Survivorship and Life History Strategies in Relation to Migration Distance in Western and Semipalmated Sandpipers in Perú

by

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Ethics Statement

Abstract

This thesis explored the relationships between life history, migration distance, survivorship components of fitness, and molt strategies of Western and Semipalmated Sandpipers in one of the most austral non-breeding sites for both species, at Paracas, Perú. I asked how migration distance relates to pre-migratory preparation, survivorship and migratory decisions for different age classes and ecological circumstances between species and within populations. I focused particularly on how timing of first breeding relates to survivorship and thus future overall fitness. I found that adults from both species prepare for northward migration, but no juvenile Western Sandpipers did so, confirming a non-migratory over-summering 'slow' life history strategy for more southerly non-breeding populations. Juvenile Semipalmated Sandpipers showed bimodality in migration strategy. Most showed no migratory preparation, but ~30% fattened, molted into breeding plumage, and performed partial post-juvenal wing molt (PPW) during the pre-migratory period. The frequency of PPW is positively related to culmen length (as a proxy for eastern breeding birds with a shorter migration distance). To decompose survivorship between migrant and oversummering (resident) Semipalmated Sandpipers, I used a multi-state model with 5 years of data and found survivorship 8 percentage point higher for oversummering juveniles and 21 percentage points higher for oversummering adults compared to same aged migrant birds, as expected as compensation for the loss of a breeding opportunity. I estimated annual survivorship with an open robust multi state model using 7 years of mark-resighting data from several thousand shorebirds marked at Paracas. As predicted by some migration theories, both species had higher annual survival estimates than those obtained previously at non-breeding sites further north. Western Sandpiper juveniles also had substantially higher annual survival estimates than adults, in line with the predicted survivorship benefits needed to offset their delayed reproduction. I found that the size of the survival advantage in juvenile Semipalmated Sandpipers is migration distance dependent. Western, but not Semipalmated Sandpipers showed a negative relationship in survival with the ENSO warm phase, probably due to the former's closer association with the Pacific migratory flyway. Finally, I corroborated that the size of the survival advantage is distance dependent. My results provide novel information on non-breeding shorebird survivorship and perspective on the interrelationships that drive avian life history strategies. I confirm that Paracas is also a site with high demographic value.

Keywords: shorebirds; survivorship; migration distance; oversummering; pre-migratory molt; Paracas

Dedication

To All Shorebirds in Perú

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Chapter 1.

Introduction

1.1. General Introduction

1.1.1. On Life History Strategies and Migration Theory

The Earth is an ever-fluctuating environment revolving around the Sun on a tilted axis, which creates oscillations of food availability and temperature, strong selective forces in the evolution of life (Alerstam 1990). Shorebirds, like many other migratory animals, have a variety of behavioral adaptations to cope with the challenges of seasonal survival while they alternate between phases of their annual life cycle: breeding, molt, non-breeding survival and migration (Buehler and Piersma 2008). These phases must be perfectly timed, and individuals use phenotypic flexibility when switching from one to another, in order to maximize fitness (Wingfield 2008). What proximate and ultimate processes determine whether it is best for a bird to migrate or not, and if so, how to do so?

Darwin (1859) invented the idea of fitness to explain natural selection, an evolutionary mechanism whereby individuals better suited to an environment than others have greater reproductive success and/or survival. Consequently, over generations, their descendants continuously refine their adaptation to their environment and track changes in it. Shorebirds are known for their great adaptations to specific habitats and their features associated with their migratory nature (Colwell 2010). These adaptations include the use of more energy, greater daily energy expenditure and the maintenance of higher metabolic rates than other comparably sized birds (Castro 1987, Kersten and Piersma 1987, Lindström and Klaassen 2003); physiological and behavioral changes such as gut and musculature changes associated with powered flight (Piersma and Gill 1998); changes in size of the digestive organs and their enzymes' activity (Stein et al 2005); the extent of nocturnal and diurnal foraging (McNeill et al 1992); inter and intraspecific variation in seasonal timing for flight-feather molt (Prater et al 1977, Pyle et al 2008); and the variation in migratory behavior itself, which is shaped mainly by managing time, energy and predation danger (Alerstam and Lindström 1990).

Optimal bird migration theory addresses how migratory behavior should be structured under different set of constraints cost and benefits (Alerstam 2011). Migratory behaviors in populations with partial migrants, where there is considerable variation in the movements of individuals, are largely viewed as plastic, possibly shaped by the environment experienced by juvenile birds (Colwell et al 2007). Partial migration systems may be ‘facultative’ when they result from a condition-dependent strategy varying within individuals over their lifetime (Ketterson and Nolan 1983) and when migratory decisions are subject to trade-offs influenced by environmental and individual condition (Boyle 2008). In other species young or immature birds regularly forego migration back to breeding grounds, and adults injured or in poor condition may opt out of migration and breeding for a season (McNeill et al 1994) this would still be ‘facultative’ in some sense. There is thus, substantial inter- and intraspecific variation in migratory behavior, resulting in an enormous diversity of life history strategies beyond a simple dichotomy as migratory or a non-migratory status (aka. ‘resident’ vs. ‘migratory’) bird (Holberton and Dufty 2005). Further, residents, experience a different set of social and physical environment changes during the nonbreeding seasons, such if there is an alteration in their habitats linked to their primary source of food this might lead to negative consequences for survival and population size (Newton 2004, Santisteban et al 2012). However, when migrants arrive, resident birds have to deal with the challenge of competition for food and territory and this can lead to different types of aggressive behavior (Wingfield and Hahn 1994).

Piersma (1987) summarized shorebird migration strategies as a set of continuous events, based primarily on the distance traveled between consecutive stop-over and staging sites. Long-distance migration as typically displayed by shorebirds is a complex property that requires genetic instructions about timing and duration of movements in the organism's temporal/circannual program, physiological adaptations for the storage of nutrients (fat and proteins) that play the role of fuel to reach the next scale on the trip as well as the associated metabolism, behavioral adaptations to face environmental variables such as wind and weather conditions during the journey and control of orientation and navigation (Berthold 2001). Migration represents a critical stage of the annual life cycle and shorebirds face migratory decisions to capture the essence of their optimal annual routines and mediated them through life-history trade-offs (McNamara et al 1998). Migrants move along flyways with knowledge of their ever-changing conditions and the decision to remain at a site or move might be strongly influenced by the nature of habitat present on the landscape and the presence and quality of food resources (Colwell 2010). Behavioral decisions enable individuals to determine the timing of migration with respect to a variety of different factors, including the form of the relationships between date-specific reproductive value and environmental conditions, including food availability and the level of predation danger (McNamara and Houston 1990, McNamara et al 1998, Lank et al 2003, Ydenberg et al 2007). These life-history trade-offs are usually dependent on environmental conditions and are linked to physiological changes such as a bird's energy reserves and condition (McNamara et al 1998), change of the size of flight muscles/organs (Piersma and Lindström 1997), or related to other life history stages like molt and its variability in timing and feather condition (Barta et al 2008). Taken together, these factors create a huge range of behavioral possibilities, and selection will favor shorebirds that find optimal trade-off strategies, namely the strategy the action (or combination of actions) chosen at a specific time (McNamara and Houston 2008) to maximize their survival and reproduction throughout the entire annual life cycle.

1.1.2. Non-breeding sites are important

Shorebird demography, and annual survivorship in particular, will be strongly influenced by events at non-breeding areas, where they typically spend up to 8-10 months of each year. Many of the most productive non-breeding sites are situated at southernmost latitudes, below the Tropic of Cancer and Tropic of Capricorn, coincident with the austral summer and a pulse of productivity (Hockey et al 1992, Butler et al 2001). Non-breeding shorebird social systems among species range from extensive flocking and roosting to individual territoriality (resource defense) and can be highly variable within and between species (Hale 1980, Myers 1984, Colwell 2000, Rogers et al 2006). Dispersion patterns and social organization of foraging shorebirds during the non-breeding season are strongly influenced by the selective forces associated with finding food and avoiding predation danger (Colwell 2010, Johnston-González 2019).

How we can measure the benefits of a good non-breeding area for individual species? We can measure some benefits through annual adult survival estimates and subsequent juvenile recruitment (Gonzalez 2007). Early studies of population dynamics focused only on temporal variation in demographic parameters (Errington 1945, Lack

1964). Recent studies tried to (a) incorporate processes operating across the full annual cycle like density dependence, migratory connectivity and seasonal interactions (Hostetler et al 2015), (b) understand how spatial and temporal variation in demography influence local and regional population growth (Rushing et al 2017), (c) quantify survival for migratory periods and how this influences population dynamics (Rushing 2019). This thesis seeks to fill a gap in non-breeding ecology of western hemisphere shorebirds by trying to (1) determine factors that drive shorebird life history strategies during the non-breeding season (2) outline the benefits of an oversummering strategy and (3) determine what influences annual survivorship and monthly residency survivorship at what is for several species one of the most southern non-breeding areas, the Paracas National Reserve in Perú.

1.1.3. The Oversummering Strategy

Since the early nineteenth century, shorebirds of many migratory species were known to occur in non-breeding areas during their breeding seasons of May to July (Kennedy 1953, Loftin 1962). ‘Oversummering’ is a term that has been recently used to describe when a typically migratory bird defers migration and stays at the non-breeding grounds during the arctic breeding season (or boreal summer) (McNeil et al 1994). Oversummering as a life history strategy, particularly for juveniles, has been associated with migration distance. Juvenile birds, and those species travelling longer distances, have a greater propensity to oversummer (Summers et al 1995, Tavera et al 2016).

Proximate mechanistic explanations for the phenomenon include: sexual immaturity (Eisenmann 1951, Soto-Montoya et al 2009); helminthic infestation (McNeill et al 1994); sterility, injuries or illness (Wetmore 1927); less efficient foraging (Puttick 1979); under-developed alternate (breeding) plumage (Johnson and Johnson 1983); and flight cost on primary wear (O’Hara 2002). Ultimate explanations focus on behavioral adaptations to distance-dependent costs (Lank et al 2003, Ydenberg et al 2004, 2007), low chances of successful first breeding seasons (Summers et al 1995), and the offsetting life-history benefit of a higher probability of survival in non-breeding areas (Fernández et al 2004). If such a widespread behavior pattern is adaptive, we expect that the decision to become an oversummering (resident) bird and to remain on the non-breeding grounds therefore foregoing a breeding opportunity, involves a substantial survivorship trade-off that compensates enough to offset the fitness loss of a year’s potential reproductive success. This will demand a substantially higher survival rate during the migration and breeding seasons than that of migrants.

1.1.4. Molt occurs at oversummering sites, mostly

Most non-breeding shorebirds also need to molt flight feathers. This major component of the annual life cycle is one of the most highly energetically demanding tasks which can affect body condition, survival and future reproductive success (Barshep et al 2013). The renewal of flight feathers needs to be done periodically because of the deterioration that physical wear, sunlight and feather parasites can cause (Newton 2009). Flight feathers molt and its completeness, timing and location of occurrence, depend on a variety of life history features, such as residence duration and food availability (Holmgren and Hedenström 1995, Barta et al 2008, Dietz et al 2013). Flight capacity is diminished by the loss of an old flight feather before the new one can appear; and the loss of an outer primary affects flight speed and agility (Jenni and Winkler 1994, Swaddle and Witter 1997, Hedenström and Sunada 1999). Therefore, the repairing and maintenance of high-quality plumage takes energy and time and should be under intense selection forces. For example, Jukema et al (2013) found the replacement of secondaries to be an adaptation for very long demanding (non-stop) flights of the Pacific and American Golden Plovers. Arctic breeding shorebirds in general, are faced with very tight time schedules, especially the species migrating >16,000km between breeding and non-breeding areas (e.g. Holmgren and Hedenström 1995, Barta et al. 2008, Buehler and Piersma 2008, Conklin and Battley 2012). Most species molt (partly or completely) when they reach their non-breeding grounds (e.g. Buehler and Piersma 2008, Conklin and Battley 2012), but some molt during migration, as the *rufa* Red knot subspecies do while migrating southbound through Argentina (Gonzalez et al 2006).

Age of first breeding is often integrated with migration and molting schedules, as in juvenile American Golden Plovers that perform an extra wing molt at an age of about 0.5-year-old as a possible adaptation to make their first return flight to the breeding grounds (Jukema et al 2013). Of particular interest in the current study, some Semipalmated Sandpiper juveniles perform a Partial Post-Juvenal Wing Molt (PPW), in which individuals replace only 1-6 outer primaries on each wing just prior northbound migration (Gratto and Morrison 1981, Tavera et al 2016). Shorebirds that oversummer also need to schedule the best time for them to molt, like Western Sandpiper staying at

Panamá who advanced the timing of molt, doing so more than a month before migrants return from the Arctic (O'Hara 2002).

1.1.5. Migration Distance, Molt, Oversummering and Survival

Figure 1 presents a conceptual model of the hypothesized adaptive relationships between the survivorship components of fitness with respect to migration distance, and life history and molt strategies, particularly for juvenile shorebirds. Each line depicts the predicted annual survivorship rate of birds using a particular life history and molt tactic. The expected highest fitness tactics at different migration distances are written at the bottom. The first assumption for the figure is that migrating longer distances entails higher intrinsic survivorship cost, which may be offset by other factors. The second assumption is that there is some survivorship cost to molting feathers.

The line drawn for oversummering has the highest survivorship rate at all distances but will accrue no additional fitness because of forgone reproduction. Also, we are assuming that oversummering is independent of migration distance. In contrast, the line drawn for migrating without molting has a negative slope, assuming that the greater wing wear associated with migrating greater distances will entail a survivorship cost that outweighs the more favorable environmental conditions at more distant sites. On the left side of the diagram, the total fitness of migrants will be higher than that of oversummering birds if a large enough reproductive contribution is added. The line drawn for PPW has a lower survivorship at short distances because of the cost of molting, but the shallower slope is the resulting mitigation of the wing-wear-related survivorship cost achieved by maintaining flight performance with new feathers. PPW thus becomes the better tactic at intermediate distances, where the lines cross (vertical solid line), assuming similar reproductive payoffs are added to both molt strategies. As migration distances increase further, however, the additional fitness contribution from migration and breeding is insufficient to offset the cost to survivorship. At this point (vertical dashed and solid line), the highest fitness will be achieved by oversummering instead of migrating north.

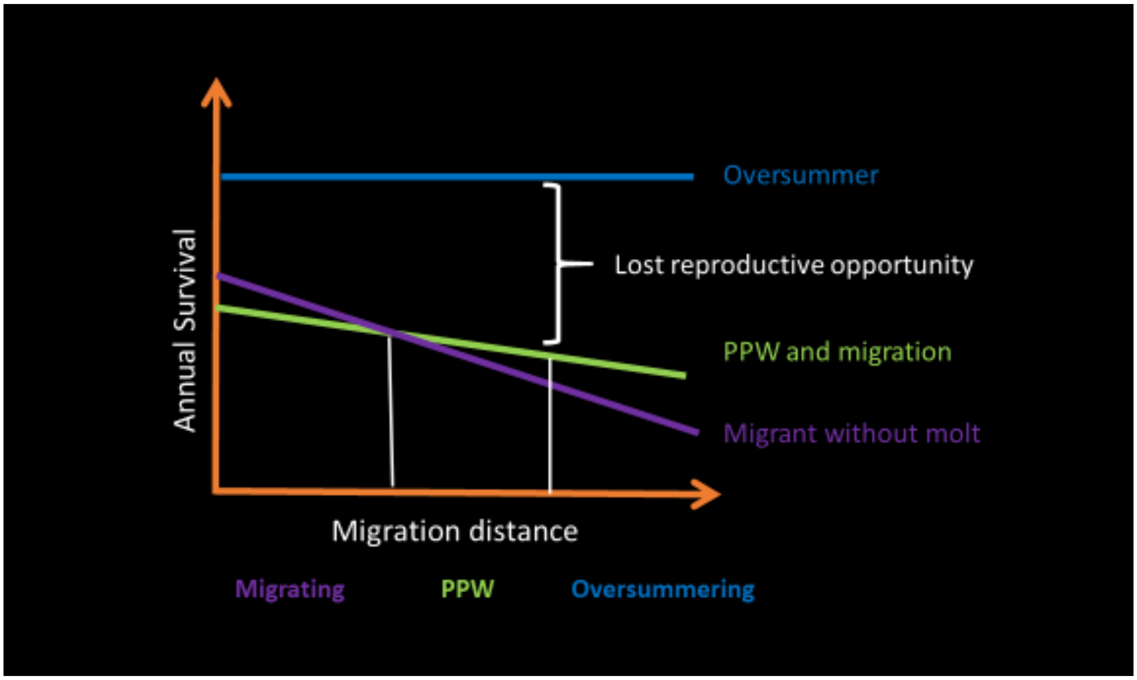

Figure 1.1. **Conceptual model of hypothesized relationships between the fitness components of migration and molt strategies, in relation to migration distance. Lines depicts the predicted annual (October – October) survivorship of tactics that oversummer, and migrate with or without partial post-juvenile wing molt (PPW).**

(i) The survivorship of oversummering (blue line) is independent of migration distance.
(ii) Survivorship with migration (green and purple lines) is lower than that of oversummering, due to the costs of long-distance migration. These costs increase with migration distance, and so the lines have negative slope.
(iii) Survivorship falls less quickly with distance if some primaries are replaced (PPW) and hence the green line has a shallower slope than the purple line.
(iv) However, even partial molt has a cost, so the intercept of the green (PPW) line is below that of the purple line. This means that PPW is worthwhile only beyond a threshold migration distance (solid white vertical line).
(v) Beyond a greater distance (second white vertical line) the migratory cost, even with PPW, exceeds the fitness cost of a missed breeding season (‘lost reproductive opportunity’), making oversummering the better strategy. A full wing and body molt (which juveniles do not undertake) is required to make migration worthwhile beyond this threshold.
(vi) With these assumptions PPW is never associated with oversummering.

1.2. Study species

My thesis focuses primarily on non-breeding Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*Calidris pusilla)*, among the smallest scolopacid sandpipers in the Americas. The species overlap in morphological traits (Table 1, Paulson 1993, Haig et al 1997), are very alike in basic plumage (Phillips 1975, Sibley 2000), and a proportion of the populations of each of these species spends the non-breeding season in South America, where they often flock together. The species have similar breeding biology, forming territorial biparental pairs. Adults of both species abandon their chicks shortly after fledging, with females first to desert and depart on migration (Holmes 1972, Gratto-Trevor 1991, Ruthrauff et al 2009, Jamieson et al 2014). Juveniles depart south just after growing to full size, about a month after the adults (Stein and Williams 2002). The species differ in the timing of both northward and southward migration, with Western Sandpipers migrating about one month before central and eastern populations of Semipalmated Sandpipers (Lank et al 2003, Ydenberg et al 2005, Niehaus and Ydenberg 2006, Hicklin and Gratto-Trevor 2010, Franks et al 2014). Both species' behavior on migration and non-breeding sites, and possibly even departure timing from the breeding grounds is influenced by predation danger from falcons, primarily Peregrine and Merlins (*Falco peregrinus* and *F. columbarius)* (Lank et al 2003, Jamieson et al 2014, Hope et al 2014, Johnston-González 2019).

Western Sandpipers migrate from their breeding range in western and northern Alaska and eastern Siberia to sites along the Pacific coast from Washington State to Peru, in much smaller numbers, on the Atlantic coast from the southeast coast of the United States to Surinam (Franks et al 2014). On migration, there is very little temporal overlap at stopover sites between adults and juveniles, with adults moving through on average one month before juveniles (Butler et al 1987, Ydenberg et al 2005). They show differential migration by sex, with a higher proportion of males at northern sites (Nebel et al 2002). Previous studies report over-summering (termed a 'slow' life history) strategy for juveniles spending their first non-breeding season in Panama, in contrast to a 'fast' life history without oversummering for those in Mexico, where most are reported to migrate north in their first year (Fernández et al 2004, O'Hara et al 2005).

Semipalmated Sandpipers breed on the arctic Alaskan coast, where they partially overlap the breeding range of Western Sandpipers. Breeding sites range eastward across the Canadian tundra to northern Quebec. They spend the non-breeding season on the Atlantic coast from Florida to the central Brazilian coast, and on the Pacific coast from southern Mexico to Peru (Harrington and Morrison 1979, Hicklin and Gratto-Trevor 2010). Semipalmated Sandpipers exhibit a cline in bill length across their breeding range, with bill of eastern birds being ~8–12% longer than those of western birds (Manning et al 1956, Harrington and Morrison 1979, Gratto-Trevor et al 2012), despite minimal population genetic differentiation (Miller et al 2013). Gratto-Trevor et al (2012) provided the widely-used guideline, which I also follow, for assigning birds captured outside breeding areas to ‘western’, ‘central’ or ‘eastern’ arctic populations. Most of the eastern population (84%) of Semipalmated Sandpipers spends the non-breeding season in northeastern South America (Morrison et al 2012), whereas the western and central populations appear to favor western South America as a non-breeding sites. Recent tracking studies have shown that regardless where they come from in the breeding range, they all stage on southward migration and make long flights directly to South America (Brown et al 2017).

I explore how interrelated components of life history strategies differ between far southerly-non-breeding populations of Western and Semipalmated Sandpipers, between eastern and western populations of Semipalmated Sandpipers, and how these compare with more northerly non-breeding populations of Western Sandpipers. I focus on juveniles because the age of first breeding is variable and has large effect on the demography of small shorebirds (Weiser et al 2020). Specifically, I compare a set of life history traits between age classes, populations and taxa, including: variation in juvenile molt mode and preparation for northward migration, the probability of oversummering by juveniles, annual survival differences between migrants and non-migrants and annual and monthly residency survivorship rates of juvenile and adult sandpipers. I relate differences among groups to variation in migration distance, in the context of the conceptual framework presented in Fig. 1.1.

Table 1.1. **Morphological traits, migration distances to Peru, oversummering, molt strategies and migration route of Western Sandpipers (Peru and Mexico) and Semipalmated Sandpipers (different breeding populations: western, central and eastern).**

	Species / Population				
Trait	SESA west	SESA central	SESA east	WESA (Peru)	WESA (Mexico)
Wing length	95.64 ± 0.37	97.80 ± 1.13	97.31 ± 0.41	101.7 ± 2.63	99.0 ± 0.7
Culmen length (exposed)	17.94 ± 0.18	18.56 ± 0.21	20.04 ± 0.21	26.33 ± 1.69	26.09 ± 0.28
Sexual dimorphism (by culmen)	Female: 18.7 Male: 17.1	Female: 20.2 Male: 18.3	Female: 21.5 Male: 19.8	Female: 27.01 Male: 23.26	Female: 26.09 Male: 22.31
Migration distance	~ 11,000km	~ 9,500k	~ 8,000k	~ 11,000km	~ 5,700km
% juvenile oversummering	69%	Unknown	Unknown	100%	0%
% PPW	69%	Unknown	Unknown	0%	0%
Migration route	Pacific Flyway (through the interior of North America)	Mississippi Central Flyway	Atlantic Flyway	Pacific Flyway	Pacific Flyway

1.3. Shorebird Studies in Perú, Study Site and Field Work

Throughout the 1970s and 1980s, shorebirds in Perú were a largely neglected subject and so little-studied that data on their distribution and abundance were only obtained incidentally as part of other bird studies (Hughes 1970, Hughes 1972, Hughes 1976, Koepcke 1970, Schulenberg and Parker 1981, Parker et al 1982). The first shorebird study that helped to promote shorebird research in the country was done by Duffy et al (1981), whose focus on non-breeding season competition encouraged a discussion about Nearctic shorebird behavioral ecology during the non-breeding season and promoted ornithologists´ curiosity to be redirected to the southern hemisphere. Shortly after that, many different entities, Peruvian non-governmental organizations, the Philadelphia Academy of Natural Sciences, the Panamerican Shorebird Program, the former National Wildlife Authority (INFOR), the Peruvian Oceanic Institute (IMARPE) among others helped to organize and undertook the first studies of shorebird migration in Perú. Shorebird censuses in 1982 and the first long-term study marking of Sanderlings, led by J.P. Myers, began shortly thereafter that in three different sites: Mejia Lagoons, Villa Wetlands and Paracas National Reserve (Pulido 1983). These efforts became the first shorebird behavioral ecology studies in the country (Castro 1985, Castro and Myers 1987, Castro et al 1988).

By the end of 1990s and into the 2000s, there was a marked reduction in the interest of shorebirds studies in Peru. It was not until 2010 that the Centre for Ornithology and Biodiversity (CORBIDI) with support from the Cornell Lab of Ornithology led the first Peruvian national shorebird coastal survey, building local capacity with more than 300 volunteers. Shortly after, by the end of 2011, shorebird studies were resumed at Paracas National Reserve led by CORBIDI as a long-term project with the support of the U.S. Neotropical Migratory Bird Conservation Act program. My thesis is based on data from this long-term project and it is a model for future shorebird research studies in the country.

