC). Variation in reproductive success has been reported both within (Knetter et al. 2002) and among breeding seasons (Jung et al. 1998; Murphy et al. 2000). Factors that are thought to limit reproduction include predation, habitat alteration and destruction, water management, weather, food availability, and contamination (Haig 1992). Population models based on reproductive rates in the prairie suggest that the probability of persistence of the piping plover population is low (Plissner 2000; Ryan et al. 1993).

The Great Plains are thought to provide the best opportunity for long-term conservation of this species due to low human populations and a relatively large proportion of the piping plover population occurring there (Prindville-Gaines & Ryan 1988). Plovers are heterogeneously distributed throughout the Great Plains at low densities (Haig 1992). The International Piping Plover Breeding Census (IPPBC) indicates that the prairie supports 49%-63% of the North American breeding population (Dunlop 2001). Within the Great Plains, Saskatchewan is recognized as an important breeding region for piping plovers in that it supports up to 23% of the North American breeding population (Skeel et al. 1997). Alkali habitats supported 62% and 84% of the piping plovers recorded during the 1991 and 1996 IPPBC, respectively (Murphy et al. 2000). Despite this, few studies have measured plover productivity on alkali lakes (Prindville-Gaines & Ryan 1988; Mayer & Ryan 1991– Williams Preserve, North Dakota; Murphy et al. 2000 – Lostwood, North Dakota and Stateline, Montana; Whyte 1985 - Big Quill Lake, Saskatchewan). Furthermore, breeding pairs using alkali habitats tend to fledge more young than those nesting on freshwater reservoirs (Larson et al. 2000).

Chaplin Lake is a large alkali lake in southern Saskatchewan. Results from the IPPBC show that Chaplin Lake has supported 22% of the Saskatchewan population and 3.5% of the continental population (Skeel 1996). Despite the importance of this lake as a breeding site, relatively few studies have been conducted there (Dundas 1999). The primary objective of my study was to document the general reproductive ecology of piping plovers breeding at this site, which included quantifying the variation of nest and brood survival using continuous explanatory variables.

2.2 METHODS

Study species

The piping plover is a small migratory shorebird (mean adult mass 53 g) species that breeds on sparsely vegetated beaches of freshwater lakes and reservoirs, alkali lakes, and rivers and coastal areas of North America (Haig 1992). Typically, the female lays 4 eggs in the nest, which is a shallow scrape in the ground. Pairs are generally socially monogamous for the breeding season. They will re-nest if the first attempt fails, but typically only raise one brood per year. Both parents are known to participate in incubation (see Chapter 3) and one or both parents provide care until fledging. However, female desertion of the young after the eggs hatch has been reported (Haig 1992). Typically, eggs are laid every 36 hours resulting in a 7-day laying period, followed by a 28-day incubation period. Young fledge (age at which they are capable of flight) between 18-25 days post hatching. Breeding typically begins in early May and flocks of fledglings and adults are often seen in mid-August; however, some individuals whose nesting attempts fail may leave the breeding area earlier in the season.

Study site:

My study focused on birds nesting at Chaplin Lake, Saskatchewan (50° 26' N, 106° 40' W) during the 2002-2004 breeding seasons. Chaplin Lake is a large saline lake in the Missouri Coteau region covering approximately 11,777 ha (178 km²). High salinity of the lake is due to a glacial sodium sulfate deposit. The lake is composed of 10 interconnected basins, which are used to manage water levels. The water levels are managed for the commercial extraction of sodium sulfate (Fig. 2.1) and are regulated by the solution mining operation as well as by natural precipitation and evaporation. Water levels vary both between and within years, but water management ensures that there is shoreline habitat available to plovers even in drought years. Typically, the highest water level occurs in spring and declines as the summer progresses. The width of shoreline beaches varied, but primary breeding areas typically had beaches that were approximately 100 m wide (MacDonald et. al. 2003). The beaches consist of a combination of mud, gravel and cobble; all with high alkali content (MacDonald et. al. 2003). The shorelines are mostly un-vegetated, becoming patchy with sparse vegetation towards the uplands. The dominant plant species included alkali grass (*Puccinellia nuttallinana*), salt grass (*Distichlis stricta*), seaside arrow-grass (*Triglochin maritima*) and wire rush (*Juncus balticus*; MacDonald et. al. 2003). The area surrounding the lake is predominantly native grassland pasture and wetlands. Cattle had access to all beaches but one (approx. 5 km long) along the north side of the west basin.

Nest monitoring

I conducted nest searches and monitoring from early May until mid August in each year. I attempted to locate every plover nest on the entire lake. The methodology I used followed Murphy *et. al.* (1999). Nest searches were conducted between 06:00 and 17:00. Searches were restricted to the morning (06:00-12:00) on days when the temperature was predicted to exceed 29° C in order to minimize the exposure of eggs or young to heat if parent birds flushed from the nest. Nest searches included systematic surveys of all available habitats around the lake. A complete survey of the entire shoreline was conducted at least every 5 days. During surveys, the locations of individuals and pairs were documented using a Global Positioning System (GPS). In all areas with documented individuals, especially territorial pairs, search effort was intensified to locate nests. Nests were located by finding and observing breeding pairs of adults. Nest searches were conducted on foot or by surveying from all-terrain vehicles. When all-terrain vehicles were employed, driving was limited to areas with vegetation to decrease damage to the beaches and minimize the risk of inadvertently destroying plover habitat and nests. To determine nest initiation dates for nests found during incubation, 2 eggs from each nest were floated to determine the developmental stage from which nest initiation date was back counted (Alberico et al 1995; Murphy et al 1999). Using nest initiation dates, hatching dates were predicted based on estimates of a seven-day laying period and 28-day incubation (Murphy et al 1999). Estimation of hatching dates allowed for increased accuracy in calculating nest survival (Mayfield 1975, Shaffer 2004) and success in banding young in or near the nest. Clutch initiation date was defined as the

Julian date on which the first egg was laid. I considered hatching dates to be the day that the first chick in the brood hatched. Nests were marked with a 15 cm wooden stick (1 m away from the nest) and a small (10 cm high) rock cairn (built 5 m away) placed in such a way that the cairn, wooden sticks and nests formed a straight line. The location of the nest was also recorded with a hand held GPS. Nests were checked every 3-5 days to assess success or failure. Nest attempts were considered successful if at least one egg hatched (Murphy et al. 1999; Armstrong et al. 2002).

Chicks were monitored every 2-3 days from hatching until fledging. They were caught by hand in the nest bowl or near the nest bowl soon after hatch. In 2002-2003, each chick in the brood received the same colour band combination. In 2004, chicks received band combinations that either uniquely identified each individual in the brood (individual band) or identified individuals from the same brood (brood band). To locate all chicks, 1 hour was allocated to search the area where the brood was previously located. Sites with nests where broods that were suspected to have failed were checked an additional three times before being recorded as “failed”. I considered chicks surviving to 18 days of age to have fledged (Murphy et al. 1999), but continued to monitor chicks until we could no longer locate them. Overall fledging rate was determined using the mean number of young fledged per breeding pair on Chaplin Lake (Murphy et al. 1999). The number of breeding pairs used in this calculation was based on the number of breeding pairs documented during the weekly surveys.

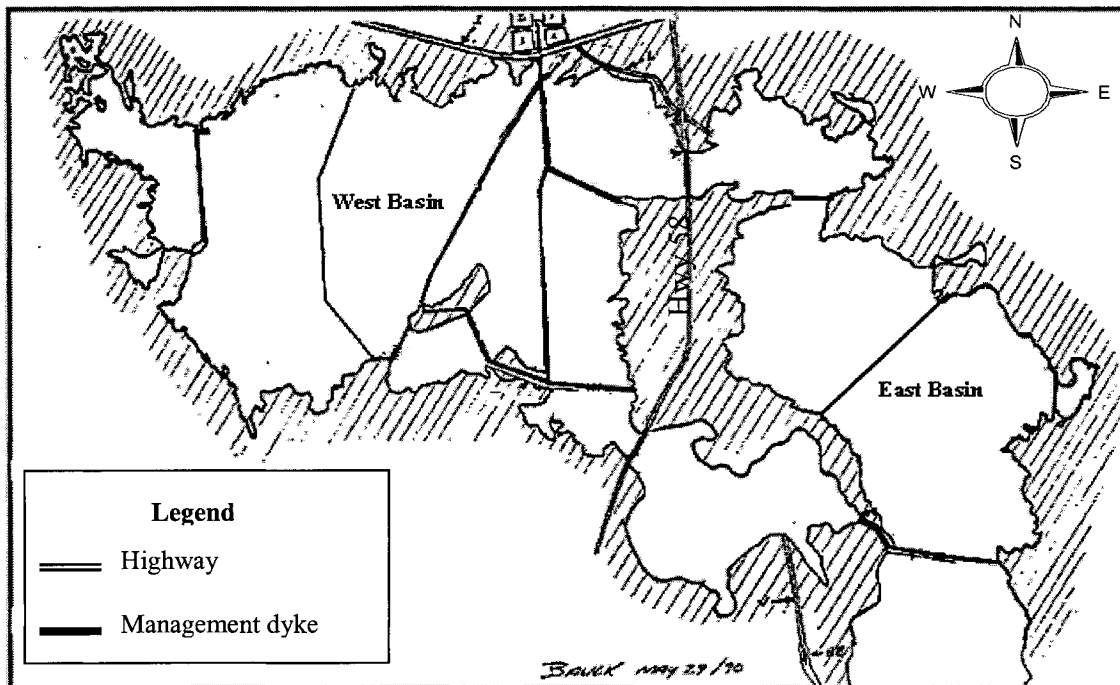


Figure 2.1. Study area at Chaplin Lake, Saskatchewan. The basin is divided into 10 Management basins. Dark lines represent dykes and grades, which divide the management basins. East and west basins are divided by a gravel road (Highway 58).

Video Monitoring

I used 4 video systems (B&E electronics Inc. Regina, SK) to monitor 23 nests during the 3 breeding seasons. Small (29 mm diameter, 74 mm long) remote colour/infrared cameras (National Electronics Bullet C/IR) were placed at randomly selected plover nests around the lake. Nests were chosen using a random number generator to select the nest number of active nests. The cameras provided colour video images during the day and black and white footage at night. Cameras were placed approximately 50 – 100 cm from the nest to balance the tradeoff between proper infrared illumination and minimizing disturbance. Cameras were hidden in an artificial rock and all cables were buried underground. Cameras were always deployed facing north to minimize glare from the sun at sunrise and sunset. Video was continuously recorded on a time lapse VCR (Sanyo Real Time SRT 2400DC or Sanyo Real Time 4040AC). The VCRs were located in protective waterproof cases 75-100 m from the nest. Rechargeable deep cycle 12-volt batteries were used to power the VCR and video camera. Video systems were operational from the time the nest was located until it was either depredated or the eggs successfully hatched. Nest checks were done both by physically checking the nest as well as remotely from the site of the VCR using a 5.6" National Electronic Colour LCD monitor. Checking remotely allowed me to test the video equipment to ensure it was working properly. I attempted to begin monitoring a nest as early in the incubation stage as possible, but I did deploy cameras at nests in the middle or late stages. Installation of video systems took approximately 20 min, after which direct observations were made to ensure that the adults returned to the nest. The University of Regina Animal Care Committee approved all protocols.

Statistical Analysis:

To determine the synchrony of nest initiation and hatching, I calculated standard deviation (Nol et al 1997; Westneat 1992). Nest success was calculated using Mayfield's estimator of nest success (Mayfield 1961, 1975) and apparent nest success to allow for comparison with previous studies. To determine nest success I calculated the daily survival rate based on the total number of exposure days and used an exponent of 35 days (7 days laying and 28 days incubation).

Nest and brood survival:

I used an information theoretic approach and the logistic exposure method (Shaffer 2004) to determine whether time-specific effects of nest/brood age, Julian date and year influenced nest and brood survival. Julian date allowed me to determine the seasonal patterns of nest and brood survival. I used generalized linear models (PROC GENMOD, SAS Institute 1999) to fit logistic exposure models for both broods and nests. Due to the binomial distribution of the Mayfield estimator, a logistic regression can be employed to explore the effects of explanatory variables on nest success (Hazler 2004). However, logistic regressions do not account for exposure time; thus, they have the same bias as apparent estimators (Shaffer 2004). The logistic exposure regression model is based on a binomial distribution (interval nest fate = 0 if failed and 1 if successful) and a logit link function to estimate daily survival (Shaffer 2004). Nest fate refers to the outcome of the nest during the monitoring interval. I considered a nest/brood “successful” if at least one egg/young survived the interval between nest visits, and

considered the nest to have “failed” if it was destroyed or abandoned (Stanley 2002). The link function included in the model was a modified logit link function ($g(\theta) = \log_e (\theta^{1/t} / [1 - \theta^{1/t}])$; Shaffer 2004), where θ is the interval survival rate and t is the length of the interval in days. The logit function for this logistic regression was modified to account for monitoring intervals that were greater than 1 day and varied in length. Each monitoring interval for a nest was treated as an observation and the mid-point age (days) and date (Julian date) was determined for each interval (Shaffer 2004). This allowed for the modeling of nest age and date by allowing the values to change among monitoring intervals, but the value was assumed to remain constant within that interval (Shaffer 2004). This method differs from the Mayfield method in that constant survival is not assumed and known date of failure is not required (Schaffer 2004). The interval ending with the date on which the nest was last active was used for monitoring intervals where fate was unknown (Manolis 2000). The halfway point of the monitoring interval was used for nests with known fate (Johnson 1979). My analysis was conducted on a per nest and per brood basis to avoid the complication of the lack of independence between eggs/chicks in a brood (Dzus & Clark 1998).

I considered models with the lowest Akaike’s Information Criterion score corrected for small sample size (AIC_c) to be the best models fitting the data. I used the effective sample size (Rotella et al. 2004) to determine AIC_c and ranked models for each reproductive stage from most to least supported (Burham & Anderson 2002). I calculated ΔAIC_c , the difference between the lowest observed AIC_c value and the best model, to rank the candidate models (Burnham & Anderson 2002). The larger the AIC_c value the less plausible it is the best model. Generally, ΔAIC_c of 0-2 suggest that the models have

substantial support based on the data (Burnham & Anderson 2002). In addition, AIC weights (ω_i) were calculated and provide a measure of support for the current model (Burnham & Anderson 2002). I used the AICc weights to calculate model averaged parameter estimates and unconditional standard errors (Burnham & Anderson 2002). AIC is based on the principle of parsimony, that is the model of best fit with the fewest number of parameters that provides an adequate explanation for the data is chosen (Burnham & Anderson 2002).

I established a set of 20 *a priori* nest survival models, which included linear effects of age, date and year, and quadratic effects of age and date. Quadratic models included both a linear function (x) and a quadratic function (x^2). The set of candidate models also included a null model of constant survival and a global model. I tested for camera effects by comparing the best time-specific model with and without camera effects. A set of 23 models were used to test camera effects. This analysis was repeated to determine whether brood survival varied as a function of year, nest age and date. I established a set of 19 candidate brood models that included the same temporal variables as used for nest survival.

2.3 RESULTS

I located 36, 41 and 75 nests during 2002, 2003 and 2004, respectively (Table 2.1). Nest initiation dates varied among years. The median nest initiation date in 2002 was 18 days later than in 2003 and 10 days later than in 2004 (Fig. 2.2). Nesting was generally synchronous in all three years, with standard deviations of 9.7 days, 10.2 days and 11.3 days for the 3 years, respectively. The duration of the incubation period ranged

from 22 - 38 days and was similar among years with an overall mean of 28.03 ± 2.6 days (Table 2.1). Hatching date chronology reflected the pattern observed for clutch initiation dates. The median hatching date for 2002 was 14 days and 7 days later than the median hatching dates from 2003 and 2004, respectively (Fig. 2.3). Hatching was also synchronous with standard deviations of 7.7 days, 8.3 days and 11.2 days for 2002, 2003 and 2004 respectively.

Nest fate was known for 34 of the 36 nests I monitored in 2002, 40 of 41 nests in 2003 and all 75 in 2004. Predation was the major cause of nest failure, accounting for the majority of nest failures (Table 2.1). Additional causes of nest failure included abandonment, livestock trampling, and flooding. Of the abandoned nests recorded in 2002, one was deserted at the 2-egg stage after a video monitoring system was deployed, while the second nest contained 4 eggs and reasons for abandonment were not apparent. The nest abandoned in 2004, contained 4 infertile eggs and had a prolonged incubation period. Nests with unknown fate were those for which I could not identify the cause of nest loss or the nests could not be relocated. Clutch size was similar among years (Table 2.2). The proportion of hatched eggs varied among years (Table 2.2), but 86-87% of the eggs laid in successful nests ultimately hatched. Post hatch abandonment, infertile eggs, and partial predation accounted for most egg losses in successful nests (Table 2.2).

Table 2.1. Nest fate of piping plovers at Chaplin Lake, 2002-2004. Data presented are the total number of nests (n), the mean incubation length (\pm SD), daily survival rate, Mayfield nest success, number of successful, depredated, trampled, flooded, and abandoned nests and nests with unknown fate.

