BREEDING BIOLOGY AND HABITAT SELECTION OF THE MAGELLANIC PLOVER (*Pluvianellus socialis*)

A thesis submitted to the Committee on Graduate Studies in partial fulfillment of the requirements for the degree of Master of Science in the Faculty of Arts and Science

TRENT UNIVERSITY
Peterborough, Ontario, Canada

Environmental and Life Sciences Graduate Program

September 2008

ABSTRACT

BREEDING BIOLOGY AND HABITAT SELECTION OF THE MAGELLANIC PLOVER (*Pluvianellus socialis*)

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Rare species are more vulnerable to extinction than common species. The objective of this study of *Pluvianellus socialis* was to address four factors related to rarity and vulnerability: geographic distribution, habitat specificity, local abundance, and demographics. Breeding location of *P. socialis* were searched and monitored in two breeding seasons: 2006-2007 and 2007. The species was found to have a restricted geographic range in Southern Argentina. By comparing used sites with unused, available, sites at three spatial scales results showed that birds selected specific habitat characteristics: saline lakes with well-developed aeolian lunettes, territories near freshwater channels with minimal vegetation cover, and microsites with minimal clay. The species exhibited small local population sizes where 1 - 4 pairs occupied a single lake. One lake was an exception and supported 14 breeding pairs. Nests contained 1 - 2 eggs. Pairs double- or triple-brooded when annual precipitation and lake water levels were favourable. Average number of young raised per season was 1.36. Finite population growth rate, using survivorship estimates based on a mass-survival rate equation, was estimated as 0.80, indicating a declining population. Restricted geographic range, ephemeral nesting habitat, low local abundance and low annual fecundity suggest that *P. socialis* is vulnerable to extinction.

Keywords: Magellanic plover, *Pluvianellus socialis*, Patagonia, endemic, shorebird, habitat selection, breeding biology, rare, vulnerable

ACKNOWLEDGEMENTS

I am grateful to the many individuals who provided field and logistic support in Santa Cruz, Argentina: S. Imberti, M. McNamara, G. Montero, R. López, K. Clark, M. Sejas, S. Alvarado, M. Ganchegui, R. Lovera, W. Lishman, M. Vindel, L. Najgebauer, and F. Paz. For private land access: Estancia. Killik Aike Norte, Ea. Los Pozos, Ea. La Angelina, Ea. Tres de Enero, Ea. Otern Aike, Ea. Rupai Pacha, Ea. Morro Chico, Ea. Glen Cross, Ea. Los Luises, Ea. El Bosque, Ea. La Martina, Ea. La Leona, and Ea. Don Raul. To individuals who provided advice on data analysis: Joe Nocera, Linh Nguyen, and Koji Tominaga. Suggestions and support from Ken Abraham, Jim Schaefer, Linda Cardwell, Santiago Imberti, and David Winkler were also greatly appreciated. This study was funded by Trent University, Universidad Nacional de la Patagonia Austral, and the Natural Science and Engineering Research Council of Canada.

Two people deserve special thanks. My supervisor, Erica Nol, was supportive of my hard-headed determination to study the pseudo-plover at the end of the Americas. She put a great deal of faith in me, supported my efforts and always had valuable input for the project. Santiago Imberti was the first to suggest the idea of studying *Pluvianellus socialis* to me. Although he took many risks in supporting my efforts, his unending encouragement and input was invaluable. In short, thanks a million to both of you.

I can’t express enough gratitude to my friends and family members who kept me in their hearts during this whole process: Cadence, Ma & Pa, Aaron & Ivy, Geordie, Leslie, Linh, Brian, Rita, Kim, Hepburn, Ania, Marina, Ina, Mike, Stacy, Chris, Bee and, of course, Della. Finalmente doy millones de gracias al Chorlito Ceniciento. Por todo.

FORWARD

This thesis has been formatted according the guidelines set out by Trent University Office of Graduate Studies.

Chapter Two: Data from this thesis were collected by C. Lishman and contributed significantly to the following publication: Ferrari, S., C. Albrieu, S. Imberti, and C. Lishman. 2008. Estado actual del conocimiento de un chorlo endémico de la Patagonia austral, el Chorlito Ceniciento (*Pluvianellus socialis*): reuniendo las piezas de un reompecabezas. Ornitología Netropical 19:433-443.

Chapter Three: Lishman, C., and E. Nol. (*Unpublished data*). Multi-scale habitat selection of the Magellanic Plover (*Pluvianellus socialis*). Data collected and analyzed by C. Lishman.

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CHAPTER 1: General Introduction

In the interest of preserving biological diversity, conservationists strive to understand patterns of extinctions and vulnerability. Rare species attract the attention of conservation research as they are more vulnerable to extinction (Rabinowitz et al. 1986). While there is evidence that rare species play an important role in ecosystem function and community structure (see Power et al. 1996, Lyons and Schwartz 2001), this is still debated among ecologists (Lyons et al. 2005). The total species richness of an ecosystem is usually comprised of several common species, and many more small populations of uncommon species (McArdle 1990). In this way, rare species are an important part of local species richness and there is evidence to suggest that more species in a community contributes to community stability (see Ives et al. 2001). In the interest of preserving biodiversity and community stability, rare species are often a priority for research and conservation efforts.

An important question concerning rarity is: what makes a species rare and not common? Rabinowitz et al. (1986) addressed this question and suggested that rarity takes on seven different forms and is caused by three unrelated dichotomous factors: geographic range (wide or narrow), habitat specificity (broad or restricted), and local abundance (abundant or scarce). From these three factors a three dimensional table is constructed and a species is classified into one of eight cells, seven of which makes the species rare in one or more dimensions (Table 1.1). Some forms of rarity are inherently more vulnerable to extinction than others, as Rabinowitz et al. (1986) observed, and for this reason a scheme with which to identify the different forms of rarity is an important tool in biodiversity management. The most extreme, and consequently the most

Table 1.1 A classification scheme for rare species (Rabinowitz et al. 1986). Seven forms of rarity are identified according to a dichotomous categorization of three independent factors. Numbers in the cells are ordered by vulnerability from 1 (most vulnerable) to 7 (least vulnerable). Using these factors, the form of rarity of *Pluvianellus socialis* can be determined.

		Geographic Distribution			
		Wide		*Narrow*	
	Habitat Specificity	*Broad*	*Restricted*	*Broad*	*Restricted*
Local Abundance	*Abundant*	common	6	4	2
	Scarce	7	5	3	1

vulnerable form of rarity (form 1, Table 1.1) is a species with a narrow geographic range, restricted habitat specificity and low abundance (which Rabinowitz et al. 1986 termed "scarce"; Manne and Pimm 2001).

The classification scheme designed by Rabinowitz et al. (1986) was first applied to the plants of Great Britain, but has since been applied to other groups of organisms such as passerine birds, primates or insect assemblages (Kattan 1992, Novotry and Basset 2000, Harcourt et al. 2002, Walker 2006). For example, Kattan (1992) studied the forms of rarity in Colombian avifauna by reviewing census data and provided a breakdown of the species with their respective category of rarity. Not all species can be classified appropriately by Rabinowitz et al.'s classification scheme (1986), e.g. species whose habitat use changes throughout their annual cycle (see Kunin and Gaston 1997). Despite its flaws, this system has been applied to various populations (Kattan 1992, Harcourt et al. 2002, Davies et al. 2004). Authors recognize that while it is effective at identifying rarity of a species, the extension of the concept of rarity to vulnerability to extinction should be done only when a fourth factor, population growth rate, is considered (Kattan 1992, Harcourt et al. 2002, Davies et al. 2004).

Certain life history and demographic characteristics of a rare species may predispose it to extinction risk more than other rare species (Pimm et al. 1988, Bennett and Owens 1997). Reproductive traits such as clutch size in birds (fecundity) and annual reproductive output have an influence on the population growth rate. Bennett and Owens (1997) compared the fecundity (measured as clutch size) of both non-threatened and threatened bird species (1111 species) at a global scale and found that lower fecundity was associated with extinction risk. It makes intuitive sense as species with low intrinsic rates of increase, r, and population growth rates, λ, would not be as resilient to mortality events (Pimm et al. 1988).

FOCAL SPECIES: THE MAGELLANIC PLOVER, *PLUVIANELLUS SOCIALIS*

Pluvianellus socialis, the focal species of my thesis, is a shorebird endemic to Patagonia, a non-politically recognized region spanning Chile and Argentina in southern South America (Figure 1.1). The range of *P. socialis* extends from the southernmost Andes mountains in the west to the Atlantic coast in the east and from as far south as the island of Tierra del Fuego to as far north as southern Buenos Aires province (Figure 1.1; Jehl 1975, Chiurla 1996). The majority of *P. socialis'* breeding range falls within Argentina; however some locations in Chile's Tierra del Fuego are also used by the species (Ferrari et al. 2003, Ferrari et al. 2008).

P. socialis is a dove-sized (~85 g) shorebird with light grey upper parts and head with white underparts (Figure 1.2 A). The species has a black bill and a pink or red iris. Juveniles and adults are distinguished by the colour of the legs which are yellow-orange and pink, respectively. The shape and manner of *P. socialis* is reminiscent of a dove since it is more squat and rounded than true plovers. In flight, *P. socialis* is characterized by the white wing stripe and white outer tail feathers. Sexes are similar although males are slightly larger and have darker features than females (Jehl 1975, pers. obs.). Eggs are greyish-green with dark brown spots (Figure 1.2 B). Chicks are mottled greyish-green. The adults and their chicks are very cryptic on their nesting substrates and essentially disappear from view when not moving. Eggs are also highly cryptic (Figure 1.2 B).

Groups are known to spend the austral winter (March-August) on estuaries and sheltered bays on the Atlantic coast of Argentina (Figure 1.1). During the breeding

Figure 1.1 The presumed global distribution of *P. socialis*. Map was modified from IUCN (2006).

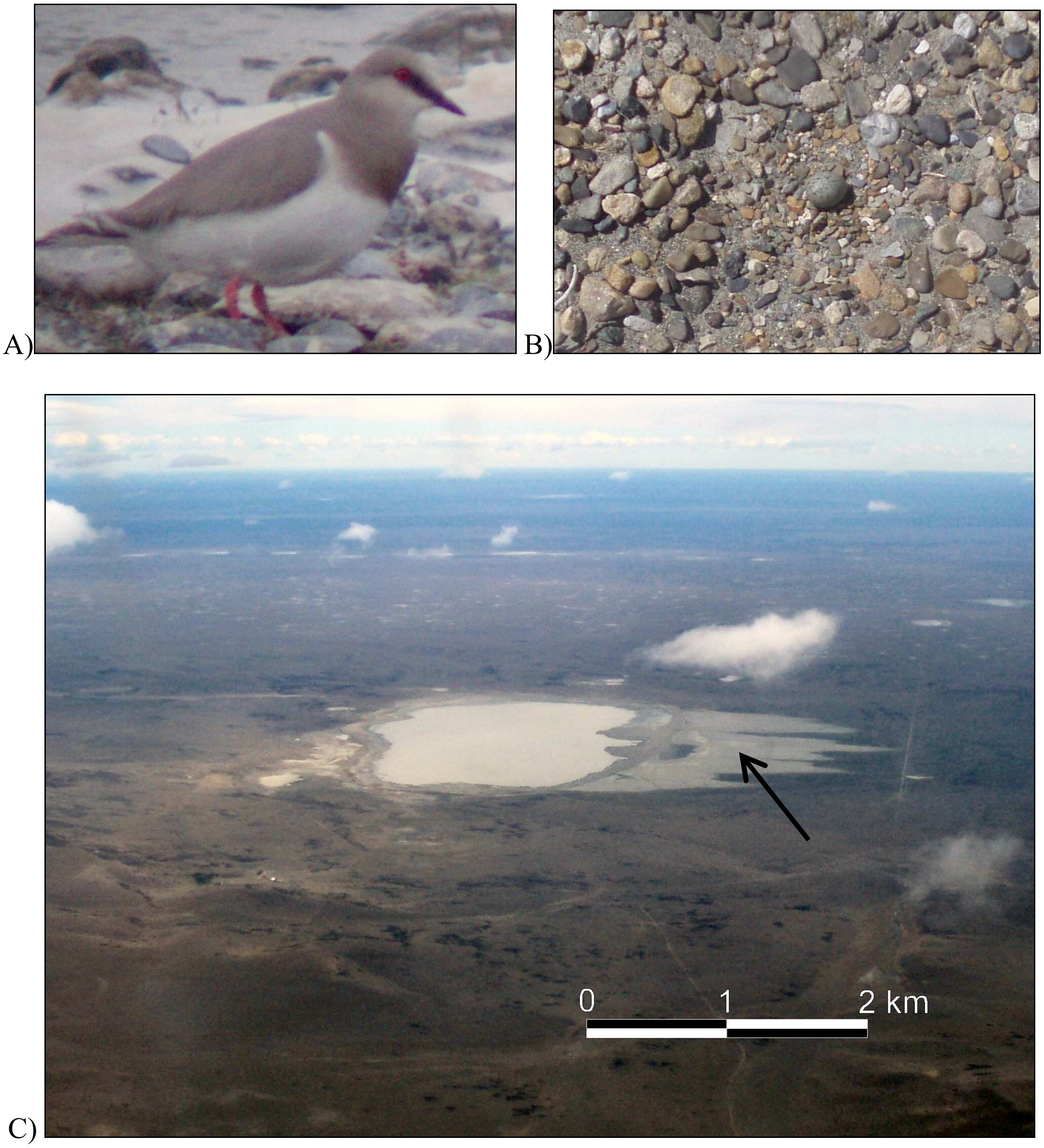

Figure 1.2 A) Photograph of an adult Magellanic Plover, *Pluvianellus socialis*. B) A nest of *P. socialis*. C) A typical lake in Santa Cruz Province, Argentina, on the shores of which *P. socialis* nest. The arrow points to a feature of the lake, called the aeolian lunette caused by wind erosion. All photographs by Carmen Lishman.

season *P. socialis* occupy the southern half of Santa Cruz province and northern area of Tierra del Fuego province (Figure 1.1). Pairs establish breeding territories and nest on the shores of lakes of the semi-arid grasslands of the Patagonian steppe (Figure 1.2 C). They may also nest on the shorelines of rivers (Ferrari et al. 2003). Jehl (1975) examined the stomach contents of a few individuals to find that they forage on invertebrates, mostly dipteran larvae and eggs. Further details on diet are unavailable.

Several aspects of the biology and behaviour of *P. socialis* indicate it is not a true plover, as its common name suggests, although several aspects of its ecology resemble that of members of the Charadriidae (Piersma and Wiersma 1996). Most authors recognize that *P. socialis* is monotypic; however, there is some uncertainty as to which family the genus *Pluvianellus* belongs (Jehl 1975, Chu 1995, Piersma and Wiersma 1996, Paton et al. 2003). The most recent molecular studies have confirmed suspicions that it is a member of the sheathbill family, Chionidae (Chu 1995, Paton et al. 2003). *P. socialis* may be sufficiently distinct to be designated to a family of its own, Pluvianellidae (Jehl 1975).

Census data on *P. socialis* indicate low population numbers (fewer than 1000-1500 individuals in the global population). Thus the species has been classified as “near threatened” on the IUCN Red List and by BirdLife International (2006). Population estimates of *P. socialis* are highly speculative since no systematic census has been conducted. The problem of estimating the *P. socialis* population is confounded by the fact that it is endemic to a sparsely inhabited part of the world, and it is highly cryptic. Accordingly, numerous authors have emphasized the urgency of greater effort to study *P. socialis* (Jehl 1975, Ferrari et al. 2003, Imberti 2003).

Most of the documentation of the biology of *P. socialis* came from the work of Jehl (1975) who observed five breeding pairs near the city of Río Grande, Tierra del Fuego in southern Argentina. Jehl (1975) assembled a comprehensive publication on the natural history of the species with valuable information on behaviour, breeding, and morphometrics. The depth of the paper's content, however, was limited by the small number of encounters, sample size, and the circumstances of his efforts. While travelling north through Santa Cruz province Jehl (1975) surveyed areas of suitable habitat and reported that *P. socialis* was also present in that province (Figure 1.1). With this information and incidental observations from other observers throughout Patagonia, he created a rough distribution map. Several questions arose in light of Jehl's publication, e.g. the taxonomic relationships of the species, survival of its nests and offspring and why it is such a rare species.

In 1999, Ferrari et al. (2003) surveyed the avifauna in the estuaries near the city of Río Gallegos, Santa Cruz province (over 250 km north of Río Grande on continental Argentina) and discovered the presence of large groups (ca. 140 individuals) of *P. socialis* wintering on the estuaries. Ferrari et al. (2003) published a collection of both winter and summer encounters throughout the province of Santa Cruz. They were unable to estimate the population size from their study and they expressed concern for the conservation of this rare and endemic species.