My study site is within the Paracas National Reserve, a Natural Protected Area (ANP) of 335,000 hectares, 65% of which are marine ecosystems, located in the department on Ica, Peru (Fig. 1.2). The Paracas National Reserve was one of the pioneer sites that served as a steppingstone for shorebird studies and banding campaigns in the southern hemisphere from 1987 to 1991 (Pulido et al 1996). The importance of the Reserve for shorebird conservation was promptly recognized hemispherically and the site was recognized as part of the Western Hemisphere Shorebird Reserve Network in 1991, as a RAMSAR Wetland in 1992 and as an Important Bird Area (IBA) in 2003.

Fieldwork was conducted on an intertidal mudflat <2 km long called La Aguada Beach. A total of 50 field ‘campaigns’ were conducted monthly each yearduring the non-breeding season (October – March), each a nine-day field period during the new moon phase.Sandpipers were captured in mistnets set on La Aguada Beach at night. Each captured sandpiper was marked with an aluminum leg band and a conspicuous leg flag (made from darvic material and with a 3-coded letter-number-letter engraved). Data were collected by capturing and conspicuously marking individuals and resighting those previously marked. Beginning in October 2014, five-day monthly campaigns to resight banded birds were continued during the oversummering (breeding) season (April – September). The numbers of each species captured and resighted are detailed in Figure 1.3 and Tables 1.2 and 1.3.

Table 1.2. **Captures, recaptures and resighting effort of Semipalmated Sandpiper juveniles and adults from 2012 to 2019 at Paracas National Reserve.**

	# Capture		# Recapture		Effort mist-net hour	#Resights	Effort resights/hour
Year	**Juvenile**	**Adult**	**Juvenile**	**Adult**			
2011-12	10	49	0	0	80	0	0
2012-13	195	244	5	11	336	0	0
2013-14	397	892	17	83	472	575	30
2014-15	91	444	19	101	256	1134	54
2015-16	89	100	0	33	136	2351	210
2016-17	209	111	9	31	192	2114	348
2017-18	71	55	0	11	184	1427	306
2018-19	24	14	0	0	96	1957	306
TOTAL	1086	1909	50	270	2052	9558	1254

Table 1.3. **Captures, recaptures and resighting effort of Western Sandpiper juveniles and adults from 2012 to 2019 at Paracas National Reserve.**

	# Capture / age class		# Recapture / age class		Effort Mist-net hour	#Resights	Effort resights/hour
Year	Juvenile	Adult	Juvenile	Adult			
2011-12	16	48	0	0	56	0	0
2012-13	113	65	8	2	224	0	0
2013-14	169	158	13	8	288	121	33
2014-15	26	179	1	21	224	380	54
2015-16	73	86	3	9	168	1200	129
2016-17	73	119	0	10	160	1239	192
2017-18	41	86	1	9	144	1225	171
2018-19	4	18	0	4	72	1210	171
TOTAL	515	759	26	63	1336	5375	750

Figure 1.2. Location of Perú in the Americas, zoom in to Peru and the location of the Department of Ica (in black) and last zoom in at La Aguada Beach (in yellow) at Paracas National Reserve.

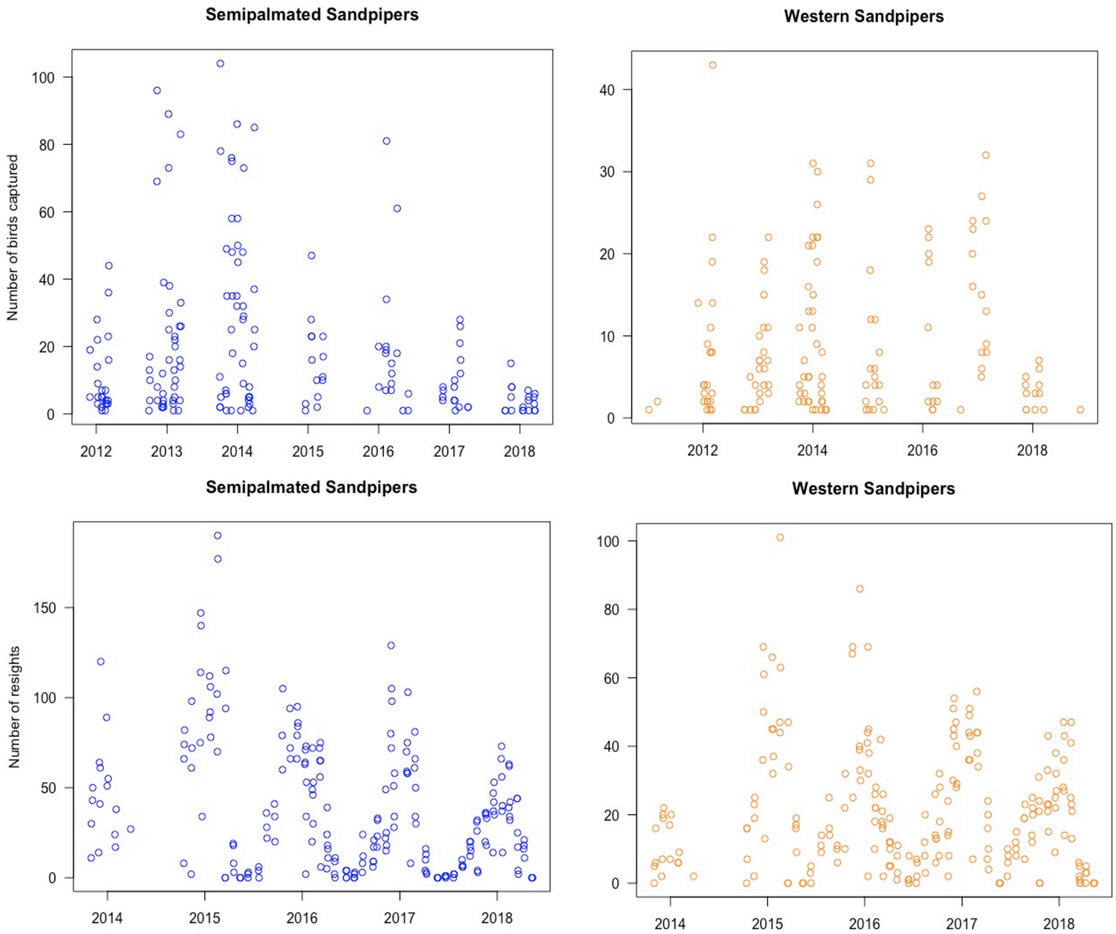

Figure 1.3. **Numbers of Semipalmated Sandpipers (left) and Western Sandpipers (right) captured (upper panels) from 2012 to 2018 and resighted (lower panels) from 2014 to 2018 at Paracas National Reserve. Each blue or yellow dot is one field occasion.**

1.4. Thesis Outline

The overall goal of this thesis is to dissect aspects of the life history strategies of non-breeding shorebirds and relate them to survival estimates, molt strategies and migratory decisions. I use a wide variety of data sets collected for from 3 to 6 years, some non-stop throughout the year with emphasis during the non-breeding season, at the same non-breeding site to analyze different aspects of shorebird behavioral ecology in the southern hemisphere.

In Chapter 2, I examine the relationship between migration distance and life history strategies within and between both Semipalmated and Western Sandpipers. There are no data from other studies conducted so far south with the same species to which I can relate my work. At Paracas, Western and Semipalmated Sandpipers flock together and behave in a very similar way, they feed at the same time and locations, share vigilance time against predators, and they look for roosting sites and roost together. But despite these similarities, the species, and population within species, have different migration distances, and do not arrive and leave Paracas at the same time. Individual behavior by juveniles (first year birds) differs within and between species. I use three years (2012-2015) of data collected only during the non-breeding season and examine the differences in timing of migratory preparation by adults and also the oversummering probability by juveniles, using body molt, weight and the post-juvenal wing molt as pre-migratory indices. Finally, I estimate the probability of migration by different breeding populations of juvenile Semipalmated Sandpipers with different migration distances, assessed using culmen length as a proxy to distinguish breeding location and therefore approximate migration distance to Paracas. I plot the probability of migration versus oversummering in these different populations by seeing the relationship between the presence or absence of PPW and culmen length, controlling other factors.

The main objective of Chapter 3 is to quantify the potential survivorship cost of migration compared with oversummering. I compare survivorship rates of juvenile and adult Semipalmated Sandpipers following each strategy. To estimate rates, I defined the two seasons the non-breeding (October – March) and the oversummering (April – September) and assigned encounter data with individuals to one of 6 different states, considering age class, season and migration status during April-September (transition probability). If oversummering compensates for the fitness cost of migration and a potential loss of breeding opportunity, I expect that oversummering birds would have a higher survivorship than migrants. To test this, I use a Multi-State Mark-Recapture model with 5 years of data collected through each year from 2015 to 2019 and model 5 sets of survival variations to have a total of 15 models all together. I plot the differences between transition survival estimates for oversummering and resident birds by age class, during a six-month period of time.

In my fourth chapter, I present the first set of annual survival and non-breeding monthly residency estimates for both Semipalmated and Western Sandpiper at a non-breeding site so far south in the hemisphere. I use 7 years of non-breeding mark-resighting data and a Multi-State Open Robust Design model with 5 different parameters, to calculate apparent survival estimates for both species. I include year, age, sex, bill length, wing length, and an ENSO (El Niño) index as covariates to test for effects on survivorship within and between species. I tested all possible combinations among parameters and covariates to generate a set of 'best models' for each species. I use these models to produce specific annual and seasonal survival estimates for both species and calculate monthly residency probabilities as potential indices of non-breeding seasonal survivorship. I test a set of predictions about the relative survivorship estimates of species and age based on life history theory and migration distance, to try to understand strength of selective factors involved. I examine the relationships between non-breeding seasonal and annual survivorship estimates for different age and species categories to make inferences about their annual cycle strategies, and compare these rates to those found at other non-breeding locations. The answers help clarify interpretations of population trends and to potentially help identify threats before detectable abundance declines occur.

Last, Chapter 5 provides a general discussion of my results. I summarize the contributions I have made to our understanding of shorebird non-breeding biology and population trends in the southern hemisphere, in the context of the conservation and management of shorebirds in Perú and in the western hemisphere.

Chapter 2.

Effects of migration distance on life history strategies of Western and Semipalmated Sandpipers in Perú

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2.1. Abstract

Migration distances of shorebird species correlate with life history strategies. To assess age-specific migratory preparation and adult wing-molt strategies, we studied Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*C. pusilla*) with different migration routes at the Paracas National Reserve in Perú, one of the most austral non-breeding areas for these sandpipers, from 2012 to 2015. Western Sandpipers breed near the Bering Sea, ~11,000 km from Paracas as well as Semipalmated Sandpiper short-billed birds from western arctic breeding sites. Paracas hosts a mixture of short-billed and long-billed Semipalmated Sandpipers from eastern sites, ~8000 km distant. Adults of both species arrive in October with primary feathers already partially renewed so wing molt starts at sites further north. Semipalmated Sandpipers with longer bills completed wing molt later than shorter-billed birds. Adults of both species prepared for migration in February and March. No juvenile Western Sandpipers prepared for migration, confirming the “slow” over-summering life history strategy of more southerly non-breeding populations. Juvenile Semipalmated Sandpipers showed bimodality in strategies, most showed no migratory preparation, but, during three non-breeding periods, from 27 to 31% fattened, molted, and partially replaced outer primaries during the pre-migratory period. Long-billed juveniles were heavier and tended to have more alternate plumage. Also, juveniles partially molting primaries had longer bills and more alternate plumage. Juvenile long-billed eastern-breeding populations of Semipalmated Sandpipers thus have a higher propensity for a fast life history strategy, and western birds a slow one, at this non-breeding site in Peru.

Short-billed western-breeding Semipalmated Sandpiper populations thus resemble Western Sandpipers, suggesting a common, possibly distance-related, effect on life history strategy.

Key words: culmen length, molt strategies, over-summering, Paracas, shorebirds

2.2. Introduction

Long-distance migration has been recognized as an evolutionary adaptation to maximize the survival and reproductive success of individuals by exploiting seasonal peaks of resource abundance and avoiding seasonal resource depression (Alerstam et al. 2003). Migration strategies thus balance costs against benefits and studying the diversity of migration patterns will help identify the relative importance of different selective factors. Life history strategies of migratory shorebirds vary among short-, medium-, and long-distance migrants (Buehler and Piersma 1998, Nebel et al. 2000, Fernandez et al. 2004, Morrison et al. 2005, O'Hara et al. 2005, Remisiewicz et al. 2014) and, for some species, among age classes (O'Hara 2002, Fernández and Lank 2007, Remisiewicz et al. 2010). As a dramatic example, not all individuals in populations migrate from non-breeding areas and attempt to breed every year; such "over-summering" birds spend a "gap year" on non-breeding grounds (Loftin 1962, Johnson and Johnson 1983, McNeill et al. 1994, Hockey et al. 1998, Pyle 2008). Juveniles that over-summer are pursuing a 'slow' life history strategy, postponing their first potential breeding opportunity. Proximate explanations to account for over-summering by juvenile shorebirds include sexual immaturity (Eisenmann 1951, Loftin 1962, Johnson and Johnson 1983), helminthic infestation (McNeill et al. 1994), sterility, injuries, or illness (Wetmore 1927), and less efficient foraging (Puttick 1979, Hockey et al. 1998). Ultimate explanations include low probabilities of having a successful breeding season (Summers et al. 1995), higher likelihood of surviving on non-breeding grounds (Fernández et al. 2004), condition-dependence on primary feather wear (O'Hara 2002), and other distance-dependent costs (Myers et al. 1985, Lank et al. 2003, Ydenberg et al. 2004, 2007).

Feather molt is another factor integrated with migratory strategy. Birds generally avoid overlapping molting with other energy-expensive activities such breeding or migration, adopting a variety of schedules to separate these activities (Ginn and Melville

1983, Zwarts 1990). Molt strategy varies with breeding success, migration distance, availability of food, non-breeding latitude, and type of habitat (Prater 1981, Barta et al. 2006, Howell 2010, Remisiewicz 2011, Rogers et al. 2014, Dietz et al. 2015). For example, adults of many species, such as Little Stints (*Calidris minuta*), Red Knots (*Calidris canutus*), and Wood Sandpipers (*Tringa glareola*), molt almost exclusively in non-breeding areas (Pearson 1984, Remisiewicz et al. 2009, Summers et al. 2010). Other species, like Wilson's Phalaropes (*Phalaropus tricolor*), start to molt at stopover sites, but then suspend it and resume in non-breeding areas (Jehl 1987). Molt suspension is common among shorebirds and is known to be a strategy for coping with temporary food scarcity (Prater 1981) and facilitating short-distance movements (Remisiewicz 2011). Adult Common Greenshanks (*Tringa nebularia*) arrive to Kenya with a suspended molt and resume it there from September to January (Pearson 1974). Molting at staging sites is also not uncommon. For example, Red Knots take advantage of seasonal peaks in food availability at specific stopover sites during fall migration to molt (Harrington et al. 2010). Finally, some taxa pursue alternative strategies, such as some subspecies of Dunlins (*Calidris alpina*) that start molting on or near breeding areas (Kania 1990, Holmgren et al. 2001, Warnock et al. 2013).

Molt strategies also vary with age-classes. Some juveniles molt all of their primaries before their first northward migration (e.g., Little Stints, Tree 1974), others retain their first set of primaries and complete the first migration with the same feathers (Prater et al. 1977), and some retain their first set of primaries for up to 17 months (e.g., Western Sandpipers, O'Hara et al. 2005). A peculiar addition to this set of molt-chronology variability in juvenile shorebirds is the molt strategy known as the Partial Post-Juvenile Wing Molt (PPW), where juveniles drop and replace only 1-6 outer primaries on each wing (Gratto and Morrison 1981).

Western Sandpipers (*Calidris mauri*) and Semipalmated Sandpipers (*C. pusilla*) are among the smallest scolopacid sandpipers in the Americas. They overlap in morphological traits (Paulson 1993, Haig et al. 1997), look alike in basic plumage (Phillips 1975, Sibley 2000), and have similar breeding biology (Holmes 1972, Gratto-Trevor 1991, Ruthrauff et al. 2009). A proportion of the populations of each of these species spends the non-breeding season in South America, where they often flock together. However, they differ in the timing of southward migration, with Western Sandpipers migrating about one month before central and eastern populations of

Semipalmated Sandpipers (Lank et al. 2003, Hicklin and Gratto-Trevor 2010, Franks et al. 2014).

Western Sandpipers migrate from their breeding range in western and northern Alaska and eastern Siberia to Perú along the Pacific coast, and to the east coast of the United States to Surinam on the Atlantic coast (Franks et al. 2014). They show a differential migration by sex, with a higher proportion of males at northern than at southern sites (Nebel et al. 2002). Previous studies report a slow, over-summering life-history strategy for the juveniles spending their first non-breeding season in Panamá, in contrast to a fast life history for those in México, where most migrate north in their first year (Fernández et al. 2004, O'Hara et al. 2005).

Semipalmated Sandpipers breed on the Subarctic Alaskan coast, where they partially overlap with Western Sandpipers, and east across the Canadian tundra to northern Quebec. They spend the non-breeding season from Florida to the central Brazilian coast on the Atlantic coast, and from southern México to Perú on the Pacific coast (Harrington and Morrison 1979, Hicklin and Gratto-Trevor 2010). The species shows a cline in bill length across its breeding range, with eastern birds having ~8-12% longer bills than western birds (Manning et al. 1956, Harrington and Morrison 1979, Gratto-Trevor et al. 2012), despite minimal population genetic differentiation (Miller et al. 2013). Most of the eastern population (84%) of Semipalmated Sandpipers spends the non-breeding season in northeastern South America (Morrison et al. 2012), whereas the western and central populations appear to favor western South America as a non-breeding site. Based on mean bill lengths, Gratto-Trevor et al. (2012) suggested that the central breeding population predominates in Perú. However, Tavera (2013) found a confluence of eastern and western populations on the Peruvian coasts, as assessed by bill lengths. The migration distance from western breeding sites of Semipalmated Sandpipers to Perú is ~11,000 km, whereas eastern populations migrate ~8000 km. Based on one year's data, Tavera (2013) showed differences in life history strategies between coexisting populations in Perú, including arrival timing and body molt-chronology prior to spring departure, which may be related to the differences in migration distance.

We examined non-breeding populations of Western and Semipalmated Sandpipers in Perú to test predictions about the effects of migratory distance and age class on life history strategies. After inferring the geographical breeding origins of Semipalmated Sandpipers at Paracas, our study had three objectives. (1) We quantified the propensity for over-summering behavior by first-year birds. Nearly all young Western Sandpipers spending their first non-breeding season in Panamá oversummer, but few of those at México do so. We expected high rates in Perú. For Semipalmated Sandpipers, over-summering by juveniles has been reported (Spaans 1976, Pyle 2008), but has not been quantified at any location. We used changes in mass, plumage, and wing molt during the adult pre-migratory season as potential indicators of migration propensity. (2) We compared wing-molt chronologies of adult and juveniles of each species. For Western Sandpipers, southward migrating adults have been reported to drop the first five primaries almost simultaneously upon arrival in Panamá (Watts 1998). Semipalmated Sandpipers are reported to begin primary molt after arrival in Brazil (Spaans 1981), but patterns of molt have not been documented further south for either species. For juveniles, we expected Western Sandpipers to follow the slow life history strategy previously shown in Panamá and, therefore, to not undergo wing molt during their first non-breeding season. For Semipalmated Sandpipers, a study at James Bay revealed variation in the extent of PPW, ranging from half to all migrants originally banded as juveniles and recaptured as first-year birds (Gratto and Morrison 1981). However, the probability of PPW varying among breeding or non-breeding populations and whether those birds undergoing PPW have a different probability of pursuing a fast versus slow life history strategies are unknown. (3) For juvenile Semipalmated Sandpipers, we tested for differences in migratory strategies between breeding populations coexisting in Perú. Specifically, we expected that migratory strategies differed as a function of migration distance, using bill length as an indicator of the location of breeding populations. If longer-distance migrants have a greater propensity to over-summer, a smaller proportion of juvenile Semipalmated Sandpipers with shorter bill lengths should prepare for migration.

2.3. Methods

2.3.1. Study site

The Paracas National Reserve is a Natural Protected Area in Perú located in the Department of Ica. We conducted field work on La Aguada beach (13º51'35.47"S 76º16'16.16"W), an intertidal mudflat <2 km long and surrounded by coastal desert (Fig. 2.1). The near-shore section of the mudflat has no vegetation and most of the lower intertidal zone is covered with soft mud filled with polychaetes, fly larvae, microscopic sea shrimp, and beetles (Pellissier 2013), and covered by biofilm and decaying algae.

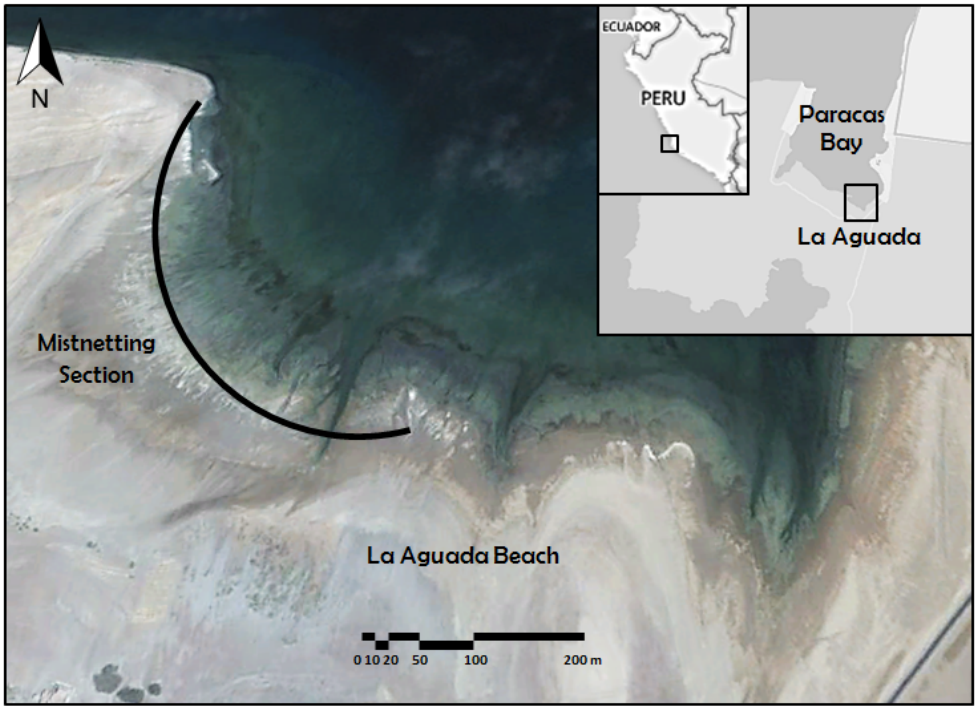


Figure 2.1. Location of the fieldwork on "La Aguada" beach in Paracas National Reserve, Perú.

2.3.2. Data collection

Migrant Western and Semipalmated Sandpipers arrive in Paracas in early October and were captured during three consecutive non-breeding seasons (October 2012–March 2013, October 2013–April 2014, and December 2014–April 2015). Nine-day campaigns were conducted per month during the new moon phase. Shorebirds were captured primarily at night with mist-nets. Time of capture depended on the tide cycle; we always began three hours after the evening high tide and ended three hours before the next high tide, ranging between 21:00 and 06:00. Fewer than 10% of the birds were captured with bungie-powered whoosh nets on rising tides between 06:00 and 09:00. Captured birds were banded on the right tarsus with an incoloy metal band (CORBIDI Bird-Banding Program, the Peruvian bird-banding scheme). A 3-character-coded yellow flag was placed on the left tibia, following the Panamerican Shorebird Program protocol (Myers et al. 1983, Myers 1984) to identify individuals and enable gathering local resighting data and documenting long-distance movements. Birds were assigned age classes as juveniles or adults based on plumage. Juveniles (individuals in their first non-breeding season, from 0 to 12 months old) were aged by the retained juvenile-type inner greater coverts, and adults (12+ months old) were aged by wing and flight feather characteristics (Prater et al. 1977, but see Franks et al. 2014). Data on body mass were obtained using a digital scale (± 0.5 g).

2.3.3. Alternate plumage scores

Most small sandpipers undergo a pre-alternate molt from basic (dull non-breeding) into alternate (bright breeding) plumage in spring (Prater et al. 1997, Wilson 1994, Hicklin and Gratto-Trevor 2010, Franks et al. 2014). Alternate plumage of captured birds of both species was identified using feather characteristics for each species, including the degree of black-centered and rufous-edged coloration (Prater et al. 1977). The crown, cheeks, mantle, upper scapulars, and tertials were scored following O’Hara et al. (2005) as: 1 = no rufous anywhere, 2 = trace of rufous on any tract such as the mantle, upper scapulars, tertials, or crown, 3 = traces of rufous on more than one tract, 4 = presence of rufous in three or four tracts, 5 = rufous on lower scapulars and other tracts, and 6 = full alternate plumage.