Year	2002	2003	2004
n	36	41	75
Incubation Length (\pm SD)	27.3 \pm 2.1	28.3 \pm 1.9	28.5 \pm 3.2
Mayfield's Daily Survival Rate	0.98 \pm 0.01	0.99 \pm 0.01	0.97 \pm 0.02
Mayfield nest success	51%	77%	33%
Successful nests (%)	23 (63 %)	36 (87%)	40 (53%)
Depredated (%)	7 (19%)	4 (10%)	28 (38%)
Trampled (%)	-	1 (2.4%)	1 (1.3%)
Flooded (%)	1 (2.7%)	-	4 (6.7%)
Abandoned (%)	2 (5.5%)	-	2 (2.6%)
Unknown (%)	3 (8.3%)	1 (2.4%)	-

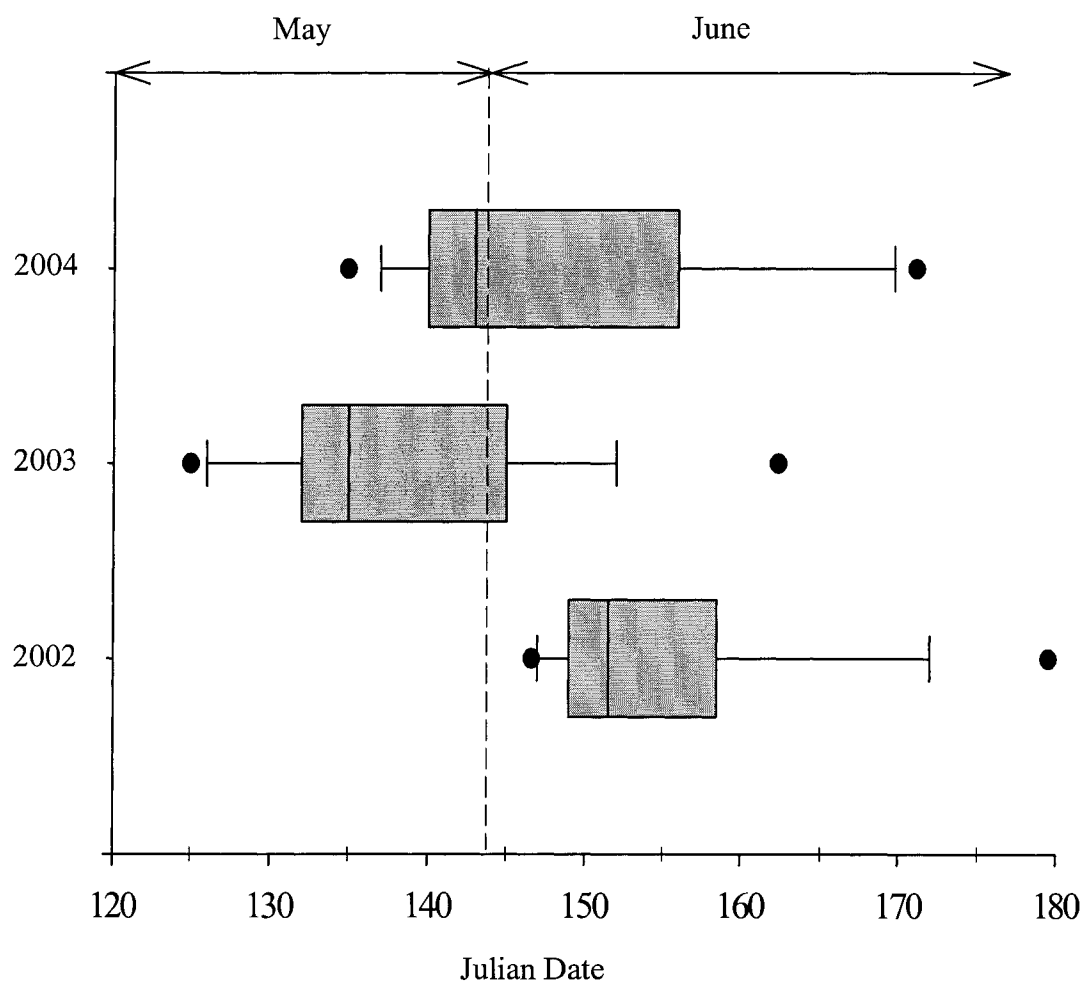


Figure 2.2. Temporal pattern of nest initiation on Chaplin Lake; 2002- 2004. Box plots illustrate distribution of nest initiation dates. Middle lines represent the median, boxes represent the quartile range, whiskers represent the 90th and 10th percentile and dots represent the 5th and 95th percentiles. The dotted line divides the months of May and June.

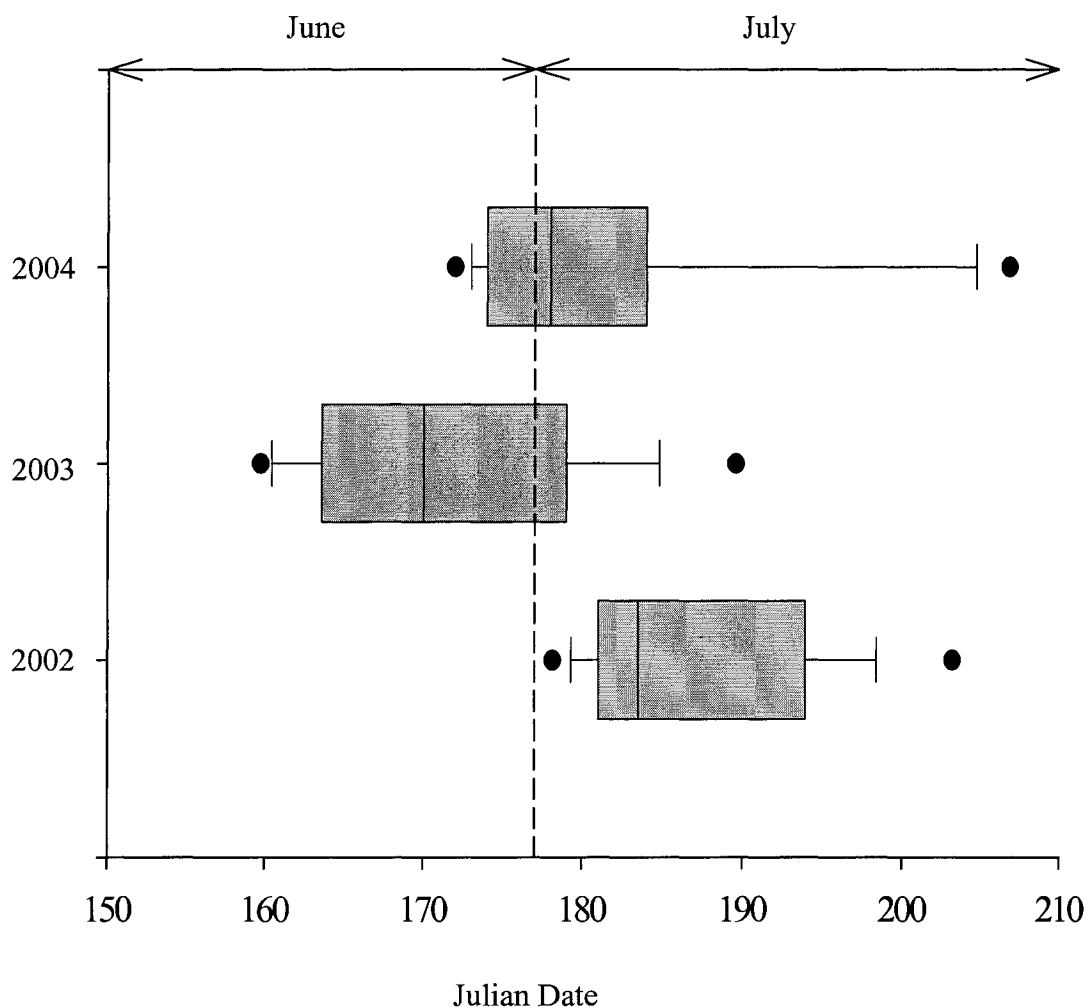


Figure 2.3. Temporal hatching pattern of piping plover eggs at Chaplin Lake, 2002- 2004. Box plots illustrate distribution of hatching dates. Middle lines represent the median, boxes represent the quartile range, whiskers represent the 90th and 10th percentile and dots represent the 5th and 95th percentiles. The dotted line divides the months of June and July.

Table 2.2. Piping Plover clutch size and egg fate at Chaplin Lake, 2002-2004. Data presented as the mean clutch size (\pm SD) and the total number of eggs laid. Egg fate is presented as the number and percent of eggs lost to partial predation, known accidental egg removal, and post hatch abandonment. The development stage of abandoned eggs is presented as the number of eggs. In 2002, the numbers of post hatch abandoned eggs and development stage were not recorded.

Year	2002	2003	2004
Clutch Size	3.5 \pm 0.9	3.6 \pm 0.7	3.7 \pm 0.7
Total eggs laid	136	145	277
Eggs hatched (%)	73 (54)	113 (77)	130 (47)
Partial Predation (%)	8 (11)	9 (8)	5 (4)
Accidental egg removal (%)	1 (1.0)	1 (1)	1 (0.5)
Post-Hatch Abandonment (%)	-	6 (4)	13 (9)
Unfertilized	-	3.0	6.0
Partially developed embryo	-	1.0	3.0
Developed Embryo	-	2.0	4.0

One hundred and fifty-two nests were monitored over the 3-year study period resulting in 602 monitoring intervals. Nest survival was most influenced by year, and date (Table 2.3). Daily survival rates of the nest decreased as the breeding season progressed (coefficient estimated -0.14 ± 0.20). The daily survival rates in 2003 (coefficient estimate 1.29 ± 0.49) and 2002 (coefficient estimate 1.25 ± 0.40) were similar. However, daily survival rates were higher in 2003 and 2002 when compared to 2004. The null model of constant survival was ranked 18th of the 20 models (Table 2.3). Furthermore, when video monitoring was added to the set of candidate models the most supported model included year, date and video effects. The presence of video cameras had a positive effect on nest survival. Nest survival for video monitored nests was 87% (DSR = 0.99 ± 0.04) compared to 53% (DSR = 0.98 ± 0.02) for non-video nests. Based on Mayfield's estimate of daily survival, nest success for 2002, 2003, and 2004, was 51%, 77% and 33%, respectively (Table 2.1).

During the three-year period, 220 young from 94 broods were banded using Murphy et al.'s (1999) formula to calculate fledging rate, plovers at Chaplin Lake produced 0.69 chicks/pair in 2002 (n = 36), 0.75 chicks/pair in 2003 (n = 41) and 0.86 chicks/pair in 2004 (n=75; Table 2.4). Despite the slight increase in the fledging rates during the past 3 years, the rate remains lower than the recovery goal of 1.25 chicks/pair. However, my calculated rates may be biased due to the difficulties in determining the exact number of breeding pairs; consequently, my data for fledging rates represent a conservative minimum estimate.

Table 2.3. Selection results for models explaining variation in nest survival as a function of time-specific effects for piping plovers at Chaplin Lake. Models include the best model (lowest AICc value), candidate models within $\Delta 2$ AICc units from best model, and null (constant survival) models. Values for the global model and the null (constant) model are included for comparison. YEAR is the linear effect of year. AGE is the linear effect of age, AGE² is the quadratic polynomial effect of age. DATE is the linear effect of date, DATE² is the quadratic polynomial effect of date. The global model included linear effect of year, age, date and an interaction of age and date in addition to quadratic age and date. A total of 20 models were considered. Effective sample size was 2373 intervals.

Model	K	AIC _C	Δ AICc	ω_i
YEAR + DATE	4	379.29	0.00	0.21
YEAR + DATE + AGE ²	6	379.89	0.60	0.16
YEAR + DATE ² + AGE ²	7	380.05	0.76	0.14
YEAR + DATE + AGE	5	380.14	0.88	0.14
DATE ² + YEAR	5	380.48	1.22	0.11
GLOBAL MODEL	8	380.77	1.48	0.10
YEAR + DATE ² + AGE	6	380.95	1.66	0.09
NULL (Constant)	1	402.624	28.1479	0.00

Table 2.4. The number of piping plover young banded and monitored at Chaplin Lake, 2002-2004. Data are presented as the number of broods to receive bands, broods monitored, banded young, successful broods and the mean number of chicks fledged per monitored brood (\pm SD) and the mean number of chicks fledged per breeding pair.

Year	2002	2003	2004
Broods received bands	19	34	41
Number of monitored broods	17	34	41
Number of banded young	51	75	94
Number of successful broods	8	16	34
Chicks fledged/brood	1.5 \pm 0.4	1.1 \pm 1.3	1.6 \pm 1.2
Chicks fledged/breeding pair	0.69	0.75	0.86

A total of 92 broods were monitored from 2002-2004, resulting in 356 monitoring intervals. The model with the most support was $\text{Date}^2 + \text{Age} + \text{Year}$ (Table 2.5). Age had a positive influence on survival and was found in all the top models (Fig. 2.3). Brood survival also varied as a function of date with daily survival rates being high initially and then declining followed by an increase later in the season (Fig 2.4). Lastly, year effects suggest that 2003 (coefficient estimate = -0.52 ± 0.22) had lower daily survival rates than 2004 while 2002 (coefficient estimate = 0.18 ± 0.38) had higher daily survival rates than 2004. The null model of constant survival was the least supported of all 19 models.

Table 2.5. Selection results for models explaining variation in brood survival as a function of time-specific effects for piping plovers at Chaplin Lake. Models include the best model (lowest AICc value), candidate models within $\Delta 2$ AICc units from best model, and null (constant survival) model. Values for the global and null (constant) models are included for comparison. AGE is the linear effect of age, DATE is the linear effect of date, YEAR is the linear effect of year, AGE² is the quadratic polynomial effect of age, and DATE² is the quadratic polynomial effect of date. The global model included linear effect of year, age, and date in addition to quadratic age and date. A total of 19 models were considered. Sample size (effective sample size) was 1251 intervals.

Model	K	Δ AICC	AIC _c	w_i
AGE + DATE ² + YEAR	6	257.8	0.0	0.32
AGE + DATE ²	4	259.5	1.7	0.14
GLOBAL MODEL	7	259.8	2.0	0.12
NULL (Constant)	1	294.4	36.6	0.00

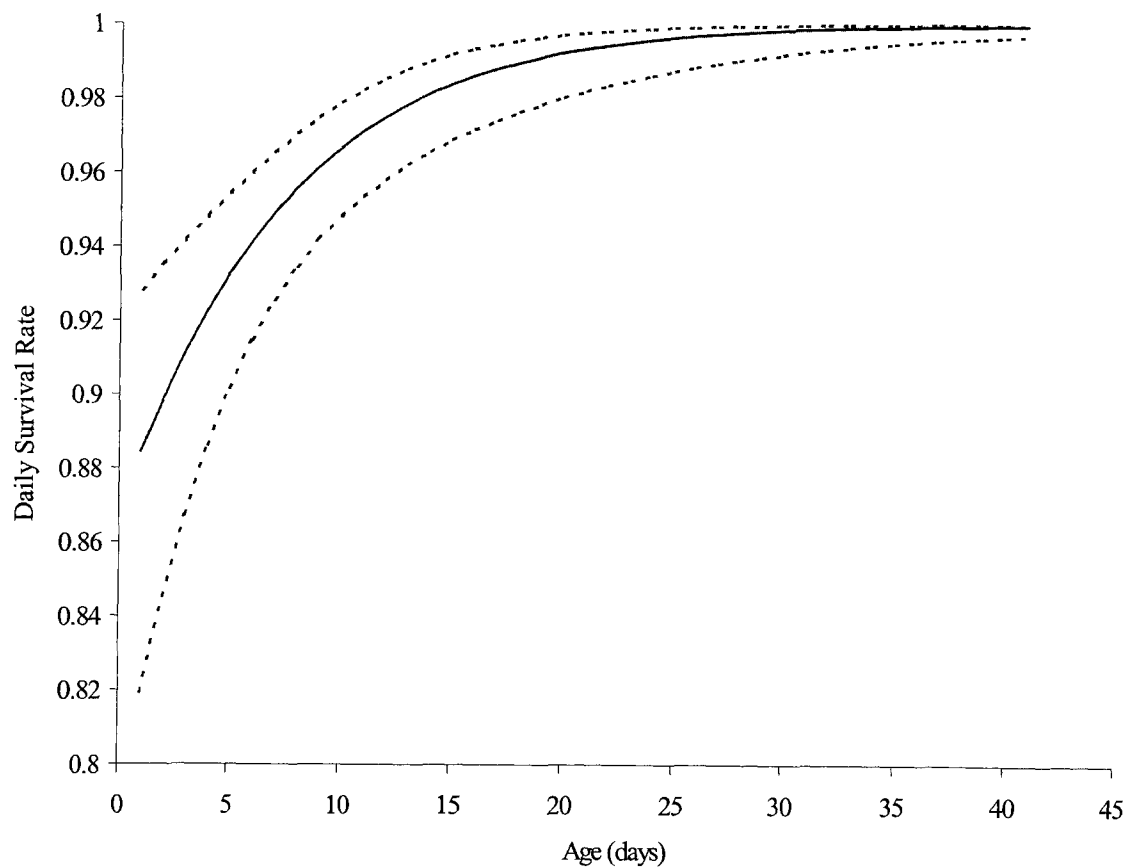


Figure 2.4. The daily survival rate of piping plover broods increases with brood age (days) at Chaplin Lake, 2003-2004. The dashed lines represent the 90% confidence intervals.

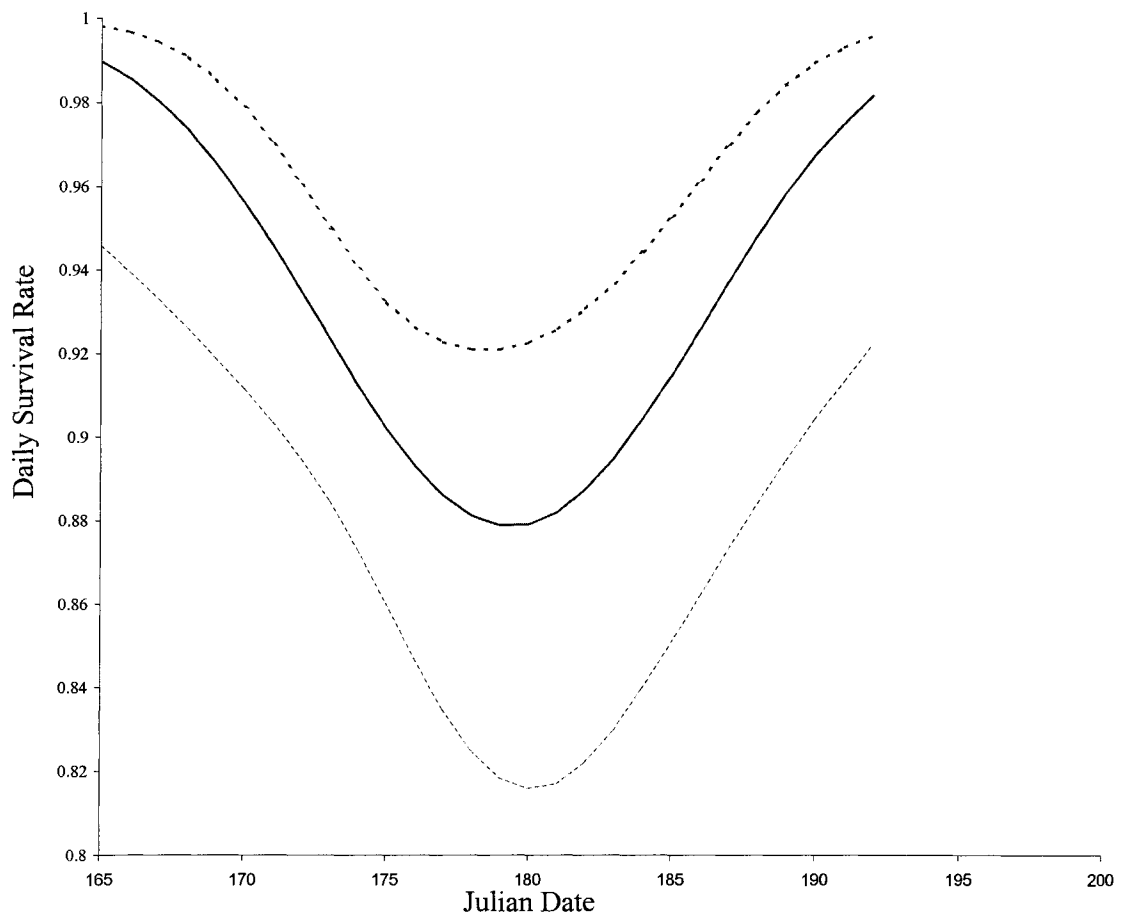


Figure 2.5. The daily survival rate for piping plover broods in relation to date at Chaplin Lake, 2002-2004. Dashed line represents the 90% confidence intervals.