Apart from the two aforementioned publications, the documentation of *P. socialis* in institutional (e.g. IUCN 2006) and academic publications is limited to a mere mention. This very low quantity of documentation is not unusual for a South American endemic as most research funding is biased towards neotropical migrants. Piersma et al. (1997)

identified a “wealth of research opportunities” for the endemic shorebird species of South America and made explicit mention of the potential vulnerability of *P. socialis* due to nest trampling by introduced sheep in Patagonia.

PURPOSE AND OBJECTIVES

The purpose of my thesis is to address the question: Is *P. socialis* a vulnerable species and why? To address this broad question, four specific questions should be addressed:

1) Does *P. socialis* have a wide or narrow geographic distribution?
2) Does *P. socialis* exhibit broad or narrow habitat specificity?
3) Is *P. socialis* locally abundant or scarce?
4) Does the species possess life history characteristics that predispose it to extinction risk?

The first three questions are derived from the classification scheme devised by Rabinowitz et al. (1986). The fourth question relates to life history characteristics. This scheme was selected to describe *P. socialis* because it is simple and a useful model to understand causes of rarity. Additionally, the emphasis on habitat use seemed appropriate given that it is an important aspect of the biology and ecology of an organism and provides important information used in conservation applications.

Chapter 2 documents the breeding biology of *P. socialis*. In this chapter, I provide information on geographic distribution, breeding biology, life history traits and population growth rates. The objectives in this portion of my study are to (a) categorize *P. socialis* according to local abundance and geographic distribution and (b) estimate demographic parameters such as annual reproductive output and population growth rate. Achieving these objectives allow me to address questions 1), 3) and 4) above.

Chapter 3 is a habitat selection study conducted at three spatial scales of *P. socialis'* habitat. My objective in this chapter is to determine whether habitat use of *P. socialis* is non-random in relation to availability. By achieving this objective, I will be able to comment on the habitat specificity of *P. socialis,* thus addressing question 2) above.

In Chapter 4 I summarize the information from the studies in chapters Two and Three and draw conclusions on the classification of rarity that best describe this species and whether *P. socialis* should be considered a species vulnerable to extinction. I then report observations and speculate on why it is or is not a vulnerable species. Finally, I recommend directions for future research on *P. socialis*.

CHAPTER 2: Breeding Biology of the Magellanic Plover (*Pluvianellus socialis*)

ABSTRACT.--- The Magellanic Plover, *Pluvianellus socialis,* is a poorly studied, monotypic, endemic shorebird of Patagonia. I studied the breeding biology of *P. socialis* in southern Santa Cruz province, Argentina during breeding seasons in 2006 and 2007. Earliest nesting began in mid-September and clutch size was 1 or 2 eggs (*n* = 8 and 6, respectively). Eggs were laid on gravel or gravel-clay substrates on the shoreline of endorheic lakes in the semi-arid Patagonian Steppe. Eggs were incubated 24 days and 12 of 17 monitored nests had at least one egg hatch successfully (70%; Mayfield daily survival estimate = 0.975 and nest success estimate = 0.550). The observations of multiple within-season nesting (*n* = 7) in a 6-month breeding season, survival of siblings to fledgling age (*n* = 2), and a one-year old breeding individual provide new information on the breeding biology of the species and indicate that annual reproductive output of *P. socialis* is higher than previously believed. The data indicate an approximate annual output of 1.36 chicks per female. I modeled a scenario to estimate population growth rate, λ, using real values from this study and assumptions based on other shorebird species. The result was a λ of 0.80, a value that represents a decreasing population. The ability to nest multiple times in one season may be related to annual precipitation and water levels in the endorheic lakes. Proximal conservation efforts should be directed towards reducing the risk of trampling by grazing livestock, perhaps by excluding livestock from portions of the endorheic lakeshores.

Keywords: Magellanic Plover, *Pluvianellus socialis*, Patagonia, breeding biology, endemic, shorebird

INTRODUCTION

The Patagonian steppe, the arid grassland ecotone at the southern tip of South America, is a region renowned for relatively undisturbed natural systems and rich native fauna (Soriano 1983). The Magellanic Plover, *Pluvianellus socialis,* is an endemic shorebird of southern Patagonia. The biology of *P. socialis* has been poorly documented (Jehl 1975, Ferrari et al. 2003).

Population estimates of the species range from 1000 to 10,000 individuals (Jehl 1975, BirdLife International, 2006, respectively). Classified as "near threatened" on the IUCN Red List (2006), there is very little understanding of the threats that the species faces or whether it should be considered a species at risk at all.

P. socialis is not a true plover, as its common name suggests. Several characteristics of *P. socialis* noted by Jehl (1975) distinguish it from other members of the Charadriidae including regurgitation of food to the young and semi-precocity of the young (Jehl 1975). As such, it is a monotypic clade of the Charadriiformes. The genus *Pluvianellus* has tentatively been placed in the family Chionidae (the sheathbills) based on molecular evidence (Verheyden and Jouventin 1991, Paton et al. 2003, Van Tuinen et al. 2004) or based on ecology and morphology, considered the sole member of its own family, Pluvianellidae (Jehl 1975, Chu 1995).

Given the lack of basic knowledge of *P. socialis* and concern for its conservation status, several authors have emphasized the urgency of greater effort to study this species (Jehl 1975, Piersma et al. 1997, Ferrari et al. 2003). In this paper, I report on the breeding biology of *P. socialis* from south-central Santa Cruz Province, Argentina. The purpose of this research is to use new information provided by this study to describe the reproductive strategy and speculate on population dynamics of *P. socialis*. I report on breeding phenology, incubation period, egg dimensions, nest success, growth and morphology of chicks, and movements. As a heuristic method of estimating demographic parameters for *P. socialis*, I use information from this study and some supplementary information from the literature to estimate population growth rate, λ.

METHODS

Study area.--- This study was conducted during two consecutive breeding seasons in the austral spring and summer from October 2006 to March 2007 (hereafter, “2006 season”) and during the month of December 2007 (hereafter “2007 season”) in southern Santa Cruz Province, Argentina (51° 20’ S, 69° 30’ W). The semi-arid Patagonian steppe region was characterized by a cold, dry (<200 mm annual rainfall) climate with a strong persistent wind from the west (Soriano 1983). The flat grassland landscape supported many endorheic basins (Soriano 1983). Endorheic basins are watershed basins that do not drain to the ocean, and each basin usually contained one or more lakes, termed endorheic lakes, that vary in salinity, size and geomorphological development (Soriano 1983, Quirós and Drago 1999). I searched 53 endorheic lakes, 35 of which I visited in both seasons. I also searched portions of Lake Argentino (50° 19’ S, 72° 15’ W), a large (~700 km^2) freshwater lake that accumulates from Andean glacial water and drains to the Atlantic Ocean via the Santa Cruz river. All endorheic lakes included in the study (hereafter referred to simply as “lakes”) had clay bottoms and unvegetated shorelines, and all but one, inside the Argentinean National Park “Parque Nacional Monte León,” are on privately-owned sheep ranches. The summer of 2007 was a particularly dry year in this region and many lakes (~ 40%) that contained water in the 2006 season were completely dry when visited in the following year.

I searched the perimeter of each lake with 2 - 3 observers abreast walking in parallel transects around the circumference of the lake. As *P. socialis* is both cryptic and quiet on its breeding territories (Jehl 1975), observers stopped every 100-150 m to do a complete 360° scan with a 40x spotting scope. Forty pairs were found on 20 lakes, including 19 endorheic lakes and Lake Argentino.

Nest searching.--- When *P. socialis* was found, I made further observations using a spotting scope and/or binoculars from a distance of < 40 m, for up to several hours. I assumed individuals were transient visitors to the lake if they were walking or flying long distances (e.g. 500 - 2000 m) within the lake area, not associating with another individual, not exhibiting territorial behaviours, and foraging for extended periods of time (> 2 hours). I considered individuals to be territorial if they vocalized in the presence of an observer or conspecific, were aggressive with conspecifics or heterospecifics, associated strongly with a mate (copulating, following, or giving joint territorial displays), incubated a nest or brooded or fed a chick. I georeferenced the UTM coordinates and behaviours of the birds and territories. To avoid counting each waypoint as one territory, I examined the spatial distribution of breeding observations and considered waypoints < 200 m apart to be within one territory. This technique seemed effective, especially because waypoint clumps were either the only ones on one lake, or were evenly spaced around the shore of the same lake. In the 2007 season, I revisited 22 territories that had been found in the Austral spring of the previous year (October 2006).

Twenty nests (scrape with eggs) were found in the 2006 season (~120 days of effort) and four in the 2007 season (12 days of effort). I measured egg length and width using dial calipers to the nearest 0.1 mm and mass using a Pesola scale to the nearest 0.1 g. I calculated egg volume using the equation $[(0.4482 \text{ x egg length x egg width}^2) - 0.269]/1000$ following the technique developed for the Common Ringed Plover (*Charadrius hiaticula*, Väisänen 1977). I monitored 17 nests in the 2006 season by visiting every 2 – 8 days and determined nest fate. I considered a nest to be successful if one or more eggs hatched and unsuccessful if there was no eggshell evidence of hatching nor birds present on the territory (Mabee 1997). The cause of nest failure was determined from evidence near the nest. If eggs were absent I assumed that predation was the cause of nest failure. If eggs were crushed inside the scrape, I presumed it was trampled. I calculated daily nest survival using the Mayfield (1961) technique (Johnson 1979).

Chick banding.--- Chicks are inactive for the first week after hatch and, up until fledging age, crouch silently when faced with a threat. This behaviour allowed me to easily capture chicks of varying ages. I individually marked 26 chicks (17 in the 2006 season and nine in the 2007 season) with one or two self-closing darvic color bands in unique combinations, on the tarsi. The nine individuals banded in the 2007 season were also marked with a single aluminum band on the left tarsus registered with the Museo Argentino de Ciencias Naturales. All observations of marked individuals were recorded with date, location, and estimated age. I measured culmen length, tarsus length, and head length (excluding culmen) using dial calipers to the nearest 0.1 mm, and mass to the nearest gram using a 100 g pesola spring scale. Measurement data are included as an appendix to this thesis.

Population growth rate estimate.--- I calculated population growth rate, λ, and intrinsic rate of increase, *r.* Values of $\lambda < 1$ indicate that a population is decreasing, when $\lambda = 1$ the population size is stable and when $\lambda > 1$ the population is growing. The intrinsic rate of increase, *r*, is a function of the natural logarithm of λ. I used a three age-class ($i = 0$ years for juvenile, $i = 1$ years and $i \geq 2$ years for adult) Leslie matrix (A) where fertility values (F_i) are in the first row and survival probabilities (S_i) at age class *i* are on the subdiagonal (Leslie 1945):

$$A = \begin{vmatrix} F_J & F_A & F_A \\ S_0 & 0 & 0 \\ 0 & S_A & S_A \end{vmatrix}$$

F_i was calculated with the following equation:

$$F_i = 0.5 * prbreed_i * nhatch_i * fledgeS * S_0 * nests/season$$

where $prbreed_i$ is the probability of breeding at age *i*, $nhatch_i$ is the number of eggs hatched per nest by a female of age class *i*, *fledgeS* is pre-fledging survival rate, and S_0 is the probability of surviving from fledging to one year of age (juvenile survival). As F_i is representative of the fertility per season, I added the term *nests/season* which represents the number of independent nesting events of a single female in one breeding season. The equation is multiplied by 0.5 so that all parameters are estimated only for females, which is assuming an equal sex ratio.

I assumed that fertility rates (F_A) and survival rates (S_A) among the two adult classes were equal. I made this basic assumption so that a three age-class matrix could be constructed. I estimated the probability of breeding for juveniles, $prbreed_J$, to be 0, because there is no evidence that juvenile *P. socialis* breed. Therefore, $F_J = 0$. I calculated $nhatch_A$ from the data as the number of eggs hatched per nest for the first monitored nests of each pair. $Prbreed_A$ was calculated from my data as the proportion of adults I observed between August and December 2006 that were defending territories. My estimate of *fledgeS* was calculated as the number of fledged banded individuals seen, divided by the total number of banded chicks in the study.

There is a positive relationship between body size and survival rate in adult birds (Sæther 1989). Knowing this, I estimated adult survival rates by using data from two previous studies. Sæther (1989) described relationships between body size and survival estimates of European bird species. Sandercock (2003) reviewed the literature for survival estimates of 15 shorebird species. The estimate of survivorship to first year is an averaged value of semi-precocial species, such as gulls (*Larus* spp.), terns (*Sterna* spp.), and oystercatchers (*Haemotopus* spp.; Sæther 1989). The adult body mass of *Pluvianellus* was taken from Jehl (1975). I averaged the estimate from the fit equation derived from Sandercock's (2003) review and the fit equation in Sæther (1989) for the adult survival rate estimate. To estimate the *nests/year* term, I used an estimate based on the findings of this study.

RESULTS

Breeding phenology and locations.--- *P. socialis* left the wintering sites in early to mid-August and arrived on the shores of frozen endorheic lakes in groups to forage and began the process of pair formation (Figure 2.1, Ferrari et al. 2003). In these groups, individuals engaged in pre-copulatory displays (Jehl 1975). Pairs, when formed, act aggressively towards unpaired individuals, forcing them out of the immediate area. Once territories were established, some pairs persisted at those sites throughout the breeding

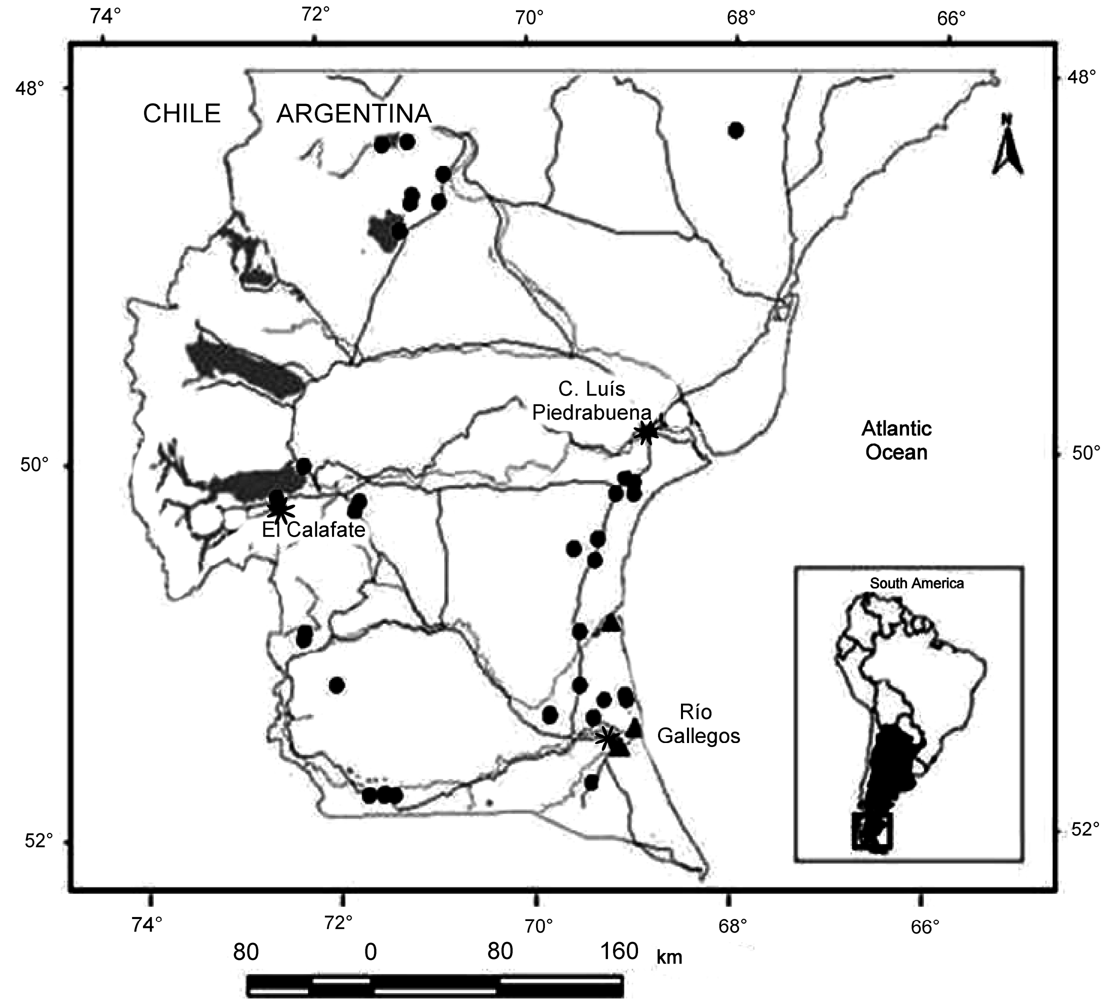

Figure 2.1 Breeding sites (circles) and non-breeding sites (triangles) of *Pluvianellus socialis* in southern Santa Cruz Province, Argentina. Locations from this study and from Ferrari et al. (2003).

season until February. However, the dry conditions of summer caused some lakes to dry completely by December and this caused pairs to abandon their territories earlier in the season. Pre-copulatory displays and copulation were observed throughout the breeding season. Only on a few occasions were these displays followed by scrape displays and nest initiation (see complete description in Jehl 1975). I located a total of 40 territories during the 2006 season, of which 22 were visited throughout the 2006 season and revisited in December 2007. Pairs remained present on territories until their ultimate brood had fledged which, for some pairs, was late February.