2.3.4. Wing molt scores

We classified captured birds as having completed wing molt (all new feathers), being in suspended molt (e.g. having old and fully-grown feathers, but no missing or pin feathers), being in active molt, or not having started wing molt (all old feathers). Individual primaries were numbered in the order they normally molt, from the innermost primary (P1) to the outermost (P10) (Pyle 2008). The stage of primary molt was recorded as a molt formula using the British Trust for Ornithology method (Ginn and Melville 1983), a string of 10 digits, whereby individual feathers were assigned a score (0 = old feather, 1 = feather in pin, 2 = brush stage, 3 = two-thirds grown, 4 = four-fifths grown, and 5 = new feather). The sum of the scores for all 10 primaries was the primary molt score (PMS), which ranged from 0 (all old primaries, molt not started) to 50 (all new primaries, molt completed).

2.3.5. Data analyses

To infer the geographical origins of the Semipalmated Sandpipers captured at Paracas, we compared the frequency distribution of culmen lengths, with (1) the range of population mean values for western, central, and eastern populations (Gratto-Trever et al. 2012), and with (2) the mean and standard deviation of simulated regional populations with 50:50 sex ratios, derived from metrics of museum specimens (Table 2 in Harrington and Morrison 1979), with 1 mm added to account for shrinkage. For the Paracas population, we determined measures of centrality and skewness, and tested for deviation from normality with the Kolmogorov-Smirnov *D* statistic.

Patterns of mass change and the alternate plumage status were examined by dividing the non-breeding season into “residency” and “pre-migratory” periods. Because individuals of both species of sandpipers started to increase in mass above non-breeding levels starting in early February, we defined the residency period as extending from the beginning of field work (October) through the end of January, and the pre-migratory period as starting on 1 February. Mass and plumage variation were compared among age categories and analyzed separately for each period and for each year of the study. For the pre-migratory period only, we tested whether the potential indicators of migratory readiness were concordant using logistic regression of plumage scores as a function of mass, and by modeling the presence/absence of PPW as a function of date-specific mass and plumage. We included data from first captures of all birds (*N* = 2965) plus individuals recaptured more than four weeks later (*N* = 236) that were treated as independent observations. Only captures with both mass and plumage scores were used. Species were analyzed separately.

We quantified patterns of mass with general linear models in relation to the fixed effects of time, age and their interaction. Alternate plumage scores were treated as an ordinal response variable, and analyzed with respect to age, mass, date and year using logistic regression models. We initially tested full models including interactions for year and age differences, and reran reduced models eliminating non-significant interaction terms. All tests used a Type III SS, which controls for other model effects, to assess the significance of particular variables ($\alpha = 0.05$ for main effects, and $\alpha = 0.10$ for interactions). We expected our potential indices of migratory readiness to positively covary during the pre-migratory period and tested for a relationship between mass and plumage class with logistic regression models. For juvenile Semipalmated Sandpipers, we tested for correlations among PPW, body mass gain, and plumage score during the pre-migratory period with logistic regression models.

To look for evidence that life history traits of Semipalmated Sandpipers varied with migration distance, we tested whether the timing of post-breeding wing molt of adults during the residency period, and the pre-migratory mass, plumage score, and PPW of juveniles, varied with respect to culmen length, which was used as a proxy for their breeding population of origin. We modeled mass using multiple regression and plumage score with logistic regression, with predictors of culmen length, date, and their potential interaction. We modeled the presence or absence of PPW for birds captured after 8 March, when PPW was first detected, using logistic regression, with mass at capture, body molt score, and culmen length as predictors. To provide a detailed picture of these relationships, we plotted the frequency distributions of culmen lengths for samples with or without PPW and compared these with sex-specific distributions of culmen lengths from eastern and western breeding grounds (Gratto-Trevor et al. 2012). Western Sandpipers can be reliably sexed by bill length differences, but Semipalmated Sandpipers cannot. Preliminary analyses of sex effects for Western Sandpipers showed no differences in molt or plumage variables, thus these were not considered further. Potential effects of sex differences on our interpretation of patterns in Semipalmated Sandpipers are considered in the discussion. All analyses were performed using SAS

(2012; v. 9.4). We used AIC scores to choose the most parsimonious of competing models. We report significance of individual factors in logistic regression with Wald χ^2 and two-tailed tests.

2.4. Results

2.4.1. Non-breeding population of Semipalmated Sandpipers

Semipalmated Sandpipers captured at Paracas had a distribution of culmen lengths that spanned that of their entire breeding range (Fig. 2.2). The distribution was positively-skewed and non-normal (N = 2439, mean = 18.6 mm, median and mode = 18.5 mm, skewness = 0.20, Kolmogorov-Smirnov normality test D = 0.05, P < 0.01), showing a species-wide distribution with an over-representation of western birds.

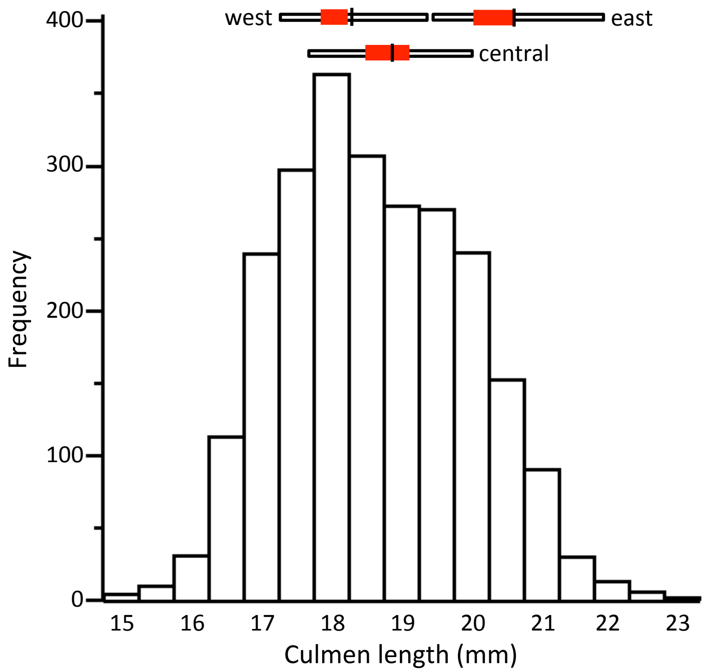


Figure 2.2. Distribution of culmen lengths of Semipalmated Sandpipers captured (N = 2439) at the Paracas Nation Reserve during the non-breeding seasons from 2012 to 2015. The distribution was non-normal (see text). Solid bars indicate the range of means for western, central, and eastern breeding populations (Fig. 1 in Gratto-Trevor et al. 2012). Vertical lines and open boxes indicate the mean and standard deviation of simulated regional populations with 50:50 sex ratios derived from museum specimen metrics (Table 2 in Harrington and Morrison 1979), with 1 mm added to account for shrinkage.

2.4.2. Residency period

Both species had low masses and stable basic plumage scores during the non-breeding residency period, followed by fattening and the development of alternate plumages by most, but not all, components of the populations during the pre-migratory period (Fig. 2.3, Table 2.1). During the residency period, adult Western Sandpipers were heavier than juveniles in all years (Table 2.1, Fig. 2.3), with no significant interactions among years or age classes (all *P* > 0.18). Masses were stable during 2012–2013 and 2014–2015, but increased for both classes during 2013–2014. Adult Western Sandpipers started to develop alternate plumage by the end of January, but no juveniles did so. Adult Semipalmated Sandpipers were heavier than juveniles during 2012–2013, but we found no other age differences in plumage scores or mass (Table 2.1, Fig. 2.3).

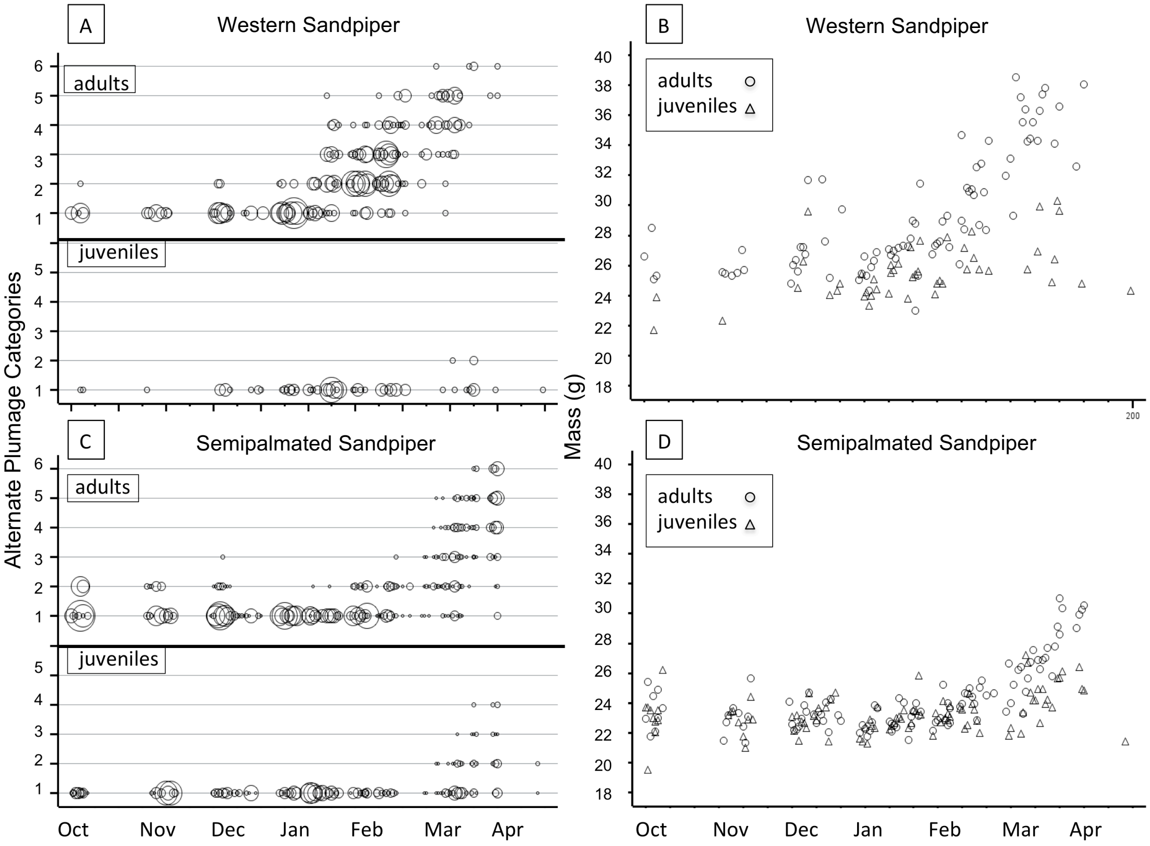


Figure 2.3. **Seasonal alternate plumage scores and patterns of mass for Western and Semipalmated Sandpipers pooled over years during the residency (October–January) and pre-migratory periods (February–April) in Paracas National Reserve, Perú, 2012–2015. (A and B) Western Sandpipers, and (C and D) Semipalmated Sandpipers.**

Table 2.1. **Patterns of mass (g) of Western Sandpipers (WESA) and Semipalmated Sandpipers (SESA) during two periods of the non-migratory season at Paracas, Perú, 2012–2015, modeled as a function of age, day in the season and their interactions, where significant. Least-squared mean values are shown for age classes. 1 df for age and day. P values with bold font are statistically significant.**

			Residency Period					Pre-migratory Period				
Species	Year		***n***	***F***	***P***	**Xadult**	**Xjuv**	***n***	***F***	***P***	**Xadult**	**Xjuv**
WESA	2012-13	Age	54	7.41	**0.01**	26.8	24.9	188	3.60	0.059	31.9	27.1
		Day		0.04	0.84				9.50	0.002		
		Age*Day		-	-				5.42	0.021		
	2013-14	Age	288	25.93	**<0.001**	26.4	24.7	81	7.61	0.007	31.1	27.2
		Day		25.59	**<0.001**				4.06	**0.047**		
		Age*Day		-	-				11.96	**<0.001**		
	2014-15	Age	104	32.46	**<0.001**	28.5	25.7	42	33.11	**<0.001**	33.5	26.9
		Day		0.19	0.66				4.08	**0.050**		
		Age*Day		-	-				-	-		
SESA	2012-13	Age	533	5.52	0.02	23.1	22.7	310	7.50	**0.007**	25.8	23.8
		Day		1.35	0.25				28.95	**<0.001**		
		Age*Day		-	-				11.47	**<0.001**		
	2013-14	Age	1060	0.34	0.56	22.8	22.7	299	17.45	**<0.001**	27.4	24.2
		Day		3.01	0.08				117.27	**<0.001**		
		Age*Day		-	-				32.11	**<0.001**		
	2014-15	Age	138	0.45	0.50	23.0	23.2	81	6.74	**0.011**	27.9	25.1
		Day		0.19	0.66				5.09	**0.026**		
		Age*Day							9.01	**0.003**		

2.4.3. Pre-migratory period

From early February onwards, adult Western Sandpipers gained mass, but juveniles did not (Fig. 2.3, Table 2.1). Although mean masses of juvenile Western Sandpipers were consistently lower than those of adults during the pre-migratory period, we only detected a significant difference in the third year of our study (Table 2.1). Adults acquired alternate plumage, whereas only three juveniles did so (age x date terms, 1 df: 2012–2013: Wald $\chi^2 = 34.4$, $P < 0.0001$; 2014–2015: $\chi^2 = 20.9$, $P < 0.0001$; insufficient data for 2013–2014).

Adult Semipalmated Sandpipers were heavier than juveniles during the pre-migratory period (Table 2.1). Adults started to molt into alternate plumage by early February, and 27% of juveniles did so starting in early March (55/206 with plumage classes > 1, pooled over years). We found no significant differences in plumage scores between age classes during the first two years (age x date, 1 df: 2012–2013: Wald $\chi^2 = 0.4$, $P = 0.50$; 2013–2014: Wald $\chi^2 = 1.7$, $P = 0.19$). In year 3, significantly more adults than juveniles molted into alternate plumage (Wald $\chi^2 = 9.3$, $P = 0.002$).

Mass and plumage scores provided similar signals of migratory propensities (Table 2.2). For both age classes of Semipalmated Sandpipers and for adult Western Sandpipers, mass had a substantial positive effect in logistic models of plumage category that included date in season and year. Juvenile Western Sandpipers that were not expected to prepare for migration exhibited little variation in either plumage or mass (Fig. 2.3).

Table 2.2. **Tests for a relationship between alternate plumage scores and body mass during the pre-migratory period for adult and juvenile Western Sandpipers (WESA) and Semipalmated Sandpipers (SESA). We report values for mass terms (1 df) from logistic models predicting plumage category that included day in season and year terms; models including year had substantially better fits (AIC scores > 10 lower) than models pooled over years. Sample sizes match those in Table 1. P values with bold font are statistically significant.**

	Estimate ± SD	Wald 95% (CL)	Wald X2	Pr>X2
WESA Adult	0.217 ± 0.039	0.139 – 0.294	30.02	**<0.001**
WESA Juvenile	0.068 ± 0.192	-0.307 – 0.444	0.13	0.7219
SESA Adult	0.262 ± 0.036	0.191 – 0.333	52.49	**<0.001**
SESA Juvenile	0.409 ± 0.078	0.256 – 0.561	27.59	**<0.001**

Table 2.3. **Primary molt scores (PMS) and Mean (± SD) of adult Western and Semipalmated Sandpipers captured each month during the non-breeding season at Paracas National Reserve, Perú, 2012–2015.**

	Western Sandpiper		Semipalmated Sandpiper	
Month	N	PMS ± SD	N	PMS ± SD
October	19	33.5 ±7.4	398	28.3±10.1
November	24	45.3±5.7	232	35±9.6
December	107	44.7±5.5	842	40.8±7.9
January	214	47.1±2.4	445	43.6±4.8
February	205	50	242	43.3±9.3
March	71	50	428	46.5±2.5

2.4.4. Primary molt

Adult Western Sandpipers captured in October had an average Primary Molt Score of 33 (replacement of 1–6 inner primaries); 84% were in active primary molt, and the rest had already completed it (Fig. 2.4A). By January, only 4% were still molting primaries, with an average PMS of 47 (molt almost completed except for half of the last outer primary). Suspended molt was found in only two birds, one in mid-November and one in mid-December, both with a PMS of 35 (1–7 new inner primaries were new), and all adults finished primary molt by February (Table 2.3).

Adult Semipalmated Sandpipers were also in active molt by early October, with 88% having an average PMS of 28 or greater, indicating that they had completed more than half of the wing molt (Fig. 2.4B). The remaining 12% had either completed primary molt or had suspended molt (4%), with an average PMS of 30 (1–6 inner primaries were new). The proportion of birds with suspended molt appeared to increase in December. By February, 85% of the individuals had completed primary molt and the rest were almost finished, with an average PMS of 43 (1–9 inner primaries were new). No adults were found with suspended molt by March, when 96% had a full set of new primaries. Adults captured in different molt status categories (active, suspended, or completed; only two were scored as not started) differed in culmen length (F = 15.8, 4,1634 df, $P <$ 0.0001 controlling for day in season and day in season squared). Adults with completed molt had significantly shorter bills than those in active or suspended molt (Tukey post-hoc tests, $P < 0.05$); those with suspended molt had the longest mean bill lengths (Table 2.4).

No juvenile Western Sandpipers molted primaries. By contrast, 31% of juvenile Semipalmated Sandpipers captured during March were in active outer primary molt. Annual average PMS varied from 8 to 14, meaning that these birds were replacing between two to four outer primaries, and even six in a few cases (Table 2.5).

Table 2.4. Relationship between wing-molt status and mean culmen lengths of adult Semipalmated Sandpipers captured during the non-breeding season at Paracas, Perú, 2012–2015.

Molt Status	N	Mean Culmen Length	95% Confident limits
Active	556	18.73	18.63–18.83
Suspended	55	19.04	18.72–19.37
Completed	543	18.55	18.44–18.66

Table 2.5. The percentage of juvenile Semipalmated Sandpipers captured annually during March with Partial Post-Juvenile Wing Molt (PPW), their mean primary molt scores (PMS), and the main group of outer primary feathers molted.

Year	N	PPW (%)	PMS ± SD	Primaries molted
2013	77	22	10.8 ± 6.24	P8–P10
2014	39	38.4	8.8 ± 4.58	P9–P10
2015	27	44.4	13.8 ± 5.74	P7–P10

Table 2.6. ANOVA model predicting mass of juvenile Semipalmated Sandpipers caught during the pre-migratory periods at Paracas, Peru, as a function of culmen length, day in season, and their interaction. Fvalue presented for full model; t value for estimates of parameter values.

Parameters	dF	Estimate	SD	*F* or *t*	*P*
Full model	3, 203	-	-	22.3	<0.0001
Culmen	1	-0.913	0.89	-1.03	0.31
Date	1	-0.160	0.11	-1.50	0.14
Culmen*Date	1	0.010	0.01	1.83	0.07

Table 2.7. Logistic regression modeling the probability of presence of PPW in juvenile Semipalmated Sandpipers captured at Paracas, Peru, during the non-breeding season, 2012–2015. See Methods section for modeling details. P values with bold font are statistically significant.

Parameters	DF	Estimate	SD	Wald 95% (CL)	Wald X^2	Pr>X^2
Date	1	-0.058	0.148	-0.348 – 0.233	0.15	0.697
Year 1	1	-2.178	1.234	-4.597 – 0.241	3.12	0.078
Year 2	1	-0.010	1.528	-3.005 – 2.985	0.00	0.995
Year 3	0	0	0	0	0	0
Breeding plumage	1	0.728	0.332	0.0781 – 1.378	4.82	**0.028**
Mass	1	-0.565	0.137	-0.833 – -0.297	17.03	**<0.0001**
Culmen	1	0.555	0.187	0.189 – 0.921	8.84	**0.003**

2.4.5. Life history differences among juvenile Semipalmated Sandpipers

Did culmen length, acting as a surrogate for breeding population of origin, predict the likelihood of migration, as assessed by mass, plumage development, and/or wing molt strategy? For mass, a full model including culmen length, date, and their interaction was significant (Table 2.6). The interaction occurs because there is no relationship early in the season but culmen length predicted mass positively and strongly only during the last part of the pre-migratory period when birds with longer bills tended to be heavier. For plumage category, logistic regression as a function of culmen length and date showed a strong date effect and a non-significant, but positive, trend with culmen length (estimate for culmen length = 0.205 ± 0.14 [SD], 95% Wald *CI* = -0.07–0.48, Wald χ^2 = 2.2, *P* = 0.14, *N* = 208). For PPW, juvenile Semipalmated Sandpipers with more alternate plumage, lower masses at capture, and longer culmen lengths were more likely to show PPW (Table 2.7). We had expected mass to increase with PPW probability, as two potential indicators of migratory propensity, but the opposite occurred. PPW was more likely to occur in years 2 and 3 of our study than in year 1. We found no significant effect of date on its correlation with other variables (Table 2.7).

The culmen length frequency distribution of juveniles showing PPW was unimodal and biased towards longer-billed birds, whereas that of birds not showing PPW was bimodal (Fig. 2.5, Table 2.7). The smaller mode (17.5 mm) was missing from the PPW distribution (Fig. 2.5). To provide a breeding population context, we provide the mean and standard deviations of male and female culmen lengths from western and eastern breeding regions (Fig. 2.5).

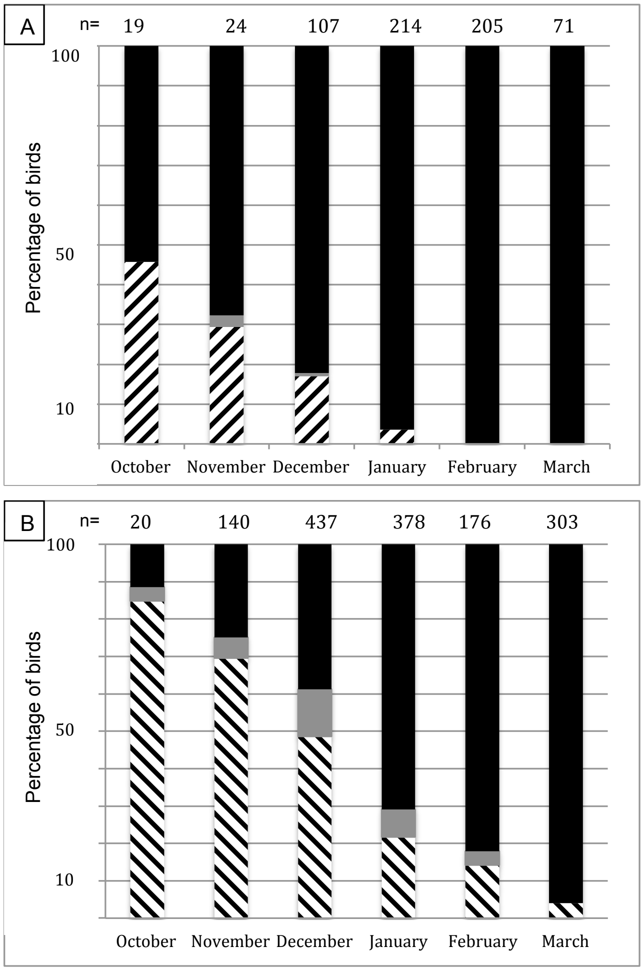


Figure 2.4. Monthly percentages of adult sandpipers at Paracas National Reserve, Perú, in three wing molt categories: active molt (hatched), suspended molt (gray) and finished molt (black). Sample sizes shown above the bars. (A) Western Sandpipers, (B) Semipalmated Sandpipers.