2.4 DISCUSSION

Monitoring reproductive success of piping plovers at Chaplin Lake for 3 years allowed me to document annual variation in breeding chronology, nest survival and brood survival. This is the first analysis of piping plover nest survival and brood survival using continuous temporal variables. Nest survival was not constant throughout the laying and incubation period, rather I found that it was influenced by date and year. Brood survival was also not constant and varied as a function of age and date. Overall, fledging rates ranged from 0.69-0.86 chicks per pair, which is below the goal of 1.25 chicks/pair proposed for population stability for the Northern Great Plains population (Goossen et al 2002).

Chronology and breeding synchrony have been shown to influence reproductive success (Parsons 1975; Siikamaki 1998; Verhulst et al. 1995; Westneat 1992). Nests on Chaplin Lake were typically laid in mid May (2nd and 3rd weeks of May), which is similar to the reports from other areas of Saskatchewan, Manitoba, Nova Scotia, and North Dakota (Haig 1992). Nest initiation dates were synchronous at Chaplin Lake, however initiation dates in 2002 were delayed relative to both 2003 and 2004 (Fig. 2.2). This delay was also reflected in delayed hatching dates. Many factors are thought to influence nest initiation dates including age, habitat quality, availability of mates, length of the breeding season, body condition (Kelly & Van Horne 1997), spring weather conditions (Hannon et al. 1988; Nol et al. 1997; Westneat 1992), prey abundance (Nol 1997; Verhulst et al. 1995), and predation rates (Verhulst et al. 1995). Synchronous breeding may also act as an anti-predator strategy, swamping predators with eggs or young (Parsons 1975; Westneat 1997). The delay in piping plover breeding in 2002 was likely the result of poor

springtime conditions (Prairie Farm Rehabilitation Administration, drought watch www.agr.gc.ca/pfra/drought). Cool springtime temperatures and extremely dry conditions possibly influenced habitat quality and prey abundance. The delayed nest initiation date in 2002 resulted in higher nesting synchrony compared to 2003 and 2004. This trend for higher nest synchrony when breeding is delayed due to poor conditions has been documented in other avian species (Westneat 1992).

Mean clutch size in temperate and arctic nesting shorebirds is 4 eggs, while 3 eggs are often found in tropical nesting shorebirds (Walters 1984). The clutch size on Chaplin Lake did not differ between years. The clutch sizes I found are similar to clutch sizes reported from other breeding locations in Saskatchewan (3.3 eggs, Whyte 1985; 3.9, Jung 1998), North Dakota (3.5-3.7 eggs, Prindville-Gaines and Ryan 1988), New York (3.8 eggs, Wilcox 1959); New Jersey (2.8-3.9 eggs, Burger 1987), and Nova Scotia (3.9 eggs, Cairns 1982). One nest in 2004 had 5 eggs, this clutch size is rare but has been documented before (Haig 1992). Clutch size in shorebirds is conservative and typically does not vary within or between seasons (Szekely et al. 1994), and is thought to maximize the efficiency of incubation heat transfer (Norton 1973). Reduction in clutch size as a result of poor weather conditions on the breeding grounds has been recorded in two arctic nesting species; semipalmated plovers (*Charadrius semipalmatus*; Nol 1997) and grey phalaropes (*Phalaropus fulicarius*; Kistchinski 1975). However, reduced clutch size has rarely been documented because shorebirds may fail to breed in poor conditions (Pitelka & Holmes 1974; Gratto-Trevor 1991).

The duration of incubation has been reported in relatively few studies. A 28-day incubation period has been used for the calculation of daily survival rates in piping

plovers (Murphy 1991). The incubation length at Chaplin Lake over the past three years did not differ among years and was found to be 28 days, consistent with incubation periods reported by Whyte (1985; Big Quill Lake), Cairns (1977; Nova Scotia) and Wilcox (1959; New York). However, Haig and Oring (1988) reported a shorter incubation period of 25.7 days at Lake Manitoba.

The number of nests I monitored at Chaplin Lake increased from 36 to 75 over the 3 years of monitoring. This could be indicative of an increase in the breeding population, but it may also indicate changes in habitat availability, researcher ability or effort (i.e. detectability; Keyser et al. 2004). Annual variation in breeding populations have been reported in previous studies (Murphy et al. 2000; Murphy et al. 2001; Canadian Wildlife Service 2002) and shifts in the abundance of breeding plovers have been documented in the International Breeding Piping Plover Census (e.g., 2001; Dunlop 2001). Shorebirds are highly mobile and opportunistic and may concentrate or disperse in response to habitat availability (Gratto-Trevor 2001). Movement in response to habitat availability results in variable numbers of breeding piping plovers on the lake. An increase in the breeding population between 2002 compared to both 2003 and 2004 is supported by an increase in the total number of individuals recorded during the annual Chaplin Lake census (Davis & McMaster 2003; White 2003, 2004). However, the census revealed no increase in the total population on the lake between 2003 and 2004. As a result, the increased number of monitored nests during the 2004 breeding season may reflect the high nest failure in 2004. Piping plovers will replace clutches if the first nesting attempt fails; however, it was difficult to determine if late nests were re-nesting attempts made by unbanded birds. It is likely that most of late nests were re-nests since

they were located in areas that had high rates of predation and were located within an appropriate time frame. The increase in the number of nests in 2004 may have also been related to the researcher ability. Increased experience with the study system may have increased detection rates (Sauer et al. 1994).

Mayfield nest success rates at Chaplin Lake varied from 32% in 2004 to 77% in 2003, with a mean of 53%. Prindville-Gaines & Ryan (1988) reported rates of 41% and 42% in 1984 and 1985 respectively in Williams Preserve, North Dakota. Piping plovers breeding on Chaplin Lake had a higher nest success rate than reported from alkali lakes in Stateline and Lostwood regions of ND and MT (mean = 38%; range 16% - 53%; Murphy 2000), and Lake Diefenbaker, SK (29% for 1997; Jung et al. 1998). Predation was the major cause of nest failure at Chaplin Lake during the 3 years of monitoring, accounting for 60-85% of failed nests. Overall, nest success at Chaplin Lake was relatively high compared to other sites.

Partial predation and un-hatched eggs accounted for 13 - 22% of all eggs laid in a year. Partial nest predation alone accounted for 4.5 - 11.0% of the eggs laid in successful nests. In each of the three years, my analysis of video footage indicates that one egg was lost due to accidental parental removal. In each case, the egg adhered to the belly feathers and was carried away by the incubating adult. This type of accidental parental removal of eggs from the nest may be mistakenly classified as partial predation. In 2 of the 3 events the adult searched for the egg within the video camera field of view. In one case the egg was incubated where it fell and successfully hatched. In the second case the egg was rolled back into the nest bowl but the egg was damaged and did not hatch. In the third event, the adults did not search for the egg within the field of view of the camera and was

not located during the next nest check. Similar observations of accidental parental egg removal have been documented in black stilts (*Himantopus novaezelandiae*), black fronted terns (*Sterna albobriata*), and banded dotterels (*Charadrius bicinctus*; Sanders & Maloney 2002).

Often the goal of nest success studies is to understand how nest success varies in response to a change in one or more explanatory variables (Shaffer 2004; Hazler 2004). In many cases, assuming a constant rate of survival may be unrealistic and the modeling of time or age specific survival reveals biologically meaningful patterns (Manly & Schumtz 2001; Grant et al. 2004). However, the assumptions of Mayfield's estimator have limited our ability to explore the effect of these continuous explanatory variables. New analytical techniques such as the logistic exposure method allow for the incorporation of explanatory variables (Shaffer 2004). The results of my analysis suggest that the assumption of constant survival of piping plover nests and broods is inappropriate (Table 2.2 & 2.3). However, the estimates provided by the logistic exposure method can be directly compared with results from studies that report Mayfield's daily survival rates (Shaffer 2004). This approach allowed me to determine biologically meaningful trends in the daily survival rates of piping plover nests and broods, which will provide insight into the threats to reproductive success of plovers in general.

Daily survival rates of piping plovers' nests and broods on Chaplin Lake were influenced by temporal variables. Nest survival varied among years and decreased with date. I also found that video monitoring had a positive effect on nest survival. Seasonal declines in nest success have been attributed to environmental factors related to date (Ens 1992; Velhurst 1992; Berg et al. 1992), variation in predation rates (Peak et al. 2004), or

variation in cues used by predators (Peak et al. 2004). The incubation period also represents the longest of the reproductive periods (laying, incubation and brood rearing) and as a result this seasonal decline may simply reflect exposure to risk (Westneat 1992; Grant et al. 2004). The longer the nest exists the more likely it will lose eggs to predation, weather or other factors (Grant et al. 2004). Furthermore, increased nest survival associated with earlier nesting has been reported for a number of species (Siikamäki 1998; Verhulst et al. 1995). Many of the late nests at Chaplin Lake are likely re-nest attempts; these replacement clutches have a lower daily survival rate and are at increased risk of failure. Since predation accounts for the largest proportion of nest losses on Chaplin Lake it seems reasonable that the decline in the number of successful nests reflects a shift in predator pressure, in addition to the long period of exposure to risk during the incubation period. Video monitoring at Chaplin Lake confirmed that coyotes depredated 2 nests (White 2003; White 2004). However, there is little information regarding the predator community (Ivan & Murphy 2002). Further research is needed to understand the seasonal dynamics and the predator community, in addition to other date related environmental factors.

I recorded annual variation in reproductive success for piping plovers at Chaplin Lake. Annual variation in productivity has been reported for many shorebirds (Beintema & Muskens 1987; Evans 1991; Gratto-Trevor 1991; Murphy 2000; Knetter 2002; White 2004). Variation in daily survival rates between breeding seasons has been associated with shifts in the predator community (Evans 1991) or predator-prey cycles (Beintema & Muskens 1987; Westworth 2003). Predation rates on shorebird nests may be cyclical depending on prey availability. In some years ground nesting shorebird nests may

provide an alternate prey source (Evans 1991). Predation rates on crewlew sandpipers (*Calidris ferruginea*) in Siberia were related to local lemming cycles (Roselaar 1979 referenced in Beintema & Muskens 1987). Beintema & Muskens (1987) found a similar trend between predation rates on redshank (*Tringa totanus*) nests and the local vole population. In my study, low daily survival rates for nests in 2004 are likely related to predation, as predation rates were higher than the previous 2 years and accounted for most nest failures (Table 2.1). Predation rates were especially high along a 5 km stretch of beach. Of the 18 nests along this stretch only 3 hatched successfully, 13 were depredated and 2 flooded. Predation along this section of the lake accounted for 46% of the total predation events documented for Chaplin Lake in 2004. These high rates may have been indirectly caused by 2 cattle carcasses which attracted potential predators. Flocks of ring-billed gulls (*Larus delawarensis*) were commonly recorded at or near the carcasses. In addition, coyotes (*Canis latrans*) were often observed in the area and video monitoring confirmed coyote depredation of one plover nest (White 2004). Video monitoring also recorded coyotes visiting a nest along this section of beach without depredating it. Fluctuating predator pressure seems to influence annual nest success at Chaplin Lake; however, additional confounding environmental factors may also play a significant role (e.g., weather).

Video cameras have become a commonly used technique for monitoring nests. At Chaplin Lake the nests that were monitored by video cameras had higher daily survival rates in all three years than nests that were monitored by humans. Thompson (1999) found similar results for field sparrows (*Spizella pusilla*). Peitz and Granfors (2000) reported a tendency for predation to be lower on grassland passerine nests with cameras

compared to nests without camera. Other studies have found no effect of cameras on nest success (Keedwell & Sanders 2002; Sanders & Maloney 2002; Williams & Wood 2002). Keedwell & Sanders (2002) suggested that predators were not attracted directly by the presence of video equipment since predators did not initially approach the camera, rather they were likely using alternative cues to locate the nest. The cues that predators are using to select nests are unknown; some predators are attracted to novel objects in the environment (e.g., corvids), while others avoid novel objects (coyotes; see Pietz & Granfors 2000). Consequently, some predators may avoid nests with cameras (Pietz & Granfors 2000). Caution should be taken when using video data to identify a list of predators since a bias in visitation by certain species may exist (Thompson et al. 1999; Pietz & Granfors 2000).

Piping plover brood survival has been reported in only a few other published studies (Prindville-Gaines & Ryan 1988; Loegering & Fraser 1995; Patterson et al. 1991). I found that brood survival at Chaplin Lake was influenced primarily by chick age. Survival around the time of hatch was lowest but as time progressed daily survival rates increased (Prindville Gaines & Ryan 1988; Jung 1998; Murphy 2000). I documented that daily survival rates were low for the first 12 –15 days and then leveled off. Patterson et al. (1991) and Loegering and Fraser (1995) documented lower daily survival rates for chicks less than 10 days of age. Furthermore, Murphy (2000) noted that many chick losses occurred in the first 5 days after hatch. Increased mortality of young individuals has also been reported in other bird species with precocial young (Grand & Flint 1997; Dzus & Clark 1998; Schekermann & Visser 2001). The decreased daily survival rates of young piping plovers have been attributed to a lack of food (Loegering & Fraser 1995)

and levels of disturbance (Patterson et al. 1991). Loegering & Fraser (1995) suggested that high levels of mortality may be due to starvation or starvation-induced weakness in areas with decreased food abundance. Starvation or starvation-induced mortality has been reported in young eiders (Swenon 1989). However, this has not been investigated in piping plovers. Environmental conditions may also affect the survival of young that have not achieved thermal independence. Murphy (2000) noted a high number of deaths in young birds due to poor conditions within a couple days of hatching. This age effect may be associated with predation, poor weather conditions, or food abundance, in addition to effects caused by an interaction of these factors. It is difficult to determine the precise cause of brood loss at Chaplin Lake because no dead young were found, growth rates were not determined, and measurements of predator abundance, food availability, and parasite loads were not undertaken.

In addition to age, Julian date and year were also found to have an effect on brood survival at Chaplin Lake. A quadratic date effect influenced the daily survival rate, such that there was a decrease in daily survival corresponding to the peak hatching period in each year (Fig. 2.2). Age and date were correlated ($r = 0.533$ $p = 0.001$ $n = 418$) in all three years. There were many young chicks with low rates of survival occurring at approximately the same time each year. Therefore, the quadratic date effect may reflect the age effect. However, it is likely that this quadratic date effect reflects additional variation due to variables that were not measured. Year effects seemed to be quite weak since the standard error of the coefficient estimates were large (Table 2.4), suggesting that the same pressures are placed on broods each year. Year has been found to influence brood survival in other studies (Murphy et al. 2000; Knetter et al. 2002).

Fledging rates ranged from 0.69 to 0.86 over the 3 years of the study. These are similar to the mean fledging rates found in alkali habitat in Montana and North Dakota of 0.76 ± 0.20 chicks per pair (Stateline MT and Lostwood, ND Murphy et al. 2002), however the rates reported at Williams Preserve were higher (1.48 - 1.04 Prindville-Gaines & Ryan 1988). Overall, fledging rates at Chaplin Lake are similar to the mean fledging rate for alkali habitats used in the demographic model (Larson et al. 2002). The “alkali” fledging rate used in the model incorporated fledging rates from Mountrail and Stateline County (Murphy 2000), Williams Preserve, ND (Mayer & Ryan 1991), and Big Quill Lake, SK (Whyte 1985). Fledging rates in alkali habitats are typically higher than on river systems such as Diefenbaker Lake (1989-2001 average of 0.53 fledglings/pair Canadian Wildlife Service 2002) and the Missouri River (0.86 fledged chicks/pair; Mayer 1993). Conversely, freshwater lakes in the Great Plains appear to have higher fledging rates, with a range of 0.9 (Lake Manitoba; Haig 1987) to 1.30 (Lake of the Woods, MN; Haig & Oring 1987). Despite the slight increase in the fledging rates at Chaplin Lake over the 3 years, the rate remains lower than the recovery goal of 1.25 chicks/pair, as are the fledging rates across the Great Plains (Goossen 2002; Westworth 2003). However, my results for fledging rates likely represent a conservative estimate due to the difficulties in determining the exact number of breeding pairs.

Productivity rates of piping plovers at Chaplin Lake seem to be consistent with the productivity documented in other alkali habitats in the prairie. Despite this, fledging rates remain lower than believed to be necessary for a stable population. The results from my logistic exposure method revealed that the daily survival rates of nests and broods are not constant throughout breeding period. I determined that there was a year, date and

video effect on nest survival, while brood survival was strongly influenced by the brood age. Predation is the largest cause of nest loss on Chaplin Lake and shifts in predation rates may explain some of the annual or seasonal variability in daily survival rates; however, weather effects (which were not included in this analysis) cannot be discounted. Continued monitoring and research regarding piping plover productivity is required to understand the dynamics and threats placed on the breeding population of piping plovers at Chaplin Lake.

2.5 LITERATURE CITED

- Alberico, J.A.R. 1995. Floating eggs to estimate incubation stage does not affect hatchability. *Wildlife Society Bulletin* 23, 212-216
- Armstrong, D.P., Raeburn, E.H., Powlesland, R.G., Howard, M., Christensen, B. and Ewen, J.G. (2002). Obtaining meaningful comparisons of nest success: data from New Zealand robin (*Petroica australis*) populations. *New Zealand Journal of Ecology* 26: 1-13.
- Beintema, A. J. & G. J. D. M. Muskens 1987. Nesting success of birds breeding in Dutch agricultural grasslands. *The Journal of Applied Ecology* 24, 743-758.
- Berg, A., T. Kubberg & K. G. Kallebrink.1992. Hatching success of lapwings on farmland: differences between habitat types and colonies of different sizes. *The Journal of Animal Ecology* 61, 469-476.
- Burger, J. 1987. Physical and Social determinants of nest-site select in Piping Plover in New Jersey . *Condor* 89, 811-818.
- Burger J, I. C. T. Nisbet, C. Safia & M. Gochfeild. 1996. Temporal patterns in reproductive success in endangered roseate tern (*Sterna dougallii*) nesting on Long Island, New York and Bird Island, Massachusetts. *Auk* 113, 131-142.
- Burnham, K. P. & D. R. Anderson. 2002. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. New York: Springer Verlag Inc.
- Cairns, W.E. 1982. Biology and behaviour of breeding Piping Plovers. *The Wilson Bulletin* 94, 531-545.
- Canadian Wildlife Service. 2002. Piping Plover Conservation Plan for Lake Diefenbaker.

Unpublished Report. 43pp + Appendices.