I found the earliest evidence of breeding, a chick estimated at 8 days of age, on 10 October 2006. This corresponds to a nest initiation date in the second week of September. I confirmed multiple within-season nesting of seven breeding pairs by observing adults feeding a chick and incubating a nest within the same one-hour observation period. One pair that was monitored throughout the 2006 season (from October to February) fledged its first chick and simultaneously initiated a second nest on 10 November 2006, from which fledged a second chick. On 20 January 2007, they initiated a third nest which had been depredated when I visited it on 27 January 2007. Pairs re-nested after successful nests (*n* = 2). The final nesting observation of the austral summer was a new nest on 23 January 2007, and the latest observation of a chick of pre-fledgling age was on 28 February 2007. This last nest, if successful, would have resulted in chicks on territories in mid-March. Thus, the breeding season for this population can last up to six months (September – March).

Of the 53 endorheic lakes searched in the 2006 season, 19 had territorial pairs present (Table 2.1): 14 lakes had one territory each, one lake had two territories, two

Table 2.1 Locations of lakes included in this study and number of *P. socialis* breeding territories per lake in Santa Cruz province, Argentina.

Location name and coordinates		Number of *P.socialis* territories
Estancia Killik Aike Norte	51º32'S 69º24'W	1
Ea. Coy Aike	51º04'S 69º32'W	1
Estancia Cañadón Rancho	50º20'S 69º12'W	4
Estancia Cañadón Rancho	50º41'S 69º24'W	1
Estancia Cañadón Rancho	50º20'S 69º11'W	1
National Route 3	50º16'S 69º03'W	1
Monte León National Park	50º19'S 69º03'W	1
Estancia Moy Aike	51º21'S 69º33'W	1
National Route 3	50º34'S 69º22'W	1
National Route 3	50º15'S 69º07'W	1
Estancia Tres de Enero	51º52'S 69º26'W	1
Estancia Los Pozos	51º26'S 69º49'W	14
Estancia La Leona	51º32'S 69º49'W	3
Estancia La Angostura	48º46'S 70º44'W	1
Estancia La Angostura	48º37'S 70º41'W	1
Estancia Los Luises	50º37'S 69º25'W	2
Estancia La Angelina	51º24'S 69º07'W	3
Estancia La Martina	50º21'S 71º31'W	1
Encadenada Lake	48º44'S 71º00'W	1

lakes had three territories, one lake had four territories, and 1 lake had 14 territories (Table 2.1). One pair was seen with a pre-fledged chick on the shore of Lake Argentino. Of the 22 territories I revisited in the 2007 field season, I observed 16 pairs (73%) occupying territories at the exact locations as observed in 2006. The remaining 6 territories were unoccupied in the 2007 season and were on lakes that had dried early in the summer because of the dry conditions.

Nests.--- I found three nests at the laying stage and 21 nests at the incubation stage over both field seasons. Nest microhabitat varied from pure clay, clay-gravel matrix, dry sandy gravel, or cobble-gravel mix (Chapter 3). Nest cups were unmodified slight depressions except for the occasional lining of small pebbles. Twelve nests had one egg and six nests had two eggs throughout incubation. Seven nests were not monitored after their discovery, all of which contained one egg when found. Egg measurements (mean ± SD) were: length = 34.7 mm ± 1.2 $n = 25$; width = 25.2 mm ± 0.6 $n = 25$; volume = 10.0 cm^3 ± 0.7 $n = 25$ and mass 10.9 g ± 1.1 $n = 5$. I measured the mass of a freshly-laid egg as 11.8 g. Incubation began the day the first egg was laid and eggs hatched 24 days later ($n = 2$). One egg hatched one day before the second egg in two-egg clutches that were monitored ($n = 2$). Incubation duties were shared between adults with 20-50 min incubation shifts ($n = 2$ pairs observed for 4 and 6 consecutive shifts respectively). Non-incubating adults foraged between 50-150 m of nest.

Seventy percent (12 / 17) of nests were successful in having one or both eggs hatch. Four nests were depredated and one nest was destroyed by trampling. In total, 14 eggs hatched from 17 nests. In two of the six 2-egg nests only one egg hatched successfully and the second egg remained in the nest abandoned or damaged. I determined a Mayfield estimate of daily nest survival of 0.975 (n = 17) and nest survival of 0.550 (n = 17, t = 24, Mayfield 1961, Johnson 1979). Predators that I observed near breeding sites included the culpeo fox (*Pseudalopex culpaeus*), chilla fox (*P. griseus*), domestic dog (*Canis familiaris*), common skunk (*Conepatus chinga*), Chilean Skua (*Stercorarius chilensis*), Southern Crested Caracara (*Caracara plancus*), Kelp Gull (*Larus dominicanus*), and the Black-chested Buzzard Eagle (*Geranoaetus melanoleucus*).

Offspring.--- Newly hatched chicks were downy when hatched and capable of locomotion (as evidenced by movement from the nest site within the first few hours of hatching) but received feedings from parents and did not move much, if at all, from their location within the first four days of hatching. These attributes, by definition, are characteristic of semi-precocity (Ricklefs 1979). At the early stage, pairs either cared for both chicks equally (n = 2) or reduced their brood by caring only for the first chick to hatch and neglecting the other (n = 2). Feedings were provided by adults in short visits to their chicks, either offering food morsels or regurgitated material from the crop, the latter method occurring more frequently in early stage chicks. During the first week, adults brooded their chicks in adverse weather conditions. Between 4 - 9 days of age, chicks became more active, moving several metres and foraging independently. At 11 - 40 days of age chicks foraged independently near the adults and receive frequent feedings (5-8 feedings per minute for a 15 day-old chick, n = 2).

Juveniles were seen receiving occasional feedings from their parents up to 45 days of age (n = 3 observations). Juveniles fledged between 28-35 days of age, although individuals remained associated with adults on their natal territory until 45-50 days of age. Adults began chasing their young at this stage, presumably causing them to disperse off their natal territory. Juveniles came together throughout the season in small groups (4-12 individuals) to forage on the same lakes occupied by breeding adults. Of 26 chicks banded, 11 were observed after fledging which represents a minimum estimate of 42% survivorship to fledging age (*fledgeS* = 0.423). At least 30 eggs definitely hatched (a chick was found, or nest was monitored to successful hatch) from 22 monitored territories in the 2006 season. In keeping with the assumption that females remain on the same territories throughout a season this represents a seasonal reproductive output of 1.36 chicks hatched per female.

Movements and Re-sightings.--- Of the 17 offspring banded in the 2006 season, five were re-encountered as juveniles or adults. Three banded individuals were re-encountered late in their natal breeding season in post-breeding groups at juvenile age: two on their natal lake and one at a site approximately 12 km from its natal lake. I made three more re-sightings in the subsequent breeding season; all had adult plumage and all individuals were observed on lakes that were not their natal lakes (minimum estimate of survival to 1 year of age = 3/17 = 0.18). I determined that individuals can breed at one year of age from the observation of an individual, banded in October 2006 as a nestling, which was re-encountered in December 2007, with a mate and brooding a chick on a lake 12 km from its natal site. The chick fledged successfully.

Demographic estimates.--- To eliminate the lack of independence that occurs by using multiple nesting by pairs, four of the 17 monitored nests were excluded in the calculation and the first monitored nest of those pairs was included. The estimate of $nhatch_A$ is the number of chicks hatched per monitored nest (11 chicks / 13 nests = 0.846). I observed 86 adults during my searches between August and December 2006, of which 80 were determined to be breeding. Therefore, $\mathit{prbreed}_A$ was 0.93 (= 80 / 86). My estimate of *fledgeS* was 0.423, representing the number of banded chicks fledged ($n = 11$) divided by the total number of banded chicks in the study ($n = 26$). From the data, I estimated that roughly half the pairs I monitored in the 2006 season from spring through to fall nested twice. From this I estimated a value of 1.5 for *nests/season*. I assume the same values of nhatch_i and *fledgeS* for different within season nest attempts.

I calculated the following adult fertility value:

$$F_i = 0.5 * \mathit{prbreed}_i * \mathit{nhatch}_i * \mathit{fledgeS} * S_0 * \mathit{nests/season}$$

$$F_A = 0.5 * 0.93 * 0.846 * 0.423 * 0.56 * 1.5 = 0.1398$$

There is a significant positive relationship between body size (g) and adult survival rate of 15 North American shorebird species ($r = 0.676$, $p = 0.0008$; Sandercock 2003). Sæther (1989) reported a significant relationship in 27 European Charadriiform species ($r = 0.45$ $p < 0.05$). I used a mean body mass for *P. socialis* of 84.5 g (Jehl 1975) and determined adult survivorship of $S_A = 0.70$ by averaging the values calculated from the following fit equations:

$$s_i = 0.2674 + 0.2314 * \log_{10}(\text{body size}) \text{ (Sandercock 2003)}$$

$$s_i = 0.2674 + 0.2314 * \log_{10}(84.5) = 0.7133$$

$$s_i = e^{-0.68 + 0.07 * \ln(\text{body size})} \text{ (Sæther 1989)}$$

$$s_i = e^{-0.68 + 0.07 * \ln(84.5)} = 0.6914$$

Adult Lesser Sheathbills (*Chionis minor*, mean body mass = 467 g, Verheyden and Jouventin 1991) are the closest known relatives of *P. socialis* and were predicted to have survival rates of 0.89 and 0.78 from the Sandercock (2003) and Sæther (1989) fit equations respectively. These values are close to the local survival estimate of 0.85 determined by Verheyden and Jouventin (1991), which indicates that the body mass – survival relationship may be applicable to the *Chionis* family.

The Leslie matrix that I used is as follows:

$$A = \begin{vmatrix} 0 & 0.1398 & 0.1398 \\ 0.5560 & 0 & 0 \\ 0 & 0.7023 & 0.7023 \end{vmatrix}$$

The estimate of λ was 0.7995 and intrinsic rate of increase, $r = -0.2238$. This estimate indicates that the population of *P. socialis* in Santa Cruz province was decreasing at approximately 20% per year.

DISCUSSION

New information on breeding and implications.--- This study is the first to document a full breeding season of the Magellanic Plover and the first to study breeding sites consecutively over two seasons. Jehl (1975) observed only two-egg clutches in his study, and suggested that one-egg clutches resulted from partial depredation or loss of one egg from flooding. Jehl's (1975) observation of a few two-egg clutches in Tierra del Fuego may not have been representative of the species across its range. My findings suggest that both one- and two-egg clutches occur. The frequency distribution of one- or two-egg clutches may vary spatially and temporally. It is considerably drier in southern Santa Cruz than Tierra del Fuego where Jehl (1975) observed two-egg clutches and climate may influence clutch size by affecting the availability of food and resources on breeding sites (Paruelo et al., Meltofte et al. 2007). I also report the first confirmed cases of both siblings surviving to fledging age. The data indicate relatively high nest and fledging success (70% hatch success and 44% minimum survivorship to fledging age) compared to shorebirds nesting at similar northern latitudes (Meltofte et al. 2007).

Multiple within-season nesting is the first documentation of its kind for this species. *P. socialis* appeared to have the longest breeding season among heterospecifics nesting on the endorheic lakes of Santa Cruz. No other endemic shorebird species of Patagonia (i.e. two-banded plover, *Charadrius falklandicus,* Magellanic oystercatcher, *Haemotopus leucapodus,* or least seedsnipe, *Thinocorus rumicivorus*) were observed nesting on the lakes in December or January when *P. socialis* pairs were initiating their second or third nests (Maclean 1987). Multiple small clutches is a reproductive strategy seen in species nesting at lower latitudes, but is unusual for temperate ground-nesting shorebirds (Maclean 1987, Piersma and Wiersma 1996).

P. socialis females were previously assumed to produce < 1 chick per season (Jehl 1975). In my study, average annual output from one *P. socialis* territory during the 2006 season was 1.36 chicks and pairs may potentially fledge two or possibly three chicks per season either by raising both chicks from a two-egg clutch or raising successive broods. The observation of a one-year old breeding adult also provides the first information on *P. socialis* age at first breeding.

From the observation that 16 of 22 *P. socialis* territories were occupied in both field seasons, I hypothesize that territories are consistent between years. Although I did not individually mark adults and cannot comment on site tenacity, this is possible since many shorebird species are site faithful, including the Lesser Sheathbill (*Chionis minor*, Greenwood and Harvey 1982, Bried and Jouventin 1998). Alternatively, the habitat specificity of *P. socialis* (Chapter 3) may suggest there are relatively few suitable sites that will be occupied every year if sufficient numbers of the species are present. Those territories that were not occupied in my visit in 2007 were on lakes that were dried, suggesting annual precipitation may influence territory occupation by *P. socialis*. As birds often forage on the shoreline of inundated lakes, they may not be capable of breeding on dry lakes. Reduced annual precipitation may cause *P. socialis* to migrate from breeding areas to wintering estuaries early in the season and forgo opportunities to nest multiple times (Paruelo and Sala 1995). Small groups of *P. socialis* were observed on the Chico river estuary in late January and early February 2008, which was a particularly dry year (R. Lopez pers. comm.). Breeding synchrony and success of shorebirds were strongly related to annual precipitation patterns in the wetlands of the Playa Lakes region of Texas, an area with similar geomorphology to the endorheic lakes of Patagonia (Conway et al. 2005).

The lake with 14 breeding pairs discovered in this study is the largest concentration of breeding *P. socialis* ever documented. This, in combination with the large non-breeding groups (ca. 140 individuals) reported from the Río Gallegos estuary in winter, confirms that southern Santa Cruz is the region of highest reported abundances of the species in the world (Ferrari et al. 2003).

Relationship to other avian taxa.--- The relatively recent taxonomic placement of *Pluvianallus* in the sheathbill family, Chionidae (Van Tuinen et al. 2004), is additionally justified by similar aspects of breeding biology that I report here. Both the *Pluvianellus* and *Choinis* genera (one and two species respectively) share asynchronous hatching, semi-precocial young and brood reduction (Burger 1996). Other Charadriiformes with semiprecocial young include oystercatchers (*Haematopus* spp.), the monotypic crab plover (*Dromas ardeola*), gulls (*Larus* spp.), and terns (*Sterna* spp.). Precocity is a desirable trait in ground-nesting shorebirds because it conserves energy for adults, allows for greater movement to food sources from the home range, and improves the chicks ability to escape predation (Ricklefs 1979). Semiprecocity is beneficial when the food items on which the birds depend are difficult or impossible for chicks to obtain on their own (Ricklefs 1979). In the case of gulls and terns, this is logical since food is obtained by flying, usually at some distance from the nest. Oystercatchers and crab plovers must develop skills in opening bivalves. I observed *P. socialis* feeding on small prey items throughout their territory, prey that would presumably be easy for hatchlings to obtain. It is interesting, then, to consider why semiprecocity was selected for in *P. socialis*. It is possible that this is a trait that has persisted since the divergence from *Chionis*, when the bird's feeding ecology was different (Ricklefs 1979).

The sheathbills are obligate klepto-parasites that forage opportunistically in seabird colonies of the Antarctic and subantarctic regions (Burger 1981). The specialized ecology of the sheathbills makes ecological comparisons with *P. socialis* difficult. Ecologically, *P. socialis* is similar to numerous other shorebird species. In foraging it exhibits the spin foraging behaviour of the Phalarope, *Phalaropus* spp., and the rock-flipping of the Turnstone, *Arenaria* spp. The micro-habitat and crypsis of *P. socialis* on the dry gravel and cobble is similar to many of the small plover species, *Charadrius* spp. On its breeding grounds, it often forages with heterospecifics such as the two-banded plover, Magellanic Oystercatcher, White-rumped Sandpiper, *Calidris fuscicollis*, Baird's Sandpiper, *C. bairdii*, and Lesser Yellowlegs, *Tringa flavipes.*

The minimal scrape construction by *P. socialis* that I observed in the Santa Cruz population was unlike the description of nests by Jehl (1975). The nests in my study were barely recognizable features and although a few were lined with pebbles, as Jehl (1975) described, most were nothing more than eggs placed in a very slight dip, if any, directly on the gravel. This very low degree of scrape development is comparable to the Nighthawks (Family Caprimulgidae).