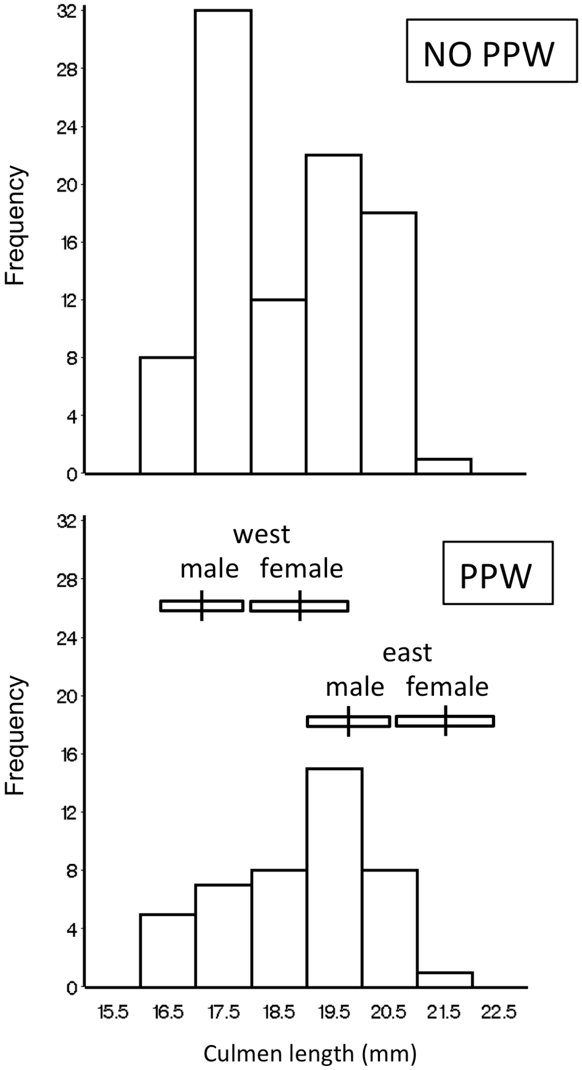


Figure 2.5. **Frequency distributions of exposed culmen lengths of juvenile Semipalmated Sandpipers exhibiting (N = 44) or not exhibiting (N = 93) Post-juvenile Partial Wing (PPW) molt in Paracas National Reserve, Perú, 2012–2015. For comparison, insets show the culmen lengths (mean ±SD) of males and females from western and eastern-breeding populations (Gratto-Trevor et al. 2012, Table 2).**

2.5. Discussion

2.5.1. Slow vs. fast life history strategies

We present evidence for inter- and intraspecific differences in life history strategies of first-year Western and Semipalmated Sandpipers preparing to migrate north from southern Perú. Juvenile Western Sandpipers did not increase in mass or undergo a pre-alternate molt, behavior strongly indicative of over-summering birds and similar to patterns reported in Panama but contrasting with those in México where most juveniles prepared for northward migration (Fernández et al. 2004, O'Hara et al. 2005). In contrast, a quarter to a third of juvenile Semipalmated Sandpipers in our study prepared for migration during their first April, based on the proportion either molting into alternate plumage or replacing outer primaries. Patterns of mass in juvenile Semipalmated Sandpipers have a complex interaction with molt strategy, our third predictor of migratory propensity (see below). Censuses and resighting of individually marked birds at Paracas conducted during the breeding season (June and July 2015) confirm that small groups (150 – 300) of juvenile Western and Semipalmated Sandpipers feed in the area (P. Pellissier, pers. comm.), corroborating our inference of over-summering based on indicators of migratory preparation.

For Semipalmated Sandpipers, bimodality in first-year life history strategy was previously suggested based on observations of both over-summering juveniles in northern South America (Spaans 1979) and recaptures of first-year breeders on southward migration (Gratto-Trevor 1988). No information was previously available with respect to either the breeding or non-breeding geographical distribution of the two life history strategies. Our results provide direct validation of a life history strategy difference based on data from a single non-breeding area; both strategies occur with reasonable frequency, at least in Perú. Although this is not likely to be the case elsewhere, we found that from 27 to 31% of juveniles were preparing for migration in different years, which is consistent with Gratto-Trevor and Morrison's (1981) suggestion that about a third of Semipalmated Sandpipers return to breeding areas in their first year of life.

The migration strategy of Western Sandpipers is geographically segregated, being largely a function of migration distance from their compact breeding range around the Bering Sea. Despite overlap in strategies at a single site, we suggest that a migration-distance explanation may similarly apply to the difference in life-histories of juvenile Semipalmated Sandpipers. Shorter-billed juvenile Semipalmated Sandpipers, which are partially sympatric with breeding Western Sandpipers in Alaska (~11,000 km from Paracas), were less likely to prepare for migration than longer-billed birds (~8000 km from breeding areas in eastern Canada), as assessed by patterns of mass, molt into alternate plumage, and likelihood of molting their outer primaries. Thus, western populations of Semipalmated Sandpipers follow a strategy similar to that of Western Sandpipers, spending the non-breeding season at Paracas. These results provide intraspecific support for the hypothesis that longer migration distances are associated with slower life history strategies (e. g., Myers et al. 1985, O'Hara et al. 2005).

An alternative interpretation of the effects of culmen length in Semipalmated Sandpipers would invoke sex-specific life history strategies. Biases consistent with our results could occur if males, with short bills, were less likely to migrate than females, with longer bills, combined with particular non-breeding sex ratios. The location of the PPW mode relative to the breeding distributions (Fig. 2.5) indicates that the larger culmen length bias detected was not simply due to females being more likely to engage in PPW than males, but, rather, there is a bias towards PPW in eastern- rather than western-breeding birds. The extent of sex ratio clines in non-breeding Semipalmated Sandpipers and their sex ratio at Paracas are unknown.

The presence of two populations at Paracas is also indicated because Semipalmated Sandpipers with longer mean culmen lengths arrive at the site later in the season (Tavera 2013). The increased prevalence of birds with suspended molts in December probably reflects a wave of eastern migrants.

2.5.2. Variation in primary molt strategies

Adult Western and Semipalmated Sandpipers at Paracas conform to a Southern Hemisphere molt strategy (Pyle 2008, Howell 2010), with the timing of adult primary molt extending from October through February. Western Sandpipers are 3–4 weeks ahead of Semipalmated Sandpipers, consistent with their earlier breeding and migration (Lank et al. 2003).

At least some adults of both species appeared to initiate wing molt prior to arrival in Paracas. About 4% of both species clearly did so because they were captured with suspended molt, providing a minimum estimate of occurrence. Significant numbers of sandpipers begin arriving during September and, by October, most birds (84% of Westerns and 88% of Semipalmated Sandpipers) had already molted more than half of their primaries and most birds were in active molt. Many of these may have arrived with suspended molt in September or early October but resumed molt by the time of capture. Western Sandpipers tend to initiate molt rapidly at Panamá Bay (Watts 1998), where they typically dropped 4–6 inner primaries upon arrival. Watts (1998) documented a peak population present in October, with numbers decreasing thereafter and suggesting continued southward migration. Wing molt of Western Sandpipers can begin as far north as Kansas (Senner and Martinez 1982), but Semipalmated Sandpipers do not appear to start wing molt until they are further south. In Kansas, there was no evidence of molt of Semipalmated Sandpipers, but a small proportion of Western Sandpipers were undergoing wing molt (S. Franks, pers. comm.), and all primary feathers were old when birds arrived in Suriname (Spaans 1979, 1984). Geolocator data from an individual Semipalmated Sandpiper captured at Nome, Alaska, in May 2014, and recaptured in May 2015, showed a migration route and timing that fits with molting farther north (E. B. Kwon, pers. comm.). The bird arrived on the coast of Ecuador in mid-August, where it stayed for three months before flying to northern Perú. Thus, northern South America seems a probable site for migrant Semipalmated Sandpipers to undergo partial molt prior to continuing on to Paracas.

Adult Semipalmated Sandpipers captured with different molt statuses during the residency period differed in average culmen lengths, controlling for date of capture. Those with longer bills, indicative of eastern population origins, were biased towards having either suspended or active molt, whereas those with shorter bills were biased towards having completed molt. This pattern is consistent with later seasonal breeding, migration, and molt timing by eastern birds, but also with a higher probability of engaging in a partial molt stopover by eastern birds, leading to suspended molt.

About a third of juvenile Semipalmated Sandpipers captured during March in Paracas were undergoing PPW (Table 2.5). Individuals with more alternate plumage, lighter in mass and with longer culmens (eastern population origins) were more likely to express PPW. More alternate plumage is expected if PPW correlates with migratory propensity, but, contrary to what one might expect, these birds were lighter rather than heavier. However, this makes sense in the context of molting, when birds typically reduce their body mass for energetic and safety reasons (Swaddle and Witter 1997, Hedenström and Sunada 1999, Lind and Jakobsson 2001).

Partial post-juvenile wing molt is assumed to be an economizing compromise supporting long migratory flights by juveniles attempting to breed in their first year, by renewing some, but not all of the primaries they grew rapidly in the breeding areas (Spaans 1976). The PPW strategy usually involves between 2 to 6 outer primaries (Videler 2005, Remisiewicz et al. 2010), those experiencing the most wear. Some species with long-distance flights perform a complete wing molt prior their first northward migration (e.g., Ringed Plovers, *Charadrius hiaticula*; Tree 1977). At the other extreme, shorter-distance migrants may not molt at all, such as Western Sandpipers spending the non-breeding season in México where juveniles perform three migrations with the same set of feathers (Fernández et al. 2004). For Semipalmated Sandpipers, the difference in migration distance between 8000 and 11,000 km likely alters the selective balance between undergoing PPW, migrating, and attempting to breed in the first year versus retaining juvenile flight feathers and oversummering or, in Pyle's (2008) terms, following a northern versus southern molt strategies.

2.6. Conclusion

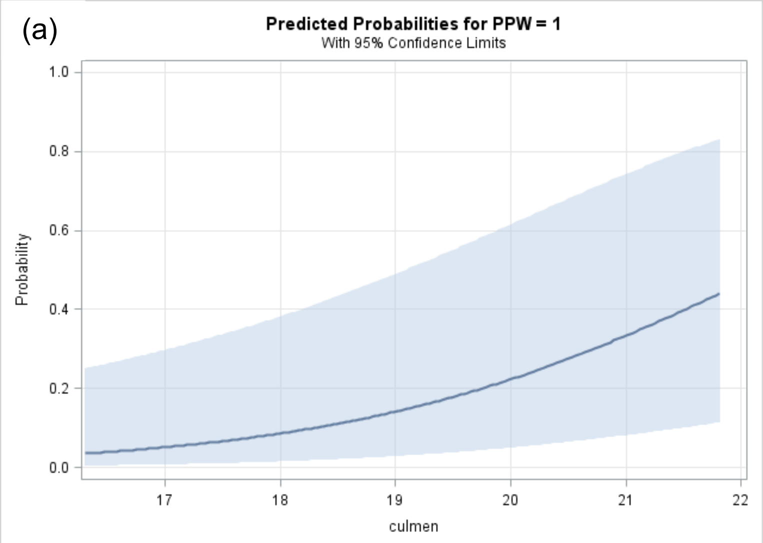
Among the hypotheses accounting for life history variation outlined in the introduction, the broad patterns of our results are consistent with being driven by differences in migration distance. The mechanisms driving a relationship between wing molt strategy and migration distance remain unclear. Direct degradation of flight efficiency is an obvious possibility (O'Hara 2002), but other incremental costs associated with predation risk during migration (Lank et al. 2003, Ydenberg et al. 2004, 2007), weather (Xu et al. 2015), and energetic risks (Baker et al. 2004) might influence molt and migration chronology decisions. The decision to migrate or not is likely related to the cost of migration. If this cost increases sufficiently with distance (Pienkowski and Evans 1985) and the reproductive payoff of juvenile breeders is low (Gratto 1983), over-summering behavior would be favored.

Addendum: Chapter 2

Migration Distance and Probability of Migration

In the published paper on which Chapter 2 is based, I concluded that no juvenile Western Sandpipers prepared for migration in their first spring of life. In contrast, I found that ca. 31% of juvenile Semipalmated Sandpipers had a partial post-juvenal wing molt (PPW), indicating that they were preparing to migrate in their first spring. Consistent with this, many Semipalmated Sandpiper juveniles put on breeding plumage and increased their mass during March and April (Figure 2.3). Juveniles with PPW were biased towards longer-billed, eastern bred, shorter-distance migrant birds rather than shorter-billed, western-bred, longer distance migrants (chapter Figure 2.5, Table 2.7). Using culmen length as an index for breeding population of origin and thus migration distance to Paracas, western-breeding Semipalmated Sandpiper juveniles therefore behaved similar to the Western Sandpipers that bred in the same areas and migrated the same distances.

To obtain a more detailed view of the relationship between migration distance and PPW, I now isolate the independent effect of culmen on the probability of PPW. Rates of PPW were lowest in the pre-migratory season of 2013, and highest in 2015, ranging from 22.0—44.4% (Tables 2.5). Table 2.7 presented the results of a logistic regression model with culmen length, mass, breeding plumage index, year, and day in the year as predictor variables of PPW. Figure A2.1 plots the effect of culmen from that model for each of the three years of the study, with other variables set to unbiased values. All three years show higher rates of PPW at longer culmen lengths, with the strongest relationship with the narrowest confidence limits occurring when PPW was most common (44.4%), in 2015. It's clear from this that PPW rises gradually across the culmen length gradient, implying that longer distance juveniles are more likely to oversummer. We therefore used values from this relationship in subsequent analyses estimating the survivorship of migrants as function of culmen length, and therefore migration distance, presented in Chapter 3.


(a)
Predicted Probabilities for PPW = 1
With 95% Confidence Limits
Probability
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22
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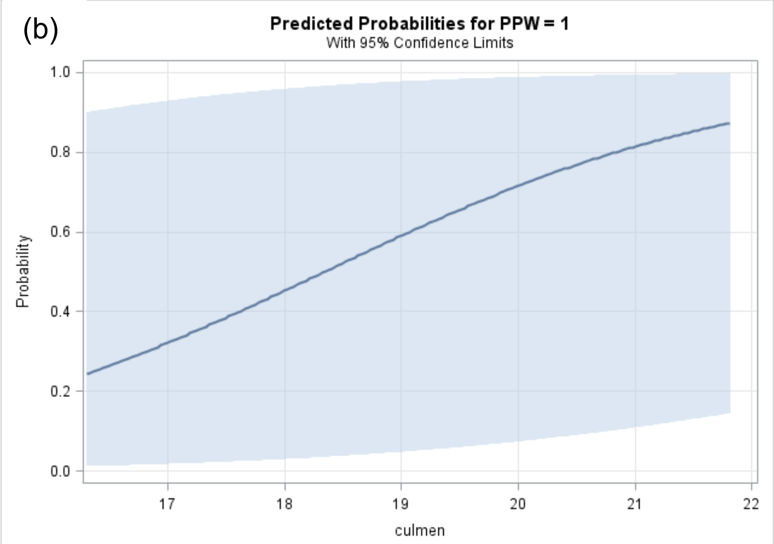
(b)
Predicted Probabilities for PPW = 1
With 95% Confidence Limits
Probability
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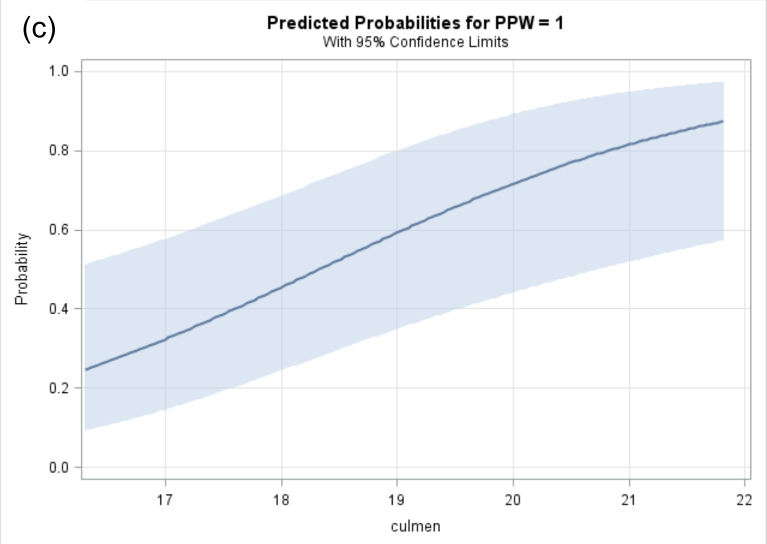
(c)
Predicted Probabilities for PPW = 1
With 95% Confidence Limits
Probability
0.0
0.2
0.4
0.6
0.8
1.0
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culmen

Figure A2.1 Probability of Partial Post-Juvenal Wing Molt in juvenile Semipalmated Sandpipers captured at Paracas, during the pre-migratory seasons of (a) 2013 (b) 2014 and (c) 2015, based on the logistic regression model presented in Table 2.7. These yearly slices were computed with day in year at 168.1, breeding plumage index at 1.54, and mass at 24.63, which minimize bias. The narrowest confidence limits occurred in 2015, when rates of PPW were highest, and range from probabilities of ca. 0.22 for the shortest bills to 0.83 for the longest.

Chapter 3.

Migrate or oversummer? Survival trade-off for Semipalmated Sandpipers at Paracas, Perú.

3.1. Abstract

The timing of first breeding plays an essential role in fitness. Most small shorebirds attempt to breed during their first year of life, despite documented lower reproductive success. Lower reproductive payoffs for young birds could favor selection for delaying the first breeding attempt. At Paracas, Perú, ~70% of Semipalmated Sandpiper juveniles oversummer, deferring their first northward migration and breeding attempt until the second year of life. A small proportion of adults also annually opt out of migration and breeding, and instead oversummer. We use this bimodality to examine underlying assumptions about the costs of migration relative to oversummering. For oversummering to compensate for the loss of breeding opportunity, oversummering birds must have sufficiently higher survival than migrants during the breeding season. We tested this prediction using a Multi-state Mark-Recapture model to estimate seasonal parameters based on extensive marking, recapture, and resighting data obtained at Paracas year-round over 5 years. For both age classes, oversummering gave higher survival than migration, and the difference was greater for adults. Our results are consistent with the life history hypothesis that oversummering birds compensate for the loss of breeding opportunities with a higher survivorship than that of migrants.

3.2. Introduction

Life history theory predicts that a substantial contribution to maximizing fitness comes from balancing survivorship and reproductive effect, through selection on timing of breeding (Stearns 1992). The timing of first breeding can be a particularly powerful variable because reproduction earlier in life compounds fitness faster than reproduction later in life. Age of first breeding (or non-breeders) can have substantial effects on population growth rates, and cases were individuals appear to forgo early breeding opportunities are therefore of intrinsic interest (Lee et al 2017).

Demographic models of small shorebirds emphasize the importance of juvenile and adult survivorship on population growth rates over both annual reproductive success and age of first breeding (Weiser et al 2018). In small shorebird species, most individuals attempt to breed in their first year of life, e.g. Dunlin *Calidris alpina* (Holmes 1966), Temminck's Stint *Calidris temminckii* (Hilden 1978), Least Sandpiper *Calidris minutilla* (Miller 1979) and Semipalmated Sandpipers (Gratto et al 1983). However, in birds in general, first year breeders often have lower reproductive success than older individuals (Saether 1990), and this has been specifically documented in small sandpipers (Gratto et al 1983, Kwon in prep.). Inexperienced birds often migrate and breed later than older birds; Gratto et al (1983) found that despite no nesting habitat differences, first year Semipalmated Sandpipers had mean hatch dates of two days later, significantly smaller egg size, and achieved substantially lower nesting success than older birds. Kwon et al (in prep.) found similar results for Western Sandpipers breeding at Nome, Alaska, where first year breeding females had lower fecundity rate compared to second years and adults. In Piping Plovers *Charadrius melodus* Gratto-Trevor (2010) found that more females bred as first years than did males and suggested that this was due to primary feather wear which may reduce the ability of first year males to perform aerial breeding displays. With potentially lower reproductive payoffs for younger birds, selection can favour delayed breeding, and factors that increase the risk or cost of breeding may make a difference.

Western Sandpipers *Calidris mauri*, and Sanderlings *Calidris alba* appear to provide good illustrations of this theory. Both have a migration-distance related difference in age of first breeding. Individuals spending their first non-breeding season at more southerly areas, further from arctic breeding grounds do not moult into breeding plumages and migrate northward, while those at more northerly locations do so (Myers 1981, O'Hara 2002, Fernández et al 2004, O'Hara et al 2005, Chapter 2). 'Oversummering' is a term that has been used to describe when a typically migratory bird defers migration and stays at the non-breeding grounds during the breeding season (or boreal summer) (McNeil et al 1994). Oversummering as a life history strategy for juveniles has been associated with migration distance. Juvenile birds, and those travelling longer distances, have a greater propensity to oversummer (Summer et al 1995, Tavera et al 2016). Some explanations for the phenomenon include: sexual immaturity (Eisenmann 1951, Soto-Montoya et al 2009); helminthic infestation (McNeill et al 1994); sterility, injuries or illness (Wetmore 1927); less efficient foraging (Puttick 1979); flight cost on primary wear (O'Hara 2002); behavioral adaptations to distance-dependent costs (Lank et al 2003, Ydenberg et al 2004, 2007); low chances of successful first breeding seasons (Summers et al 1995) and the offsetting life-history benefit of a higher probability of survival in non-breeding areas (Fernández et al 2004).

If such behavior pattern is adaptive, we expect that the decision to become a resident bird and to remain on the non-breeding grounds, foregoing a breeding opportunity, involves a substantial survivorship benefit that compensates enough to offset the fitness loss of a year's potential reproductive success, demanding a substantially higher survival rate during the migration and breeding seasons than that of migrants. This study addresses this question for Semipalmated Sandpipers spending their non-breeding season at Paracas, Perú. Semipalmated Sandpipers are one of the smallest calidrid sandpipers in the western hemisphere, who migrate twice a year from the subarctic Alaskan coast and east across the Canadian tundra to the southern hemisphere (Harrington and Morrison 1979, Hicklin and Gratto-Trevor 2010), more specifically to Perú approx. from 8,000—11,000km. At Paracas, ~70% of first year Semipalmated Sandpipers oversummer, deferring their first northward migration until their second year of life (Tavera et al 2016). Small numbers of adults also may forego breeding. This migration decision dichotomy provides the opportunity to compare the annual survivorship rates between migrant or non-migrant individuals and infer the strategic consequences. To produce estimates to test for differences, we created a Multi-state capture-resighting model with two age classes (juveniles or adults) and two migration strategies (residency or migration), during five annual time seasons, and estimated survival transition probabilities, between states, including the observable and unobservable states (migration). If oversummering compensates for the loss of breeding opportunities with sufficiently higher survivorship, we predict that oversummering birds should have a substantially higher survival during the potential breeding season than migrants. Further, since adults have a greater probability of breeding successfully than juveniles, those adults that oversummer should gain more in terms of survivorship than juveniles by doing so.

3.3. Methods

3.3.1. Study Site

We captured, marked, released and resighted Semipalmated Sandpipers at the Paracas National Reserve in Perú a Natural Protected Area, located in the Department of Ica, 250Km south of Lima city. Fieldwork was conducted on La Aguada beach (13°51‘35.47″S 76°16‘16.16″W), an intertidal mudflat <2 km long and surrounded by coastal desert (Chapter 2, Fig. 2.1). The near-shore section of the mudflat has no vegetation and most of the lower intertidal zone is covered with soft mud filled with polychaetes, fly larvae, microscopic sea shrimp, and beetles, and covered by biofilm and decaying algae in shallow water (Senner and Angulo 2014).

3.3.2. Data Collection

We collected capture–mark–resighting data on several thousand birds on a monthly basis between 1 October 2014 - 31 March 2019. Data were collected during the non-breeding season (October to March) and also during migration and breeding season (April to September). During the non-breeding season we conducted seven-day capture-resighting campaigns during each new moon phase of each month, with trapping-resighting occasions separated by a minimum of 20 days. During the migration and breeding season we carried out 5-day resighting campaigns each month, with resighting occasions separated by 25 days.

Shorebirds were captured at night with mist-nets. Time of capture depended on the tide cycle, beginning three hours after the evening high tide and ending three hours before the subsequent high tide, ranging between 20:00h-06:00h. Captured birds were marked on the right tarsus with an incoloy metal band obtained from the CORBIDI Bird-

Banding Program (the Peruvian bird-banding scheme). Also, a three-character-coded yellow flag was placed on the left tibia (e.g. 3AT), following the Panamerican Shorebird Program protocol (Myers et al 1983, Morrison 1984), to identify individuals and allow collection of resighting data.

Captured birds were assigned to two age categories based on plumage characteristics. Juveniles (individuals in their first non-breeding season from 0 to 12 months old) were recognized by the retained juvenile type inner greater coverts, and adults (12+ months old) by wing and flight feather characteristics (Prater et al 1977, but see Hicklin and Gratto-Trevor 2010). All capture efforts were carried under the supervision of a NABC (North American Banding Council) certified shorebird trainer (principal author of this study) with 5 field assistants and 5 volunteers.

Resighting effort was similar across years, with 3 persons/day effort and 3 hours of intensive survey each morning between 06:00h-09:00h, by 3 experienced observers who located, identify and recorded marked individuals across the entire beach. Individuals that couldn't be reliable identified (e.g. flag partially covered with sediments and one letter/number could not be read) were not added to the final daily list of resighted birds. Repeated observations of individuals and non-existent flags were filtered and removed from the final daily list.

3.3.3. Multi-State Models

Multi-State Mark-Recapture (MSMR) models use capture-mark-resighting data from a set of sampling occasions, where at each occasion newly marked birds are released, previously marked birds are identified, and additionally the 'state' of each bird is recorded (Nichols and Kendall 1995). Some states may be 'unobservable' (e.g. when birds have left the local area; Bailey et al 2009; Arnason 1972, Lebreton and Pradel 2002). MSMR models estimate transition probabilities between states, including the transitions to or from unobservable states. These "survival transition probabilities" are estimated as the product of a conditional probability of survival and of a transition probability. They depend only on the last state reached by the individual, and not on preceding stated (i.e., transitions are first-order Markovian; Lebreton and Pradel 2002). The models also assume that marks are not lost, that marks are correctly recorded and that animals behave independently.