- Cartar, R.V. & R. D. M. Montogmerie, 1985. The influence of weather on incubation scheduling of the white rumped sandpiper (*Calidris fuscicollis*): A uniparenal incubator in a cold environment. *Behaviour* 95, 261-289.
- Clutton-Brock, T.H. 1988. *Reproductive Success. Studies of individual variation in contrasting breeding systems*. Chicago: University of Chicago.
- Colbert J. & J.D. Lebreton 1991. Estimation of demographic parameters in bird populations. In: *Bird Population Studies: Relevance to Conservation and Management* (Eds. by C.M. Perrins, J.D. Lebreton & G .J. M. Hirons), Oxford: Oxford University Press. pp. 75-105.
- Davis, S. K. and D. G. McMaster. 2003. Identifying nest predators and assessing productivity of Piping Plovers (*Charadrius melodus circumcinctus*) at Chaplin Lake, SK, 2002. Final report for Canadian Wildlife Service. 10 pp + appendices. 2003.
- Delaney, D. K. & T. G. Grubb. 1999. Activity patterns of nesting Mexican Spotted Owls. *Condor* 101, 42-49.
- Drietz V. J., W.M. Kitchens & D. L. DeAngelis. 2004. Effects of natal departure and water level on survival of juvenile snail kites (*Rostrhamus sociabilis*) in Florida. *Auk* 121, 894-903.
- Dundas, H.A. 1995. Breeding habitat selection by Piping Plovers in southern Saskatchewan. MSc. Thesis. University of Saskatchewan, Saskatoon, SK.
- Dunlop, L. 2001. The 2001 International Piping Plover Breeding Census – Saskatchewan. Saskatchewan. Unpublished report for Saskatchewan Environment and Resource Management. 22pp. + appendices.
- Dzus, E. & R. G. Clark 1998a. Brood survival and recruitment of mallards in relation to wetland density and hatching date. *Auk* 115, 311-318.
- Ens, B. J., M. Kersten, A. Brenninkmeijer & J. B. Hulscher. 1992. Territory quality, parental effort and reproductive success of Oystercatchers (*Haematopus ostralegus*). *Journal of Animal Ecology* 61, 703-716.
- Evans P.R. 1991. Seasonal and annual patterns of mortality in migratory shorebirds: some conservation implications. In: *Bird Population Studies: Relevance to Conservation and Management* (Eds. by C.M. Perrins, J.D. Lebreton & G .J. M. Hirons), Oxford: Oxford University Press. pp. 346-359
- Goossen, J.P., D.L. Amirault, J. Arndt, R. Borge, S. Boates, J. Brazil, S. Brechtel, R. Chaisson, G.N. Corbett, R. Curley, M. Elderskin, S.P. Flemming, W. Harris, L. Heyens, D. Hjertass, M. Hout, B. Johnson, R. Jones, W. Koonz, P. Laporte, D. McAskill,

- R.I.G. Morrison, S. Richard, R. Schaffer, C. Stewart, L. Swanson, and E. Wiltse. 2002. National recovery plan for the Piping Plover (*Charadrius melodus*). National Recovery Plan No. 22. Recovery of Nationally Endangered Wildlife. Ottawa. 47pp.
- Grand J. B. & P. L. Flint 1997. Productivity of nesting spectacled eiders on the lower Kashunuk River, Alaska. *Condor* 99, 926-932.
- Gratto-Trevor, C. Beyersbergen, G. Dickson, L. Erickson, P. MacFarlane, B. Raillard, M. Sadler. 2001. *Prairie Canada Shorebird Conservation Plan*. Prairie Habitat Joint Venture Publication.
- Gratto-Trevor, C. L. 1991. Parental care in Semipalmated Sandpipers *Calidris pusilla*: brood desertion by females. *Ibis* 133, 394-399.
- Green, R.E. 1988. Effects of environmental factors on the timing and success of breeding of common snipe gallinago (Aves: scolopacidae). *The Journal of Applied Ecology* 25, 79-93.
- Haig S. M. & L. W. Oring. 1987. Population studies of piping plovers at Lake of the Woods, Minnesota, 1982-1987. *Loon* 59, 113-117.
- Haig, S. M. 1987. The Population Biology and Life History Patterns of the Piping Plover. PhD Thesis. University of North Dakota, Grand Forks, ND.
- Haig, S. M. & L. W. Oring. 1988. Mate, site, and territory fidelity in Piping Plovers. *Auk* 105, 268-277.
- Haig, S. M. 1992. Piping Plover. *In* The Birds of North America, No. 2 (A. Poole, P. Stettenheim and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences; Washington, DC: The American Ornithologist Union.
- Hannon, S. J., K. Martin & J. O. Schieck. 1988. Timing of reproduction in two populations of willow ptarmigan in northern Canada. *Auk* 105, 330-338.
- Hazler K. R. 2004. Mayfield logistic regression: a practical approach for analysis of nest survival. *Auk* 121, 707-716.
- Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of Midcontinental Mallards. *Journal of Wildlife Management* 66, 883-901.
- Ivan, J. S. and R. K. Murphy. 2002. What preys on piping plover eggs and chicks? *unpublished report*. 11pp. + appendix.
- Johnson, D.H. 1979. Estimating Nest success: the Mayfield method and an alternative. *Auk* 96, 651-661.

- Johnson, M. & L.W. Oring. 2002. Are nest enclosures an effective tool in plover conservation? *Waterbirds* 25, 184-190.
- Jung, T. S., J. P. Goossen, B. Aitken, and I. A. Bisson. 1998. Conservation biology of piping plovers at Lake Diefenbaker, Saskatchewan: 1997 progress report. Unpublished Canadian Wildlife Service report, Prairie Northern Region, Edmonton, Alberta. 49pp + appendices.
- Keedwell, R. J. & M. D. Sanders 2002. Nest monitoring and predator visitation of banded dotterels. *Condor* 104, 899-902.
- Kelly, J. F. & B. Van Horne. 1997. Effects of food supplementation on timing of nest initiation in belted kingfishers. *Ecology* 78, 2504-2511.
- Keyser A.J., M.T. Keyser & D. E. L. Promislow. 2004. Life-history variation and demography in western bluebirds (*Sialia mexicana*) in Oregon. *Auk* 121, 118-133.
- Knetter, J. M., R. S. Lutz, J. R. Cary & R. K. Murphy 2002. A multi-scale investigation of piping plover productivity on Great Plain alkali lakes, 1994-2000. *Wildlife Society Bulletin* 30, 683-694.
- Kistchinski, A. A. 1975. Breeding biology and behaviour of the Grey Phalarope *Phalaropus fulicarius* in east siberia. *Ibis* 117:285-301.
- Larson, M.A., M.R. Ryan & R. K. Murphy. 2002. Population viability of piping plovers: effects of predator enclosures. *Journal of Wildlife Management* 66, 361-371.
- Laut, M. E., P. C. Banko & E. M. Gray 2003. Nesting behavior of Piping Plover, as assessed from video recording. *Pacific Science* 57, 385-392.
- Loefering, J. P. & J. D. Fraser 1995. Factors affecting piping plover chick survival in different brood rearing habitats. *Journal of Wildlife Management* 59, 646-655.
- Lukacs P. M., V. J. Dreitz, F. L. Knopf & K. P. Burnham. 2004. Estimating survival probabilities of unmarked dependent young when detection is imperfect. *Condor* 106, 926-931.
- MacDonald, D., C. White, S. Davis, K. Connick, D. Beverage, & R. MacDonald. 2003. The Piping Plover Basin Site Plans for Southern Saskatchewan. Unpublished report for Saskatchewan Watershed Authority. 170pp. + appendix
- Manly, B. F. & J. A. Schumtz. 2001. Estimation of brood and nest survival: comparative methods in the presence of heterogeneity. *Journal of Wildlife Management* 65, 258-270.
- Manolis, J. C., D. E. Andersen, & F. J. Cuthbert. 2000. Uncertain nest fates in songbird studies and variation in Mayfield estimation. *Auk* 117, 615-626.

- Mayer, P. M. 1993. Conservation Biology of Piping Plovers in the Northern Great Plains. M.Sc. Thesis. University of Missouri, Kansas City, Missouri.
- Mayfield, H. F. 1961. Nesting success calculated from exposure. *The Wilson Bulletin* 73, 255-261.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *The Wilson Bulletin* 87, 456-466.
- McNamara J. M. & A. I. Houston. 1987. Starvation and predation as factors in limiting population size. *Ecology* 68, 1515-1519.
- McQuillen, H. L. & L.W. Brewer. 2000. Methodological consideration for monitoring wild bird nests using video technology. *Journal of Field Ornithology* 71, 167-172.
- Miller, B. J. & F. L. Knopf. 1994. Growth and survival of mountain plovers. *Journal of Field Ornithology* 64, 500-506.
- Murphy, R. K., K. A. Smith, B. R. Casler & D. P. Althoff. 2001. Reproduction and spacing of piping plovers breeding at high density at Appam Lake, North Dakota. *Wilson Bulletin* 113, 331-335.
- Murphy, R. K., M. J. Rabenberg, M. L. Sondreal, B. R. Casler & D. A. Guenther. 2000. Reproductive success of Piping Plovers on alkali lakes in North Dakota and Montana. *The Prairie Naturalist* 32, 233-241.
- Murphy, R. K., B. G. Root, P. M. Mayer, J. P. Goossen, K. A. Smith. 1999. A draft protocol for assessing Piping Plover reproductive success on Great Plains alkali lakes. Pp. 90-107 in Proceedings, Piping Plover and Least Terns of the Great Plains and nearby (Higgins, K.F., M.R. Brashier and C.D. Kruse, eds.) South Dakota State University, Brookings.
- Nol, E., M. S. Blanken & L. Flynn. 1997. Sources of variation in clutch size, egg size, and clutch completion dates of semipalmated plovers in Churchill, Manitoba. *Condor* 99, 289-296.
- Norton, D. W. 1973. Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph D. Thesis. University of Alaska, Fairbanks, AK.
- Parsons, J. 1975. Seasonal variation in the breeding success of the herring gull: an experimental approach to pre-fledging success. *The Journal of Animal Ecology* 44, 553-573.
- Patterson, M. E., J. D. Fraser & J. W. Roggenbuck. 1991. Factors affecting piping plover productivity on Assateague Island. *Journal of Wildlife Management* 55, 525-531.
- Peak R. C., F.R. Thompson III & T.L. Shaffer, 2004. Factors affecting songbird nest survival in riparian forests in a midwestern agricultural landscape. *Auk* 121, 726-

- Pietz, P. J. & Granfors, D. A. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64, 71-87.
- Pitelka, F. A. & R.T. Holmes, 1974. Ecology and evolution of social organization in Arctic Sandpipers. *American Zoologist* 14, 185-204.
- Plissner, J. H. & S. M. Haig. 2000. Viability of Piping Plover *Charadrius melodus* metapopulations. *Biological Conservation* 93, 163-173.
- Prindville-Gaines, E. & M. R. Ryan. 1988. Piping Plover habitat use and reproductive success in North Dakota. *Journal of Wildlife Management* 52, 266-273.
- Ramos, J. A. 2003. Intraspecific aggression by roseate tern adults on chicks in a tropical colony. *Waterbirds* 26, 160-165.
- Ricklefs, R.E. 1973. Fecundity, Mortality, and Avian Demography. In: *Breeding Biology of Birds: Proceedings of a Symposium on Breeding Behaviour and Reproductive Physiology in Birds* (Ed. by D.S. Farner), Washington, D.C. National Academy of Sciences. Pages 366-439.
- Roselarr, C. S. 1979. Fluctuaties in aantallen krombekstranlopers *Calidris ferruginea* (in Dutch). *Watervogels* 4, 202-210.
- Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. Modelling nest survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27,1-19.
- Ryan, M. R., B. G. Root & P. M. Mayer 1993. Status of Piping Plovers in the Great Plains of North America: A Demographic Simulation Model. *Conservation Biology* 7, 581-585.
- Sanders, M. D. & R. F. Maloney. 2002. Causes of mortality ant nests of ground nesting birds in the Upper Waiteaki Basin, South Island, New Zealand: a 5 year video study. *Biological Conservation* 106, 225-236.
- Sarno, R. J., W. R. Clark, M. S. Bank, W. S. Prexl, M. J. Behl, W. E. Johnson, & W. L. Franklin. 1999. Juvenile guanaco survival: Management and conservation implications. *Journal of Applied Ecology* 36, 937-945
- Sauer, J. R., B.G. Peterjohn & W. A. Link. 1994. Observer differences in North American breeding bird survey. *Auk* 111, 50-62.
- Schekermann, H. & G. H. Visser. 2001. Prefledging energy requirements in shorebirds: energetic implications of self-feeding precocial development. *Auk* 118, 944-957.
- Shaffer T. 2004. A unified approach to analyzing nest success. *Auk* 121, 526-540.

- Sheridan J. A., S. R. Beissinger & C. R. Hughes. 2004. Week associations between measures of health and reproductive success in green rumped parrotlets (*Forpus passerinus*) in Venezuela. *Auk* 121, 717-725.
- Siikamäki, P. 1998. Limitation of reproductive success by food availability and breeding time in pied flycatchers. *Ecology* 79, 1789-1796.
- Skeel, M. A., D. C. Duncan, and E. R. Wiltse. 1996. The 1996 International Piping Plover breeding census – Saskatchewan. Unpublished report for Saskatchewan Wetland Conservation Corporation and Saskatchewan Environment and Resource Management. 22pp. + appendices.
- Sockmann, K. W. 1997. Variation in life-history traits and nest-site selection affects risk of nest predation in the California gnatcatcher. *The Auk* 114, 324-332.
- Stanley, T. C. 2000. Modeling and estimates of stage specific daily survival probabilities. *Ecology* 81, 2048-2053.
- Stearns, S. C. 1980. A new view of life-history evolution. *Oikos*. 35, 266-281.
- Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Szekely, T., I. Karsi, & T.D. Williams 1994. Determination of clutch size on Kentish Plovers *Charadrius alexandrinus*. *Ibis* 136, 341-348.
- Thibault, M. & R. McNeil, 1995. Day- and night-time parental investment by incubating Wilson's Plovers in a tropical environment. *Canadian Journal of Zoology* 73, 879-886.
- Thomas, C. & J. C. Coulson 1988. Reproductive Success of Kittiwake Gulls, *Rissa tridactyla*. In *Reproductive Success. Studies of individual variation in contrasting breeding systems*. Chicago, USA. University of Chicago Press. Pages 251-262.
- Thompson, F. R., W. Dijk & D. E. Burhans 1999. Video identification of Predators at Songbird nests in old fields. *Auk* 116, 259-264.
- Verhulst, S., J. H. Van Balen & J. M. Tinbergen 1995. Seasonal decline in reproductive success of the great tit: variation in time or quality? *Ecology* 76, 2392-2403.
- Walk J. W., K. Wentworth, E. L. Kershner, E. K. Bollinger & R. E. Warner 2004. Renesting decisions and annual fecundity of female dickcissels (*Spiza americana*) in Illinois. *Auk* 121, 1250-1261.
- Walters, J. R. 1984. The evolution of parental behaviour and clutch size in shorebirds. In: *Shorebirds: breeding behaviour and populations*. (Eds. J. Burger and B. L. Olla) Plenum, New York. pp. 243-287.
- Westneat D. F. 1992. Nesting synchrony by female red-wing black bird: effects of

- predation on nest success. *Ecology* 73, 2284-2294.
- Westworth S. M., D. Martens, C. Gratto-Trevor, J. P. Goossen, and S. Davis. 2004. Northern Great Plains Piping Plover Science Workshop. Regina, SK. Nov. 2003.
- White, C. L. 2003. Piping Plover and Sanderling Monitoring at Chaplin Lake, Saskatchewan. 7pp + appendix. 2003.
- White, C. L. 2004. 2004 Piping Plover and Sanderling Monitoring at Chaplin Lake, Saskatchewan. Unpublished report for The Saskatchewan Watershed Authority, 25 pp + appendix.
- Williams, G. E. & P. B. Wood. 2002. Are traditional methods of determining nest predators and nest fates reliable? An experiment with wood thrushes (*Hylocichla mustelina*) using miniature video cameras. *Auk* 119, 1126-1132.
- Whyte, A. J. 1985. Breeding ecology of the Piping Plover (*Charadrius melodus*) in central Saskatchewan. MSc. Thesis, University of Saskatchewan, Saskatoon, SK.

CHAPTER 3: PIPING PLOVER (*Charadrius melodus*) PARENTAL CARE AT CHAPLIN LAKE, SASKATCHEWAN: INCUBATION ATTENTIVENESS IN MALES AND FEMALES

3.1 INTRODUCTION

The evolution of life histories, in particular mating strategies, involves a series of tradeoffs between the number and quality of offspring and adult reproductive effort, survival, and future reproduction (Houston & Davies 1985; Charnov & Krebs 1974; Lessels 1991; Reynolds 1996; Wallander & Malte 2003). The breeding period is generally a limiting stage in life history and typically results in many life history bottlenecks for individuals (Brunton 1988a). Knowledge of behaviour, in addition to the ecology of a species, is vital to understanding its life history. Many studies have focussed on mating systems while parental care strategies were largely ignored until the 1970s (Clutton-Brock 1991). Questions regarding mating strategies often represent the co-evolution of two strategies, for male and female, which are rarely identical (Trivers 1972, Lazarus 1990). Thus, parental care strategies are of central importance because the striking differences in male and female reproductive strategies are often associated with variations in their involvement in parental care (reviewed by Clutton-Brock 1991).

Parental care is a key component of life histories and breeding systems and is defined as any behavior that increases the probability of offspring survival at a cost to the parent (reviewed by Clutton-Brock 1991). One principle function of parental care in endothermic organisms is to regulate the thermal environment of fertilized eggs, providing optimal conditions for embryo development (Clutton-Brock 1991). Some form of parental care is found in 99% of avian species (Buntin 1996). Parental care is

characteristic of most avian species because of the requirement to incubate and protect eggs before they hatch (Hauber 2002; Reid et al. 2002a), but there is considerable variation in the care provided to young (Knetterson & Nolan 1994). In birds, monogamy combined with bi-parental care occurs in 90% of extant species (Brunton, 1988, Clutton-Brock 1991, Alcock 1998), whereas it is uncommon in most other animal taxa (Clutton-Brock 1991, Alcock 1998). Birds provide an interesting model organism for studies of parental care in that both males and females of many species exhibit parental care (Alcock 1998). Male and female participation may not be equal and the extent of male care in many species is not well documented (Reid et al. 2002b). As a result of the variation in parental care systems, many questions regarding parental care arise pertaining to the extent of participation by males and females (Burger 1981; Bergstrom 1986).

Shorebirds (suborder Charadrii) have the greatest diversity of parental care of any suborder of birds (Szekely & Reynolds 1995). The diverse parental care strategies found in shorebirds make them a good group of organisms to evaluate general questions about reproductive behavior (Reynolds & Szekely 1997; Kosztolányi & Székely 2002; Deeming 2002; Thibault & McNeil 1995). Many studies have focused on parental effort in shorebirds (Norton 1972; Bergstrom 1981; Bergstrom 1986, 1989; Cartar 1985; Brunton 1988a, b). Parental care strategies in shorebirds include variations of uni- to bi-parental care. For example, male and female black oystercatchers (*Haematopus bachmani*) and purple sandpipers (*Calidris maritima*) share incubation duties (Kosztolanyi & Szekely 1997). However, in northern lapwings (*Vanellus vanellus*), females alone incubate the eggs and care for the young (Parish & Coulson 1998). Conversely,

incubation and parental care is the male's responsibility in some phalarope species (*Phalaropus spp.*; Thibault & McNeil 1995). Furthermore, in mountain plovers (*Charadrius montanus*; Graul 1975) and Temminck's stint (*Calidris temminckii*; Breiehagen T. 1989), the first clutch is the male's responsibility while the female cares for the second (). Parental care systems in shorebirds are diverse and the time devoted to parental care varies with species and sex (Thibault & McNeil 1995).