Status and conservation.--- I estimated the population growth rate of *P. socialis* in Santa Cruz province as $\lambda = 0.8$. If true, the population is decreasing at a rate of 20% per year. Although this is a low value, estimates such as this one are commonly found in population demographic studies on shorebirds (e.g. Hitchcock and Gratto-Trevor 1997). Some parameters of this calculated value are based on conservative estimates, such as *fledgeS* = 0.423, and could be an underestimate. Other parameters are averaged literature values where none exist for *P. socialis.* The estimate, whether an underestimate or not, is based on various assumptions and at the moment we lack the data to improve the confidence of the value. That being said, the exercise was heuristic and provides insight into the effect that different aspects of fertility may have on λ. For example, I expect that the parameter *nests/season* will vary with annual precipitation, and therefore so will λ. Figure 2.2 shows the theoretic relationship between *nests/season* and λ, demonstrating that a year where all pairs are able to breed twice corresponds to a λ of 0.83. Years where lakes dry early and pairs can breed only once will cause λ to drop to 0.77.

The most direct anthropogenic threat to *P. socialis* on its breeding grounds appears to be nest trampling by livestock (Jehl 1975, Piersma et al. 1997). The results of my study did not show that trampling is a significant cause of nest failure since only one

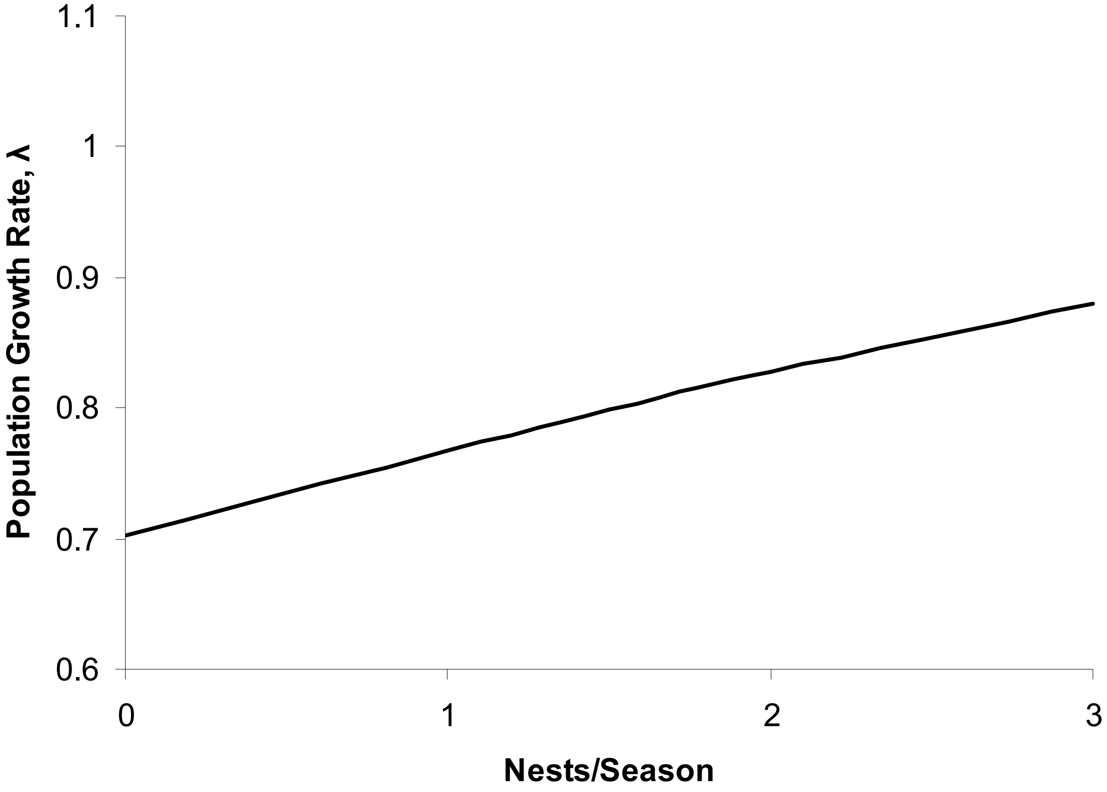

Figure 2.2 Theoretical relationship between number of nests per season per female and the population growth rate, λ of *Pluvianellus socialis*. Estimates assume that all other parameters (fledging success, hatch success, survival rates, etc.) are equal.

of 17 nests was trampled. However, I am cautious to suggest that it is not an important concern to conservation of the species as endorheic lake shorelines are heavily used by livestock (pers. obs.) and nest trampling may occur more frequently than I could detect. Other activity from the ranches may also contribute some disturbance since many ranch-owners keep dogs and use all-terrain vehicles on the shores of their mostly privately owned lakes.

The introduced culpeo fox (*Pseudalopex culpaeus*) likely had an effect on all native birds early in the 1900s when it was introduced, but the impact now would be difficult to detect (Novaro et al. 2000). Certainly, there is a valid concern with the rapid urban development and associated explosion of feral dog populations which undoubtedly affect wintering *P. socialis*, although there is no evidence of such effect on breeding birds, which are generally far from city centres (Ferrari et al. 2003). One pair was documented nesting on the shore of Lake Argentino, within the city limits of El Calafate, a busy tourist centre at the foot of the Andes Mountains. The pair and their unfledged chick (age estimated at 17-20 days old) were foraging along a high-use beach where locals, tourists and many dogs spend time. This was a striking observation and provokes questions about how much this lakeshore was used in the past (before the rapid development in the recent decade) and how resilient *P. socialis* may be to human disturbance.

Indirect anthropogenic impacts include degradation and desertification of the Patagonian steppe environment by introduced grazing livestock (Soriano 1983, Aagesen 2000), the contamination of groundwater from oil pipelines (Quirós and Drago 1999), invasive species, and climate change. All of these factors may influence the stability of the semi-arid ecosystem and the chemistry of the lakes on which *P. socialis* depend for nesting habitat. As has been demonstrated in the previous sections, several aspects of the annual reproductive output of *P. socialis* may be strongly influenced by precipitation. Increased drying of the semi-arid Patagonian Steppe and decreases in annual rainfall attributed to climate change can be expected to decrease the annual reproductive output of *P. socialis* (Thompson and Solomon 2002).

Addressing large-scale environmental issues such as climate change, ecotourism and accountability for oil spills will certainly relieve some pressures from *P. socialis*. Proximal conservation efforts should be directed towards reducing the impact of livestock grazing, perhaps by excluding livestock from portions of the endorheic lakeshores where *P. socialis* is most likely to nest.

CHAPTER 3: Multi-scale habitat selection of the Magellanic Plover.

ABSTRACT.--- Studies of habitat selection attempt to understand the disproportionate use of a habitat in relation to its availability. In this study, I aimed to characterize the habitat selected by Magellanic plovers (*Pluvianellus socialis*) in Santa Cruz province, southern Argentina. I measured habitat characteristics at three spatial scales: lake (first-order selection), mesosite (second-order selection) and microsite (third-order selection). Characteristics were compared between used and unused, available sites at each spatial scale. I also compared some characteristics between successful and unsuccessful nest sites. I found that *P. socialis* prefers to occupy saline endorheic lakes that have large aeolian lunettes. At the mesoscale, birds selected locations farther from vegetation and closer to freshwater channels than available. Used mesosites also had less vegetation within a 15 m radius of the centrepoint than available. Within their territories, *P. socialis* avoid placing their nests on clay substrates. I suggest that some habitat preferences at the meso- and microsite scales are anti-predator adaptations and are meant to maximize crypsis of nests and chicks. I detected no differences in habitat characteristics between successful and unsuccessful nest sites; however, caution should be taken with these results since sample size was small (n = 17 nests). I recommend future efforts to characterize habitat across a broader area of the species' range (e.g. Tierra del Fuego) to compare with my results.

Key words: Magellanic Plover, Habitat Selection, Patagonian Steppe, *Pluvianellus socialis*, endemic shorebird.

INTRODUCTION

Birds, like all organisms, meet their survival and reproductive needs by accessing the resources and conditions in their surroundings, or habitat (Cody 1985, Jones 2001). The habitat used by a breeding bird is a result of the habitat selection process, a topic which is of interest to ecologists (Cody 1985, Jones 2001). Studies of "habitat selection" in birds attempt to understand the disproportionate use of a habitat relative to its availability (Kristan 2003, Johnson 2007).

Many methods have been used to study breeding habitat selection in birds (Pribil and Picman 1997, Jones 2001). The traditional method correlates variation in breeding success (often a binomial variable, i.e. successful/unsuccessful) with variation in the attributes of breeding sites. This method attempts to demonstrate the adaptive significance of habitat selection, or that quality sites are those where individuals experience increased reproductive success. Another method, sometimes referred to as the direct method, compares variation in habitat attributes between occupied (or 'used') breeding sites and available sites (Pribil and Picman 1997, Jones 2001). Occupied sites are those that are currently used and available sites may or may not be currently used by the species (Jones 2001). In studies using the direct method, available areas are delineated by the researchers as some biologically meaningful area to the species (Jones 2001, Johnson 2007). Available sites may be used by the bird but generally are not at the time the study is conducted (Jones 2001).

The selection of habitat may be regarded as a hierarchical process that occurs at different spatial scales (Orians and Wittenberger 1991). Because individuals must make choices about where to breed at broad, intermediate and fine spatial scales, the variation of habitat characteristics at each scale is important to consider (Orians and Wittenberger 1991). At the largest scale of a species' geographic breeding distribution, there is heterogeneity between different areas, referred to as first-order selection (Johnson 1980). For example, Found et al. (2008) considered how wetland birds of the boreal forest must choose to occupy wetlands that vary in size, chemistry, depth, and vegetative characteristics. Each species selects for certain features disproportionate to what is available (Found et al. 2008). Once birds arrive at a wetland, there is another scale of spatial heterogeneity and individuals are faced with decisions of where to establish a territory within this available area, called second-order selection (Johnson 1980). At this scale, variables such as ground cover and proximity to food resources are presumably going to impact the decision to establish in that location. Finally, once an individual has chosen and established a territory they must make a decision on the location of the nest-site, referred to as third-order selection (Johnson 1980). The choices made by an individual at each scale will have implications for the fitness of the bird and its young (Cody 1985, Pribil and Picman 1997, Jones 2001, Kristan 2003). By studying habitat selection of a population, we gain information that is valuable to conservation and general ecological knowledge of that species.

In this study, I examined the patterns of breeding habitat selection of the Magellanic plover (*Pluvianellus socialis*) using both the traditional and the direct method. *P. socialis* is a territorial ground-nesting shorebird that breeds on the shores of wetlands in the semi-arid grasslands of Patagonia from September to February (Jehl 1975, Ferrari et al. 2003). My study spanned two breeding seasons, from October 2006 to February 2007 (hereafter the 2006 season) and another in December 2007 (hereafter the 2007 season). I conducted my study in south-central Santa Cruz province, Argentina, where the species exists in its highest known densities (Ferrari et al. 2003).

P. socialis is endemic to the Patagonian steppe, which is the semiarid grassland of southernmost South America (Aagesen 2000). The Patagonian steppe was colonized by European sheep ranchers in the late 19th century (Soriano 1983). Sheep ranching is the cause of widespread degradation of the vegetation and soils (Defossé and Robberecht 1987, Aagesen 2000). Another recent (ca. 15 years) wave of development in Patagonia has brought oil and gas exploration, urban expansion, and tourism (Aagesen 2000). European settlement in Patagonia brought predators, alien plant species, increased human traffic and generally altered the landscape (Piersma et al. 1997, Aagesen 2000). Thus understanding which habitats are selected by *P. socialis* can help elucidate impacts of landscape level changes on the species.

I compared characteristics of used and unused breeding habitat at three spatial scales and of successful and unsuccessful nest sites at two spatial scales (Johnson 1980). I aimed to address the following questions: 1) What chemical and physical characteristics of endorheic lakes do *P. socialis* prefer during the breeding season and are these characteristics related to number of territories on an occupied lake? 2) Which substrates do *P. socialis* select? 3) What proximate features are good predictors for the location of *P. socialis* breeding sites? and 4) Do habitat characteristics of successful nests differ from those of unsuccessful nests?

METHODS

Study area.--- My study was conducted in southern Santa Cruz province, Argentina. Fifty-three endorheic lakes were searched within an area of approximately 62 000 km^2 between "Estancia Morro Chico" (51°57' S, 71°33' W) in the southwest, the town of El

Calafate (50°20' S, 72°16' W) in the west, "Estancia La Angostura" (48°37' S, 70°31' W) in the north, the village of C. Luis Piedrabuena (49°59' S, 68°54' W) in the east, and "Estancia Tres de Enero" (51°52' S, 69°26' W) in the southeast (Figure 3.1). The study area was an arid bunch-grass (*Festuca* sp. and *Poa* sp.) dominated steppe environment with an annual precipitation of < 300 mm (Soriano 1983). Westerly winds were the most dominant climatic feature, with mean annual speeds of 30-70 km/h and occasionally reaching 180 km/h in spring and summer (Soriano 1983, Paruelo et al. 1998). Many geomorphological features of the Patagonian steppe were influenced by the strong winds (Soriano 1983). Depressions in the flat landscape created aeolian lunettes, which are slow-growing unvegetated areas characterized by dunes of aeolian loess (wind-generated mineral dust) and gravel/cobble substrates (Iriondo 1989, Quirós and Drago 1999). Some of the depressions in the Patagonian plateau support endorheic basins and endorheic lakes (hereafter referred to simply as lakes) that have no water flowing to the ocean and whose characteristics, such as size and salinity, vary with the geologic age of the basin (Soriano 1983, Quirós and Drago 1999, Diaz et al. 2000). Aeolian lunettes were often associated with the downwind (eastern) side of the endorheic lakes (Soriano 1983, Quirós and Drago 1999). Exorheic wetland basins (i.e. lakes or ponds in river basins that ultimately drain to the ocean) are occasionally used by *P. socialis* however these were excluded from my study because occupation of *P. socialis* of these wetlands is apparently minimal (Ferrari et al. 2003, Imberti 2003, Ferrari et al. 2008, pers. obs.).