MSMR models provide estimates for survival, transition, and detection parameters, denoted as follows:

S_t^J = survival probability from time t to t+1 for individuals in state J;

ψ_t^{JI}= transition probability from state J to state I at the beginning of occasion t+1, given survival to time t+1;

and p_t^J = detection probability of an individual in state J during occasion t.

In many cases, fully time-and state-dependent parameters are not estimable, and certain constraints must be applied, especially when some of the states are not observable (Schaub et al 2004, Fugiwara and Caswell 2002). Also, some transitions may not be possible, depending on the situation (e.g., transitions from adult to juvenile). As with other non-spatially explicit capture-recapture models, permanent emigration from the population cannot be distinguished from mortality in our system, thus survivorship estimates are ‘apparent survivorship’.

To simplify our model structure, we aggregated monthly observations into one of five annual component seasons: Winter1 (from October to December), Winter2 (from January to March), Spring (April and May), Summer (June and July) and Fall (August and September). We defined four observable states:

1. Juvenile in winter (JW) = individuals in their first non-breeding season at Paracas, Winter 1 + Winter 2

2. Juvenile in summer (JS) = individuals spending their first breeding season (oversummering) as non-breeders in Paracas, Spring + Summer + Fall

3. Adult in winter (AW) = birds in at least their second non-breeding season at Paracas

4. Adult in summer (AS) = birds in at least their second non-breeding season and staying in Paracas after it

and two unobservable states:

5. Juvenile migrant (JM) = birds in their first year of life migrating north in spring and coming back to Paracas in Fall

6. Adult migrant (AM) = birds in at least their second non-breeding season migrating north in spring and returning to Paracas in Fall.

3.3.4. Modeling Transition Probabilities

Transitions in the basic model structure are shown in Figure 3.1. Most transitions are either deterministic or impossible, and fixed at 1 or 0. With these assumptions, the model estimates the transition probabilities between Winter2 and Spring, representing migration and resident (oversummering) by juveniles and adults (ψ^{JWM1}, ψ^{JWJS}, ψ^{AWM2}, ψ^{AWAS}). We could not make estimates for each year, as these models failed to converge reliably.

3.3.5. Modeling Survival and Detection Probabilities

Based on exploratory analyses, we compared five model structures to estimate survival rates S of the six states (JW, JM, AW, AS, JM, AM, as above).

Model 1: Survival varies by season (summer, winter), age (juvenile, adult) and strategy (migratory, resident).

Model 2: Survival varies by season (summer, winter), age (juvenile, adult), but not strategy.

Model 3: Survival differs only by season (summer, winter).

Model 4: Survival differs by age (juvenile, adult) and strategy (migratory, resident).

Model 5: Survival differs only by age.

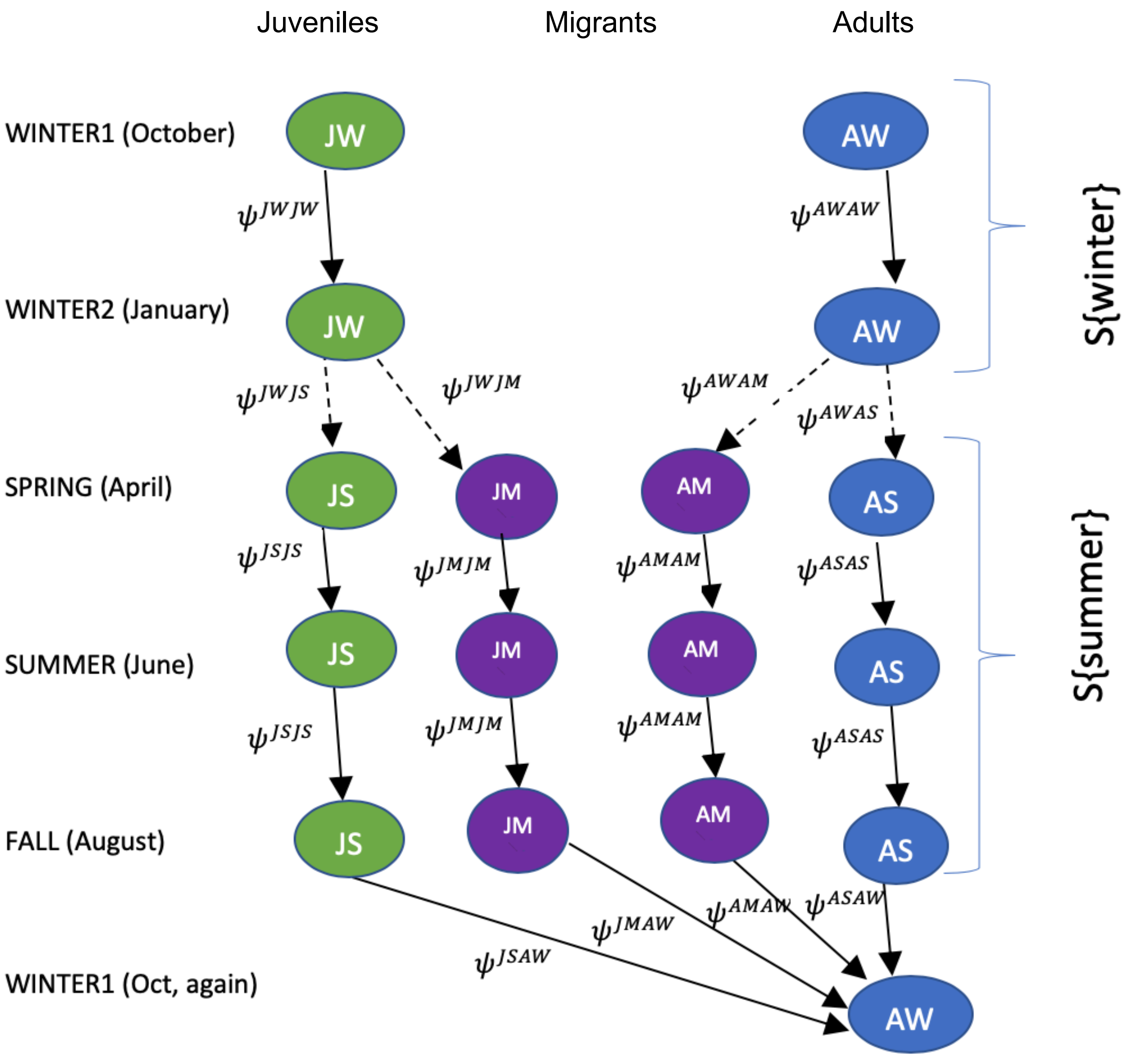

Figure 3.1. **Possible state transitions for Semipalmated Sandpipers at Paracas, Perú. Solid arrows denote deterministic transitions, and dashed transitions denote stochastic transitions estimated in the MSMR model. All other transitions are not possible. States are as defined in the text: JW (Juvenile in winter), JS (Juvenile in summer), AW (Adult in winter), AS (Adult in summer), JM (Juvenile migrant), and AM (Adult migrant)**

In each of these models, Winter1 and Winter2 are each three months long and survival can vary with age class. At the end of Winter2, Semipalmated Sandpipers can either remain as resident juveniles or adults, or can transition to the unobservable migratory states (JM, AM). Spring and Summer are each two months long, and both can vary by age or by strategy (oversummering or migrant). Fall is also two months long and can vary by age or by strategy. At the end of Fall, all birds deterministically transition to state AW. We accounted for different period lengths (e.g., Winter1 was 3/12 years, and Spring was 2/12 years in length) by scaling the reported estimates to six months to make them directly comparable. Therefore, survivorship for the entire 6-month 'Summer season' included the Spring, Summer, and Fall sampling occasions, similarly, the 6-month 'Winter season' included both winter occasions. As with transition probability, we constrained survival probability to be equal across the five years of observations.

In MSMR models typically it is necessary to set survival probability of an unobservable state equal to that of one of the observable states – it not possible to estimate unique survival rates for unobservable states (Schaub et al 2004). However, in our case there is a great deal of determinism in transitions, including the constraint that all individuals in unobservable states must become observable in Winter (Fig. 3.1). We conducted simulations that suggested that the determinism in transition probabilities for an unobservable state rendered survival probability separately estimable for that state, although precision suffered with sparse data. Details on simulations are given in Appendix D.

Detection probability p_t^J was allowed to vary by age (juvenile, adult) or by age and season (summer, winter). We did not consider a model with constant detection probability, because we had occasions with different lengths. We set the detection probability *p* = 0 for all unobservable states, and as with transitions and survival, we did not model inter-annual differences in detection probability.

3.3.6. Data Analysis

The encounter history assigned birds captured between midnight and 09:00 to the previous date for simplicity. We assigned a state to each encounter based on age and dates. 'Adult' and 'juvenile' status were assigned based on plumage (Prater et al 1977). Juveniles first seen before July 19 (d-o-y 200) were assumed to have been born the year before (and hence were non-migrants), while those first seen after July 19 were assumed born in the same year.

Encountered data from 55 months were aggregated into 22 sampling occasions over a five-year period from October 2014 to March 2019, based on the two or three-month sub-seasonal definitions given above. We used data from first encounters (first capture, or first resighting for birds marked before October 2014) (n=1,963) and their respective resighting observations (n=3,229), all treated as independent observations. An average of 43% of Semipalmated Sandpipers were never seen after first capture, ranging from 31% to 55% annually. Reencountered birds were seen on 1 to 16 subsequent sampling occasions averaging 2.91 occasions, ranging from 2.28 to 3.15 annually, excluding the last season. Further information on the distribution encounters by occasion and year is given in Appendix E.

We fit 15 model combinations with 5 structures for S, 1 structure for ψ ($\psi\ state$), and 3 structures for p, for Semipalmated Sandpiper encounter histories (Table 3.1). We used a multinomial logit (mlogit) link function to estimate beta coefficients and real parameters for ψ and logit links for S and p. The most parsimonious models were selected based on the Akaike information criterion corrected for the effective sample size (AIC_c; Burnham and Anderson 2002). Models with ΔAIC <2 were considered the best ones supporting the data and were used to estimate parameters and respective standard errors (SEs; Burnham and Anderson 2002). We fitted models in program MARK (White and Burnham 1999) using the Rpackage “Rmark” interface (Laake 2013) within program R, version 3.5.1 (R Core Team 2016).

Table 3.1. **Set of models fitted for Semipalmated Sandpipers with five different structures for annual survival (S), three different structures for probability of resighting (p) and one structure for transition probability (ψ).**

Model (S)	Model (p)	Model (ψ)
S(age+season+strategy+age.season+age.strategy)	p(age+season)	state
S(age+season+age.season)	p(age+season)	state
S(season)	p(age+season)	state
S(age+strategy+age.strategy)	p(age+season)	state
S(age)	p(age+season)	state
S(age+season+strategy+age.season+age.strategy)	p(season)	state
S(age+season+age.season)	p(season)	state
S(season)	p(season)	state
S(age+strategy+age.strategy)	p(season)	state
S(age)	p(season)	state
S(age+season+strategy+age.season+age.strategy)	p(age+season+age.season)	state
S(age+season+age.season)	p(age+season+age.season)	state
S(season)	p(age+season+age.season)	state
S(age+strategy+age.strategy)	p(age+season+age.season)	state
S(age)	p(age+season+age.season)	state

3.4. Results

A top model (model 14) was identified from 15 models run, with a ΔAICc ≤ 2 (Table 3.2). This most parsimonious model had survival described as a function of age and migratory strategy, such that juveniles had lower survival than adults and migration imposed a survival costs that varied by age. Detection probability was allowed to vary by age and by season. We compare the best model with the second best model (11, ΔAICc = 3.766), that also allows survival of juveniles and adults to vary with season.

Transition probability estimates from resident to migratory state in model 14 were 0.72 ± SE 0.26 (LCL 0.67 UCL 0.77) for juveniles and 0.81 ± SE 0.009 (LCL 0.79 UCL 0.82) for adults. Detection probabilities ranged among age and season classes from 0.218 to 0.603, being slightly higher during winter than summer for both age classes. During the summer period, adults had a higher detection probability than juveniles (Table 3.3).

The six-month survival estimates for each state for both models are shown in Table 3.4. In both models, adult's survival is higher than juveniles' within the observable (Resident) states, independently of the season (winter or summer): JuvW: 0.789 ± 0.001 SE; AdW: 0.904 ± 0.001 SE. Within the migratory states, juvenile migrants have a slightly higher survival than adult migrants: JuvM: 0.700± 0.002 SE; AdM: 0.676 ± 0.001 SE.

Estimates between juvenile residents versus juvenile migrants showed 0.09 points of difference, with a slightly higher survival for the resident juveniles than migrants (JuvM: 0.700 ± 0.002 SE; JuvW: 0.789± 0.001 SE). Adults follow the same pattern but with a bigger difference of 0.22 points between estimates with residents with a higher survival than migratory adults (AdM: 0.676 ± 0.001 SE; AdW: 0.904 ± 0.001 SE) (Fig. 3.4).

The annual survival estimates are created as the product of the appropriate 6-months estimates for resident (winter*summer) and migrants (winter*migration) and are shown in Table 3.5. In general, the values of the two models are similar. Migrants of both age classes had lower survivorship rates than residents: JM: 0.554 ± 0.001 SE, JR: 0.625 ± 0.001 SE; AM: 0.613 ± 0.001 SE; AR: 0.819 ± 0.001 SE.

Table 3.2. The three top survival models for Semipalmated Sandpipers. The first row specifies the number of model, the second row specifies the type of model within its parameters: S for Survival, p as the probability of recapture/resighting and ψ as transition survival probability.

Model	Factors (S, P, ψ)	AICc	ΔAICc	ω AIC	Deviance	K
14	S(age+strategy+age.strategy) p(age+season+age.season) ψ [state]	15889.45	0	0.87	5554.56	10
11	S(age+season+strategy+age.season+age.strategy) p(age+season+age.season) ψ [state]	15893.22	3.77	0.13	5554.31	12
15	S(age) p(age+season+age.season) ψ [state]	15916.89	27.44	9.57E-07	5586.02	8

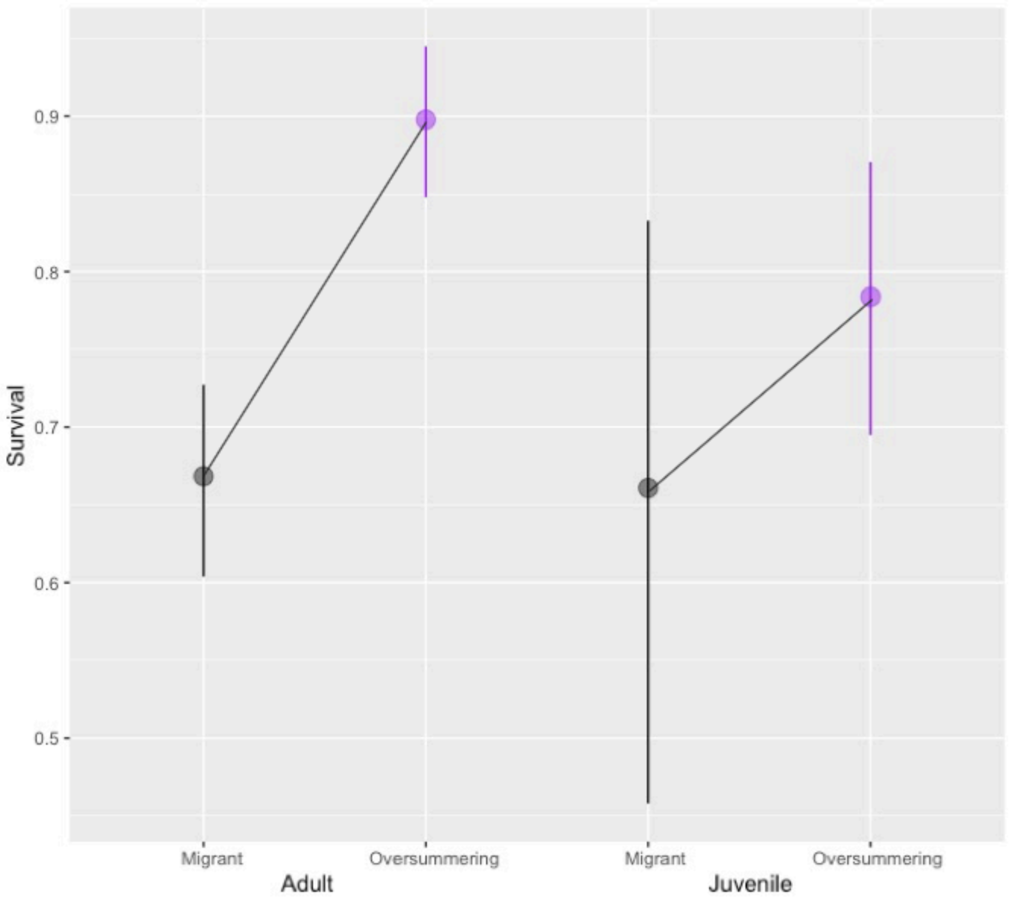

Figure 3.2. **Six-month survivorship for Semipalmated Sandpiper adults (left) and juveniles (right), for migrant and resident (oversummering) birds. Vertical lines are 95% confidence intervals.**

Table 3.3. **Detection probabilities for model 14 of Semipalmated Sandpiper juvenile and adults within Winter and Summer seasons.**

Model 14	Estimate	SE	LCL	UCL
J winter	0.603	0.051	0.500	0.697
J summer	0.218	0.025	0.174	0.27
A winter	0.448	0.009	0.424	0.463
A summer	0.389	0.009	0.371	0.408

Table 3.4. **The six-month survival estimates for each state for the best two best models (model 14 and model 11). SE as Standard Errors, UCL and LCL as Upper and Lower Confidence Limits (95%).**

6-months States	Model 14	SE ±	UCL95%	LCL95%	Model 11	SE ±	UCL95%	LCL95%
J winter	0.7895	0.0012	0.8610	0.7129	0.8176	0.0043	1	0.4976
J summer	0.7895	0.0012	0.8610	0.7129	0.7839	0.0014	0.8706	0.6948
A winter	0.9043	0.0006	0.9408	0.8674	0.9128	0.0011	0.9810	0.8437
A summer	0.9043	0.0006	0.9408	0.8674	0.8978	0.0008	0.9451	0.8480
M juvenile	0.7002	0.0020	0.8175	0.5743	0.6608	0.0031	0.8328	0.4578
M adult	0.6763	0.0007	0.7197	0.6305	0.6684	0.0010	0.7272	0.6039

Table 3.5. **The annualized survival estimates for the two best models (model 14 and model 11). SE as Standard Errors, UCL and LCL as Upper and Lower Confidence Limits (95%).**

Annualized States	Model 14	SE ±	UCL95%	LCL95%	Model 11	SE ±	UCL95%	LCL95%
Resident Juvenile	0.6253	0.0014	0.7147	0.5399	0.6411	0.0035	0.8233	0.3908
Migrant Juvenile	0.5541	0.0017	0.6603	0.4407	0.5469	0.0038	0.7725	0.2992
Resident Adult	0.8191	0.0008	0.8645	0.7717	0.8195	0.0012	0.8962	0.7425
Migrant Adult	0.6137	0.0007	0.6578	0.5688	0.6100	0.0012	0.6808	0.5357

3.5. Discussion

Migratory adaptations or migratory ‘strategies’ are affected by selective forces such as time, energy and predation minimization under different seasons and environmental conditions (Alerstam and Lindström 1990). Our main hypothesis involves comparing survivorship rates of residents versus migrants during the potential migratory season, as predicted by life history theory. Oversummering Semipalmated Sandpipers did have a higher survivorship than migrants. The survivorship rate of resident adults was 0.205 higher than that of adult migrants, representing an increase of 33%. The rate for resident juveniles was 0.07 higher than that of juvenile migrants, representing an increase of 13% (Fig. 3.2; Table 3.5).

Palacin et al (2017) found extremely large survival rate differences between migrants and resident bustards, on the order of 2.5–3 times, largely as a result of collisions with power lines. The authors attributed a historical change in the proportion of migrant versus resident birds to changes in individual behavior, which was observed, and possibly also to selection against migrants. A second example of how juveniles can alter their migratory behavior and change life history decisions over only a few decades is shown by a study on storks where the majority of juveniles chose to migrate a shorter distance and spend the winter in the “closer” non-breeding site associating this decision with higher survival (Cheng et al 2019).

Our survivorship differences are smaller in magnitude than those found in bustards, but we can estimate the probable effect on population growth rate from birds following one strategy or another, using existing demographic models for Semipalmated Sandpipers and other small arctic breeding shorebirds. Growth rates in shorebirds in general are much more sensitive to variation in survivorship than in annual fecundity. We can use the elasticity of parameters on population growth rates to provide perspective on this question. The decision to breed or not as a juvenile Semipalmated Sandpiper has an elasticity of ca. 0.03 (Hitchcock and Gratto-Trevor 1997) - 0.04 (Weiser et al 2020). In contrast, elasticities for juvenile survivorship of Semipalmated sandpipers are far higher, on the order 0.11-0.21 in the two studies. Given these numbers, the proportional variation in survivorship of 13% for juveniles is high enough to offset the fecundity loss. For adults, the elasticities are on the order of 0.69 to 0.34 in the two studies, respectively, compared with a 33% higher survivorship for oversummering birds. Finding a greater change in survivorship for adults than in juveniles was also predicted, as outlined in the introduction, because their loss of reproduction would be greater.

The effect of life history decision on population growth rate also depends on the proportion of birds adopting each strategy. This model estimated that 72% of juveniles and 81% of adults migrate. The value for juveniles is substantially higher than the average of 31% that we estimated based on the proportion of juveniles doing PPW in Chapter 2. Apparently, some proportion of juveniles migrate without doing PPW (Gratto and Morrison 1981), and/or the proportion of juvenile migrants may have been increasing through the study period. Season 2014-2015, the last year considered in Chapter 2, had the highest rate of PPW, occurring in 44% of juveniles. Furthermore, a more recent study based on shorebird vital rates (Weiser et al 2020) found that Semipalmated Sandpiper juveniles had 67% probability of returning to their breeding sites, similar to our transition probability estimate for migrant juveniles. The model estimate for the proportion of migrating adults is lower than we would have predicted. This appears to be driven by an unusual proportion of adults not migrating in 2018.

One consideration in interpreting our residency/migration comparison is that the populations of migrants and non-migrants were likely not completely otherwise equivalent in this observational study. We could not assign birds to migration/residency states at random, as would be done in an experimental study. Thus, the comparison is imperfect as a quantification of what might be the consequences for individuals making the alternative decision. There also may be biases in permanent emigration, which we might *a priori* expect to be in the direction of a higher proportion of migratory individuals not returning. Despite these caveats, we view these results as reflective of a substantial survivorship advantage for oversummering residents of both ages during the potential breeding season.

Our results from the resident strategies of both age classes show a similar pattern to the annual survival results (see Chapter 4), in that adults had a higher survival than juveniles. However, the magnitude of difference was 0.12 in survival probability in the MSMR estimates (Table 3.5), compared with 0.04 in annual survivorships in the MSORD model (Chapter 4). The lower magnitude of the difference in the MSORD model could be accounted for by the similar survival probabilities of the migratory portion of the populations, which are also included in the annual estimates. The point estimate of migratory juveniles is in fact a little higher than those of migratory adults, which would help balance out the large juvenile disadvantage among residents.

Age differences of this kind are often found as juveniles are usually at more risk than adults, mostly attributed to a lack of experience in coping with migration, foraging and predators (Lima 1986, Kus et al 1984, Anderson et al 1985, Sandercock and Gratto-Trevor 1997). Wintering juvenile Redshanks *Tringa totanus* on a Scottish estuary were socially constrained by adults to feed on salt marshes despite a high mortality rate from raptors (Cresswell 1994). Alternatively, juveniles may be naive and need to learn to avoid dangerous sites, as argued for migrating juvenile Dunlins *Calidris alpina* at Helgoland (Dierschke 1998). However, our survival results for resident juveniles are not much lower than those of adults, which suggests relatively little influence of competition with adults or other selective pressure from inexperience (Anderson et al 2019).

3.6. Conclusion

Our results are consistent with the life history hypothesis that oversummering (resident) birds compensate for the loss of breeding opportunities with a higher survivorship than migrant birds. Migration distance has been previously identified as a factor associated with migratory propensity, but other factors will also be important in affecting the balance. The Semipalmated Sandpipers studied at Paracas may be particularly sensitive to changes in other factors, since both strategies are currently maintained in the population. Factors affecting pre-migratory body condition, such as El Niño may be affecting the annual trade-off (O'Hara et al 2007), and climate change could alter the balance over the longer term. Changes in danger from increasing falcon population (Lank et al 2003, Ydenberg et al 2007) can also do so if the rates differ between Paracas and the migration/breeding. If migration has become relatively more dangerous, oversummering would be more greatly favored. On the other hand, if local populations of resident raptors increased local danger more than changes on migration, migration would be favored. The information gathered in this study provides a description of the system against which future studies may be compared.