Costs of incubation include increased vulnerability to predators and energy and time constraints (Clutton-Brock 1991; Reid 2002c). For example, parental care often limits the time which can be allocated to foraging, or constrains mobility of the caregiver and often leaves the caregiver at a higher risk of predation (Clutton-Brock 1991). Recent studies have shown that the incubation stage imposes significant energy demands on parents (Brunton 1988a; Reid et al. 2000; Cresswell et al. 2003; Reid 2002c). In shorebirds with bi-parental care, the nest is attended 90% or more of the total incubation time (Bergstrom 1986, Thibault & McNeil 1995) and successful incubation requires both members of the pair (Bergstrom 1986; Thibault & McNeil 1995; Brunton 1988b; Clutton-Brock 1991b). In many shorebirds, including most *Charadrius spp.*, young are mobile soon after hatching and do not rely on adults for food. However, the incubation period may be relatively long because of the longer development required for the young to develop enough to be able to actively forage after hatch (Clutton-Brock 1991, Deeming 2002). Consequently, in species with precocial young, incubation represents a longer and more energetically costly component of parental investment (Brunton 1988a, b; Cresswell 2003).

Optimal incubation strategies for males and females are rarely identical (Trivers 1972) and in monogamous shorebirds there is substantial variation in the contributions of each sex (Kosztolányi & Székely 2002). Variation in the care given by males in monogamous birds ranges from none to extensive (Reid et al. 2002b). Males of many monogamous single-clutched shorebird species have a relatively large role in incubation (Soikkeli 1967; Bergstrom 1981; Hussell 1976; Miller 1985; Lenington 1980). It has been suggested that male individuals of *Charadrius* spp. adopt the primary parental role, including a principal role in nocturnal incubation (Warnock & Oring 1996). Overall however, there are limited data available on the incubation roles of sexes through the 24-hour period (Thibault & McNeil 1995). There are few data on nocturnal incubation by shorebirds with the exception of Wilson's plover (*Charadrius wilsonia*; Thibault & McNeil 1995), killdeer (*Charadrius vociferus*; Warnock & Oring 1996), snowy plover (*Charadrius alexandrinus*; Kosztolányi & Székely 2002) and semipalmated plover (*Charadrius semipalmatus*; Blanken & Nol 1998).

In the past, studies of avian parental care were done primarily through direct observations of the nests, and nocturnal incubation was assessed by nocturnal trapping or dawn/dusk nests checks (Bergstrom 1981; Mundahl 1982). However, an accurate assessment of nest attendance patterns requires detailed observations (Bottitta et al. 2002). Video monitoring enables researchers to collect data on time budgets similar to those based on observations from a blind. Video monitoring has become a relatively common technique to quantify parental behaviour (Cartar 1985; Thibault & McNeil 1995; Laut et al. 2003) and to identify nest predators (Pietz & Granfors 2000; Williams & Wood 2002; Keedwell & Sanders 2002; Sanders & Maloney 2002). Video allows for

continuous diurnal and nocturnal observation and provides the opportunity to review and store the data (McQuillen & Brewer 2000). Video systems also provide the capability to record highly detailed observations of diurnal and nocturnal behaviour at the nest with little or no observer effects (Delaney & Grubb 1999).

Piping plovers (*Charadrius melodus*) are a monogamous single-clutched species with bi-parental care and precocial young (Wilcox 1959; Haig 1992). Data on daily incubation patterns are limited and no information regarding nocturnal incubation exists (Cairns 1982; Haig 1992). The objective of my study was to quantify diurnal and nocturnal incubation patterns and determine the relative contribution of each sex to incubation in piping plovers. I tested the null hypothesis that incubation duties are equally shared by the sexes. I predicted that that since piping plovers are a monogamous, single clutched, *Charadrius* spp, that males will have an increased contribution to incubation compared to females, and that males will take on the principal role in nocturnal incubation (Warnock & Oring 1996).

3.2 METHODS

Study species

The piping plover is a small migratory shorebird (mean adult mass of 53 g; Haig 1992) species that breeds on freshwater lakes and reservoirs, alkali lakes, rivers and coastal areas of North America. Piping plovers have lifespan of approximately 7-10 years, and are thought to breed in their first year (Haig 1992). Typically, the female lays a clutch of 4 eggs in a shallow scrape in the ground. Pairs are generally monogamous for the breeding season. They will re-nest if the first attempt fails but they typically only

raise one brood per year. The incubation period is typically 28 days and young fledge 18-25 days post hatch. Breeding typically begins in early May (Chapter 2) and flocks of fledglings and adults are often seen in mid August, however some individuals whose nesting attempts fail may leave the breeding area earlier in the season.

Study site

My study focused on birds nesting at Chaplin Lake, Saskatchewan (50° 26' N, 106° 40' W) during the 2002, 2003 and 2004 breeding seasons. Chaplin Lake is a large saline lake in the Missouri Coteau region covering approximately 11,777 ha (178 km²). The lake covers a glacial sodium sulfate deposit and is composed of 10 interconnected basins. Water levels are managed for the commercial extraction of sodium sulfate (Fig. 2.1) and are regulated by the solution mining operation as well as by natural precipitation and evaporation. Water levels vary both between and within years but water management is such that there is shoreline habitat available to plovers even in drought years. Typically, the highest water level is in spring and then declines as the summer progresses. The width of shoreline beaches varies, but primary breeding areas have beaches that were approximately 100 m wide (MacDonald et. al. 2003). The beaches consist of a combination of mud, gravel and cobble; all with high alkali content (MacDonald et. al. 2003). The shorelines are mostly unvegetated, becoming patchy with sparse vegetation towards the uplands. The dominant plant species included alkali grass (*Puccinellia nuttallinana*), salt grass (*Distichlis stricta*), seaside arrow-grass (*Triglochin maritima*) and wire rush (*Juncus balticus*; MacDonald et. al. 2003). The area surrounding the lake is

predominantly native pasture and wetlands. Cattle had access to all beaches but one (approx. 5 km long) along the north side of the west basin.

Nest Monitoring

The University of Regina Animal Care Committee approved all protocols. Nest searches and monitoring were conducted from early May until mid August from 2002 to 2004. I attempted to locate all plover nests on the entire lake using methodology outlined in Murphy *et. al.* (1999). Searches were conducted between 06:00 and 17:00. However, nest monitoring and searching was restricted to the mornings (06:00 – 12:00) on days when the temperature was expected to exceed 29° C, to minimize the exposure of eggs or young to heat if parents flushed. Nest searches were systematic surveys of all available habitats around the lake. A complete survey was conducted on the lake every 5 days. During surveys, the locations of individuals and pairs were documented using a Global Positioning System (GPS). In all areas with documented individuals, especially territorial pairs, the searching effort was intensified to locate nests. Nests were located by finding and subsequently observing breeding pairs of adults. Nest searches were conducted on foot or by surveying from an all-terrain vehicles (ATV). When ATV were employed, driving was limited to areas with vegetation, to decrease damage to the beaches and minimize the chance of destroying plover nests. To determine nest initiation dates for nests found during incubation, 2 eggs from each nest were floated to determine the developmental stage from which nest initiation date was back counted (Alberico et al 1995; Murphy et al 1999). Using nest initiation dates, hatching dates were predicted based on estimates of a 7-day laying period and 28-day incubation period (Murphy et al

1999). These dates enabled me to determine the incubation stage of each nest. Nests were marked with a 15 cm wooden stick 1 m away and a small (10 cm high) rock cairn built 5 m away such that the cairn, wooden stick, and nest formed a straight line. The position of the nest was also recorded with a hand held GPS. Nests were checked every 3-5 days to assess success or failure. Nest attempts were considered successful if at least one egg hatched (Murphy et al 1999).

Video Monitoring

Four video systems (B&E electronics Inc. Regina, SK) were used to monitor nests during the 3 years. Small (29 mm diameter, 74 mm long) remote video cameras (National Electronics Bullet C/IR) were placed at randomly selected plover nests around the lake. Nests were randomly selected by using a random number generator. The cameras provided colour video during the day and black and white footage at night. The cameras had 6 light emitting diodes, which enabled me to capture sharp images under low light conditions. Cameras were placed approximately 50 – 100 cm from the nest to balance the tradeoff between proper infrared illumination and minimal disturbance. Cameras were deployed facing north to minimize glare from the sun at sunrise and sunset. Video was continuously recorded on a time lapse VCR (Sanyo Real Time SRT 2400DC or Sanyo Real Time 4040AC). The time-lapse feature allowed a complete 24 hour period to be recorded onto a standard 8 hour video cassette. The VCRs were located in waterproof cases within protective boxes 75-100 m away from the nest. Rechargeable deep cycle 12-volt batteries were used to power the VCR and video camera. Video systems were operational from the time the nest was located until it was either depredated or the eggs

successfully hatched. Videotapes were changed every twenty-four hours and the battery was changed every 48 hours. Nests were checked remotely at the site of the VCR using a 14.2 cm National Electronic Colour LCD monitor. I attempted to begin monitoring early in the incubation stage, but cameras were deployed during the middle or late incubation stages if no other nest were available. Installation of video systems took approximately 20 min, after which direct observations were made to ensure adults returned to the nest.

I divided the 28-day incubation period into three 9-day periods: early (day 1-9), middle (day 10-18) and late (day 19-27; Blanken & Nols 1998), to ascertain if parental care patterns are a function of incubation stage. Nests that were missing more than 6 days of video monitoring during the entire incubation period were excluded from all analyses. For my analysis of each nest, I randomly selected 3 tapes (24-hour periods) from each incubation stage, resulting in nine 24-hour observation periods.

For each observation period, I recorded the duration of each incubation bout as well as the duration of each absence. Bout length was considered to be the time that elapsed from the beginning of incubation by a given parent until an absence of more than 1 minute. I did not consider absences <1 minute as the beginning of a new incubation bout since the cooling rates of eggs during this period would be negligible (Norton 1972). I used the incubation bouts to determine total nest attendance for each individual. Nest attendance was defined as any time an adult was on the nest either in contact with the eggs or shading them. Using this value for nest attendance, I calculated the percent attendance as the proportion of time spent attending the nest during the observation period. Daily activity patterns were determined by dividing the observation period into 2 periods. Diurnal incubation was defined as occurring between 5:00 and 21:00, while

nocturnal incubation was between 21:00 and 5:00. These daily time periods were defined on the basis of sunrise and sunset times during the incubation period. If the incubation bout extended into the next daily time interval the incubation bout was allocated to the time period which contained a greater percent of the bout.

The sex of the incubating parent was determined using morphological characteristics and within-pair differences. In addition, individual band combinations were used when individuals in the pair were banded (4 nests). Although piping plovers are considered monomorphic, plumage brightness differences can be used to distinguish breeding males from females. Typically, males have a brighter and more extensive black breast and forehead bands and a brighter orange bill (Haig & Oring 1988; Haig 1992). In addition, males may have a black mustache in the malar region (the cheek area; Haig & Oring 1988, Haig 1992). These morphological characteristics were visible on the video footage. Furthermore, for each individual, I generated a list of characteristics including brightness, shape, and extent of breast and forehead bands, moustache presence and brightness, in addition to other specific identifying features of each individual (Delaney & Grubb 1999). To confirm the sex of individuals, ten-second video clips for each individual were extracted (Haig 1987). I surveyed both experienced and naïve observers to verify the gender of each individual. Only birds that were consistently categorized as the same sex were used in the analysis.

Statistical Analysis:

All data are presented as means \pm standard error (SE), unless otherwise stated. All data were analyzed using SAS statistical software (SAS institute 1999), with a

significance level of 0.05. I quantified the duration of time that individuals incubated as well as the duration of time the nest was unattended. I used the duration of time incubating to determine percent nest attendance, which is the proportion of the observation period that each individual attended the nest. I also used duration of incubation to determine the mean bout length (in minutes) for each individual. All data (nest attendance and bout length) were tested for normality before proceeding with parametric statistics (Zar 1999).

I used generalized linear models (PROC GENMOD) to examine the influence of sex, incubation stage (early, middle or late) and daily time period (diurnal or nocturnal) on incubation attentiveness. Since repeated observations of the same nest are not independent, I used generalized estimating equations (GEE) and an exchangeable correlation matrix to account for repeated observations of the same nest. In this analysis the proportion of time the nest was attended ($\text{event/trial} = \text{number of minutes nest attended} / \text{total number of minutes nest observed}$) was the response variable and sex, incubation stage and daily time periods were the predictor variables. The logistic analysis was based on binomial distribution and a logit link function.

A mixed model (PROC MIXED; SAS 1989) was used to determine if mean bout length varied as a function of sex, incubation stage (early middle and late) and time period (diurnal or nocturnal). I treated sex, incubation stage and time period as fixed effects and nests as random effects.

3.3 RESULTS

In total, I used data from 10 nests to quantify incubation behaviour (4 from 2002, 4 from 2003 and 2 from 2004). The relatively low number of nests in 2004 was due to technical difficulties with the camera units. Therefore, observations were made from a total of 83 tapes resulting in a total of 1945 hours of observation on 20 individuals (10 males + 10 females). There were 28, 29, 26 tapes viewed for early, middle and late incubation, respectively. The mean observation period per tape was 23.4 ± 1.4 hours (mean \pm SD; range 25.4 – 18.2 hours).

Nest attendance:

Total nest attendance (male and female combined) was $92\% \pm 2\%$ of the total time and did not differ significantly between incubation stages (Figure 3.1; $\chi^2 = 4.19$, $df=2$, $p = 0.12$). However, males spent a greater proportion of time attending the nest (Fig 3.2; Sex $\chi^2 = 5.38$, $df = 2$, $p = 0.02$), and there was no interaction between the incubation stage and sex of the incubating adult (Fig 3.2 Stage*Sex $\chi^2 = 0.62$, $df= 2$, $p=0.33$). Total nocturnal nest attendance (males and females combined; $93\% \pm 2\%$) did not differ significantly from total daytime nest attendance ($88\% \pm 1\%$; Fig. 3.3; Time period $\chi^2 = 0.097$, $df = 1$, $p=0.34$), but there was an interaction between daily time period and sex (Fig 3.4; Time period * sex $\chi^2 = 52.8$, $df = 1$, $p = 0.000$). Male and females equally shared incubation duties during the day (Fig. 3.4). However, at night males increased nest attendance while females decreased the time spent at the nest (Fig. 3.4). Nocturnal nest attendance by females was lower ($32\% \pm 2\%$)

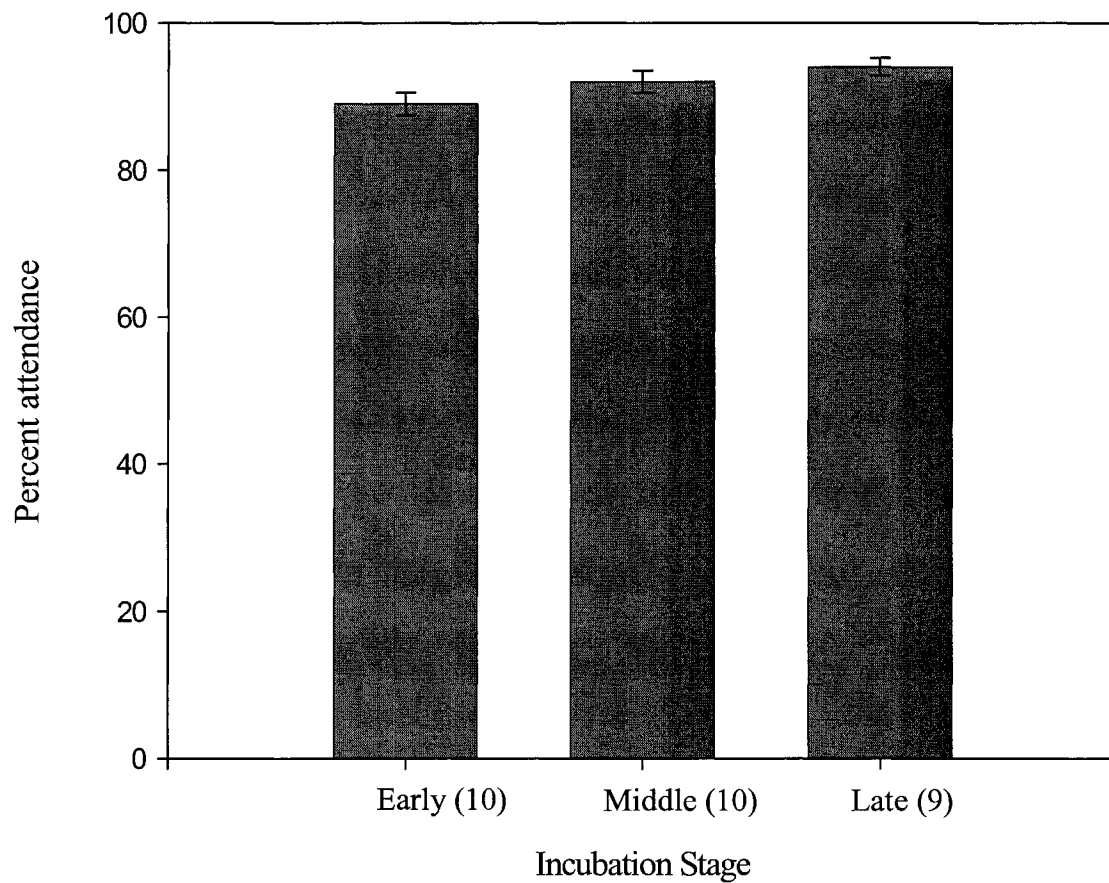


Figure 3.1. Parental nest attendance as a function of incubation stages. Data presented as mean \pm SE. Sample size represents the number of nests (indicated in parentheses).