Territory searching and nest monitoring.--- I searched for *P. socialis* by walking the circumference of the 53 endorheic lakeshores with 2 - 3 people walking abreast (Figure 3.1). I stopped every 100-150 m to complete a 360°-survey using a 40X spotting

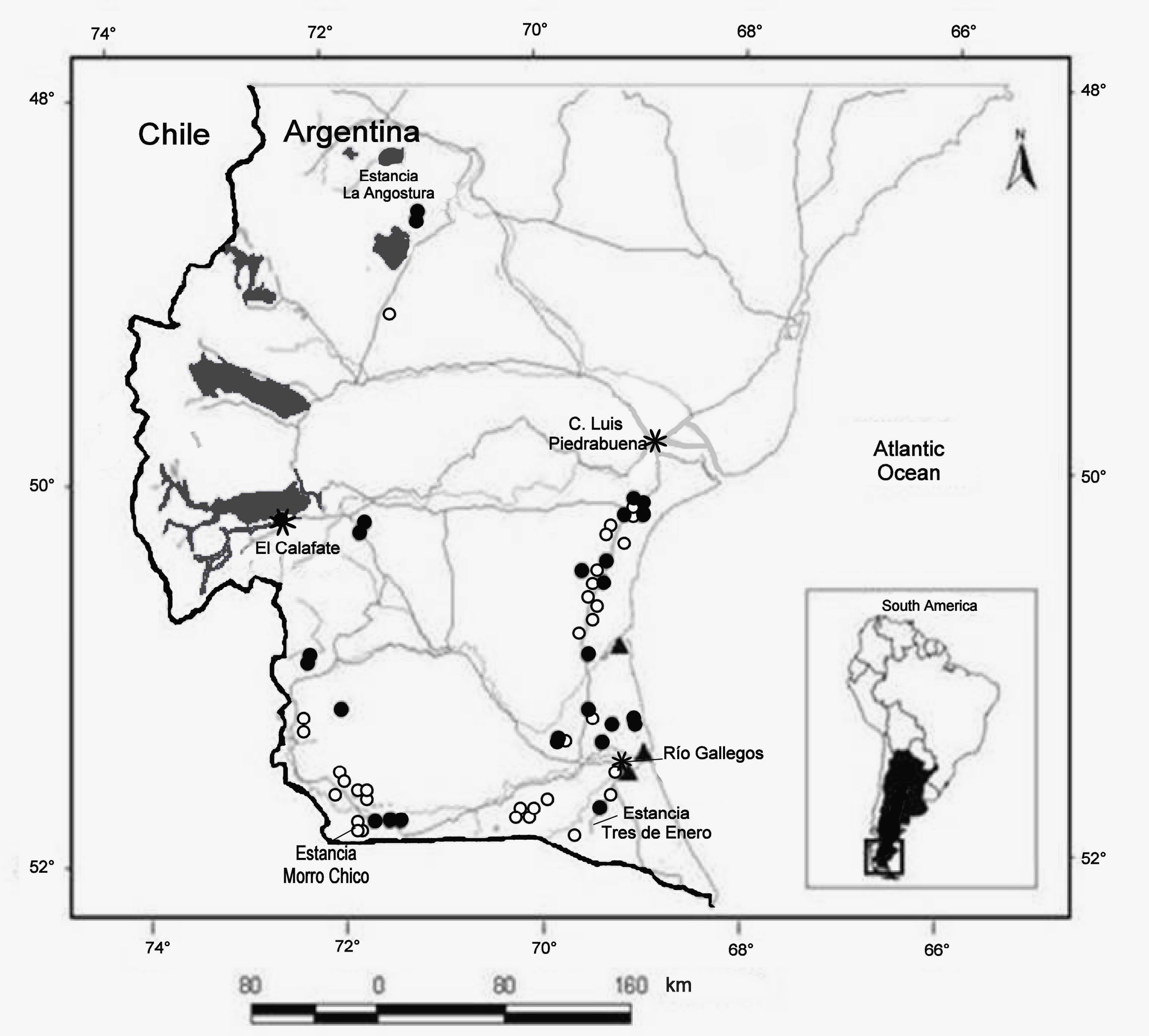

Figure 3.1 Geographic locations of endorheic lakes included in my study where searches for breeding *P. socialis* took place (circles) and three wintering sites of the species (triangles). Populated centers are marked with asterisks. Unused lakes (not occupied by *P. socialis* during my study) are represented by hollow circles while occupied lakes are represented by solid circles.

scope. All lakes included in the study were visited more than once; however, it was not logistically feasible to re-visit all 53 lakes at regular intervals. To investigate the consistency of lake occupation, I systematically searched a subset of 21 lakes on the first week of each month for four months from August - December 2006 (September excluded) and searched the same 21 lakes again in December 2007. This subset included 14 lakes located in southeastern Santa Cruz between the communities of Río Gallegos and Piedra Buena (50° S, 69° W), four lakes on Estancia Otern Aike located west of Río Gallegos, two lakes on Estancia Tres de Enero south of Río Gallegos (51°50' S, 69°25' W), and one lake "Ortiz" located on the edge of the city of Río Gallegos (51°38' S, 69°14' W).

Individuals were observed from a distance of 50-100 m using a 40x spotting scope and/or binoculars. I assumed that individuals were transient visitors to the lake if they were moving long distances (e.g. 500 m - 2 km) within the lake area, not associating with another individual, not exhibiting territorial behaviours, or foraging for extended periods of time (> 2 hours). I considered individuals to be on a territory if they vocalized in the presence of an observer or conspecific, were aggressive with conspecifics or heterospecifics, associated strongly with a mate (copulating, following, or giving joint territorial displays), incubated a nest or brooded and fed a chick. Geographic coordinates and details of every encounter with the birds were recorded.

I monitored 17 nests in the 2006 season by visiting each every 2 – 8 days and deemed a nest successful if one or more eggs hatched and unsuccessful if there was no eggshell evidence of hatching nor birds present on the territory (Mabee 1997). If eggs were absent, I assumed that predation was the cause of nest failure. One egg was crushed in the nest, and was recorded as trampled. I calculated daily nest survival using the Mayfield (1961) technique.

Habitat characterization across scales.--- I characterized the habitat of *P. socialis* at three spatial scales: lake, mesosite and microsite. These scales correspond to first-, second- and third-order selection (Johnson 1980).

Lake. At the broadest scale, I delineated the biologically meaningful "available" area of breeding *P. socialis* as the species' geographic distribution in Santa Cruz Province (Ferrari et al. 2003, 2008) and considered all endorheic lakes therein to be available to the species. I categorized lakes within this area as occupied if I encountered *P. socialis* once or more during my searches and unused if the species was not encountered at all. I used program MARK to build models and estimate the probability of an occupied lake being occupied on each visit (White and Burnham 1999). This value, termed the encounter probability, *S*, was estimated for the occupied lakes within the subset of 21 systematically searched lakes. Data were entered as binary presence (1) and absence (0) for each visit with five observation occasions (August, October, November, December 2006, and December 2007). The constant model was the most parsimonious, followed by the time dependent model. I report the encounter probabilities from model averaging of both the constant and the time dependent models.

I input waypoints from the handheld GPS unit into the software program Google Earth © and examined satellite images of the 53 endorheic lakes included in my study. I used the 'distance ruler' tool to measure lake area, aeolian lunette area, and distance to the ocean. I approximated the shape of a lake to an ellipse and measured the longest and shortest diameters of the maximum inundated zone. Area was calculated with the equation:

$$\text{area (in ha)} = \pi*[(\text{diameterA (m)} + \text{diameterB (m)})/4]^2 * 0.0001\ \text{m}^2/\text{ha}.$$

I approximated the shape of the unvegetated aeolian lunette to a rectangle and measured length and width. Area was calculated with the equation:

$$\text{area (in ha)} = \text{length (m)} * \text{width (m)} * 0.0001\ \text{m}^2/\text{ha}$$

I measured distance from the ocean as the closest straight-line distance (in km) to the Atlantic coast. Elevation of the shoreline was taken from the digital elevation model (DEM) used by Google Earth ©.

I measured salinity on a subset of lakes that were visited in December 2007, using a Eutech ECTestr™ pocket salinity tester to the nearest 0.1 ppb. Salinity measurements were all taken between 14 and 20 December 2007. Measurements greater than 19.9 ppb were beyond the scale detected by this device, so I recorded these readings as >19.9 ppb. At lakes that were dried (n = 10) I measured the conductivity of a solution of 100 ml lake bottom sediment to 100 ml distilled water.

Mesosite. At the mesoscale, I delineated the available area of a lakeshore as a 300 m buffer with the waterline of the lake as the interior limit (Figure 3.2). I measured mesosite characteristics at 33 sites that were used by *P. socialis* pairs and 33 other sites that were randomly selected within the available area of the lakeshore (hereafter referred to as 'used' and 'available' mesosites respectively). A site was considered used if a nest or chick of *P. socialis* was found, and the spatial centrepoint of the used site was assumed to be where the nest or chick was located. I randomly determined the location of available mesosites by setting an alarm to sound every 40 minutes during my lake

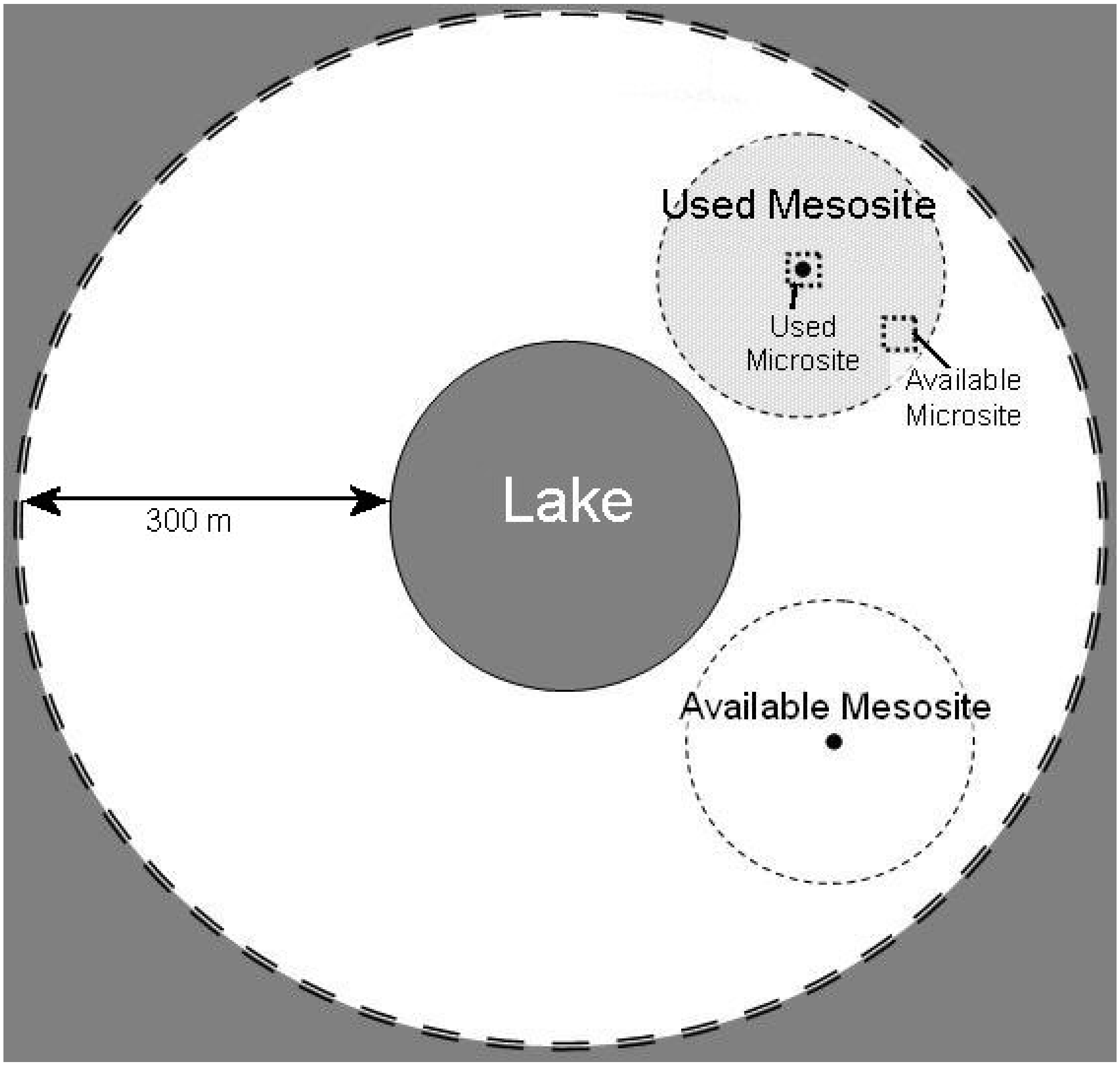

Figure 3.2 Schematic representation of available habitats on an endorheic lake at the two finest spatial scales. Grey areas outside of the 300 m lake buffer were considered unavailable to breeding *P. socialis*. White area is what was considered available for mesosite selection (buffer with a 300 m radius from lakeshore). The area within a 100 m radius of a nest site was considered available for microsite selection.

searches (see above). At the sound of the alarm, the observer holding the clock used two randomly generated lists of numbers (one list ranging from 0-359° and a second from 0-200 m) and moved to a site at a random orientation and distance. If the projected site was outside the designated available area (i.e. >300 m from the waterline or in the inundated area of the lake), I chose the next distance from the list.

From the centrepoint of all mesosites, I selected a random orientation (between 0 - 359°) from a randomly-generated number list and measured percent cover at 5, 15, 30 and 45 m distances spiraling from the centrepoint at 90° from one another. Cover was estimated by placing a 1 m^2 quadrat on the ground and visually estimating the percent of six substrate types. Cover types were categorized as: clay, vegetation, gravel (grain size <5 cm), cobble (grain size >5 cm), sand, or wrack (organic material washed up from wave action).

From the centrepoint of used and available mesosites, I measured the distance to three features within the available area: lakeshore, vegetation and channel. All distances were measured to the nearest metre using a 100 m tape measure. Distance to lakeshore was measured to the waterline of the lake at the time of measurement. Distance to vegetation was measured to the nearest vegetation patch with > 50% cover of vegetation within 1 m^2. Distance to channel was measured to locations where freshwater flows into the lake in a channel either formed by overland flow during precipitation or from a groundwater spring. If the vegetation or channel was >500 m, I walked to the feature and used the “distance to” tool on the GPS unit to find the distance to the mesosite centrepoint waypoint (accurate to 15 m).

Microsite. For the smallest scale, the microsite, I delineated the available area as a circle with a 100 m radius centered on a nest site (Figure 3.2). This delineation was based on the observation that nesting *P. socialis* typically occupy and defend a linear territory along approximately 200-300 m of the lake shore (Jehl 1975, Ferrari et al. 2008). Used microsites were nest-sites. Available microsites were selected at a random orientation (between 0-359°) and distance (between 0-100 m) from a nest using two random number lists. I placed a 1 m^2 quadrat, marked at 10 cm intervals, over the microsite and took a digital photograph using an Olympus Stylus 700 7.1 megapixel digital camera from 1.7 m above the ground. Using the software program Jasc Paintshop Pro ©, nest microsite digital photographs were overlayed with a 10 cm x 10 cm grid aligned with the quadrat in the photograph and each grid cell was assigned one of the 6 cover types for a total of 100%.

Data analysis across scales.--- I tested for normality of data using Shapiro-Wilks tests and used natural logarithm, square root, or arcsin transformations if the assumption of normality was not met. I excluded all mesosite and microsite cover types that were present in less than 25% of all quadrats [e.g. sand (9%) and wrack (7%)] from further analyses.

Lake. I tested for differences in lake size and elevation of occupied and unused lakes using independent t-tests. I tested for differences in aeolian lunette area and distance to ocean in occupied versus unused lakes using the Mann-Whitney U-test. I originally intended to include salinity as a continuous variable in my data set. However, the data were essentially binomial with all readings (n = 31 lakes) falling between 0- 0.8 ppb or >19.9 ppb. Therefore, I categorized lakes as freshwater (0-0.8 ppb) and saline

(>19.9 ppb). I tested the null hypothesis that there was no association between salinity occupancy by *P. socialis* using Fisher's exact test. I tested for correlations between number of territories per lake and all continuous variables (lake size, elevation, distance to ocean and aeolian lunette size) using the non-parametric Spearman rank order correlation. One lake in my dataset had an unusually high number of territories, so I used an unconditional logistic model to test the effect of distance from this lake with lake occupation (unused = 0, occupied = 1) of all other lakes in the data set.

I ran Spearman rank order correlations between all continuous variables and found significant correlations between aeolian lunette size and distance to ocean ($r = -0.46$, $p < 0.05$) and between aeolian lunette size and lake size ($r = 0.60$, $p < 0.05$). I used unconditional multiple logistic regression to test candidate models for the separate and combined effects of lake size, aeolian lunette size, and distance to ocean on the binary response variable of lake occupation (unused = 0, occupied = 1). I used Akaike's Information Criteria (AIC) corrected for small sample size (AIC_c, Hurvich and Tsai 1989) and Akaike's weights (ω_i) to determine the most parsimonious models (Burnham and Anderson 2002). Those models with $\Delta AIC_c < 4$ were considered the best subset. The relative importance of each variable was determined by summing Akaike weights from models including the variable of interest (Burnham and Anderson 2002).

Mesosite. I transformed all percent cover variables using an arcsin $[\sqrt{(x)}]$ transformation to minimize non-normal distributions and multi-collinearity. I modeled mesosite use (available = 0, used = 1) with the percent cover of four cover types (clay, vegetation, gravel, and cobble) at each of four distances from the mesosite centrepoint (total of 16 variables) using a generalized linear mixed-effects model (GLMM) with penalized quasi-likelihood (PQL) estimation (McCullagh and Searle 2000, *R v* 2.6.2; R Development Core Team 2008). I used a GLMM because it allowed me to separate the potential effects of co-varying independent variables, such as percent cover, on the process of habitat selection. Also, because multiple mesosites were sometimes measured on the shorelines of the same lakes, I was able to incorporate lake as a random effect in the model. I used a backward stepwise approach by inspecting the parameter estimates of one model and selectively removing non-significant covariates until a skeleton model was reached (McCullagh and Searle 2000).

To test whether proximity to mesosite features (lakeshore, vegetation and freshwater channel) varied significantly among lakes, I used a one-way ANOVA with lake as the categorical independent variable (n=10 lakes). I found no significant differences in any variables between lakes ($0.35 < p < 0.48$). I tested for relationships using the Pearson product-moment correlation between all variables and found no significant relationships. To test for the effect of proximity to features on mesosite occupation, I used unconditional, multiple logistic regression to construct seven candidate models that explained the effects of proximity to lakeshore, vegetation and channel on mesosite use. Variables were included in models separately and in all combinations, on a binary dependent variable (available = 0, used = 1). I used AIC model selection corrected for small sample sizes ($AIC_{c,}$ Hurvich and Tsai 1989) and ω_i to determine the most parsimonious models. Two of the candidate models had ΔAIC_c values < 4, so those with $\Delta QAIC_c \leq 7$ were considered the best subset. I used model averaging of this subset to calculate parameter estimates. The most important parameter(s) were determined by summing Akaike's weights, $\omega_{i,}$ from models (in the subset) including the parameter of interest (Burnham and Anderson 2002).