Chapter 4.

Annual Survival and Monthly Residency Estimates of Western and Semipalmated Sandpipers in Relation to Migration Distance and Life History Strategies

4.1. Abstract

Avian migrants are generally assumed to balance fitness benefits and costs of the travel between breeding and non-breeding destinations. We used 7 years of mark-resighting data to estimate annual apparent survivorship and monthly residence probability of Semipalmated and Western Sandpipers captured at one of the furthest south non-breeding grounds for both species, the Paracas National Reserve, Perú. We modeled survivorship and monthly residence probability with an open robust design multi-state capture-reencounter model. For both sandpiper species, we included year, age, wing length, bill length, and an ENSO (El Niño) index as covariates, plus sex for Westerns Sandpipers. Western Sandpipers differ in bill length by sex, and bill length was used for Semipalmated Sandpipers as a surrogate for breeding population of origin. Both species had higher annual survival estimates than those obtained previously at non-breeding grounds further north. In Semipalmated Sandpipers, the most parsimonious model had a pooled survivorship estimate of 0.71 ± 0.03 SE. Nearly all Western Sandpiper juveniles pursue a non-migratory oversummering strategy, and Western Sandpiper juveniles had substantially higher survival estimates than adults (0.83 ± 0.03 SE for juveniles, 0.70 ± 0.01 SE for adults), in line with the predicted survivorship benefits needed to offset delayed reproduction. Juvenile Westerns were also the most site faithful age-species category during the non-breeding season, with substantially higher average monthly residency rates than other categories (Western Sandpiper: juveniles: 0.89 ± 0.02 SE, adults: 0.82 ± 0.03 SE, Semipalmated Sandpiper: juveniles: 0.84 ± 0.03 SE, adults: 0.77 ± 0.02 SE). Culmen length was negatively related to annual survival in both species, significantly so for Semipalmated Sandpipers: -0.05 ± 0.02 SE (LCL = -0.09, UCL = -0.01). The interpretation of this analysis is complicated because a higher proportion of short-billed juvenile Semipalmated Sandpipers oversummer. After taking this into account, I estimated higher survival estimates for shorter distance (long-billed) migratory birds. Wing length showed opposite non-significant positive trend in

Semipalmated Sandpipers, and a negative trend in Western Sandpipers. Western Sandpipers with longer bill had a lower survivorship, suggesting a possible sex difference (females relative to males: -0.03 ± 0.02 SE; LCL = -0.07, UCL = 0.02). The ENSO index warm phase was significant for Western Sandpipers with a negative relationship with survival: -1.07 ± 0.07 SE (LCL = -1.20, UCL = -0.93), but not significantly associated with Semipalmated Sandpipers, perhaps due to Western Sandpipers' closer association with the Pacific migratory flyway.

4.2. Introduction

The annual life cycle of an organism is defined by a series of life-history stages of correlated morphological, physiological and behavioral traits that allow one to infer adaptation strategies to the environment (Jacobs and Wingfield 2000, Wingfield 2005, Wingfield 2008). Other physiological factors are also involved in this cycle that must be precisely timed to maximize fitness in terms of survival and reproduction (Buehler and Piersma 2008). In long-distance migratory shorebirds, survival is highly linked to migratory chronology. For example, northward migrating Red Knots (*Calidris canutus rufa*) with a late arrival date to Delaware Bay, USA, experience negative fitness consequences due to lack of time to refuel and food shortages (Baker et al 2004). Migratory strategies are also influenced by environmental conditions (Niehaus and Ydenberg 2006), climate change (Hedenström et al 2007), predation danger (Lank et al 2003, Ydenberg et al 2007), migratory distance (González 2007, Tavera et al 2016) and food availability (González et al 2006). To deal with these challenges, birds must have the capacity to choose an optimal strategy that copes with the three broad sources of mortality: starvation, predation and disease (McNamara et al 1998).

Demographic fluctuations are driven by events that occur throughout the year (Buehler & Piersma 2008), particularly for seasonal migrants exposed to different environmental conditions in geographically separated habitats. Annual survival estimates for shorebirds are available based on data from the breeding grounds (Sandercock and Gratto-Trevor 1997, Sandercock et al. 2000, Lloyd 2008, LeDee 2010, Johnson et al 2010, Hill 2012, Taylor et al 2015, Piersma et al 2016, Weiser et al 2018, Garcias and Tavecchias 2018), which comprise 63% of all shorebird survival studies in the world, compared to 6% from staging areas, and 31% from non-breeding grounds (Méndez et al 2018). Importantly, non-breeding survivorship is a strong driver of shorebird population growth rates (Calvert et al 2006) and unfortunately the Western Hemisphere has very few survival studies based on data from non-breeding grounds (Johnson et al. 2001, Fernández et al. 2003, González 2006, Rice et al 2007, O'Hara et al 2007). Demographic studies are crucial for the conservation of shorebirds, given that 60% of shorebird populations in North America are undergoing long-term population declines, mainly associated with human activities (Andres et al 2012). Efforts to identify the biological and environmental drivers of shorebird population declines can be guided by empirical quantification of survival rates across species ranges and at different stages of the annual cycle (Méndez et al 2018). Weiser et al (2018) found little effect of variation in environmental conditions at Arctic breeding grounds on adult survival rates of 5 species of shorebirds, and concluded that more might be gained by generating these annual estimates at staging and non-breeding grounds, as previously suggested by Sandercock and Jaramillo (2002) and Hostetler et al (2015).

We conducted a 7-year mark-recapture-resighting study of Semipalmated Sandpipers (*Calidris pusilla*) and Western Sandpipers (*C. mauri*) at Paracas, Perú, one of the most austral non-breeding grounds for both species, on the western Pacific coast. Western and Semipalmated Sandpipers are among the smallest scolopacid sandpipers in the Americas. They are considered 'sister-species' that overlap in many morphological traits, have similar appearance in basic plumage, and have similar breeding biology (Holmes 1972, Phillips 1975, Gratto-Trevor 1991, Paulson 1993, Haig et al 1997, Sibley 2000, Ruthrauff et al 2009). The species flock, feed and roost together in Paracas, and at many other staging and non-breeding grounds along the migratory route (Phillips 1975, Fernandez et al 2003, Rice et al 2007, Hope et al 2011). However, the species also have different life history strategies with respect to breeding population and migration distances (Tavera et al 2016, Chapter 1: Table 1.1, Chapter 2: Table 2.1, Fig. 2.3, Fig. 2.4). The central and eastern populations of Semipalmated Sandpipers migrate southward about one month later than Alaska-breeding Western and Semipalmated Sandpipers (Lank et al 2003, Hicklin and Gratto-Trevor 2010, Franks et al 2014). Their migratory routes from their breeding grounds to Perú follow different flyways and have different migration distances. Those flying from the subarctic western Alaskan coast use mainly the Pacific flyway, while those from northern Quebec use the Mississippi and Atlantic flyways (Harrington and Morrison 1979, Hicklin and Gratto-Trevor 2010, Franks et al 2014). They all arrive to Paracas at somewhat different times, with groups of birds arriving from early October (most likely second years) and others arriving in early November. Migrants return to the northern hemisphere the following March and April.

Semipalmated Sandpipers exhibit a cline in bill length across their breeding range, ranging from short bills in the west to long bills in the east (Gratto-Trevor et al 2012). The cline to some extent translates southwestward into an east-west cline on the non-breeding grounds and allows bill length to be used as a partial surrogate for identifying breeding populations of origin. Based on bill lengths, Semipalmated Sandpipers at Paracas come from across their entire breeding range, with birds of eastern origins arriving in Paracas later than western populations (Tavera et al 2016, Chapter 2). Western Sandpipers show a differential latitudinal migration by sex, with a higher proportion of males at northern than at southern sites (Nebel et al 2002). At Paracas Western Sandpipers adults have female to male ratio of ca. 3:1 (unpublished data). Juveniles of both species may use an ‘over-summering’ strategy, whereby in their first year of life individuals remain in the south during the breeding season, deferring their first northward migration and breeding attempt (Gratto-Trevor and Morrison 1981, Fernández et al 2004, O’Hara et al 2005). All Western Sandpiper juveniles, and about 69% of Semipalmated Sandpiper juveniles at Paracas do not prepare to migrate north and breed in their first year (Tavera et al 2016).

The life history strategy differences between the two species suggest that they make different tradeoffs with respect to their survival probabilities at the austral extremes of their non-breeding ranges. The species, populations, and age classes that converge at Paracas may have different non-breeding survival rates. In this study, we model annual survivorship and non-breeding residence probability for both species as a function of year, age, sex, breeding population of origin (as inferred for Semipalmated Sandpipers by bill length), selection on wing length and ENSO (El Niño) index. We implemented an open robust sampling design model in a multistate framework (ORDMS; Kendall and Nichols 2002, Kendall 2004, Schaub 2004) with a general encounter history to test all our predictions. ORDMS models estimate apparent annual survivorship **S** using an open-population approach. They also produce estimates of within season monthly residence probabilities $\boldsymbol{\phi}$. Permanent emigration within the non-breeding season cannot be distinguished from mortality, thus to the extent that birds leave the site within the non-breeding season, $\boldsymbol{\phi}$ cannot be used directly to estimate complete non-breeding seasonal survivorships.

I present a series of 9 numbered *a priori* predictions about annual shorebird survival rates and non-breeding seasonal survival rates for birds captured at Paracas, based on existing theories and models about how animals are distributed over broad landscapes in the non-breeding period, and from other empirical studies.

4.2.1. Migration Distance

We can start with the Ideal Free Distribution (IFD) model which states that overall mean fitness of individuals should be equalized across all non-breeding sites (Fretwell and Lucas 1970, Castro et al 1992). Many factors can create occasions where the IFD does not apply, such as the buffer effect combined with a dominance displacement model, to explain why some individuals (often low quality) are displaced to poorer habitats (Gill et al 2001) and consequently have lower fitness. The IFD is nonetheless useful as a null hypothesis or framework, assuming that an IFD-like process offsets costs and benefits to produce equivalent fitness across sites against which to assess alternative models (Reneerkens et al 2019).

A standard assumption is that longer migration distances carry higher survivorship costs (Chapter 1, Fig. 1.). We can add to this assumption the Time Allocation and the Physiological Tolerance models for shorebird nonbreeding distribution, which predict that non-breeding survival should increase at sites further away from the breeding area due to more benign climate or other factors (Hockey et al 1992, Myers 1981). Under an IDF, variation in non-breeding survivorship would offset variation in migration cost. If these assumptions apply, we should find: (1) similar overall annual survivorships, but (2) higher non-breeding survival estimates in Perú relative to more northern non-breeding populations of both Western and Semipalmated Sandpipers.

Using the same two assumptions, we can make predictions about the relative annual survivorship of eastern versus western Semipalmated Sandpipers. The eastern birds, with longer bills, migrate to Paracas a ≈3,000 km shorter distance than birds of western origins, about a 25-30% shorter distance. Assuming similar survivorship at Paracas during the non-breeding season, and no additional offsetting cost: (3) the shorter distance, longer-billed migrants should have higher annual survival than the shorter-billed western populations. As a complication possibly unrelated to migration distances, several lines of evidence suggest that eastern populations of Semipalmated Sandpipers underwent substantial population declines during the 1990s–2000s, while western populations were more stable (Gratto-Trevor et al 2012, Morrison et al 2012). If this were still occurring during our study years, longer-billed eastern birds should have lower annual survivorships. Such alternative processes could offset each other, resulting in no difference between regions.

4.2.2. Life History Trade-off

Under the hypothesis that oversummering compensates for the loss of breeding opportunity with higher survivorship (Chapter 1, Fig. 1.1), or following my results from Chapter 3 (Table 3.3), we predict: (4) that annual survivorship of Western Sandpiper juveniles should be higher than that of adults, since all juveniles stay as oversummering birds in Paracas. In theory, this may allow birds to conserve energy for survival and future breeding opportunities and avoid survivorship risk altogether from migration and breeding, when breeding success as a first year is low anyway (Gratto et al 1983, Reznick et al 2002, Ricklefs and Wikelski 2002, Robinson et al 2010, Kwon in prep.). For Semipalmated Sandpipers, we predict: (5) a similar trend but smaller difference in age-specific annual survivorship, because ca. 30% of juveniles attempt to migrate north and breed (Tavera et al 2016).

4.2.3. Age and Sex effects

For the age effects: if juveniles have lower foraging proficiency or due to competitive subordination (Hockey et al 1998) are excluded from safer places and/or invest less in anti-predator behavior than adults (Metcalfe and Furness 1984, Cresswell and Whitfield 2008), we predict: (6) a higher annual survival for adults than of juveniles for both species. This is the opposite of predictions 4 and 5.

Regarding the sex term, Western Sandpipers show a differential migration by sex, where more females migrate to sites further south (Nebel et al 2002, Fernández et al 2004, O'Hara et al 2006). We might therefore expect females at Paracas to have a higher survivorship than males. Alternatively, we might also expect that the few males at Paracas might have a high survival, producing an ideal free like distribution with respect to the success of the sexes at a given local sex ratio. We predict (7) no difference in annual survival estimates between sexes. For Semipalmated Sandpipers, no test of sex differences was made, given the absence of sufficiently large sexual dimorphism to allow reliable differentiation of females from males (Sandercock 1998).

4.2.4. Morphology

An intercontinental decrease of wing-length has been recently reported for Semipalmated Sandpipers, which the authors interpret as an adjustment or adaptation to a predator population increase (Lank et al 2017). Selection for greater escape performance over flight efficiency favours shorter wings (Lockwood et al 1998, Warrick et al 1998). If such selection was ongoing during our study, we should observe: (8) that shorter-winged Semipalmated Sandpipers had higher annual survival than longer-winged ones.

4.2.5. Seasonal El Niño effect

Empirically, previous work in Ecuador found a negative effect of El Niño on shorebird annual survivorship, meaning a lower survivorship in years with warmer water temperatures (O'Hara et al 2007). If this pattern is general, we should find: (9) a negative relationship between a climatic index capturing El Niño variation and our seasonal survivorships.

Finally, as a separate analysis I will answer if the size of the survival advantage is distance dependant. To do this I will use results from Chapter 2 to decompose the contributions from migrant and oversummering birds in Semipalmated Sandpipers. In Chapter 2 (Addendum) I found that the frequency of partial post-juvenal wing molt (PPW) and culmen length are positively related (Fig. A2.1). I will use this result to calculate the survival of migrants necessary to produce the annual survival level for the combined population, under the assumption that oversummering survival is independent of migration distance.

My analyses present a novel opportunity to test various hypotheses to the sandpipers spending the nonbreeding season at Paracas. The role of each one of these variables on survival could help us understand population trends during the non-breeding season, but most importantly could serve as a tool to identify threats before detectable abundance declines occur.

4.3. Methods

4.3.1. Study Site

We captured, marked, released and resighted Semipalmated and Western Sandpipers at the Paracas National Reserve in Peru, a Natural Protected Area located in the Department of Ica, 250 km south of Lima city. Fieldwork was conducted on La Aguada beach (13°51‘35.47″S 76°16‘16.16″W), an intertidal mudflat <2 km long, surrounded by coastal desert (Fig. 3.1). The near-shore section of the mudflat has no vegetation and most of the lower intertidal zone is covered with soft mud filled with polychaetes, fly larvae, microscopic sea shrimp, and beetles, and covered by biofilm and decaying algae in shallow water (Senner and Angulo 2014).

Figure 4.1. Location of the fieldwork on "La Aguada" beach in Paracas National Reserve, Perú. Black solid curve is the exact place for shorebird captures. Resightings were conducted along the entire beach.

4.3.2. Data Collection

We collected capture–mark–recapture data between October 1 and April 15 during 7 consecutive non-breeding seasons, from 2011-2018. We conducted seven to nine-day campaigns during the new moon phases within each season, with trapping occasions separated by a minimum of 20 days (Chapter 1, Fig. 1.3). Shorebirds were captured primarily at night with mist-nets. Time of capture depended on the tide cycle, beginning three hours after the evening high tide and ending three hours before the subsequent high tide, ranging between 20:00h and 06:00h. Fewer than 5% of the birds were captured with bungie-powered whoosh-nets on rising tides between 06:00h and 09:00h. Captured birds were banded on the right tarsus with an incoloy metal band obtained from the CORBIDI Bird-Banding Program (the Peruvian bird-banding scheme). Birds were color-marked with a three-character-coded yellow flag placed on the left tibia (e.g. 3AT), following the Panamerican Shorebird Program protocol (Myers et al 1983, Myers 1984) to identify individuals, and allow collection of local and foreign resighting data. Birds were assigned to two age categories based on plumage characteristics. Juveniles (individuals in their first non-breeding season from 0 to 12 months old) were recognized by the retained juvenile type inner greater coverts, and adults (12+ months old) by wing and flight feather characteristics (Prater et al 1977, but see Franks et al 2014). Western Sandpipers were sexed by culmen length, classified as male (M), female (F) (Page and Fearis 1971; for regional accuracy see Ortiz 2017). Morphometric measurements (culmen length and flattened wing) for both species were taken with a dial caliper (0.5 mm) and a wing ruler (0.5 mm). To avoid bias in measurements taken by different people, we relied on only one person to take each measurement through all the years. Birds were weighed using a digital scale (0.5 g) and released less than 10 min after capture time. All capture efforts were carried under the supervision of a NABC (North American Banding Council) certified shorebird trainer (principal author of this study) with 5 field assistants and 5-7 volunteers.

Resighting data from marked individuals were collected during the trapping field periods from autumn 2011 to spring 2018 (Chapter 1, Fig. 1.3). Resighting effort was similar across years, except that 2013 was limited to the last months of the year (November and December) and fewer resighting hours. Intensive surveys were conducted each morning between 06:00h to 09:00h, with an equal effort by 3 experienced people, who located, visually observed and recorded marked individuals across the entire beach.

4.3.3. Mark-Recapture/Resighting Survival Analysis

All capture, recapture, and resighting information from each sampling occasion (the 7–9 consecutive sampling days in each month) were combined to generate a single re-encounter value (0 = ‘no’; ‘1’ = ‘yes’) for each of the 6 months (Oct-March) in each of the seven non-breeding seasons from 2011/12 to 2017/18. For both species we included data from first captures (SESA=1,286/WESA=1,162), and their total reencounters (SESA=5,495/WESA=2,505) as well as recaptures (at least 4 weeks after being initially captured; SESA n=316, WESA n=102).

For Semipalmated Sandpipers, an average of 43% of birds were never seen after the month of capture, ranging from 26% to 63% annually, and 47% were never seen after the year of capture (excluding the birds captured the last year of the study), ranging from 37% to 73% annually. Reencountered birds were seen again on 1 to 22 subsequent occasions averaging 3.2 occasions, ranging from 2.0 to 3.5 per year. The rate of reencounters in subsequent years (after banding) averaged 1.70 over all years, ranging from 1 to 1.90 annually (excluding the logical zero from the last season). For Western Sandpipers, 34% of marked birds were never seen again after the month of capture, ranging from 16% to 55% annually and 43% were never seen after the year of capture (excluding the birds captured the last year of the study), ranging from 29% to 68% annually. Reencountered birds were seen again on 1 to 15 subsequent occasions averaging 3.2 occasions, ranging from 1.9 to 4.2 per year. The rate of reencounters in subsequent years was 1.65 in average, ranging from 1 to 1.97 annually, excluding the last year. Further information of the distribution encounters by occasion and by year are given in Appendix F.

We used a simplified version of an open robust design multi-state model (ORDMS) (Kendall and Bjorkland 2001, Kendall 2004) that did not include parameters related to observable and unobservable states. We estimated annual survival and monthly residence rates for each species, allowing survival to vary by year, age, sex (in Western Sandpipers only) as categories, and culmen length, wing length and an index value for El Niño Southern Oscillation (ENSO; see below) as linear covariates. An

ORDMS requires an ‘open’ population for the primary sampling periods, whereby individuals can enter or exit the study area, through immigration, permanent emigration or death. We defined the length of our primary sampling periods as the non-breeding capture period (October through March) during each year of the study. “Year” refers to the calendar year during which each non-breeding season’s work began (thus the 2011–2012 season is ‘2011’). We defined our secondary sampling periods as each monthly sampling occasion, treating them as ‘closed’ populations for the 7-9 days of field work during which no individuals entered or exited the study area. However, individuals were allowed to enter the population between secondary sampling periods, temporary or permanent departures between secondary periods were accounted for in apparent monthly resident rates (Pollock 1982, Kendall et al 1995). The model structure is shown in Fig.4.2.

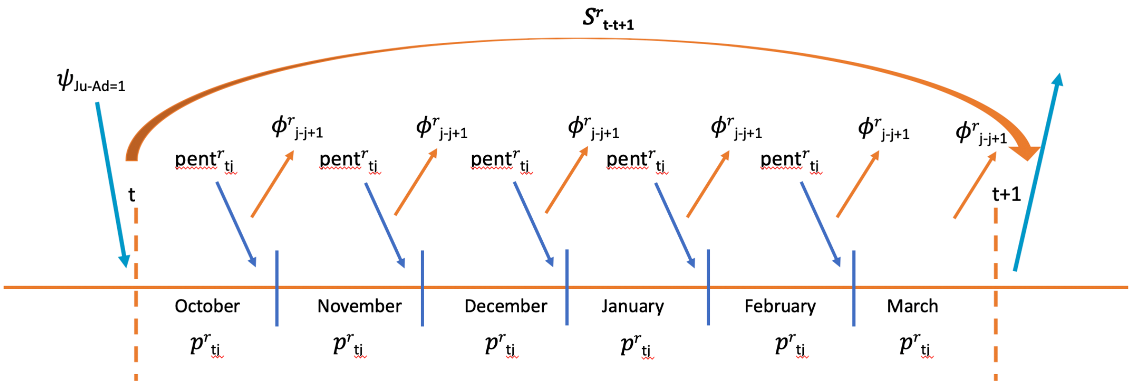

Figure 4.2. Model structure for the Open Robust Design Multistate Model (ORDMS). $S^r_{t\text{-}t+1}$ is apparent annual survival, $\phi^r_{j\text{-}j+1}$ non-breeding monthly residency, $pent^r_{tj}$ is the probability that a bird in state r is a new arrival to the study area, p^r_{tj} is the probability of detection and ψ is the probability of a bird making a transition, which are 3 fixed terms.

Our ORDMS model estimate values for five parameters:

(1) Apparent annual survival S^r, hereafter annual survival, is the probability of a bird for state r of surviving between primary occasions and not permanently emigrating;

(2) ψ_t^{rs} is the probability of a bird making a transition between state **r** to state **s** at year t.

(3) For a given primary sampling period t, $\mathbf{pent}^{r}_{t\mathbf{j}}$ is the probability that a bird in state **r** is a new arrival to the study area during secondary occasion **j**.

(4) $p^{r}_{t\mathbf{j}}$ is the probability of detection of a bird in state **r**, given that is available, during secondary occasion **j**.

(5) And $\phi^{r}_{t\mathbf{jk}}$ hereafter non-breeding monthly residency, is the probability that a bird of state **r** will stay in the study area between secondary occasions **j** and **j**+1, given that they entered **k** secondary occasions prior.

To simplify our models, we fixed ψ such that juveniles returning the next primary period become adults (fixed = 1). We modeled pent and p as varying based on real resighting effort, collapsed into monthly averages per year) to account for annual variation in effort, particularly lower resighting effort in the first two years. To look for relationships with ENSO, we used the Peruvian Coastal Thermal Index (PCTI), a recently created index which takes in account the total variation of the Sea Surface Temperature anomalies of the Peruvian Upwelling Ecosystem (Quispe-Ccalluari et al 2018). This index goes from -2 to 2 with high values meaning a warm phase of El Niño and low values a cold phase one. We used the ENSO monthly indices during the non-breeding season (from October to March) then we collapsed them per year, which were added to the design matrix as linear and quadratic factors.

The final sampling structure was a matrix of 7 occasions for each of the first six study years, and 6 occasions in the final year, for a total of 48 encounter occasions. To create a capture history, we merged the capture and resighting data, checked that all flags in the resighting data were also in the capture data, removed multiple observations of flags seen in the same sampling occasion, and ordered the data into the robust model format. We made the capture history as a character vector and wrote out the input file as a .text to be run in RMark. The final data files include an individual identifier, the capture-recapture history, the linear individual (culmen and wing length) and the categorical (year, age, sex) covariates, and the annual ENSO index.