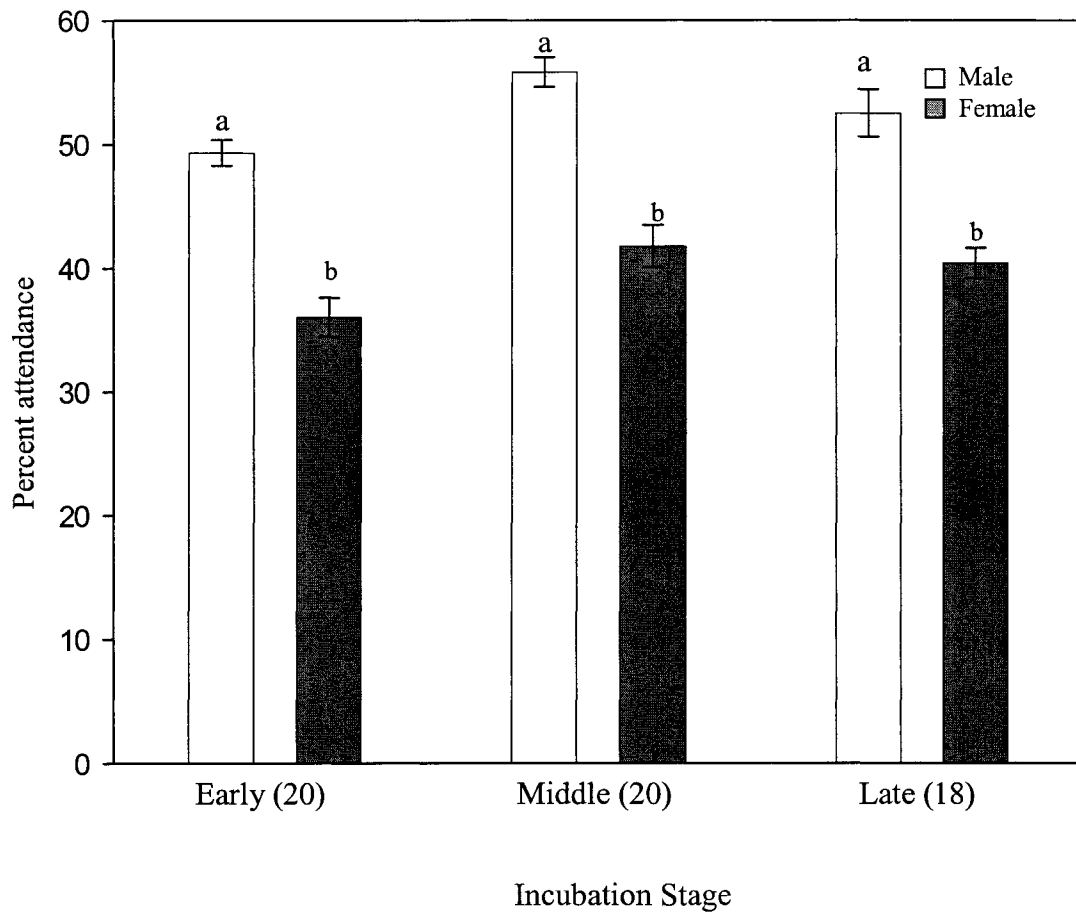


Figure 3.2. Parental nest attendance (%) as a function of sex and incubation stage. Data given as mean \pm SE. The number of individuals used in the analysis are given in parentheses and letters indicate significant results ($p < 0.05$).

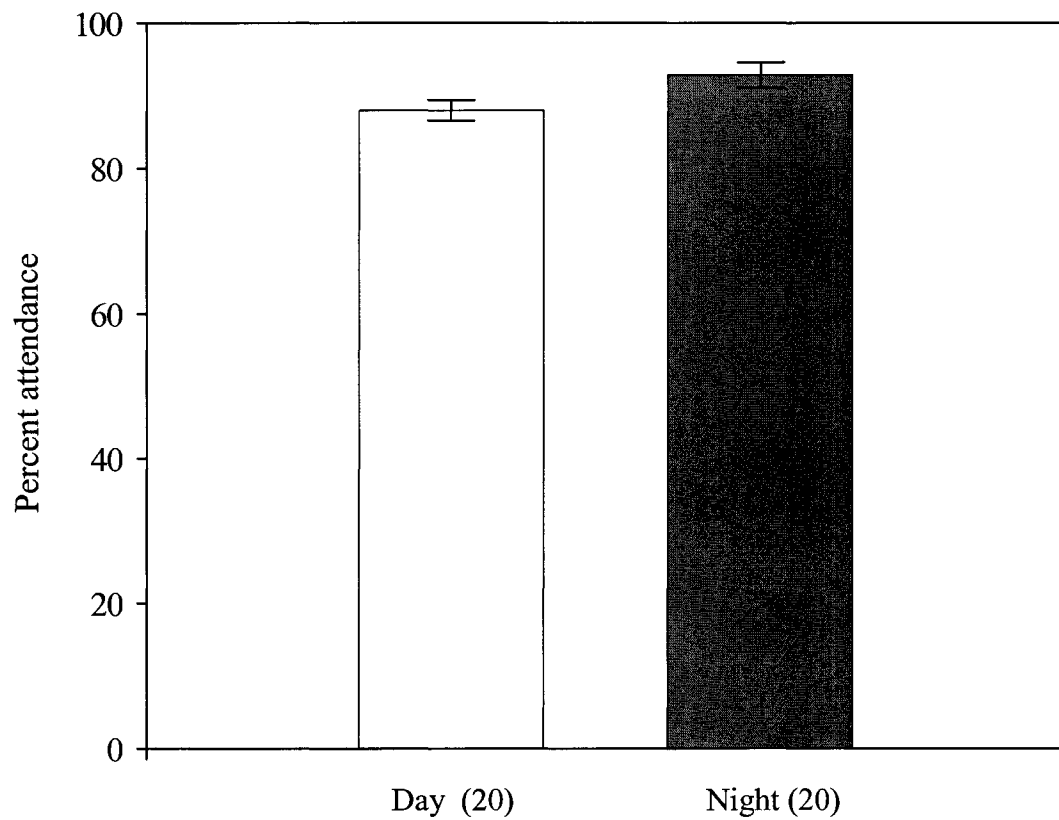


Figure 3.3. Parental nest attendance (%) as a function of daily time period (nocturnal and diurnal). Data given as mean \pm SE. The number of individuals used in the analysis are given in parentheses.

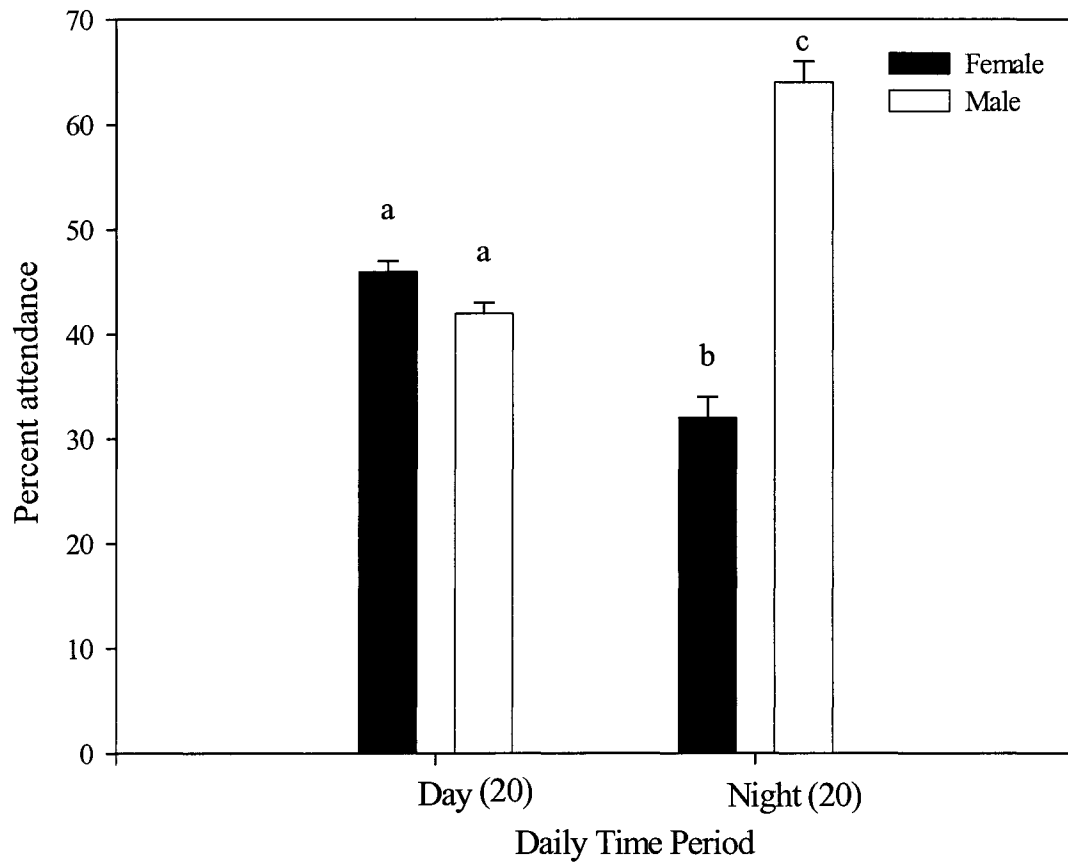


Figure 3.4. Nest attendance (%) as a function of sex and daily time period (diurnal and nocturnal). Data given as mean \pm SE. The number of individuals used in the analysis are given in parentheses and letters indicate significant results ($p < 0.05$).

compared to daytime ($46\% \pm 1.0\%$). Males increased nocturnal nests attendance ($64.8\% \pm 2.5\%$) compared to diurnal nest attendance ($42.2\% \pm 0.9\%$). Nocturnal nest attendance for both males and females ranged from 0-100%. There were 4 events of nocturnal egg neglect at three nests. All of these events occurred during the early stage of incubation. Nest neglect was not documented during diurnal observations.

Bout length:

Mean incubation bout length did not differ significantly as a function of incubation stage (Fig 3.5; $F_{2,18} = 1.26, p = 0.3$). However, mean bout length differed among sexes with males having longer incubation bouts (99.4 ± 6 minutes) than females (70.5 ± 5 minutes; Fig 3.6 Sex $F_{1,9} = 4.72, p = 0.04$). Furthermore, there was a significant interaction effect between incubation stage and sex (Stage*Sex $F_{2,18} = 5.42, p = 0.005$). Males and females had similar bout lengths during early incubation (males 70.3 ± 12 ; females 86.1 ± 11 minutes) and late incubation (males 77 ± 7 ; females 55.5 ± 7 minutes). However, males (118.0 ± 15) had longer incubation bouts during the mid incubation stage when compared to females (56.5 ± 6 minutes).

Total mean incubation bout length differed significantly between nocturnal and diurnal incubation (Fig 3.7; Daily time period $F_{1,18} = 14.2, p = 0.001$). Nocturnal incubation bouts (108.44 ± 7.6 minutes) were longer compared to diurnal incubation bouts (62.23 ± 3.7 minutes). Furthermore there was a significant interaction between daily time period and sex (Fig 3.8; Daily time period * sex $F_{1,18} = 8.32, p = 0.008$). Males

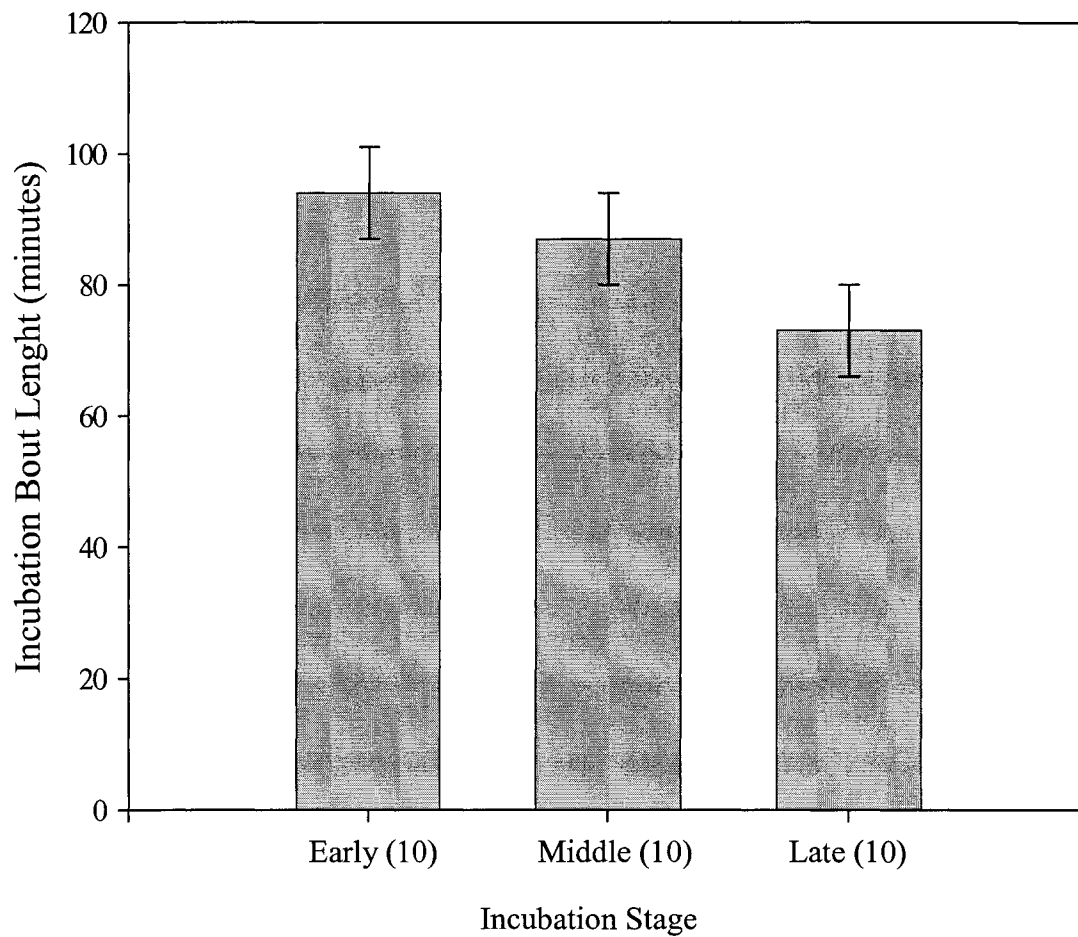


Figure 3.5. Mean incubation bout length as a function of incubation stage. Data given as mean \pm SE. The number of nests used in the analysis is given in parentheses.

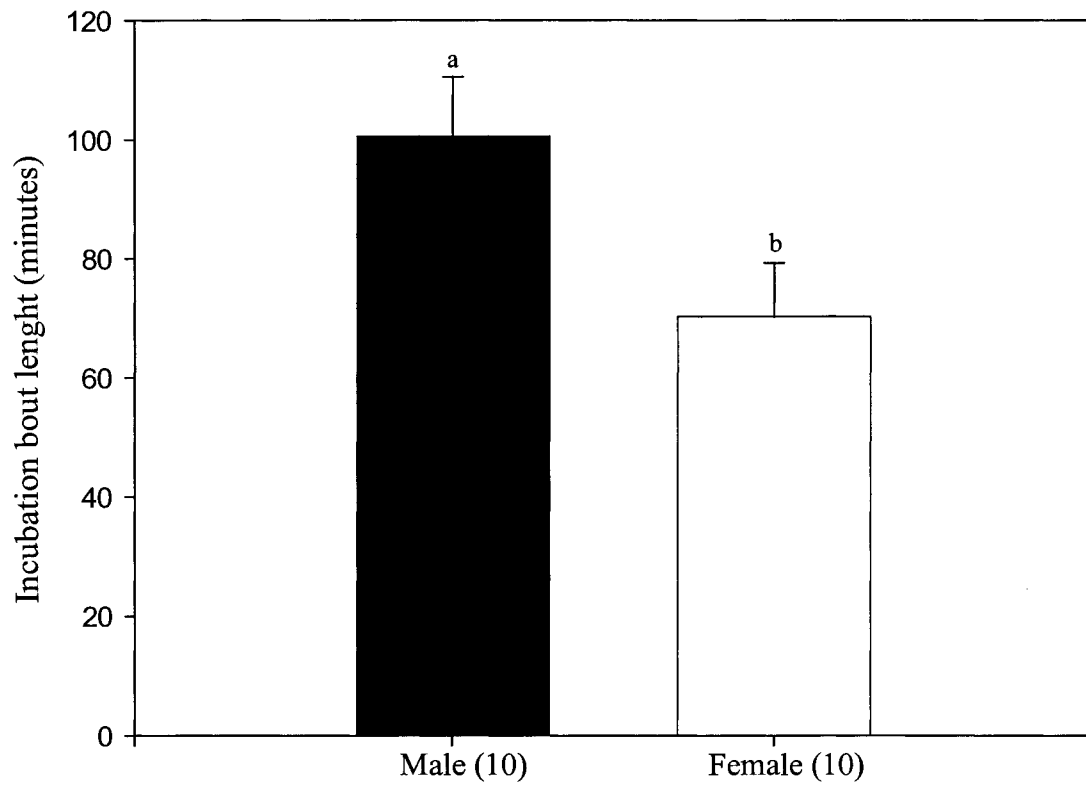


Figure 3.6. Incubation bout length as a function of sex. Data given as mean \pm SE. The number of nests used in the analysis is given in parentheses and letters indicate significant results ($p < 0.05$).

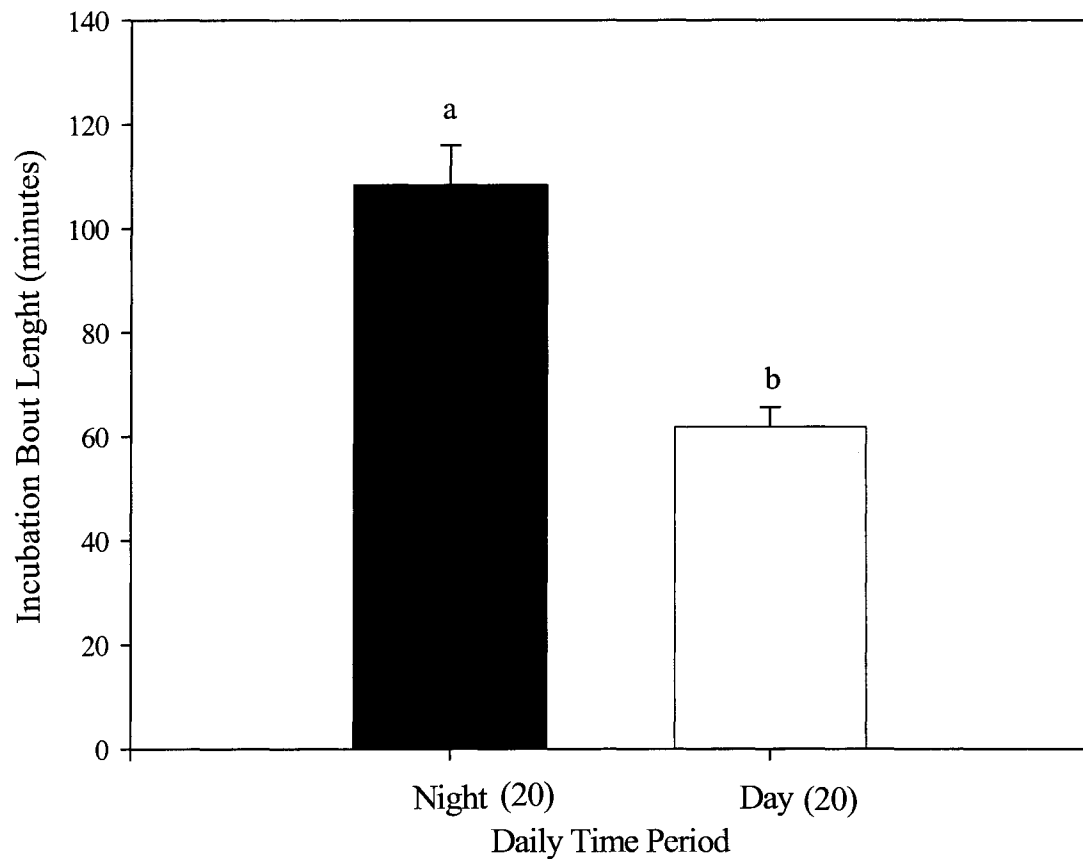


Figure 3.7. Incubation bout length as a function of daily time period (nocturnal or diurnal). Data given as mean \pm SE. The number of individuals used in the analysis are given in parentheses and letters indicate significant results ($p < 0.05$).