Microsite. I transformed percent cover of clay, vegetation, gravel, and cobble using an arcsin [$\sqrt{(x)}$] transformation to minimize non-normal distributions and multi-collinearity. The comparison of used and available microsites were not independent because they were both observed within the same home-range. For this reason, I modeled the probability of microsite use (available = 0, used = 1) as a response variable to the percent cover of clay, vegetation, gravel and cobble using conditional (paired), multiple logistic regression (*R v.* 2.6.2; Therneau and Lumley, R Development Core Team 2008). I constructed 16 candidate models based on all possible additive combinations and the constant model and used AIC model selection, corrected for small sample size, to determine the most parsimonious models (Hurvich and Tsai 1989). Models with a ΔAIC_c value < 4 were considered the best subset. I used model averaging of this subset to calculate parameter estimates. The most important parameters affecting microsite occupation were determined by summing Akaike's weights from models including the parameter of interest (Burnham and Anderson 2002).

Nest success.--- I chose not to compare mesosite cover between successful and unsuccessful sites because of small sample size (n=17 nests) and large number of parameters (K=16). I compared proximity to lakeshore, vegetation, and freshwater channel of successful and unsuccessful nest sites using independent t-tests. I compared the percent cover of all four substrates (clay, vegetation, gravel and cobble) between successful and unsuccessful nests using the non-parametric Mann-Whitney U-Test.

RESULTS

Lake occupation.--- A total of 53 lakes (23 occupied, 30 unused) were included in my study (Figure 3.1). I failed to reject the null hypothesis that *P. socialis* territories were distributed among lakes in a Poisson manner ($X^2 = 15.08$, df = 12, $p = 0.237$; Figure 3.3). Of 21 lakes that were searched systematically on five occasions, seven were occupied and 14 were never occupied by *P. socialis.* I found a high probability of re-encounter of *P. socialis* on the seven occupied lakes (model averaged parameter estimate 0.969 ± 0.041 SE).

Lake size and aeolian lunette size (Spearman's $r = 0.73$, $p < 0.05$, n = 53), and lake size and elevation were significantly correlated (Spearman's $r = -0.35$, $p < 0.05$, n = 53). From my exploratory univariate analyses, I found that occupied lakes were significantly larger, closer to the ocean and had significantly larger aeolian lunettes than unused lakes (Table 3.1, Figure 3.4). The confidence intervals of elevation and interquartile ranges of distance to ocean overlapped between occupied and unused lakes (Table 3.1). Twelve percent (2 of 17) of freshwater lakes were occupied by *P. socialis* whereas 86% (12 of 14) saline lakes were occupied; therefore, occupancy and salinity were significantly associated (Fisher's exact $p < 0.0001$). There was no significant relationship between number of territories per lake and any lake scale variable (Figure 3.5). Distance from the lake with 14 territories was not a predictor of lake occupation (logit function $X^2 = 0.0023$, df = 2, $p = 0.961$).

A model including the additive effects of aeolian lunette size and distance to the ocean was most parsimonious, with a 54% chance of best explaining variation in lake occupancy from my candidate models (Table 3.2). In comparison, the additive effects of

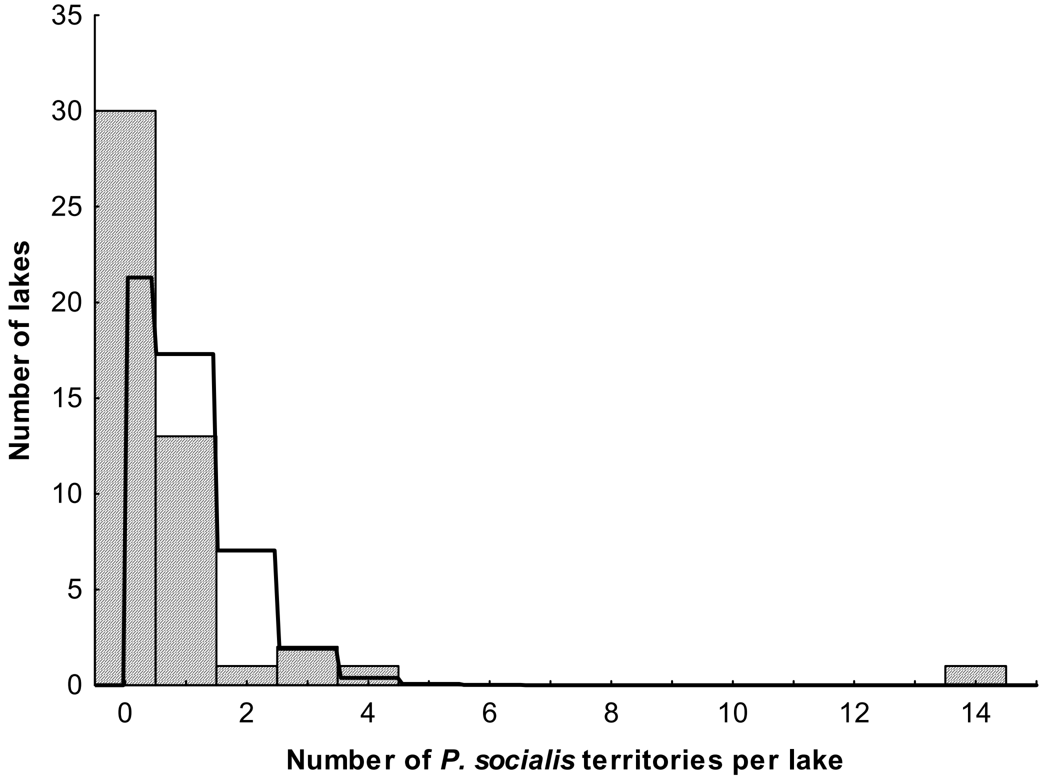

Figure 3.3 Frequency histogram of observed number of *P. socialis* territorial pairs per lake (grey bars) and expected distribution under a Poisson distribution (black line). I failed to reject the null hypothesis that *P. socialis* pairs were distributed randomly (X^2 = 15.08, df = 12, p = 0.237).

Table 3.1 Descriptive statistics and univariate results for alkaline lakes located within the geographic range of *Pluvianellus socialis,* comparing occupied and unused lakes. Independent t-tests were performed on lake size (ha) and elevation (m asl) respectively and Mann-Whitney U-test was performed on aeolian lunette area and distance to ocean.

	Occupied		Unused		Test Statistics	
	n	Mean (95% CI)	n	Mean (95% CI)	t	p
Lake Size (ha) *	23	37.7 (21.0, 67.6)	30	6.0 (3.2, 11.0)	4.37	<0.001
Elevation (m asl) **	23	185 (122, 260)	30	191(147, 240)	-0.146	0.88
	n	Median (IQR)	n	Median (IQR)	Z	p
Aeolian lunette Area (ha)	23	24.1 (7.3, 120.0)	30	0.0 (0.0, 1.2)	6.0	<0.001
Distance to Ocean (km)	23	28 (19, 168)	30	77 (12, 222)	-2.16	0.03

* variable was $\log_{10}$ transformed, values are back-transformed
** variable was square-root transformed, values are back-transformed

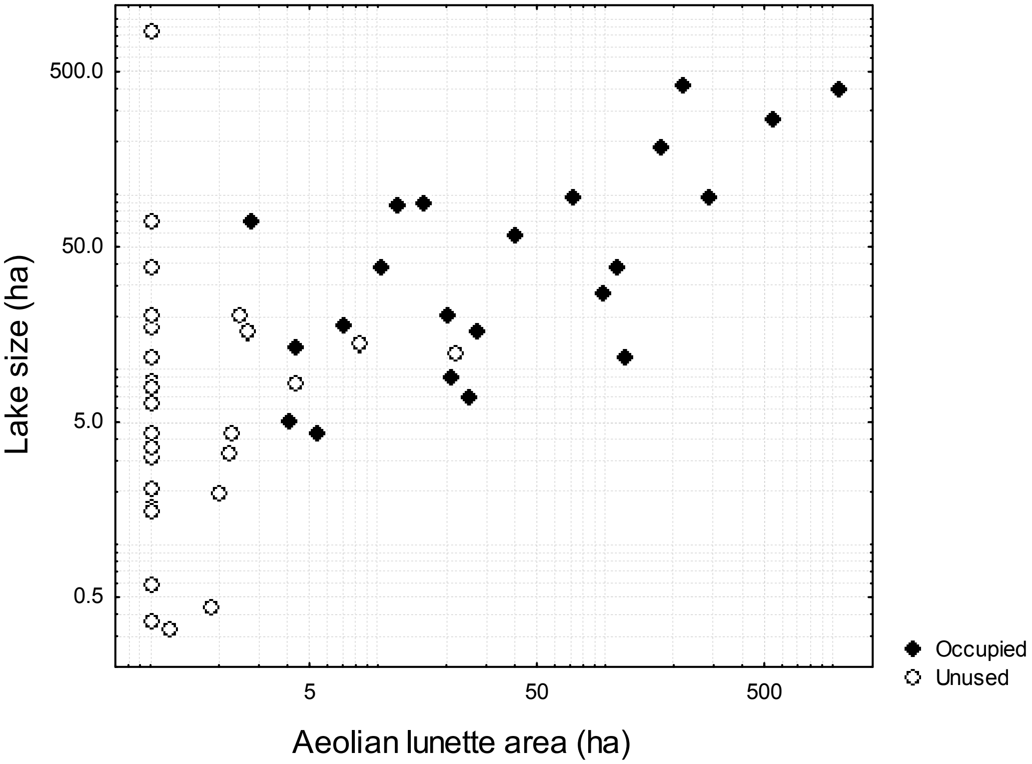

Figure 3.4 Lake size (ha) and area of the aeolian lunette (ha) of endorheic lakes of southern Santa Cruz province, Argentina, searched for occupation by *P. socialis* in 2006 and 2007. Solid points are occupied lakes (Spearman rank order $r = 0.78$, $p < 0.001$) and hollow circles are unused lakes (Spearman rank order $r = -0.0613$, $p = 0.75$).

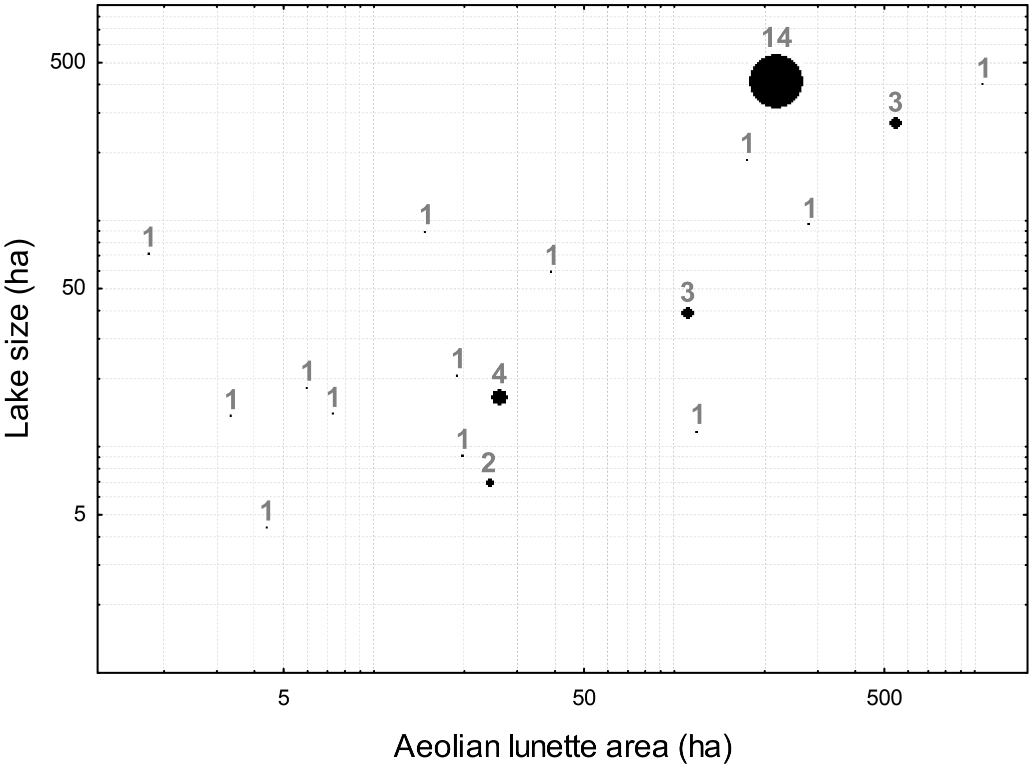

Figure 3.5 Endorheic lakes occupied by *Pluvianellus socialis* during the breeding season plotted by lake size (ha) and the area of the associated aeolian lunette (ha). Circle size and adjacent numbers correspond to the number of *P. socialis* territories present on the lake.

Table 3.2 Model selection of unconditional multiple logistic regression using Akaike's Information Criteria (AIC). Three variables of endorheic lakes (lake size, aeolian lunette size and distance to the ocean) were modeled against lake occupation by *P. socialis* in Santa Cruz province, Argentina. The table gives sample size (n), number of parameters (K), log likelihood [-2 ln (L)] values from the regression, AIC, AIC values corrected for small sample size AIC_c, the difference in AIC_c ($\Delta\mathrm{AIC}_c$) and Akaike's weights (ω_i) for top ranking models (< 4 $\Delta\mathrm{AIC}_c$) and the constant model of 16 candidate models. The total importance value for each variable is also provided, as well as the parameter estimates, their standard error (SE) and 95% confidence intervals.

Model	n	K	- 2 ln (L)	AIC	AICc	$\Delta\mathrm{AIC}_c$	ω_i
Lunette size, Distance to ocean	53	3	19.76	25.76	26.25	0.0	0.54
Full model	53	4	19.49	27.49	28.33	2.1	0.19
Lunette size	53	2	24.28	28.28	28.52	2.3	0.17
Lake size, Lunette size	53	3	23.23	29.23	29.72	3.5	0.10
Constant model	53	1	72.55	74.55	74.62	48.4	0.00

Variable	Importance Value ($\Sigma\omega_i$)	Parameter Estimate	SE	Lower 95% CI	Upper +95% CI
Lunette size	1.00	2.785*	0.979	0.820	4.750
Distance to Ocean	0.73	0.018	0.010	-0.002	0.038
Lake size	0.29	0.312**	0.456	-0.602	1.226
Intercept	0.00	-5.813	2.273	-10.374	-1.252

* parameter estimate applies to the natural logarithm (ln) transformed variable

all three lake variables in the full model had a 19% chance. Aeolian lunette size and distance to ocean had the highest importance values (Table 3.2). The parameter estimates were positive for all three variables, indicating a positive relationship with lake occupancy. The lake size and distance to ocean parameter estimates had 95% confidence overlapping zero.

Mesosite use.--- The random effect of lake on substrate cover and mesosite occupation by *P. socialis* was substantial (SD = 0.975) compared to the intercept (SD = 0.00017). Thus, it was important to include lake as a random effect in the GLMM. The skeleton model that resulted from backward stepwise variable removal included two variables with significant ($\alpha < 0.05$) p-values: vegetation at 5 m and vegetation at 15 m (Table 3.3). Both variables had negative parameter estimates suggesting that increasing the percent cover of vegetation within 15 m of the centrepoint decreases the probability of mesosite use by *P. socialis.*

The model including distance to vegetation and distance to channel was the highest ranking, with a 64% chance of best predicting mesosite occupation (Table 3.4). The sum of Akaikes weights for each variable showed that distance to vegetation and distance to channel ($\omega_i = 0.98$ and 0.95, respectively) were considerably more important than distance to lake ($\omega_i = 0.32$). The parameter estimate for distance to vegetation was positive, and that for distance to channel was negative, indicating that the probability of mesosite use by *P. socialis* increases with increasing distance from vegetation and decreasing distance to freshwater channels (Figure 3.6).

Table 3.3 Generalized linear mixed-effects model (GLMM) that predicts the effects of substrate ground cover on mesosite use by breeding *P. socialis*. The table includes the parameters (percent cover of vegetation at 5 m and 15 m from the centrepoint) that remained in a skeleton model after a backward stepwise procedure of eliminating non-significant variables (McCullagh and Searle 2000). The effect of lake (included as a random factor) was important to the model (SD = 0.975) compared to the intercept model (SD = 0.00017; McCullagh and Searle 2000).