To run the ORDMS, we first needed to specified number of primary and secondary occasions to create the design matrix. A model list was created of all possible subsets of combinations of all our covariates with no interaction terms. For

Semipalmated Sandpipers S was modelled with a series of factors and covariates with 21 options, ϕ was modelled as a series of covariates with 7 options, $p$ent was modelled with a series of covariates with 3 options, p was modelled as a series of covariates with 6 options and ψ was modelled with 1 fixed parameter. This resulted in a candidate model set with 21x7x3x6x1 = 2,646 models. A similar process was followed for Western Sandpipers with sex as an additional factor for S and ϕ producing a candidate set with 29x9x3x6x1 = 4,698 models. The detailed parameter structures are given in Appendix G.

We believed all our covariates could have a potential effect against and within in each other, therefore we allow them to remain constant or to vary among years. We used multinomial logit (mlogit) link function to estimate beta and real parameters. Most parsimonious models were selected based on the Akaike information criterion corrected for the effective sample size (AIC_c; Burnham and Anderson 2002). Models with ΔAIC <2 were considered the best ones supporting the data and were used to estimate parameters and respective standard errors (SEs; Burnham and Anderson 2002). To allow for comparisons between species and age class, we also present year and age estimates from the relevant models. Currently there is no general goodness-of-fit test for the type of ORDMS models we used in our analysis, and the median ĉ procedure implemented into program MARK (ĉ is an estimated overdispersion parameter) is not available for robust design data.

All mark-recapture models were constructed using the package “Rmark” (Laake 2013) and run with the program R version 3.5.1 (R Core Team 2016). The estimates of monthly residency times produced for the first two seasons (2011 and 2012) were unreliable because of small sample sizes of marked birds and limited reencounter data (Chapter 1, Tables 1.2, 1.3, Fig. 1.3), and are not included in our results. Similarly, the last estimate of annual survivorship (2018) was excluded because of insufficient subsequent encounter data.

4.3.4. Estimating survival as a function of migration distance for juvenile Semipalmated Sandpipers

I estimated the relationship between migration distance and survivorship rate of migrant juvenile Semipalmated Sandpipers by decomposing the overall annual rate of the population with the following equation:

SURVIVAL rate of the population = (proportion Migrants * survival rate of Migrants)

+

(proportion Oversummering birds * survival rate of Oversummering birds)

I applied this equation separately to birds to each culmen class; the weighted sum of survivorships over all classes must describe that of the population as a whole. I estimated the proportion of migrant and oversummering birds in each culmen class from Figure 2.5. The probability of migration by class was taken from the probability of partial post juvenal wing molt presented in Chapter 2 (Addendum), I assumed that the annual survival of oversummering birds was independent of culmen class (migration distance), which seems a reasonable first approximation, and used three different estimates of it. The lowest was 0.79, from Table 3.2, for juvenile Semipalmated Sandpipers. The highest was 0.93, derived from Western Sandpiper juveniles' early monthly residency rates (see below), and I also present results for an intermediate value of 0.83.

4.4. Results

4.4.1. Model Selection for Semipalmated Sandpipers

Model selection for Semipalmated Sandpipers was made from 2,646 models run. We present results from top models with a ΔAICc ≤ 2 (Table 4.1). In the top model, apparent annual survival S (henceforth annual survival) was a function of year and culmen length. The second top model, with a similar model weight, (model 1: $w_1 = 0.37$, model 2: $w_1 = 0.34$) added age class as a predictor. The third model substituted an ENSO effect for age, but the wide 95% CI of the ENSO parameter overlapped 0: -0.53 ± 32.32 SE (LCL = -63.89, UCL = 62.83). Figure 3.2. plots the beta coefficients for predictor variables.

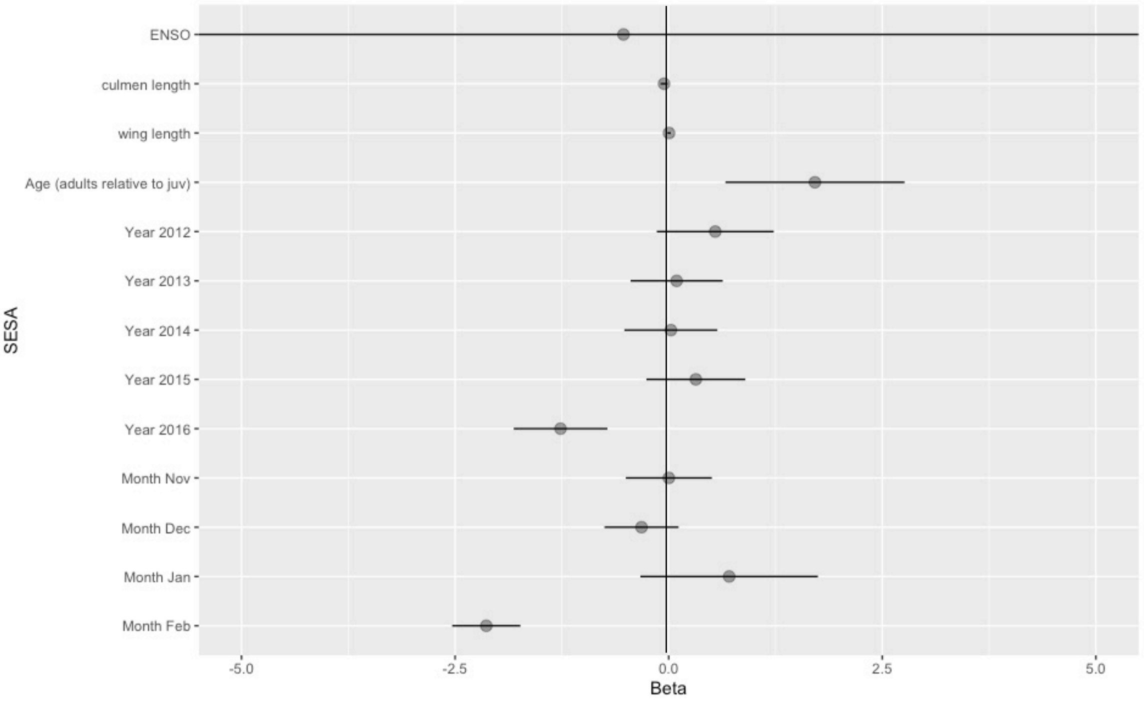

Figure 4.3. **Beta coefficients from models of annual survivorship and monthly residency for Semipalmated Sandpipers at Paracas for predictor variables ENSO, culmen length, wing length, age, year and month.**

Table 4.1. **Model selection of the best fitting survival models for Semipalmated Sandpipers. The first column specifies the number of model, the second column specifies the type of model within its parameters: S for annual survival, ψ as transition probability, pent as probability of arrival of a new bird, ϕ for monthly residency and p as the probability of resighting. K is the number of parameters.**

Model	Parameters	AICc	Δ AIC	ω AIC	Deviance	K
1512	S (time + culmen) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	*43558.37*	*0*	*0.37*	*43488.08*	*35*
2268	S (time + age + culmen) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	43558.57	0.19	0.34	43486.25	36
1638	S (time + enso + culmen) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	43560.39	2.01	0.13	43488.08	36
1890	S (time + enso + enso^2+ culmen) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	43562.41	4.03	0.04	43488.08	37
756	S (enso + enso^2 + culmen) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	43563.74	5.36	0.02	43499.49	32
2262	S (time + age + culmen) ψ (.) $pent$ (month) ϕ (year) p (year + month)	43563.89	5.51	0.02	43493.59	35
1764	S (time + enso) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	43564.90	6.53	0.01	43494.61	35
1008	S (enso + enso^2+ age + culmen) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	43565.64	7.26	0.009	43499.37	33
1632	S (time + enso + culmen) ψ (.) $pent$ (month) ϕ (year) p (year + month)	43565.72	7.34	0.009	43495.42	35
2016	S (time + enso + enso^2) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	43566.92	8.54	0.005	43494.61	36
1884	S (time + enso + enso^2 + culmen) ψ (.) $pent$ (month) ϕ (year) p (year + month)	43567.73	9.36	0.003	43495.42	36
750	S (enso + enso^2 + culmen) ψ (.) $pent$ (month) ϕ (year) p (year + month)	43568.99	10.62	0.001	43506.76	31
882	S (enso + enso^2) ψ (.) $pent$ (month) ϕ (year + age) p (year + month)	43569.41	11.03	0.001	43507.17	31
1758	S (time + enso) ψ (.) $pent$ (month) ϕ (year) p (year + month)	43570.25	11.87	0.0009	43501.97	34
1002	S (enso + enso^2 + age + culmen) ψ (.) $pent$ (month) ϕ (year) p (year + month)	43570.89	12.51	0.0007	43506.64	32
1134	S (enso + enso^2 + age) ψ (.)$pent$ (month) ϕ (year + age) p (year + month)	43571.36	12.98	0.0005	43507.11	32
2010	S (time + enso + enso^2) ψ (.) $pent$ (month) ϕ (year) p (year + month)	43572.27	13.89	0.0003	43501.97	35
876	S (enso + enso^2) ψ (.) $pent$ (month) ϕ (year) p (year + month)	43574.66	16.29	0.0001	43514.45	30

Annual survival

The average annual survival (S) in the top model was estimated as 0.71 ± 0.03 SE, across age classes, ranging from 0.67 ± 0.05 SE in 2011 to 0.73 ± 0.03 SE in 2015. The age-specific model produced somewhat lower annual survival estimates for juveniles than adults (average for juveniles: 0.68 ± 0.04 SE, average for adults: 0.72 ± 0.03 SE) (Fig. 4.3, more details in Appendix B).

Culmen length was negatively related to annual survival: -0.05 ± 0.02 SE (LCL = -0.09, UCL = -0.01) (Fig. 4.4), based on the second-best model (Table 4.1). Since age seemed important, we re-ran only the top model allowing for an interaction between culmen length and age. The effect size of culmen for juveniles was similar to that in the pooled (juveniles and adults) model: -0.05 ± 0.08 SE (LCL = -0.21, UCL = 0.10), but no effect was estimated for adults: 0.00 ± 0.09 SE (LCL = -0.17, UCL = 0.17). With lower power than the pooled analysis, the 95% CI estimate for Juveniles included zero, but juveniles rather than adults must drive the estimate of the pooled analysis.

Wing length had a slightly positive but non-significant relationship with survivorship: 0.004 ± 0.01 SE (LCL = -0.02, UCL = 0.02) (Fig. 4.5).

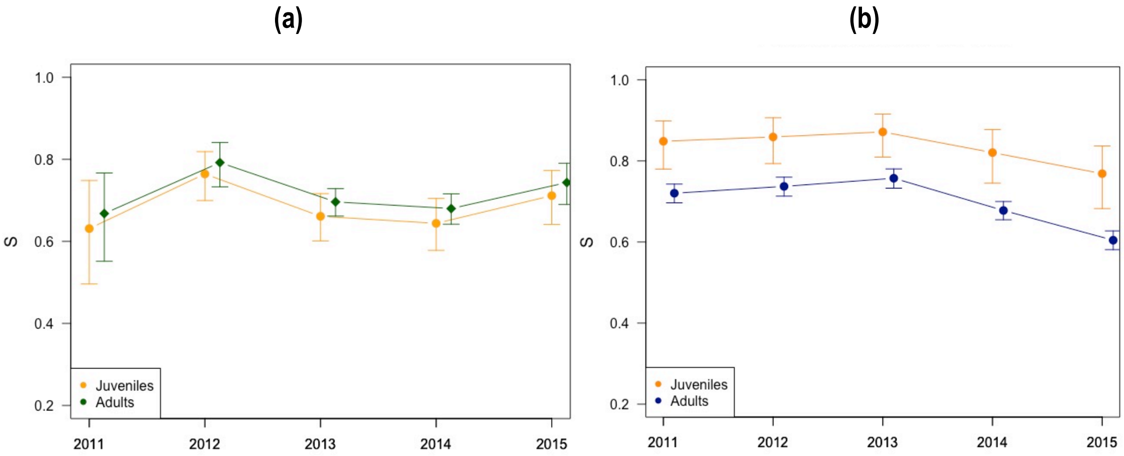

Figure 4.4. **Apparent Annual Survival estimates of adult and juvenile Semipalmated Sandpipers (a) and Western Sandpipers (b) captured at Paracas, Perú. Vertical lines show standard errors (SE). Estimates from top model (Tables 4.1; 4.2).**

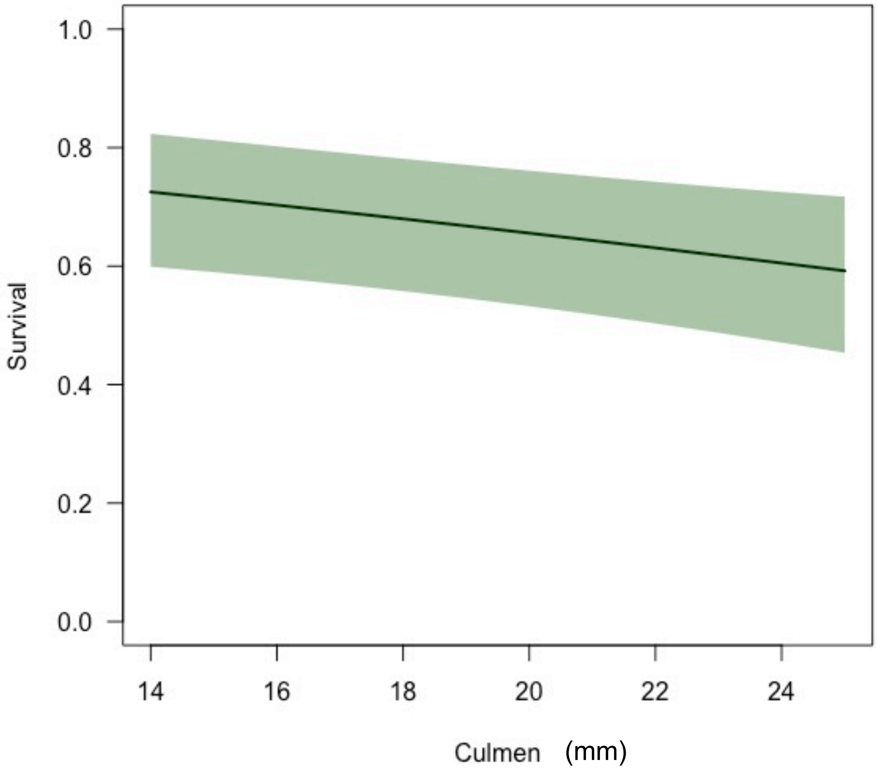

Figure 4.5. **Apparent Survival for Semipalmated Sandpipers as a function of culmen length. Shade area represents the upper and lower 95% confidence intervals.**

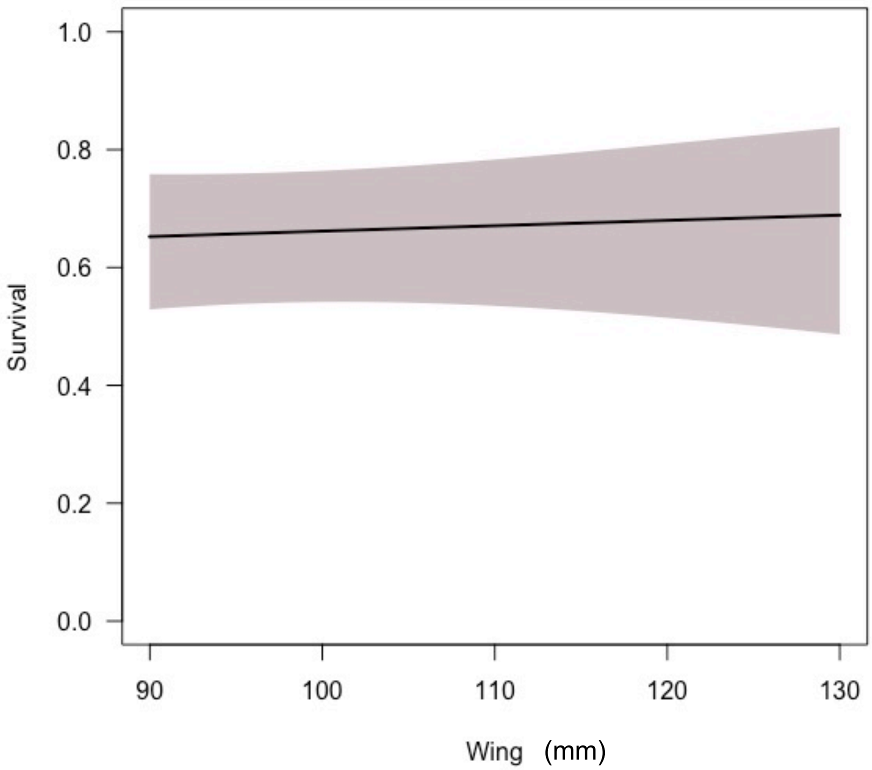

Figure 4.6. **Apparent Survival for Semipalmated Sandpipers as a function of wing length. Shaded area represents the upper and lower 95% confidence intervals.**

Monthly residency

Monthly residency (ϕ) during the non-breeding period ('residency') was best described by an interaction in year and age in all three top models (Table 4.1). Juvenile birds had higher residency estimates than adults (juveniles: 0.84 ± 0.03 SE, Adults: 0.77 ± 0.02 SE (Fig. 4.6, more details in Appendix B). Although 'month' as a predictor was not included in the top model, we believed that the candidate set should be defined by the biology of the system, therefore we examined its potential effect by re-running the best model with 'month' in it. Monthly residency of juveniles ranged annually from 0.86 ± 0.02 SE in October to 0.93 ± 0.04 in January declining to 0.44 ± 0.04 SE in February. For adults, it varied from 0.83 ± 0.03 SE in October to 0.91 ± 0.04 SE January decreasing 0.37 ± 0.02 in February when birds left the area (Fig. 4.7).

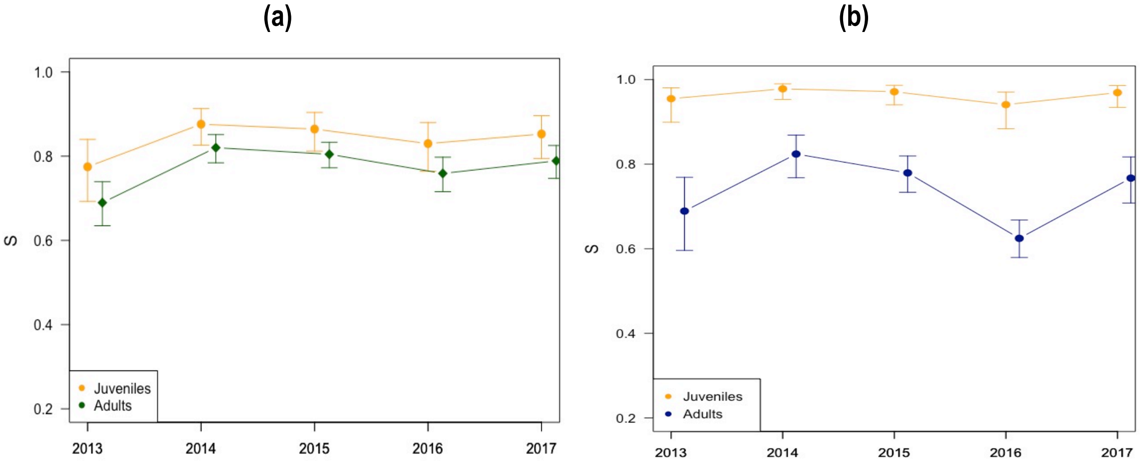

Figure 4.7. **Annual variation in Monthly Residency (ϕ) by year of adult and juvenile Semipalmated Sandpipers (a) and Western Sandpipers (b) captured at Paracas, Perú. Vertical lines show standard errors (SE).**

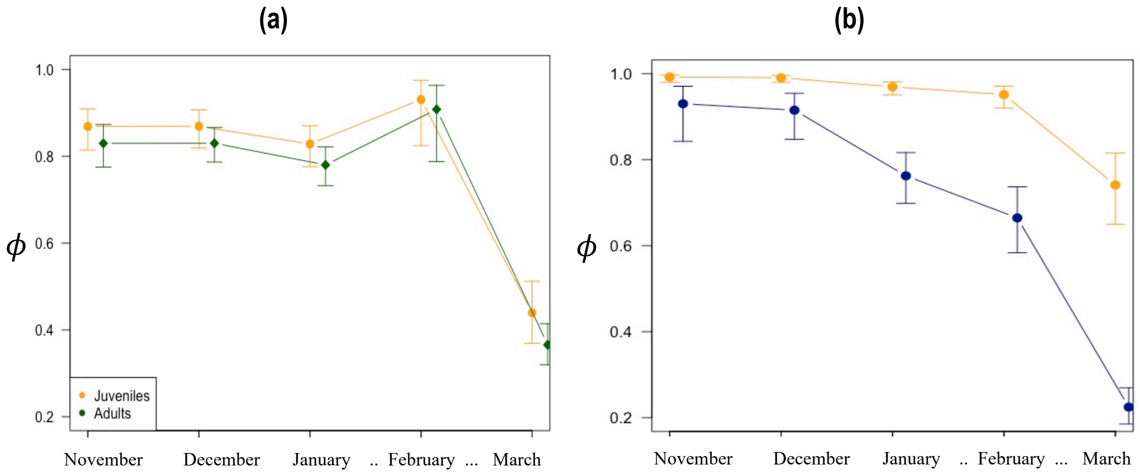

Figure 4.8. Monthly residency (ϕ) estimates of adult and juvenile Semipalmated Sandpipers (a) and Western Sandpipers (b) captured at Paracas, Perú. Vertical lines indicate standard errors (SE). Using the most parsimonious model.

4.4.2. Model Selection for Western Sandpipers

Model selection for Western Sandpipers was made from 4,698 models run. Four top models had ΔAICc ≤ 2 (Table 4.2). Age and ENSO were included in all four models as the main covariates explaining annual survival, in contrast to Semipalmated Sandpipers. The second model added culmen length, which the fourth replaced with sex, and which likely captured much of the same variation (Table 1.1). The third model included an ENSO quadratic factor in place of culmen or sex. Figure 4.8. plots the beta coefficients for predictor variables.

Table 4.2. Model selection of the best fitting survival models for Western Sandpipers. The first column specifies the number of model, the second column specifies the type of model within its parameters: S for annual survival, ψ as transition probability, pent as probability of arrival of a new bird, ϕ for monthly residency and p as the probability of resighting. K is the number of parameters.

Model	Fixed factors	AICc	Δ AIC	ω AIC	Deviance	K
948	S (enso + age) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	*16609.55*	*0*	*0.36*	*16549.04*	*30*
786	S (enso + age + culmen) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16610.43	0.87	0.23	16547.89	31
1920	S (enso + enso^2 + age) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16611.35	1.79	0.14	16548.81	31
1110	S (enso + age + sex) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16611.52	1.96	0.13	16546.94	32
2082	S (enso + enso^2 + age + sex) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16613.34	3.78	0.05	16546.73	33
4349	S (-1 + time + age) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16614.55	4.99	0.02	16545.89	34
4187	S (time + age + culmen) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16615.36	5.80	0.01	16544.67	35
4511	S (time + age + sex) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16616.64	7.08	0.01	16543.90	36
462	S (enso) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16621.46	11.90	0.0009	16562.98	29
300	S (enso + culmen) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16622.54	12.98	0.0005	16562.02	30
1434	S (enso + enso^2) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16623.26	13.70	0.0003	16562.75	30
624	S (enso + sex) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16623.71	14.15	0.0003	16561.16	31
1272	S (enso + enso^2+ culmen) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16624.37	14.81	0.0002	16561.82	31
1596	S (enso + enso^2 + sex) ψ (.) $pent$ (month) ϕ (month + age) p (year + month)	16625.54	15.98	0.0001	16560.96	32

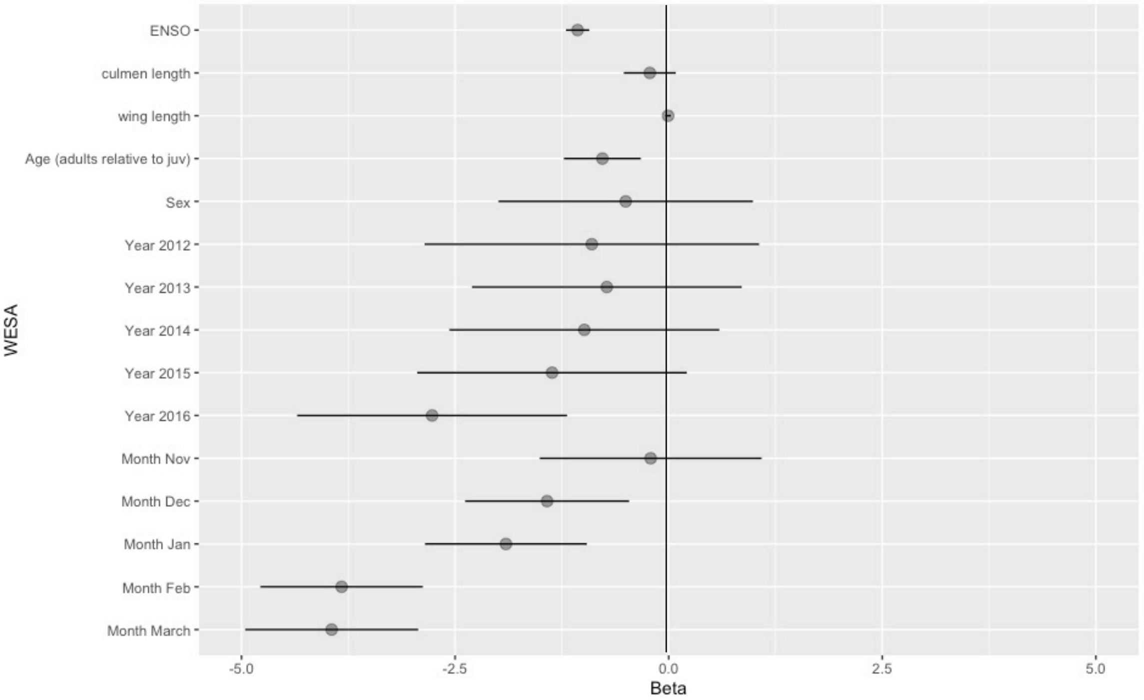

Figure 4.9. Beta coefficients from models of annual survivorship and monthly residency for Western Sandpipers at Paracas for predictor variables ENSO, culmen length, wing length, age, year and month.