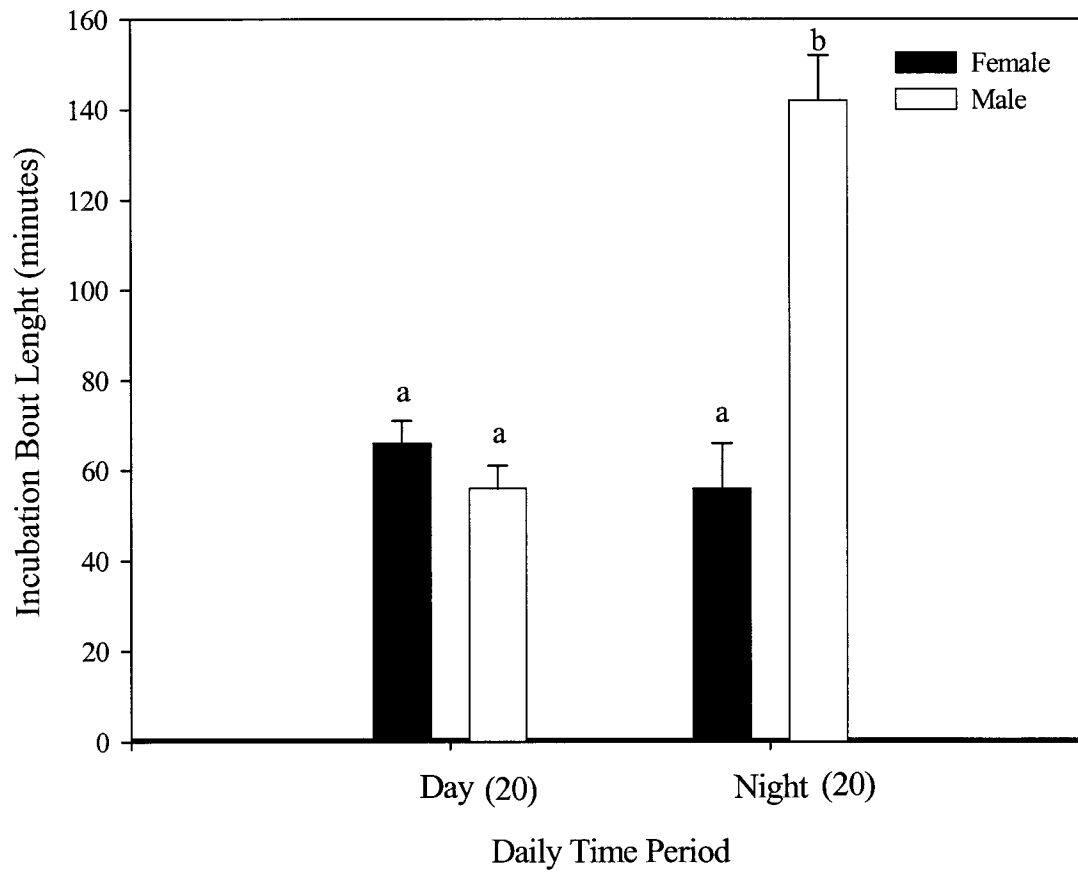


Figure 3.8. Incubation bout length as a function of sex and daily time periods. Data given as mean \pm SE. The number of individuals used in the analysis is given in parentheses and letters indicate significant results ($P < 0.05$).

and females had similar bout lengths during the diurnal incubation period. However, males increased bout length at night (142.1 ± 10 min) compared to diurnal incubation bout lengths (56.5 ± 5 min). Females had similar bout lengths during nocturnal (56 ± 10 min) and diurnal incubation bouts (66.3 ± 5 min).

3.4 DISCUSSION

The results of my study indicate that total nest attendance by piping plovers does not vary with incubation stage (early, middle or late) or the daily time period (nocturnal versus diurnal). Overall, my results did not support the null hypothesis that males and females share incubation duties equally. Rather, the data support my *a-priori* prediction that male piping plovers play the principle role in incubation, especially at night. Although males and females shared diurnal incubation duties, males increased their contribution during the night.

Shared incubation duties in piping plovers allow the nest to be attended almost continually, resulting in an overall nest attendance of 92%. Generally, shorebirds with bi-parental care have a parent attending the nest $\sim 90\%$ of the time (Bergstrom 1986) whereas shorebirds with uni-parental care attend the nest $< 90\%$ (Norton 1972, Deeming 2002). Continuous attendance may have advantages in terms of embryo development and reduced re-warming costs, which may result in shorter incubation periods, decreased predation risk and lower energy expenditures for the incubating adult (Reid 2002c).

Male piping plovers at Chaplin Lake spent a larger proportion of their daily activity incubating relative to females. Male participation is likely influenced by the opportunity to acquire mates, paternity, survival, current reproductive effort, and relative

contribution by its mate (Moller & Thornhill 1998; Reid et al. 2002b). Life history theory suggests that males participate in incubation when male care enhances offspring survival (Alcock 1998). Thus, males are expected to participate when the number of offspring that survive with bi-parental care exceeds the number that survive with uni-parental care and additional mating opportunities (Elmen & Oring 1977). In many shorebirds with bi-parental care, the cost of male desertion is high due to inevitable female nest abandonment. Mate removal studies illustrate that incubation cannot be completed with a single parent (e.g. killdeer, *Charadrius vociferus* ; Brunton 1988a; kentish plover, *Charadrius alexandrinus*; Lessels 1984; black-bellied plovers, *Pluvialis squatarola*; Hussell & Page 1976). However, female killdeer (*C. vociferus*) tend to abandon more quickly than males (Brunton 1988a), which may be indicative of increased constraints placed on the female (Brunton 1988a, b). Although it has not been tested directly, it seems likely that piping plovers may not normally be able to successfully complete incubation without a mate, and some nest abandonment may be the result of mate loss.

In migratory species, including piping plovers, the benefits derived from mate assistance may outweigh the tradeoff with mating opportunities because females are synchronously receptive to reproduction, consequently there is limited opportunity of additional matings (Elmen & Oring 1977; Patton 1995). Furthermore, low rates of extra pair copulations have been reported for shorebirds in general (Mee et al. 2004), including piping plovers (Haig 1987). The majority (95%) of first nest initiation dates for plovers at Chaplin Lake occurs within an 18-22 day period (Chapter 1). Thus, opportunity for additional mates seems to be low which suggests that males' best opportunity to enhance fitness is to increase parental care.

Males potentially play a larger role in incubation because females may be unable to maximize foraging and incubation activities simultaneously (Brunton 1988b; Clutton Brock 1991b; Lessels 1991; Lessels 1998). The incubation stage of reproduction imposes significant energy and time constraints on parents (Reid et al. 2000; Tinbergen & Williams 2002). Metabolic rates for incubating kentish plovers (*C. alexandrinus*) have been estimated at 100-106 kJd⁻¹ which is approximately 2.5 times their basal metabolic rate (BMR: 41-42 kJd⁻¹; Amat 2000). Furthermore, shorebirds, including plovers, lay large clutches relative to body size (Rahn et al. 1975). The initial production of an egg is estimated to represent at least 200% of the basal metabolic rate in killdeer (*C. vociferus*; Brunton 1988a) and spotted plovers (*Actitis macularia*; Maxon & Oring 1988). This initial investment may not constrain females to the point of inhibiting incubation, but it may limit the ability of females to provide parental care (Amat et al. 2000). Females are likely required to exploit exogenous resources to meet these energy expenditures, at the cost of a decreased ability to incubate (Conway & Martin 2000; Cresswell et al. 2003). If females have limited resources to invest in reproduction, life history theory predicts a negative relationship between time allocated to foraging and reproductive activities (Reid et al. 1999). A negative relationship has been demonstrated for female killdeer (Brunton 1988a, b). This relationship suggests a direct tradeoff between energetic costs (somatic activities) and reproductive activities. Males may adjust investment in parental care in response to a decrease in their mate's parental effort. Adjustments in response to a mate's effort has been documented in dunnoek (*Prunella modularis*), ringed turtle doves (*Streptopelia risoria*) and black-tailed godwits (*Limosa limosa*; Hegyi & Sasvari 1998). Thus, increased male incubation may compensate for decreased female participation and

allow females to recoup the costs of egg production and incubation (Brunton 1988; Clutton Brock 1991b; Lenington 1980). Mate assistance may be the most effective method for male piping plovers to increase individual fitness. Increased participation in incubation may allow males to increase their fitness by enhancing offspring survival (Mundah 1982). As the opportunity to inseminate many females may not be available due to low temporal variation in female sexual receptiveness and a short breeding season, and abandonment during incubation leads to reproductive failure (Elmen and Oring 197, Patton 1995). However, further investigation into the time activity budget of males and females during non-incubating periods would provide insight into the constraints imposed on both sexes during the incubation period.

A second (although not mutually exclusive) hypothesis suggests that for shorebirds with high rates of nest failure, increased investment by males may be required to allow females to maintain their body condition such that they can rapidly produce replacement clutches (Smith 1977; Wallander & Malte 2003). Piping plovers replace clutches if the current attempt fails (Evans 1991; Haig 1992). Hegyi & Sasvari (1998) found that larger northern lapwing (*V. vanellus*) and black-tailed godwit (*L. limosa*) females in good body condition had improved ability to replace clutches. Overall, piping plovers tend to have high rates of nest failure (Chapter 1; Prindville-Gaines & Ryan 1988). In general, the rate of nest failures in piping plovers is similar to those found in killdeer (*C. vociferus*; 60-65%; Brunton 1988a) and ringed plovers (*Charadrius hiaticula*; 67%; Wallander & Malte 2003). High rates of nest failure in conjunction with a short breeding season may result in selection pressure for females to rapidly produce new clutches.

Male piping plovers assume the primary role in nocturnal incubation. This is similar to snowy plovers (*C. alexandrinus*; Kostolanyi & Székely 2002) and killdeer (*C. vociferus*; Warnock & Oring 1996). A number of hypotheses have been proposed to explain the predominance of male nocturnal care. Nocturnal incubation may allow females to forage at night to recoup costs of incubation (Norton 1972; Burger 1981; Kosztolányi & Székely 2002). McNeil (1991) proposed the supplemental foraging hypothesis, which suggests that nocturnal foraging arises when diurnal foraging is insufficient to meet the daily energy needs. Thibault & McNeil (1995) found that male Wilson's plover (*Charadrius wilsonia*) mainly foraged during the day while females foraged at night during the incubation period. Blanken and Nols (1991) suggested that female semipalmated plovers (*C. semipalmatus*) forage at night when polychaetes are most active. Plovers are visual foragers and grey plovers (*Pluvialis aquatarola*) have been observed to forage even on dark nights, despite decreased foraging efficiency (McNeil 1991). Piping plovers have also been documented to forage at night during the breeding season (Staine & Burger 1994). Nocturnal foraging by birds in the prairie population has not been investigated. Secondly, males may need to defend the territory during the day, limiting their ability to incubate during the day (Kosztolányi & Székely 2002). However, this seems unlikely at Chaplin Lake since the non-incubating parent (male or female) is often not on the territory and may be foraging some distance away (C.W. personal observation). A third explanation may be that males and female have differing abilities to detect and escape predators at night (Blanken & Nol 1998; Kosztolányi & Székely 2002). However, Miller (1985) suggested that nocturnal predation pressures vary both temporally and spatially across a species range, consequently

predation may not provide a constant or consistent selective pressure. The piping plover predator community is thought to include coyotes, foxes, skunks, gulls, crows, and magpies in addition to other small mammals and birds. However, little is known about the spatial and temporal variation in the piping plover predator community (Ivan & Murphey 2002). Further investigation into the predator communities that threaten piping plovers is required. Amat (2004) reported increased adult mortality in male kentish plovers (*C. alexandrinus*) that incubated at night, suggesting that nocturnal incubation poses a higher risk than diurnal incubation. It has been suggested that nocturnal incubation carries increased physiological costs and predation risk; and consequently females that do not incubate at night may save energy and avoid risk (Mundahl 1982). Temperatures during the night are generally low, especially in May when nests are initiated, and furthermore ground nests are exposed and subject to greater fluctuations in temperature (Bergstrom 1989; Cresswell et al. 2003). The mean minimum nocturnal ambient temperature at Chaplin Lake in 2004 was $7.06^{\circ}\text{C} \pm 4.50 \text{ SD}$ for June and $10.5^{\circ}\text{C} \pm 2.75$ July (White unpublished data). In summary, while males of many shorebird species incubate at night, further research is required to test the hypotheses that have been proposed to explain this behaviour.

Incubation bout length is likely a function of body size, climate, the degree of conspicuousness of the incubator and energetic requirements imposed by incubation (Cartar 1987). Piping plovers at Chaplin Lake had no predictable schedule for incubation changeovers during diurnal or nocturnal incubation and bout lengths did not vary over the incubation stages. During the day, bout lengths were approximately one hour but changeovers did not consistently occur at the same time each day. Likewise, killdeer (*C.*

vociferus) and semipalmated plovers (*C. semipalmatus*) have no set incubation changeover patterns (see Blanken & Nols 1998). This may result from disturbance (e.g. humans or predators) or energy constraints or requirements (Blanken & Nols 1998; Cresswell 2003). Overall, nocturnal incubation bout lengths were longer than diurnal bout lengths. Bout lengths for females did not change when diurnal and nocturnal incubation periods were compared. However, males increase their bout length at night to approximately 2 hours before taking a recess. The constancy of female bout length may reflect reproductive constraints. Females may only be able to incubate for a certain duration of time before “hunger levels” require them to restore body reserves (Cresswell 2003). In contrast, males may be more persistent incubators as they may have more body reserves, which allow them to have longer incubation bouts (Kosztolányi & Székely 2002). The phenomenon of bout length has received relatively little attention in shorebirds (Blanken & Nols 1998) and factors thought to influence bout length in piping plovers have not been investigated.

Overall, there are limited data regarding the nocturnal activity schedule of shorebirds (McNeil 1991). Typically, researchers have assumed that if a bird is on the nest at dusk and dawn it had remained there all night (Bergstrom 1981). Other studies have defined nocturnal incubation periods based on a few nocturnal trapping events, despite the recognized bias in trapping success between males and females in some species (Mundahl 1982). McNeil (1991) suggested that shorebirds are active during the night, which may result in variable nocturnal parental care. Recent studies using night-vision equipment and video cameras confirm McNeil’s contention and show that nocturnal incubation is variable (Thibault & McNeil 1995; Warnock & Oring 1996). My

results indicate that there is variation in nocturnal incubation patterns. On two occasions there was a reversal of roles where the female incubated for most of the night, this occasional role reversal has also been documented in killdeer (Warnock & Oring 1996). Furthermore, male-only incubation occurred on 28 nights, while both parents contributed to nocturnal incubation during the other 53 nocturnal observation periods. The variability in nocturnal incubation suggests there is flexibility within incubation patterns which likely reflects environmental conditions (Thibault & McNeil 1995). The differential allocation of parental care by the two sexes in shorebirds seems to occur at night, and therefore diurnal observations may result in an underestimation of the relative contribution by each sex. Video monitoring allowed for detailed continuous 24-hour observations. There has been no formal evaluation of the potential effects of cameras (Sanders & Maloney 2002; Keedwell & Sanders 2002), however numerous studies suggest that the cameras do not influence adult parental behaviour (Delaney & Grubb 1999; Laut et al. 2003). Although nocturnal studies were difficult in the past, advances in technology enables us to collect data representative of the 24-hour time period meaning that the assumptions previously necessary can be avoided.

Overall, my study was confined to activities that occurred at or very near to the nest and did not account for all activities that would be considered parental investment. In the broadest sense, parental investment includes the preparation of nests, production of eggs, and care of young until independence (reviewed by Clutton-Brock 1991). All activities performed by an individual during the breeding season can be divided into either somatic effort (the time, energy, and risks involved in growth and maintenance) or reproductive behavior (time, energy and risk associated with reproduction; Brunton

1988b; Blanken & Nols 1998). Reproductive behaviour can further be divided into “reproductive effort” and “mating effort”. Mating effort would include activities related to courtship and establishing and maintaining a territory. Reproductive effort includes activities that enhance the survival of offspring including incubation and brood rearing. Time budget data including courtship, nest defense and incubation “off-bout” activities would provide insight into the relationships that exist between self-maintenance and reproductive activities.

Video monitoring enabled me to gather specific data regarding the parental roles of male and female piping plovers. This study overcomes one of the major assumptions that has been made in previous studies, and supports the conclusion that nocturnal incubation is more variable than previously thought (McNeil 1991; Warnock & Oring 1996). My results show that males and females have differing levels of contribution to incubation. However, investigation into the energetics and/or time budget outside of incubation would provide insight into this pattern in piping plovers. Furthermore, I found that males take on the primary role at night; however, hypotheses as to what drives this incubation pattern need to be explicitly tested.

3.5 LITERATURE CITED

- Alcock J. 1998. *Animal Behavior: an evolutionary approach*, 6th edition. Sinauer Associates, Massachusetts.
- Alberico, J.A.R. 1995. Floating eggs to estimate incubation stage does not affect hatchability. *Wildlife Society Bulletin* 23, 212-216
- Amat, J.A., G.H. Visser, A.P. Hurtada & G.M. Arroyo 2000. Brood desertion by female shorebirds: a test of differential capacity hypothesis on kentish plovers. *Proceedings of the Royal Society of London. B.* 267, 2171-2176.
- Breichagen, T. 1989. Nesting biology and mating system in an alpine population of Temminck's Stint (*Calidris temminckii*). *Ibis* 131, 389-402.