Parameter	Estimate	SE	df	t-value	*P*
(Intercept)	2.187	0.607	51	3.60	0.0007
5 m vegetation	-1.911	0.567	51	-3.37	0.0022
15 m vegetation	-3.420	1.155	45	-2.96	0.0049

Table 3.4 Model selection for unconditional logistic regression describing the effect of distance to three geographic features (lakeshore, vegetation and freshwater channel) on mesosite occupancy of *P. socialis*. The table shows sample size (n), number of parameters (K), Akaike's information criterion (AIC), AIC corrected for small sample size (AIC_c), difference in AIC_c (ΔAIC_c) and Akaike's weight (ω_i) for the top ranking candidate models ($\Delta AIC_c \leq 7$) and constant model of 16 candidate models. The total importance value for each variable is also provided, as well as the parameter estimates, their standard error (SE) and 95% confidence intervals.

Model	n	K	- 2 ln (L)	AIC	AIC_c	ΔAIC_c	ω_i
Vegetation, Channel	51	3	53.49	59.49	60.00	0.00	0.64
Full model	51	4	52.48	60.48	61.35	1.35	0.33
Vegetation	51	2	62.80	66.80	67.05	7.00	0.02
Constant model	51	1	78.58	80.58	80.66	20.66	0.00

Parameter	Importance Value ($\Sigma\omega_i$)	Parameter Estimate	SE	Lower 95% CI	Upper 95% CI
Vegetation	0.98	1.072*	0.350	0.372	1.773
Channel	0.95	-0.123**	0.096	-0.316	0.070
Lake	0.32	-0.095*	0.096	-0.287	0.098
Intercept	0.00	-2.518	1.436	-5.394	0.358

* parameter estimate applies to square root transformed variable

** parameter estimate applies to natural logarithm (ln) transformed variable

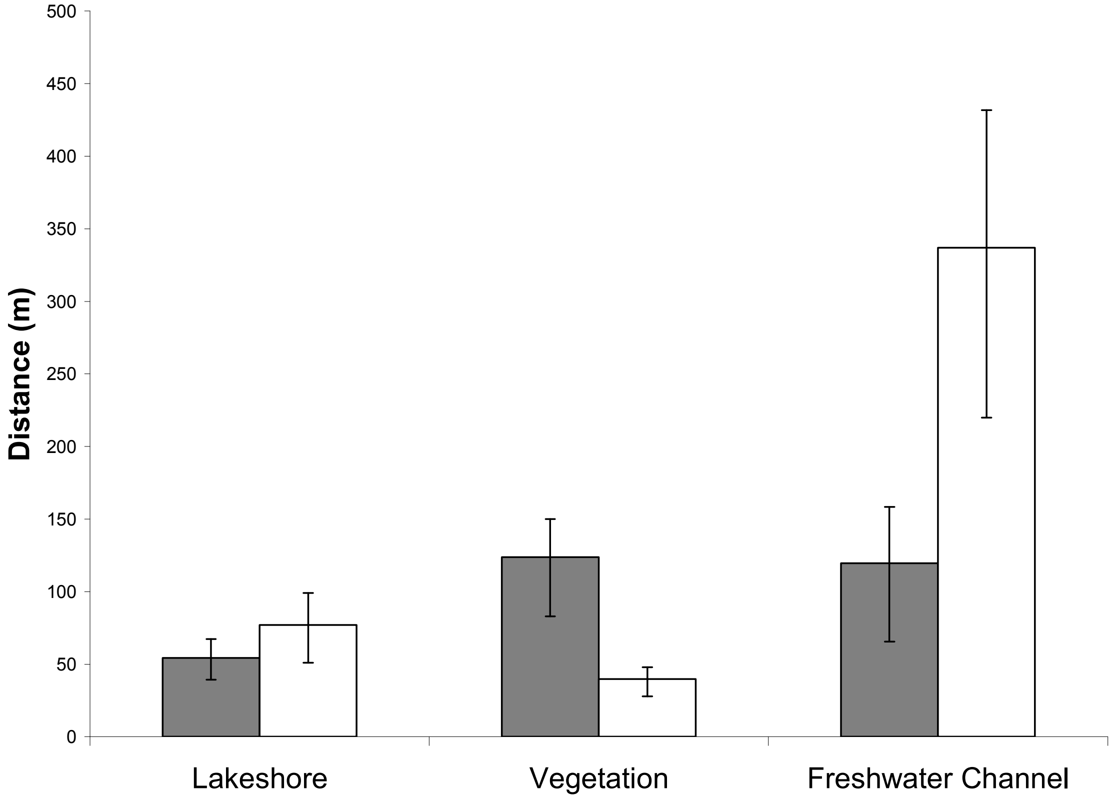

Figure 3.6 The mean and 95% confidence interval of distance to three features (endorheic lakeshore, vegetation, and freshwater channel) of *P. socialis* comparing used and available mesosites.

Microsite use.--- The model including the additive effects of percent clay and percent cobble was the most parsimonious, with a 37% chance of best describing microsite use by *P. socialis* (Table 3.5). Clay alone was the second ranking model (27%) and percent clay cover was present in all of the 5 most parsimonious models (Table 3.5; $\Delta AIC_c < 4$). Clay had the highest overall importance value of $\omega_i = 0.73$ with cobble as the next most important value ($\omega_i = 0.37$). Percent clay was lower at used sites than available sites, and percent cobble was slightly higher (Table 3.6).

Nest success and habitat characteristics.--- Seventy percent (12/17) of nests were successful in having one or both eggs hatch. Four nests were depredated and one nest was trampled. I determined a Mayfield estimate of daily nest survival of 0.975 ($n = 17$) and nest survival of 0.550 ($n = 17$, $t = 24$, Mayfield 1961, Johnson 1979). I found no significant differences in proximity to lakeshore, vegetation or freshwater channel between successful and unsuccessful nest sites (Table 3.7). I found no evidence that microsite cover differed between successful and unsuccessful nests (Table 3.7).

DISCUSSION

Lake preference.--- The altitude of lakes in my study site ranged from 10 - 800 m above sea level; climate on the lakeshore can vary considerably within this range as high altitude lakes are colder and exposed to more severe storms than those at lower altitudes, even throughout the breeding season (Soriano 1983). My results provided no evidence

Table 3.5 Model selection for conditional logistic regressions describing the effect of percent substrate cover on probability of microsite use by breeding *P. socialis* (Burnham and Anderson 2002). Sample size (n), number of parameters (K), Akaike's information criterion (AIC), AIC corrected for small sample size (AIC_c), difference in AIC_c (ΔAIC_c) and Akaike's weight (ω_i) are reported for the top five models ($\Delta AIC_c < 4$), and constant model, of 16 candidate models describing the effect of substrate cover on the microsite occupancy of *P.socialis*.

Model	n	K	AIC	AICc	ΔAIC_c	ω_i
clay, cobble	50	3	14.186	20.708	0.000	0.37
clay	50	2	17.055	21.310	0.602	0.27
clay, vegetation	50	3	17.040	23.562	2.854	0.09
clay, gravel, cobble	50	4	15.492	24.381	3.673	0.06
clav, cobble	50	3	18.065	24.587	3.879	0.05
constant	50	1	34.657	36.741	16.033	0.00

Parameter	Importance Value ($\Sigma\omega_i$)
clay	0.73
cobble	0.37
vegetation	0.09
gravel	0.00

Table 3.6 Descriptive statistics for the percent cover of clay, vegetation, gravel and cobble at used and available microsites of *P. socialis.* The sample size (n), median and interquartile range (IQR) is provided.

	Used		Available	
	n	Median (IQR)	n	Median (IQR)
% Clay	24	0 (0, 3.5)	24	42.5 (1.5, 92.5)
% Vegetation	24	0 (0, 0)	24	0 (0, 3.5)
% Gravel	24	92 (80.5, 97.5)	24	23.5 (0, 95.5)
% Cobble	24	2 (0, 8)	24	0 (0, 0)

Table 3.7 Descriptive statistics and results of univariate tests for differences between successful and unsuccessful nest sites of *P. socialis*. Mean and 95% confidence intervals of distance to lakeshore, vegetation and freshwater channel are provided with the test statistics from independent t-tests. The median and interquartile range (IQR) of percent cover of clay, vegetation, gravel and cobble at microsites are provided with the test statistics from non-parametric Mann-Whitney U-tests.

	Successful		Unsuccessful		Test Statistic	
Distance to (m):	n	Mean (95% CI)	n	Mean (95% CI)	t	p
Lakeshore*	12	47 (27, 72)	5	45 (13, 96)	0.117	0.9
Vegetation**	12	53 (28, 100)	5	122 (45, 328)	-1.65	0.12
Freshwater Channel*	12	27 (13, 53)	5	34 (6, 198)	-0.39	0.7
Microsite cover (%)	n	Median (IQR)	n	Median (IQR)	Z	p
Clay	12	1.5 (0, 6)	5	0 (0, 0)	0.79	0.43
Vegetation	12	0 (0, 0.5)	5	0 (0, 0)	0.21	0.83
Gravel	12	92 (79, 97)	5	92 (92, 97)	-0.32	0.75
Cobble	12	2.5 (0, 8.5)	5	2 (2, 6)	-0.11	0.92

* variable was square-root transformed, values are back-transformed

** variable was $\log_{10}$ transformed, values are back-transformed that *P. socialis* prefers any particular altitude within this range. As altitude did not relate to lake occupation by *P. socialis*, it suggests that the species is robust to breeding in the variable climate conditions associated with elevation.

P. socialis appears to prefer saline lakes over freshwater lakes. This finding could be explained in several ways. First, the invertebrate assemblages in the endorheic lake basins change with variations in salinity (Quirós and Drago 1999), and *P. socialis* may select saline lakes as they support a greater abundance of invertebrates, thus increasing food availability. Shorebirds use saline lakes throughout the world because of the abundance of invertebrate prey species (e.g. Verkuil et al. 2003, Conway et al. 2005). Another possible reason that *P. socialis* prefers saline lakes may be related to their depth. Freshwater endorheic lakes occur because they have been eroded deep enough to contact the water table and have freshwater input which dilutes the salts (Paruelo and Sala 1995). *P. socialis* may avoid deep basins or steep shorelines. Steep surfaces are known to be unfavorable to ground-nesting shorebirds (e.g. Whittingham et al. 2002) because nests are more vulnerable to predation or egg loss. Since nest scrapes are quite shallow in this species, it is logical that steep shorelines would be avoided. Finally, saline lakes may be preferred if competition is reduced at these lakes and there are fewer nesting species with which to compete for breeding sites. This does not seem a likely explanation, however, since all heterospecific ground-nesting birds occurred in relatively equal densities among lakes, regardless of salinity (e.g. the Two-banded Plover, *Charadrius falklandicus*; pers. obs.).

P. socialis occupied larger lakes with large aeolian lunettes. These variables were significantly correlated; however some large lakes had no aeolian lunettes. Larger lakes may be preferred by *P. socialis* because the larger lake perimeter allows birds to occupy larger territories and thus have more resources available to them when breeding. Lake size, although significant in the univariate analysis, did not come out as a strong explanatory variable in comparison to aeolian lunette size in the logistic regression models. Some smaller lakes are occupied by *P. socialis*, but lakes with little or no aeolian lunette development, regardless of size, were unused. The aeolian lunette may act as a signal of sparsely vegetated shores to *P. socialis* that are searching for suitable lakes. *P. socialis* tended to avoid vegetation within their mesosites and clay in their microsites. The substrate of the aeolian lunette contains very little clay and no vegetation and because it is highly wind-exposed, the substrate is a matrix of gravel, cobble and loess (wind-generated mineral dust).

The shorelines of the endorheic lakes of Patagonia exhibit a general pattern with a wind-sheltered side (western shore) that is composed of a clay shoreline and a wind-exposed side (eastern shore) with a gravel-cobble shoreline and aeolian lunette extending away from the lake (Soriano 1983). Although this was not quantified in my study, I did observe that *P. socialis* were more often observed on the wind-exposed side of the lake. As these features are wind-generated, it could be argued that *P. socialis*, by preferentially occupying lakes with an aeolian lunette, are selecting lakes that have high wind exposure. The wind is nearly unbearable for human observers at times (reaching up to 140 km/hour on a regular basis; pers. obs.) and could disorient olfactory-dependent ground predators like foxes and skunks, thus reducing the risk of predation for *P. socialis*. Based on behavioural observations, the species appears to be adapted to high wind exposure, e.g. facing upwind constantly while foraging.

The importance of proximity to the ocean for lake occupation by *P. socialis* could be interpreted in a number of ways. First, *P. socialis* winters on estuaries near the ocean, so the distance they migrate to breed may be important to their habitat selection decisions. Second, if the lakes occupied by *P. socialis* dry early in the summer, it may be beneficial to be near the ocean where alternate food sources are accessible to the birds. Third, proximity to the ocean is one way to describe geographic location, and because this was an important parameter for lake occupation, it suggests that the desirable lake characteristics are non-randomly distributed geographically. Proximity to ocean did not correlate with any other variable in my study, so there may be a variable that was not measured in this study but varies geographically and is also important in describing the lake preference of *P. socialis*.

Cover type and nest-site selection.--- I found little commonality between the results of analyses of substrate cover selection at the mesosite (45 m radius) and microsite (1 m^2) scales. The decisions made by breeding birds at the mesosite scale generally have different consequences at the microsite scale. At the mesosite scale, there are two contrasting pressures that would affect site selection. First, birds need access to substrates ideal for foraging (clay and wrack). Second, they need substrates in which they and their young are cryptic and can avoid detection by aerial predators (clay, gravel and cobble). Clay, gravel and cobble were not significant variables in mesosite use when lake was controlled for as a random effect. Therefore, there was no evidence that birds selected higher amounts of foraging related substrates within their mesosites (i.e. clay or gravel). *P. socialis* did, however, avoid vegetation within 15 m of the nest or chick. As the upperparts of *P. socialis* are similarly coloured to clay, gravel and cobble (light grey), but different from vegetation, this is presumably a crypsis-related preference. When birds are at or near their nest or chick, aerial predators may find them difficult to detect.

At the microsite scale, the microclimate around the nest and the crypsis of the eggs are important pressures affecting site selection. I found a clear trend that birds select sites within their territories that have less clay for nest placement. The additive effects of decreasing clay and increasing cobble was the most parsimonious model; however, the contribution of percent clay to variation in microsite use was overall nearly twice as important as that of cobble. In comparison, percent cover of gravel and vegetation were not selected for or avoided by *P. socialis* within their territory, which may be simply because percent cover of each is relatively uniform throughout their territory. The decision to avoid clay at the microsite could be for two reasons. First, the size and colour of *P. socialis* eggs is most similar to pebbles, and a single egg on clay is not nearly as cryptic as one on pebbles, which may pose a high risk of predation at clay sites (pers. obs.). Second, the cold and windy environment in which *P. socialis* breeds may select against the nest microclimate of eggs laid over clay. Clay, by definition, is a water-holding substrate and with so much convection due to wind in that environment, heat is rapidly taken from the substrate and consequently the eggs. In contrast, gravel and cobble tend to reflect heat and may provide a more favourable microclimate (Gloutney and Clark 1997).

Proximity to landscape features and nest-site selection. P. socialis appears to select sites that are farther from vegetation and closer to channels than available sites. The avoidance of vegetation appeared to be the strongest explanatory variable of *P. socialis* mesosite selection, which suggests it is an important factor in the selection decision made by birds. Other ground-nesting shorebirds also avoid vegetation (Nguyen et al. 2003), which probably obstructs an incubating bird's visibility and thus reduces its effectiveness in detecting predators (Gotmark et al. 1995). However, the vegetation near or within *P. socialis* breeding territories is typically low lying (< 2 - 5 cm in height) and so the obstruction of the bird's visibility seems unlikely. Perhaps a more relevant explanation for *P. socialis* is that the colour and patterns of *P. socialis* adults, eggs, and chicks are more similar to unvegetated sediments and mesosites that are close to, or include, vegetation reduce the overall crypsis of *P. socialis* in its environment and increase the risk of predation by aerial predators (Solís and Lope 1995).

Proximity to a freshwater channel was another strong explanatory variable of mesosite use by *P. socialis*. I suggest two possible reasons for this finding. First, as I observed in the lake level analysis, the majority of lakes occupied by *P. socialis* are saline and birds likely need a local source of freshwater from which to drink. This is particularly important for breeding adults that must be present on their territory when the young are in the early stages of development and inactive (Ferrari et al. 2008). The second explanation for this finding is that freshwater channels may be related to a food source for *P. socialis*. The small estuaries that form at the mouth of the freshwater channels into the saline lakes may have certain chemical characteristics that are ideal habitat for invertebrate food items for *P. socialis*. I observed that birds forage constantly, which may be a function of the apparently small prey size (mostly invisible to an observer, even with a spotting scope; Jehl 1975, Ferrari et al. 2008), so I assume that they must be strategic in selecting sites in proximity to food-related features, like brackish washouts (Jehl 1975, Ferrari et al. 2008). Indeed, I often observed adults, chicks and juveniles foraging in these features. The combined effects of selecting for territories that are distant from vegetation and close to freshwater channels presumably maximizes fitness.