- Bergstrom, P.W. 1981. Male incubation in Wilson's plover (*Charadrius wilsonia*). *Auk* 98, 835-838.
- Bergstrom, P.W. 1986. Daylight incubation sex roles in Wilson's plover. *Condor* 88, 113-115.
- Bergstrom, P.W. 1989. Incubation temperature of Wilson Plovers and Killdeers. *Condor* 91, 634-641.
- Blanken, M.S. & Nol, E. 1998. Factors affecting parental behavior in semipalmated plovers. *Auk* 115, 166-174.
- Bottitta, G.E., H. G. Gilchrist, A. Kift, and M. G. Meredith 2002. A pressure sensitive wireless device for continuously monitoring avian nest attendance. *Wildlife Society Bulletin* 30, 1033-1038.
- Brunton, D.H. 1988a. Energy expenditure in reproductive effort of male and female killdeer (*Charadrius vociferous*). *Auk* 105, 553-654.
- Brunton, D.H. 1988b. Sexual differences in reproductive effort: time activity budgets of monogamous killdeer, *Charadrius vociferus*. *Animal Behaviour* 36, 705-717.
- Burger, J. 1981. Sexual differences in parental activities of breeding black skimmers. *The American Naturalist* 117, 975-984.
- Byrkjedal I. 1985. Time activity budget for breeding greater golden plovers in the Norwegian Mountains. *Willson Bulletin* 97, 486-501.
- Cairns, W.E. 1982. Biology and behaviour of breeding Piping Plovers. *The Wilson Bulletin* 94, 531-545.
- Cartar, R.V.&R.D.M. 1987. Day to day variation in nest attentiveness of white-rumped sandpipers. *Condor* 89, 252-260.
- Cartar, R.V.&R.D.M. 1985. The influence of weather on incubation scheduling of the white rumped sandpiper (*Calidris fuscicollis*): A uniparental incubator in a cold environment. *Behaviour* 95, 261-289.
- Charnov E.L. & J.R. Krebs. 1974. On clutch size and fitness. *Ibis* 116:217-219.
- Clutton-Brock, T.H. 1991. *The evolution of parental care*. Princeton University Press.
- Clutton-Brock, T.H. 1991b. Parental Investment. in *Behavioural Ecology* Eds J.R. Krebs and N.B. Davies. Blackwell Scientific Publications, Oxford.
- Conway, C.J. & Martin, T.E. 2000. Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology* 11, 178-188.

- Cresswell, W., S. Holt, J.M. Reid, D.P. Whitfield & R.J. Mullanby 2003. Do energetic demands constrain incubation scheduling in a biparental species? *Behavioral Ecology* 14, 97-102.
- Davies, N.B. 1991. *Mating Systems in Behavioural Ecology*. (Eds J.R. Krebs and N.B. Davies) Blackwell Scientific Publications, Oxford.
- Delaney, D.K. & T.G. Grubb 1999. Activity patterns of nesting Mexican Spotted Owls. *Condor* 101, 42-49.
- Deeming, D.C. 2002. Behaviour patterns during incubation. In: *Avian Incubation* (Ed. by D.C. Deeming) Oxford, Oxford University Press. pp 63-85.
- Elmen, S.T. & Oring, L.W. 1977. Ecology, sexual selection, and the evolution of mating systems. *Science* 197, 215-223.
- Evans P.R. 1991. Seasonal and annual patterns of mortality in migratory shorebirds: some conservation implications. Oxford, Oxford University Press. pp. 346-359
- Graul, W.D. 1975. Breeding biology of the Mountain Plover. *Wilson Bulletin* 87, 6-29.
- Haig, S. 1987. *The Population Biology and Life History Patterns of the Piping Plover*. University of North Dakota.
- Haig, S.M. 1992. Piping Plover. In *The Birds of North America*, No. 2 (A. Poole, P. Stettenheim and F. Gill, Eds.). Philadelphia: The Academy of Natural Sciences: Washington, DC: The American Ornithologist Union.
- Haig, S.M. & L. W. Oring 1988. Mate, site, and territory fidelity in Piping Plovers. *Auk* 105, 268-277.
- Hauber, M.E. 2002. Is reduced clutch size a cost of parental care in Eastern phoebes (*Sayornis phoebe*)? *Behavioral Ecology and Sociobiology* 51, 503-509.
- Hegy, L. & L. Sasvari. 1988. Parental condition and breeding effort in waders. *Journal of Animal Ecology* 67, 41-53.
- Houston, A. I. & N. B. Davies 1985. The evolution of cooperation and life history in the dunnoek *Prunella modularis*. In: *Behavioural Ecology*. (Eds J. R. Krebs and N. B. Davies) Oxford, Blackwell Scientific Publications. pp. 471-487
- Hussell, D. J. D. & G.W. Page. 1976. Observation of the breeding biology of Black-bellied Plovers on Devin Island, N.W.T., Canada. *The Wilson Bulletin* 88, 632-653.
- Ivan, J. S. and R.K. Murphey. 2002. What preys on piping plover eggs and chicks? (*unpublished report*). 11pp. + appendix.

- Keedwell, R. J. & M. D. Sanders 2002. Nest monitoring and predator visitation of banded dotterels. *Condor* 104, 899-902.
- Knetterson, E. D. & V. Nolan, Jr. 1994. Male parental behavior in birds. *Annual Review of Ecology and Systematics* 25, 601-628.
- Kosztolányi, A. & T. Székely 2002. Using a transponder system to monitor incubation routines of Snowy Plovers. *Journal of Field Ornithology* 73, 199-205.
- Lazarus, J. 1990. The logic of mate desertion. *Animal Behavior*. 39:672-684.
- Laut, M. E., P. C. Banko & E. M. Gray 2003. Nesting behavior of Piping Plover, as assessed from video recording. *Pacific Science* 57, 385-392.
- Lenington, S. 1980. Bi-parental care in killdeer: an adaptive hypothesis. *Wilson Bulletin* 92, 8-20.
- Lessels, C. M. 1984. The mating system of Kentish Plovers *Charadrius alexandrinus*. *Ibis* 126, 474-483.
- Lessels, C. M. 1991. The evolution of life histories. In, J. R. Krebs, and N. B. Davies (eds.), *Behavioural ecology: an evolutionary approach* (3rd edition). Blackwell Scientific Publications, pp. 32-65.
- Lessels, C.M. 1998. A theoretical framework for sex-biased parental care. *Animal Behaviour* 56, 395-407.
- MacDonald, D., C. White, S. Davis, K. Connick, D. Beverage, R. MacDonald (2003) The Piping Plover Basin Site Plans for Southern Saskatchewan. Unpublished report for Saskatchewan Watershed Authority. 170pp. + appendix
- Maxon, S.J. & L.W. Oring. 1980. Breeding season time and energy budgets of the polyandrous Spotted Sandpiper. *Behaviour* 74, 200-263.
- McNeil, R. 1991. Nocturnality in shorebirds. In: Acta XX International Ornithological Congress. (Ed. B. D. Bell) Christchurch New Zealand, New Zealand Ornithological Congress Vol 2. pp1098-1104.
- McQuillen, H.L. & L.W. Brewer 2000. Methodological consideration for monitoring wild bird nests using video technology. *Journal of Field Ornithology* 71, 167-172.
- Mee, A., D. P. Whitfield, D. B. A. Thompson & T. Burke 2004. Extrapair paternity in the common sandpiper, *Actitis hypoleucos*, revealed by DNA fingerprinting. *Animal Behaviour* 67, 333-342.
- Miller, E. H. 1985. Parental behavior in the least sandpiper (*Calidris minutilla*). *Canadian Journal of Zoology* 63, 1593-1601.

- Moller, A. P. & R. Thornhill, 1998. Male parental care, differential parental investment by females and sexual selection. *Animal Behaviour* 55, 1507-1515.
- Murphy, R. K. B. G. Root, P. M. Mayer, J. P. Goossen, K. A. Smith. 1999. A draft protocol for assessing Piping Plover reproductive success on Great Plains alkali lakes. Pp. 90-107 in Proceedings, Piping Plover and Least Terns of the Great Plains and nearby. (Higgins, K. F., M. R. Brashier and C. D. Kruse, eds.) South Dakota State University, Brookings.
- Murphy, R. K., M. J. Rabenberg, M. L. Sondreal, B. R. Casler & D. A. Guenther 2000. Reproductive success of Piping Plovers on alkali lakes in North Dakota and Montana. *The Prairie Naturalist* 32, 233-241.
- Mundahl, J. T. 1982. Role specialization in the parental and territorial behavior of the killdeer. *Wilson Bulletin* 94, 515-530.
- Norton, D. 1972. Incubation schedules of four species of Calidrine Sanpipers at Barrow, Alaska. *Condor* 74, 164-176.
- Parish, D. M. B. & J. C. Coulson. 1998. Parental investment, reproductive success and polygyny in the lapwing, *Vanellus vanellus*. *Animal Behaviour* 56, 1161-1167.
- Patton P. W. C. 1995. Breeding Biology of Snowy Plovers at Great Salt Lake, Utah. *Wilson Bulletin* 107, 275-288.
- Pienkowski, M. W. 1983. Changes in the foraging pattern of plovers in relation to environmental factors. *Animal Behavior* 31, 244-264.
- Pietz, P. J. & D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *Journal of Wildlife Management* 64, 71-87.
- Prindville-Gaines, E. & M. R. Ryan. 1988. Piping Plover habitat use and reproductive success in North Dakota. *Journal of Wildlife Management* 52, 266-273.
- Rahn, H., C.V. Paganelli, A. Ar. 1975. Relation of avian egg weight to body weight. *Auk* 92, 750-765.
- Reed, J. M. 1999. The role of behavior in recent avian extinctions and endangerments. *Conservation Biology* 13, 232-241.
- Reid, J. M., Monaghan, P. & Ruxton, G.D. 1999. The effect of clutch cooling rate on Starling, *Sturnus vulgaris*, incubation strategy. *Animal Behaviour* 58, 1161-1167.
- Reid, J.M., P. Monaghan & G.D. Ruxton 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proceedings of the Royal Society of London B* 267, 37-41.
- Reid, J. M., G. D. Ruxton, P. Monaghan & G. M. Hilton. 2002a. Energetic consequences

- of clutch temperature and clutch size for a uniparental intermittent incubator: the starling. *Auk* 119, 54-61.
- Reid, J. M., P. Monaghan & G. D. Ruxton 2002b. Males matter: the occurrence and consequences of male incubation in starling (*Sturnus vulgaris*). *Behavioral ecology and Sociobiology* 51, 255-261.
- Reid, J.M., P. Monaghan & R.G. Nager. 2002c. Incubation and the cost of reproduction . In: *Avian Incubation* (Ed. by D.C. Deeming) Oxford, Oxford University Press. pp 314-321.
- Reynolds, J. D. 1996. Animal breeding systems. *Trends in Ecological Evolution* 11, 68-72.
- Reynolds J. D. & T. Székely. 1997. The evolution of parental care in shorebirds: life histories, ecology and sexual selection. *Behavioral Ecology* 8, 126-134.
- Sanders, M. D. & R. F. Maloney. 2002. Causes of mortality ant nests of ground nesting birds in the Upper Waiteaki Basin, South Island, New Zealand: a 5 year video study. *Biological Conservation* 106, 225-236.
- Smith, M. 1977. Parental investment: a prospective analysis. *Animal Behaviour* 25, 1-9.
- Soikkeli, M. 1967. Breeding cycle and population dynamics in dunlin. *Annales Zoologici Fennici* 4, 158-198.
- Skeel, M. A., D. C. Duncan, and E. R. Wiltse. 1996. The 1996 International Piping Plover breeding census – Saskatchewan. Unpublished report for Saskatchewan Wetland Conservation Corporation and Saskatchewan Environment and Resource Management. 22pp. + appendices.
- Staine, K. J. & Burger, J. 1994. Nocturnal foraging behaviour of breeding piping plovers (*Charadrius melodus*) in New Jersey. *Auk* 111, 579-587.
- Sykes, P. W.Jr., W. E. Ryman, C. B. Kepler & J. W. Hardy 1995. A 24-hour remote surveillance system for terrestrial studies. *Journal of Field Ornithology* 66, 199-211.
- Thibault, M. & McNeil, R. 1995. Day- and night-time parental investment by incubating Wilson's Plovers in a tropical environment. *Canadian Journal of Zoology* 73, 879-886.
- Thompson, F. R., W. Dijak & D. E. Burhans 1999. Vida identification of Predators at Songbird nests in old fields. *Auk* 116, 259-264.
- Trivers, R. L. 1972. Parental investment and sexual selection. In B. Campbell, ed., *Sexual Selection and the Descent of Man*, pp 136-179, Alsine, Chicago.

- Wallander, J. & Malte, A. 2003. Reproductive tactics of the ringed plover *Charadrius hiaticula*. *Journal of Avian Biology* 34, 259-266.
- Warnock, N. & Oring, L.W. 1996. Nocturnal nest attendance of killdeers: more than meets the eye. *Auk* 113, 502-504.
- Wilcox, L. 1959. A twenty year banding study of the Piping Plover. *Auk* 76, 129-152.
- Williams, G. E. & P. B. Wood 2002. Are traditional methods of determining nest predators and nest fates reliable? An experiment with wood thrushes (*Hylocichla mustelina*) using miniature video cameras. *Auk* 119, 1126-1132.
- Zar, J. H. 1999. *Biostatistical Analysis*. 4th edition. Prentice Hall, New Jersey, USA.

CHAPTER 4: GENERAL CONCLUSIONS

Factors that influence the probability of species extinction and endangerment typically involve multiple variables including behavior, life history characteristics and anthropogenic threats (Reed 1999). Information about reproductive success is critical for predicting changes in population size, and for designing effective management strategies. My study set out to assess two aspects of reproduction that are intertwined: trends in productivity and patterns of parental care.

I provided data on the reproductive ecology of piping plovers breeding near Chaplin Lake over a 3-year period. Nest initiation and hatching patterns were synchronous, however they varied over the three years (Chapter 2). Threats to piping plovers at Chaplin Lake include predation, livestock trampling, and flooding. Predation accounted for the majority of nest failures in each year. Nest survival varied among years and declined as the breeding season progressed. Analysis of daily brood survival rates indicated that age, date and year all had an influence. Younger chicks had a lower daily survival rate than older ones, which is similar to previous reports (Prindville-Gaines & Ryan 1988; Loegering & Fraser 1995; Patterson et al. 1991; Jung et al. 1998). The low rates of survival for young chicks maybe due to starvation, environmental conditions, predation, or interactions between these variables. Fledging rates ranged from 0.86 to 0.69 chicks per pair. These are similar to those reported from other alkali habitat, which have been used in recent demographic models. Generally, productivity on Chaplin Lake is less than the 1.25 chicks/pair/year, which has been proposed by the Recovery Team as the minimum required for stabilizing the population (Goossen et al. 2002).

In Chapter 3, the null hypothesis that male and female piping plovers share incubation equally was rejected; rather the results supported my *a-priori* prediction that male piping plovers play a larger role in incubation, especially at night (Warnock & Oring 1996). Overall, total nest attendance did not vary as a function of incubation stage or daily time period. However, males contributed more to incubation than females in all three incubation stages (early, middle and late). Furthermore, males exhibited an increased contribution to nocturnal incubation, whereas males and females shared diurnal incubation equally. Theories which purport to explain why these trends occur in plovers primarily address female energy budgets and deficits (Brunton 1988b; Clutton Brock 1991b; Lessels 1991; Brunton 1988b; Lessels 1998). My study did not set out to explicitly address these issues and they remain to be tested. Data for time activity budgets of non-incubating individuals would allow me to investigate these theories more directly. My data support McNeil (1991) who suggested that nocturnal incubation is more variable than previously thought. Video monitoring allowed me to successfully investigate the relative roles of male and female piping plovers during incubation and evaluate the major assumptions regarding nocturnal incubation in previous studies.

Information regarding a combination of behaviour and reproductive output is important for our understanding of the constraints placed on breeding individuals. Differences in energy allocation during the breeding season may be suggestive of a greater annual mortality in females. It has been reported that yearling females are often mated to older males but older females are not mated to younger males (Westworth 2003). This suggests that there is an unequal ratio of available males and females during the breeding season (Westworth 2003). My study is limited to activity budget information

pertaining directly to the incubation period. A more complete understanding of the interactions among parental care, energy constraints and the reproductive consequences require data on overall activity budgets including somatic activities (e.g., foraging, resting), and activity during other reproductive periods (brood rearing, laying etc.) combined with indicators of productivity.

Plover conservation as a whole requires knowledge of the factors that affect reproductive success and survival. However, data on basic breeding biology are lacking for many plover species including the piping plover (Johnson & Oring 2002). Generally, reproductive rates on Chaplin Lake are lower than those required to sustain the population. By coupling productivity monitoring with a behavioral component, we gain access to breeding biology information, which can only improve our overall knowledge of piping plovers and provide insight into more effective conservation efforts.

4.1 REFERENCES

- Brunton, D.H. 1988b. Sexual differences in reproductive effort: time activity budgets of monogamous killdeer, *Charadrius vociferus*. *Animal Behaviour* 36, 705-717.
- Clutton-Brock, T. H. 1991b. Parental Investment. in *Behavioural Ecology* Eds J.R. Krebs and N.B. Davies. Blackwell Scientific Publications, Oxford.
- Johnson, M. & L.W. Oring 2002. Are nest exclosures an effective tool in plover conservation? *Waterbirds* 25, 184-190.
- Jung, T. S., J.P. Goossen, B. Aitken, and I. A. Bisson Conservation biology of piping plovers at Lake Diefenbaker, Saskatchewan: 1997 progress report. Unpublished Canadian Wildlife Service report, Prairie Northern Region, Edmonton, Alberta. 49pp plus appendices. 98.
- Lessels, C. M. 1991. The evolution of life histories. In, J. R. Krebs, and N. B. Davies (eds.), *Behavioural ecology: an evolutionary approach* (3rd edition). Blackwell Scientific Publications, pp. 32-65.

- Lessels, C.M. 1998. A theoretical framework for sex-biased parental care. *Animal Behaviour* 56, 395-407.
- Loefering, J.P. & J. D. Fraser 1995. Factors affecting piping plover chick survival in different brood rearing habitats. *Journal of Wildlife Management* 59, 646-655.
- McNeil, R. Nocturnality in shorebirds. (B. D. Bell, Ed. Acta XX International Ornithological Congress; New Zealand Ornithological Congress. 91.
- Patterson, M. E., J. D Fraser. & J. W. Roggenbuck. 1991. Factors affecting piping plover productivity on Assateague Island. *Journal of Wildlife Management* 55, 525-531.
- Prindville-Gaines, E. & M. R. Ryan 1988. Piping Plover habitat use and reproductive success in North Dakota. *Journal of Wildlife Management* 52, 266-273.
- Reed, J.M. 1999. The role of behavior in recent avian extinctions and endangerments. *Conservation Biology* 13, 232-241.
- Warnock, N. & Oring, L.W. 1996. Nocturnal nest attendance of killdeer: more than meets the eye. *Auk* 113, 502-504.
- Westworth S.M., D. Martens, C. Grato-Trevor, J.P. Goossen, and S.Davis. 2003. Northern Great Plains Piping Plover Science Workshop. Regina, SK. Nov. 2003.

Appendix A

DATE: August 16, 2005

TO: M. Brigham
Biology

FROM: Meigen Schmidt
Office of Research Services

RE: Annual Review of Animal Use Proposal

The President's Committee on Animal Care has reviewed your memorandum dated November 25, 2003, regarding your protocol entitled, Nesting Behavior of Piping Plovers (protocol number 03-06). This protocol has now been approved. Your annual renewal date is December 3rd and your protocol will expire on December 3, 2007.

Good luck with your research project. Thank you.

Meigen Schmidt
Research & Ethics Officer

MS/sm

c. Corie White, Biology