Proximity to the lakeshore, although present in my second most parsimonious model, did not have a very high importance value relative to the other features. This finding could be a function of study design for two reasons. First, my delineation of available area was based on the lake shore, and therefore limited the possible range of values from 0-300 m. This may not have allowed us to detect differences between used and available sites. Second, the levels of water in the endorheic lakes of Santa Cruz are highly variable both within and between years, so distance measurements to the shoreline could change on a daily or weekly basis. *P. socialis*, as far as I am aware, has never been observed breeding > 300 m from a lake. Within that 300 m buffer, proximity to the lakeshore may simply have no influence on a bird's decision to establish a territory, since it is such a variable feature.

Other constraints may affect a bird's non-random use of habitat, such as competition and predation (Jones 2001). Competition for territories between *P. socialis* seems unlikely because they generally nest in low densities (with the exception of the lake with 14 pairs). However, the strong dependence on proximal freshwater channels may create constraints for the number of *P. socialis* territories that one lake can support. For example, if a lake has only two freshwater channels that drain into it, it may only support two *P. socialis* breeding territories. Unfortunately the resolution of satellite images used in my study was inadequate to count the number of channels on every lake.

Habitat characteristics and nest success.--- As I found no difference in the microsite cover or proximity to features of successful and unsuccessful nest sites, there is no evidence to suggest that habitat characteristics affect nest success. However, the small sample size of nests in my study makes it unlikely that differences would have been detected. The traditional method of habitat selection studies has been criticized by some researchers who argue that natural selection will have already acted against unfavourable nest-sites at the time nests are observed, making the exercise meaningless in inferring adaptive habitat selection (Pribil and Picman 1997). The majority of studies have not found that nest success is related to habitat characteristics (Fernández and Reboreda 2002, Nguyen et al. 2003), although there are some exceptions (see Smith et al. 2007, Walpole et al. *in press*)

Implications.--- In summary, *P. socialis* select saline endorheic lakes that have large aeolian lunettes. They prefer to locate their territories farther from vegetation and closer to freshwater channels than random sites within the available area of the lakeshore. Finally, within their territories they avoid locating their nests on clay substrates. Habitat characteristics did not differ between successful and unsuccessful nest sites. At each spatial scale I found that *P. socialis* select for specific characteristics to some degree. There was no evidence of strong selection for the substrates in their mesosites, apart from avoidance of vegetation within 15 metres of the centrepoint. The choices that birds made at all scales were presumably made in the interest of maximizing available food resources for themselves and their young and to complement antipredator adaptations such as crypsis.

A potential problem that *P. socialis* faces due to its habitat preference is the vulnerability of nests to trampling by livestock which frequently use the saline lakes and freshwater channels from which to drink (Piersma et al. 1997, Ferrari et al. 2008). The gravel substrates, which are preferred by nesting *P. socialis,* may also be preferred by livestock to access the water since the alternative substrates (e.g. clay) are soft and can cause mortality to ungulates (pers. obs.). I suggest that a simple management solution to protect *P. socialis* from this would be to fence off sections of occupied lakes where there is both gravel substrate and a nearby channel between the months of September and February, thereby excluding livestock and ensuring an increased nesting success for *P. socialis.*

CHAPTER 4: General Discussion

RARITY OF *PLUVIANELLUS SOCIALIS*

Rare species can be categorized into one of seven forms according to three factors: geographic distribution (wide or narrow), habitat specificity (broad or restricted) and local abundance (abundant and scarce; Rabinowitz et al. 1986). Intrinsic demographic characteristics can make a rare species particularly vulnerable to extinction. The objectives of my thesis were to consider how these four factors relate to *P. socialis* and thus determine why the species is rare.

Geographic distribution.--- Endemic species are often targeted by conservation research since the protection of them in their habitats will preserve biodiversity (Bonn et al. 2002). *P. socialis* is an endemic species, and probably has been since its divergence from a common ancestor with *Chionis* spp approximately 19 mya (Paton et al. 2003, Thomas et al. 2004, Fjeldså 1994). The wintering distribution of *P. socialis* spans from 53°S in the south to 38°S in the North. Occasional reports of *P. socialis* from the Atlantic coast of Buenos Aires province in Argentina (see Chiurla 1996) indicate that there may be wintering sites along the coast that have not yet been discovered. The breeding range is much smaller, extending from 53°S to 46°S covering approximately 12,000 km^2. As of yet there is no evidence that the breeding range of *P. socialis* extends any farther north than 47°S (Santa Cruz Province). *P. socialis* appears to be restricted to the driest ecotone in austral Patagonia, which illustrates habitat specialization of the species (Soriano 1983). I found that distance to the ocean was a significant variable in predicting the use of endorheic lakes in Santa Cruz. This indicates that suitable lakes are additionally limited within the geographic range of the species. There is little doubt that *P. socialis* exhibits a narrow geographic distribution.

Habitat specialization.--- Habitat use of *P. socialis* was disproportionate to its availability, and may indicate that *P. socialis* is a habitat specialist. The type of endorheic lakes that *P. socialis* chose to occupy had specific characteristics in comparison to the characteristics of available lakes. At the scale of nest-site selection, *P. socialis* non-randomly selected territory sites that were distant from vegetation and within close proximity to freshwater channels. They also preferred to occupy territories with less vegetation than those that were available. The nest-sites of *P. socialis* were located at sites with less clay than other available sites within their territories.

Another aspect of specialization that has been illustrated by my studies suggests that *P. socialis* exists within a specific band of precipitation. Areas with high precipitation (i.e. lakes close to the Andes mountains) support more vegetation on the shoreline than those preferred by *P. socialis* in eastern Santa Cruz. Conversely, very low precipitation levels cause lakes to dry early in the breeding season (Paruelo et al. 1998) and may prevent consecutive within-season nesting.

Despite this evidence that *P. socialis* is a specialist, there are a few reasons that I am apprehensive to declare that *P. socialis* is a habitat specialist based solely on my habitat selection study. First, the concept of resource specialization is a relative one, and can best be identified by comparing the niche breadth of *P. socialis* with heterospecifics or taxonomically similar species. There are little data available on the habitat use of other ground-nesting shorebirds in Patagonia. During my field work in Patagonia, I observed that *Charadrius falklandicus,* the Two-Banded Plover, was often associated with *P. socialis* on its breeding habitat and nested on nearby locations on the same lakes and gravel substrate that *P. socialis* prefers. However, *C. falklandicus* was also found nesting in dry, upland, bunch grass habitats, under shrubs, on clay substrates and on the vegetated salt flats near the ocean estuaries. These are places that I never encountered *P. socialis* during the breeding season. Second, there is some evidence that *P. socialis* may also use river banks for breeding (Ferrari et al. 2003) and due to time and budget constraints I was not able to thoroughly search riverbanks for *P. socialis*. This remains an unstudied aspect of the breeding biology of *P. socialis* and it would be interesting to confirm that they breed on rivers, thus broadening our perception of its habitat preferences. Despite these uncertainties it appears that *P. socialis* is at least, probably more of a habitat specialist than its sympatric heterospecifics.

The relationship between resource specialization and rarity is the subject of much research and remains a somewhat elusive concept (Gregory and Gaston 2000, Davies et al. 2004, Walker 2006). A species may be rare because it specialized on an abundant resource that was then reduced (Gregory and Gaston 2000, Owens and Barnett 2000). Conversely, a species may have specialized on an uncommon resource initially to avoid competitive pressure and has, therefore, always been a rare species (Gregory and Gaston 2000). Distinguishing between these different mechanisms causing rarity tells us whether a species is rare because of a change to its environment or whether it is rare by nature.

In the case of *P. socialis,* there is evidence that the non-random selection of habitat characteristics is adaptive so that birds can maximize their survivorship on their breeding sites. For example, the avoidance of vegetation in nest-site selection may be an anti-predator adaptation because eggs and incubating adults are more cryptic on unvegetated substrates. This suggests that *P. socialis* adapted to match its particular habitat (Fjeldså 1994). The strong westerly wind has been present in Patagonia for over 20 million years (Soriano 1983) and the saline endorheic basins themselves have persisted several million years (Iriondo 1989). Since these are essential aspects of the habitat of *P. socialis*, it is logical to presume that the species evolved to use the wind-exposed shorelines of these lakes early and has, therefore, always been a rare species. An important source of error in this assumption is that fluctuations in temperature and precipitation caused the quantity of vegetation-free lakeshores to increase (during dry periods) and decrease (during wet periods) in the climatic history of Patagonia (Soriano 1983).

Local abundance.--- Some species that are identified as rare by the first two factors (geographic range and habitat specialization) are difficult to assess in the third factor (local abundance; Schoener 1987). Local abundance is important to evaluate because a species that is abundant in a certain region should invite conservation efforts that focus on those particular regions (Brown 1984). Uncertainty in this third factor often occurs when we observe that a species is rare because it was infrequently detected in the census data from some portion of its range (Schoener 1987). Rabinowitz et al. (1986) referred to this form of rarity as “pseudo-rarity” since it is not truly rare throughout its range.

This has been an important issue in the history of research on *P. socialis.* The species was first studied by Jehl (1975) in what we now recognize to be a relatively small part of its range (Río Grande, Tierra del Fuego). Jehl (1975) stated that “the total population may not exceed 1000 individuals.” With the recent discovery of wintering groups (ca. 140 individuals) in Santa Cruz province by Ferrari et al. (2003) came new hope that there are potentially large populations of *P. socialis*. The IUCN Redlist now suggests that the estimated population size is "less than 10,000 individuals" where it once stated "less than 1500" (BirdLife International 2006).

One of the objectives of my thesis was to determine whether *P. socialis* is truly rare throughout its range, or if there are some areas where it is more abundant. I addressed this question by conducting systematic searches for *P. socialis* across a broad area of Santa Cruz. I found no statistical evidence that the abundance of territories per lake was distributed non-randomly on 19 lakes in Santa Cruz. Observations that were contributed by other field researchers in Patagonia indicate that *P. socialis* is never found in abundances of more than 10 individuals during the breeding season (Ferrari et al. 2008). One noteworthy observation from my study was a lake that had 14 breeding territories. This is, to my knowledge, the largest concentration of breeding *P. socialis* ever found and is an anomaly to the more common observation of 1-3 territories per lake. This observation does not necessarily suggest that *P. socialis* is common in that general area (ca. 30 km north of the city of Río Gallegos). A lake of comparable size and characteristics only 12 km away from this lake had only one territory on it. This observation, if anything, should encourage more exploration for breeding areas of *P. socialis*. If such lakes exist in abundance somewhere within the range of the species, it is possible that they have simply been overlooked.

A method developed by Schoener (1987) characterizes the local abundance factor of species by calculating the ratio of area where the species is common to the area where it is rare. By using this technique, we see that *P. socialis* is scarce throughout its range, because my study indicated that a very small fraction of the area I searched had more than three pairs in a 1 km^2 area. Therefore, by most measures we find that *P. socialis* is scarce throughout its range. I strongly encourage more exploration for anomalous densities of breeding pairs like that found in my study.

VULNERABILITY AND DEMOGRAPHICS

The demographic characteristics of *P. socialis* were considered in Chapter 2. Based on several assumptions, I projected one scenario that the population growth rate (λ) for *P. socialis* is 0.80. This value represents a declining population. If this value is true, and the global population is 1000 individuals, as Jehl (1975) estimated, the population would be close to extinct in fewer than 30 years. However, there are several questionable aspects of my estimation of λ. As there are few species with which *P. socialis* can be compared directly (as it is monotypic) assumptions around estimating values such as juvenile survival and adult survival. The survival rate estimates are possibly underestimates because many species I considered in the literature are long distance migrants, and *P. socialis* is not. Migration distance may or may not be an important factor affecting adult survivorship (see Sandercock and Jaramillo 2002). In addition, *nests/year* is a term that I added and its value may vary with annual conditions.

Taking account of the uncertainty of my assumptions and the fact that only two seasons were included in my study, it is likely that *P. socialis* has a slow population growth rate. If catastrophic mortality events fall upon the species, it may not recover. Factoring in the potential additional hazards of low population densities, i.e. negative Allee effects and inbreeding depression, it is likely that the species would become increasingly rare, and possibly extinct.

OPPORTUNITIES FOR FUTURE RESEARCH

There are four main research areas that I suggest are critical to pursue in the study of *P. socialis*. The first is the estimation of a global population size. The current estimates of population size are highly speculative because there has been little effort to determine representative densities of birds in either reproductive or non-reproductive habitats (Jehl 1975, Ferrari et al. 2003, Ferrari et al. 2008). Although there are several methods to do this, I suggest that a GIS-based habitat suitability model would be the most effective method. The work in my thesis on habitat preferences should help to create this model. Additionally, systematic field searches over a wider geographic area, can be used to estimate the mean number of birds per area of suitable habitat, and extrapolation of that value to all suitable habitats within the distribution can then be made (e.g. Long et al. 2008). Another method is to survey the species during the winter. As *P. socialis* is limited to a few wintering sites along the Argentine coast (Ferrari et al. 2008), conducting comprehensive surveys would be feasible. This would be done in a coordinated fashion over the entire winter range in a short time interval, to avoid duplicate counts due to movements. A reliable estimate of population size will give solid footing to future researchers to be aware of declines and threats. Aside from this central priority, however, innumerable opportunities remain in the study of *P. socialis*.

A second area for research is to estimate local survival rates of the *P. socialis* population in my study. Marking individuals over the course of several years will improve our understanding of movements, philopatry, site tenacity as well as survival rates. I suggest continued marking of nestlings during the breeding season and marking adult birds if a safe and effective method of capturing adults is developed. Survival rate estimates will improve the estimation of population growth rate, λ.

The third important area of research is to evaluate the impacts of human development in Patagonia on *P. socialis.* This is particularly important on the estuaries, such as that of the Chico and Gallegos rivers, where rapid urban development is likely to change drastically the species' wintering habitat. With time, pressures on all native flora and fauna in the estuaries will increase, e.g. feral dogs, introduced species, soil and water contamination, and general ambient noise and disturbance. The impacts of human activities on *P. socialis* are only speculative at this point because there are no concrete studies that have demonstrated direct threats. By conducting such studies, there is a greater opportunity to obtain funding for resources to local conservation efforts and education programs. The benefits of conservation efforts will extend to other endemic waterbird species that use the estuary, such as the Hooded Grebe (*Podiceps gallardoi*) and Magellanic Oystercatcher (*Haematopus leucopodus*; Imberti 2003).

Finally, there is a need for more information on diet of *P. socialis.* Sampling available food (invertebrate assemblages) at wintering and breeding sites and combining this information with behavioural observations and studies of energy expenditure, along with quantifying microhabitat use is suggested. Information on diet and foraging behaviour will allow researchers and natural resource managers to understand how changes to the estuaries and lakes will affect the food and energetics of *P. socialis*.

As I have demonstrated, *P. socialis* is a rare species and potentially vulnerable to extinction. Conservation of the species and its habitat is of great importance. Proximal conservation efforts should focus on excluding grazing livestock from breeding sites. At a broader scale, efforts to mitigate climate change will also ensure that *P. socialis*' breeding habitat is not altered by changing precipitation patterns. Increased awareness and environmental education in Patagonia are important aspects of avian conservation and are deserving of funding and support of any kind.

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APPENDIX

Pluvianellus socialis chick dimension and banding data

Date Banded	Age Estimate (days)	Culmen (mm)	Tarsus (mm)	Head Length (mm)	Mass (g)
10/10/2006	5	6	12	30	
10/16/2006	2	5	11		
11/1/2006	1	5	11	24	
11/1/2006	1	5.5	10	23	
11/11/2006	3				
11/20/2006	3	9	15	29	
11/20/2006	1	8	12		
12/2/2006	4	7.4			
12/2/2006	4	7.5			
12/15/2006	13	10.4	14.7		
1/5/2007	2.5	8.5	13.8	23.1	
1/5/2007	15	10	16.1	27.1	
1/11/2007		9.9	14.3	34.1	31
1/11/2007	2	7.4	11.1	24.2	17
1/11/2007		8.1	13.2	22.8	7
1/23/2007	2	9	12.4	18.1	14
12/14/2007	3	6.4	14.9	25	11
12/15/2007	17	13.2	20.7	39.4	53
12/15/2007	2	6.6	12.1	26.4	10
12/15/2007	3	6.8	12.6	23.8	8
12/15/2007		7.2	13	26.2	10
12/15/2007	3	6.8	12.8	25.8	10
12/16/2007		11.9	17.3	37.8	46
12/29/2007		7.7	15.3	26.6	10
12/29/2007		11.1	18.4	34.9	36