Annual survival

In the top model, annual survival (S) of Western Sandpipers was substantially higher for juveniles than for adults (juveniles: 0.83 ± 0.03 SE, adults: 0.70 ± 0.01 SE; parameter estimate for adults relative to juveniles: -0.78 ± 0.23 SE (LCL = -1.23, UCL = -0.32) varying little annually (Fig. 4.3, more details in Appendix C). ENSO was negatively related to annual survival: -1.07 ± 0.07 (LCL = -1.20, UCL = -0.93). The third model added a quadratic ENSO term, which was positive, but with confidence limits including zero: 0.08 ± 0.16 SE (LCL = -0.24, UCL = 0.40), indicating a slowing rate of decline or possible increase in survivorship at the highest ENSO values.

The second and fourth models showed that shorter-billed birds had higher survival rates than longer-billed birds, which could represent breeding population and/or sex differences. The estimate for culmen for the second model was -0.03 ± 0.02 SE (LCL = -0.07, UCL = 0.02), and the estimate for sex for males relative to females for the fourth model was: 0.18 ± 0.13 SE (LCL = -0.07, UCL = 0.43). To further study the possible culmen effect, we re-ran the model with and interaction between age and culmen. This model had an AICc score comparable to the top models (16610.99), suggesting it was a parsimonious one. Culmen, in general, retained a negative slope estimate: -0.22 ± 0.16 SE (LCL = -0.53, UCL = 0.08), but the 95% CI overlapped 0. adults have a positive coefficient relative to juveniles (estimate for adults relative to juveniles: 0.21 ± 0.16 SE (LCL = -0.11, UCL = 0.52)), with estimates for both overlapping zero. These results indicate that the culmen effect is primarily driven by effects in juveniles. We also re-ran the analysis to look for a culmen effect within age and sex and found again a negative relation of bill with survivorship. However, the result was less than robust and apparent only for juvenile females (-0.50 ± 0.80 SE (LCL = -1.99, UCL = 0.99)) making us believe that juvenile females must be the ones driving this potential negative relationship in the pooled analysis. When wing length replaced culmen length in the second model we found a similar trend, with a negative but non-significant relationship between wing length and survival (-0.007 ± 0.01 SE (LCL = -0.04, UCL = 0.02)).

Monthly residency

Monthly residency (ϕ) of Western Sandpipers was explained by an interaction between month and age in the most parsimonious model (Table 4.2). As with annual survivorship, juveniles had a higher average residency estimate than adults (juveniles: 0.89± 0.02 SE, Adults: 0.82± 0.03 SE, more details in Appendix C). To illustrate and compare monthly residency estimates with respect to Semipalmated Sandpipers, we ran the best model with age and year as predictors of monthly residency. Juveniles still show a higher and more constant survival rate than adults, while adults show a steep drop in survivorship in 2016 and recovery in 2017 (Fig. 4.6).

By month, estimates were substantially higher during the first part of the season, particularly for juveniles, which approach 1.00. The departure of birds from the study area is clearly visible in February and March, most distinctly for adults, reflecting the earlier migration of adults relative to juveniles (Fig. 4.7). Using the overall age-specific estimates, 0.49 of juveniles and 0.30 of adults remained at and/or survived at Paracas throughout the non-breeding season. While these are both higher than the corresponding estimates for Semipalmated Sandpipers, they are still too low to use as estimates of annual survivorship.

4.4.3. Survival as a function of migration distance

I estimated the survivorship of migrant juvenile Semipalmated Sandpipers with respect to migration distance by decomposing the annual population survivorship estimate by culmen class and migration/residency(oversummering) status, using the procedure outlined in section 4.3.4. Table 4.3. shows an example of how each value was computed over the range of culmen class lengths from 15 to 24 mm, when the annual survival rates for oversummering birds was set to 0.79 (Table 3.2). Figure 4.9 presents survivorship curves across a range of oversummering survivorship values. The highest 0.93 is derived from the early monthly residency times for Western Sandpipers (Fig. 4.8b, Appendix C: Table C2). In all cases, the migrant survival estimates were low for short culmen classes, which were Alaska-bound long-distance migrants, and level off for longer billed, shorter distance migrant birds headed for central and eastern Canadian breeding sites.

Table 4.3. Estimation of annual survivorship rate for migrant juvenile Semipalmated Sandpipers with respect to culmen length, assuming an annual rate of survivorship for oversumming individuals of 0.79. See methods for sources of information and calculation methodology.

			measured	measured	measured	predicted
Culmen classes (mm)	Proportion of population	Overall annual survival	Proportion of migrants	Proportion of non-migrants	Survival of oversummering birds	Survival of migrant birds
15.00	0.01	0.75	0.07	0.93	0.79	0.193
16.00	0.04	0.74	0.19	0.81	0.79	0.531
17.00	0.23	0.73	0.32	0.68	0.79	0.602
18.00	0.24	0.72	0.45	0.55	0.79	0.635
19.00	0.23	0.71	0.61	0.39	0.79	0.658
20.00	0.17	0.70	0.70	0.30	0.79	0.689
21.00	0.07	0.69	0.82	0.19	0.79	0.667
22.00	0.01	0.68	0.89	0.11	0.79	0.666
23.00	0.00	0.67	0.91	0.09	0.79	0.658
24.00	0.00	0.66	0.95	0.05	0.79	0.653

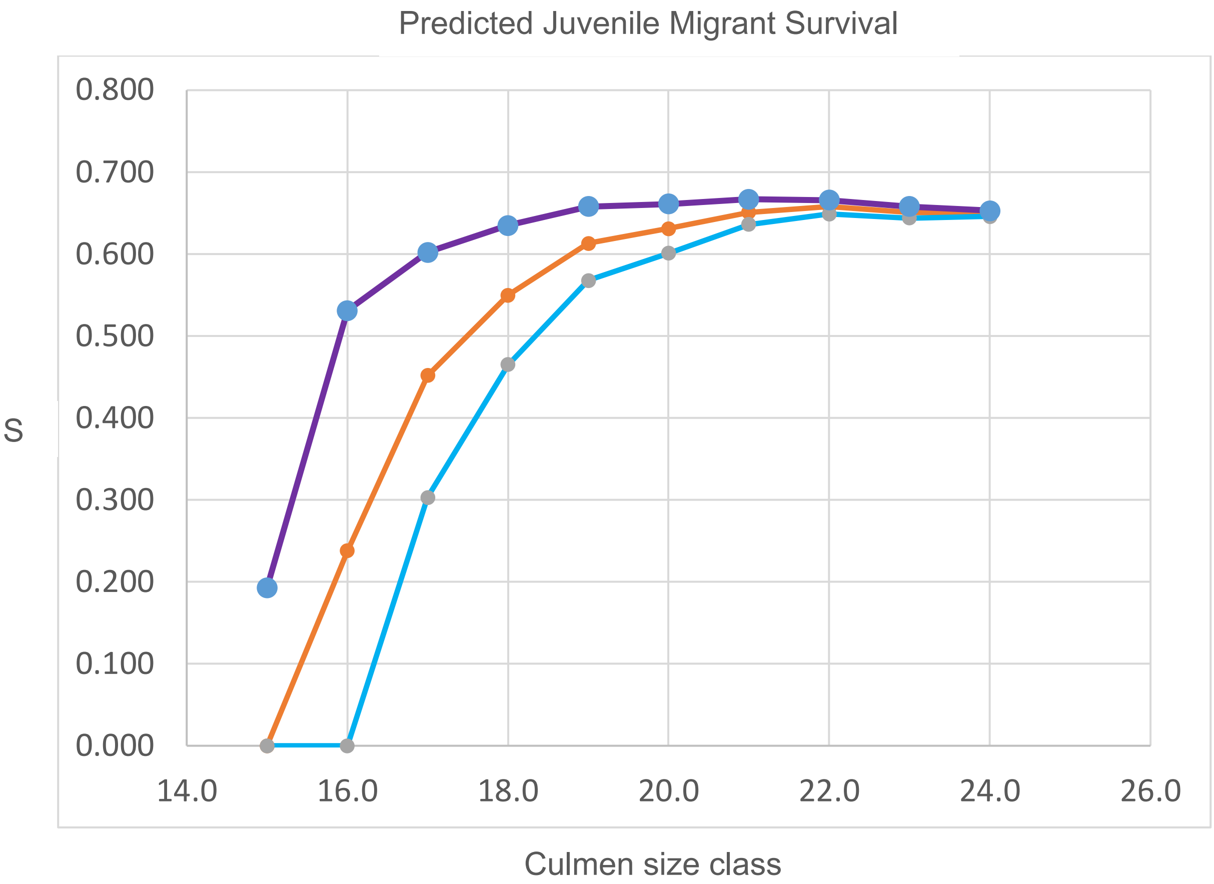

Figure 4.10. Predicted juvenile migrant survivorship of Semipalmated Sandpipers in relation to culmen length class. Estimates used for this graph were with oversummering survival set to 0.79 (purple line), 0.86 (orange line) and 0.93 (blue line).

4.5. Discussion

4.5.1. Annual survivorship

Our study provides the first set of annual survival estimates for adult and juvenile Western and Semipalmated Sandpipers at the most southern non-breeding site studied and provides information on their temporal pattern of residency at the site. Our estimates were drawn from an MSORD model which accounts for imperfect detection probability (Ruiz-Gutierrez 2016, Kendall et al 2019), allows estimation of movements in and out of the study area between years, achieving unbiased and more accurate parameter estimates (Kendall & Bjorkland 2001) and provides a flexible framework to model survival of structured migratory populations (Kendall et al 2019). We also tested for relationships between survival rates and variation in year, age, sex, culmen length, wing length and ENSO index.

Our estimates of annual survivorship for both species were substantially higher than previously published survival estimates from other non-breeding sites further north: S=0.71 for Semipalmated Sandpipers and S=0.76 for Western Sandpipers at Paracas, compared to S=0.49 for Western Sandpipers in Mexico (Fernández et al 2003), S=0.54 for Western Sandpipers in Panama (Fernández et al 2004), S=0.62 for Semipalmated Sandpipers in Puerto Rico (Rice et al 2007) and S=0.55 for both species in Ecuador (O'Hara et al 2007). If the estimates of annual survivorship from different non-breeding sites are reasonably methodologically comparable, there is not an ideal free distribution of survivorships (prediction 1), although in theory differences in reproductive performance could offset these. Birds spending the non-breeding season further north would have to have substantially higher annual reproductive success to offset lower survivorship. Given arctic sandpiper demography, in which adult survivorship has far stronger effect than annual reproductive performance on population growth rates (e.g. Hitchcock and Gratto-Trevor 1997), it is probably not possible to offset e.g. a 10-point difference in adult survivorship rate through higher reproductive performance. A similar result was recently reported for Sanderlings by Reneerkens et al (2019) wintering at sites from Europe to South Africa.

Our annual survival estimates were also closer than previous non-breeding values to the most recent annual survival study based on breeding-site data (Weiser et al 2018), which found an average of S=0.76 for Semipalmated Sandpipers compared with our 0.71, and 0.85 for Western Sandpipers compared with out 0.76. Weiser et al's estimates are nonetheless somewhat higher than the Paracas results. Breeding birds probably have higher site fidelity than non-breeding birds, and Weiser et al's model in fact incorporated spatial information into the estimates, which further raises apparent survivorship estimates towards actual survivorship values. Our finding of values this high suggests that site fidelity to Paracas is in fact nearly comparable to that from breeding sites. Our subsequent discussion therefore focuses in general on potential real survivorship differences rather than differences in permanent emigration/site fidelity.

The higher annual survivorship at Paracas is consistent with the Time Allocation and Physiological Tolerance models of shorebird non-breeding distribution (prediction 2). Both models posit that non-breeding survival increases in regions further from the breeding area through a compensation mechanism that involves a selection for climatically benign (southerly) non-breeding sites (Hockey et al 1992, Myers 1981). If we assume that mortality-related migration costs are greater to reach sites further south, and that costs during the breeding season do not differ with migration distance, the higher annual survivorship must occur due to higher non-breeding survivorship.

With respect to age, we found substantially higher juvenile than adult annual survival estimates for Western Sandpipers, which is opposite to what would be expected, based on potential lower foraging proficiency, social subordination, or riskier anti-predator behavior, which appear insufficient to produce lower rates than those of adults (prediction 6). The most probable explanation (prediction 4) is that Western Sandpiper juveniles obtain higher survival rates by following the oversummering strategy, deferring their first northward migration until their second spring of life (O'Hara et al 2007, Tavera et al 2016. This is consistent with life history theory that posits a life-history trade-off between survivorship and attempting to migrate and breed during the bird's first year of life (Gratto and Morrison 1981). This is the extreme endpoint of the 'migration distance cost' effect, and in this case apparently produces a strong effect on survivorship. Prediction 5 posited a similar, but smaller effect in Semipalmated Sandpipers, since only 30% of juveniles appear to migrate from Paracas. However, apparent survival of juvenile Semipalmated Sandpipers was in fact 0.04 lower than that of adults, so this prediction was not supported, and the results are in line with poorer age-specific performance (prediction 6). However, it is also possible that age-specific differences in site fidelity are important. Chapter 4 examines age-specific survivorship of Semipalmated Sandpipers in further detail using a different modeling approach specifically targeted at this question.

Semipalmated Sandpipers showed a significant negative correlation between culmen length and annual survivorship (Fig. 4.4), but after dichotomizing juvenile Semipalmated Sandpiper as migrants and oversummering birds by culmen size class (Table 4.3, Figure 4.9, 4.10), I found that annual survivorship was higher for long-billed (short-distance, eastern-breeding) migrant birds, and lowest for short-billed (long-distance, western-breeding) birds, consistent with the migration distance hypothesis (prediction 3). Dramatic population declines of non-breeding Semipalmated Sandpiper have been reported from the northeast coast of South America over the past 10-30 years, and it has been suggested that these were due to steep declines in eastern breeding populations (Gratto-Trevor et al 2012, Hicklin and Chardine 2012, Morrison et al 2012). For birds spending the non-breeding season at Paracas, at least, eastern populations show no sign of lower survivorship.

One of the key assumptions of this chapter is that culmen length class provides a useful metric of Semipalmated Sandpiper geographical region of origin (Harrington and Morrison 1979, Morrison 1984, Gratto-Trevor et al (2012). Although these studies highlighted geographical connectivity between breeding and non-breeding sites based on parallel clines of bill lengths, the level of uncertainty to assign an individual with a given culmen length to a specific part of the breeding range remains high. To assess the potential effect of this uncertainty on my analyses, Figure 4.10 illustrates the probability of oversummering or migration of a Semipalmated Sandpiper population as a function of culmen length in relationship to migration distance, as assessed by a regression of culmen lengths of breeding populations from Gratto-Trevor et al. (2012) at different distances from Paracas. The width of the parallelogram represents the within-population variation in culmen length. Although assignments of individuals to specific breeding locations would not possible with a high level of certainty, neither do we have a reason to assume that our conclusions are biased by within population variation.

Culmen length had a negative but not significant relationship with survival for Western Sandpipers, the 95% CI overlaps 0, therefore we obtained no difference results as we predicted (prediction 7). Our parameter coefficient for sex (males relative to females) was 0.18 ± 0.13 SE (LCL = -0.07, UCL = 0.43), again not significant, but suggesting a higher survivorship of males. Western Sandpipers show a differential migration by sex, where more females migrate to sites further south (Nebel et al 2002, Fernández et al 2004, O'Hara et al 2006), so our results show an effect based on the limited data available on local males at a southern extreme. Lastly when we look for a culmen effect between age and sex we found a negative relationship, again less than robust and apparent only for juvenile females (-0.50 ± 0.80 SE (LCL = -1.99, UCL = 0.99)) implying that juvenile females are likely to drive the potential negative relationship for the population of Western Sandpipers.

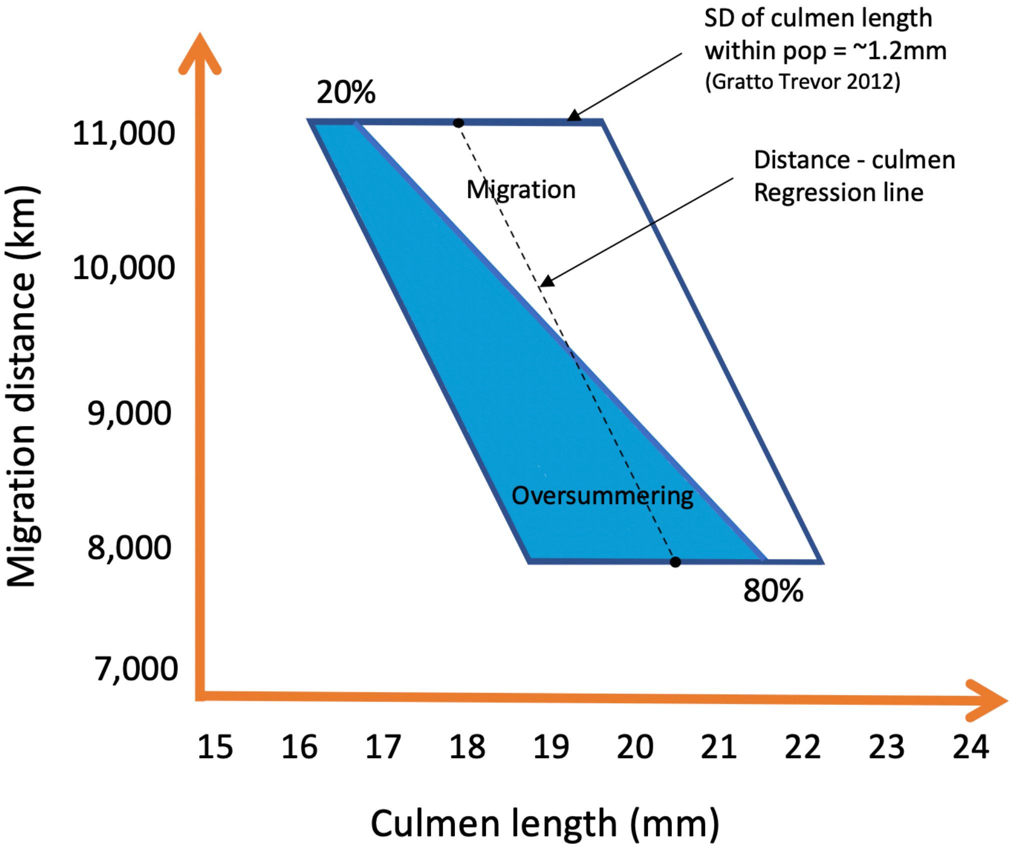

Figure 4.11. **Probability of oversummering versus migration, in with migration distance and culmen length in juvenile Semipalmated Sandpipers. Shaded area represents the oversummering propensity and non-shaded area the migration propensity. '20%' and '80%' refer to the percentage of individuals with culmens of 17 mm and 22 mm that migrate, respectively.**

To test whether wing length had any relationship with survival we replaced culmen length with wing length in the first top model for Semipalmated Sandpipers and in the second-best model for Western Sandpipers. Since bill and wing length are somewhat correlated in general (Spencer 1984, Nebel 2006), we expected a similar trend for both covariates in relation with survivorship. We found a weak positive relationship for Semipalmated Sandpipers, and for Western Sandpipers we found a negative non-significant correlation. Our result does not provide evidence of continuing selection for shorter wings in Semipalmated Sandpipers, as expected from the results from the 2000s presented by Lank et al 2016, prediction 8. If both results are credible and apply to the same populations, they suggest that selection for wing size may have equilibrated. However as with the culmen length analysis, the wing length analysis for Semipalmated Sandpiers is biased by migration strategy. Additional analysis will be needed to separate out this relationship.

The ENSO (El Niño) index had no influence on Semipalmated Sandpipers' annual survival rates, but interestingly the ENSO warming phase showed a negative relationship with annual survival of Western Sandpipers (prediction 9). We attribute this contrasting interspecific result to the use of species-specific migratory flyways. Semipalmated Sandpiper populations at Paracas predominantly use the Mississippi-Central Flyway (Harrington and Morrison 1979), with some individuals using the Atlantic Flyway until they all cross to the Pacific side to reach Paracas. However, most Western Sandpipers coming to Paracas are almost certainly restricted to the Pacific Flyway (Morrison and Myers 1987) and logically most closely tied to the Pacific currents, and thus more vulnerable to environmental cyclic anomalies of the western region of the Pacific Ocean, such as the ENSO warm phases. The quadratic ENSO term let us test for a non-linear relationship with high values of ENSO index. The estimate of our square term was positive, but overlapped 0 (0.08 ± 0.16 SE (LCL = -0.24, UCL = 0.40)), meaning we had a convex relationship between ENSO and survivorship, indicating the slowing rate of decline with further increases in ENSO values. The only other study associating ENSO with annual survival of these two species showed a weaker support for annual survival variation (O'Hara et al 2007), but this result might be due to limited power, or may have been obscured, since a quadratic term was not tested.

The Peruvian Upwelling Ecosystem (PUE) is one of the most productive zones in the tropical Pacific, driven by coastal upwelling of nutrient-rich cold waters with minimum ventilation (Pennington et al 2006). ENSO warm phases (El Niño) are known to cause a weak oxygen minimum zone, sub-oxic conditions in the sediments and low productivity of the PUE at Pisco (Paracas) region (Salvatteci et al 2014). Also, Graco et al (2016) showed how ENSO warm phases altered biochemistry conditions of the PUE surface and water column, changing pH and oxygen values, silicates concentration by nutrients and nitrate availability. Shorebirds at Paracas depend highly on available nutrients to feed and survive during the non-breeding season. If Paracas Bay productivity and accessibility of nutrients are negatively associated with ENSO warm phases through significant changes on the PUE, then our square term positive result might be showing this cyclic event with peaks of lower survivorship with higher ENSO values being mostly explained by inaccessibility to feeding resources.

4.5.2. Monthly residency

Our monthly residency estimates for both species showed a clear drop at the end of the season for both age classes. Rates for Western Sandpiper adults started to drop in December, while the juveniles remain reasonably high until February, as do both age classes of the later-migrating Semipalmated Sandpipers. The declines in local residency towards the end of the season presumably result from local movements associated with pre-migratory preparation, even for juvenile Western Sandpipers. We associate this juvenile movement to a probably local dispersion influence.

Because monthly residency was estimated under a closed population model, to estimate local apparent residency throughout a 6-month non-breeding season, we would raise e.g. the mean monthly values to the 6th power. For Western Sandpipers, using the overall age-specific estimates, only 0.35 of Juveniles and 0.11 of Adults remained at and/or survived at Paracas throughout the non-breeding season. These numbers are too low to be plausible as real non-breeding survivorship rates and suggest substantial permanent emigration from the site within the non-breeding season that we cannot separate from mortality. Similarly, for Semipalmated Sandpipers, using the overall age-specific estimates, 0.49 of juveniles and 0.30 of adults would have survived at Paracas throughout the non-breeding season. While these are both higher than the corresponding estimates for Semipalmated Sandpipers, they are still too low to plausible represent seasonal survivorship.

The residency estimates for the initial months may provide a better basis for estimating seasonal survivorship than using the overall age specific estimates, as done above. If we use values from the first 2 months and we took the average and apply them to a 6-month period as having little effect of permanent emigration, we would produce seasonal survivorship estimates of 0.43 and 0.33 for juvenile and adult Semipalmated Sandpipers and 0.95 and 0.62 for juvenile and adult Western Sandpipers.

4.6. Conclusions

This study illustrates how survivorship in two species of avian migrants can be influenced by specific life history strategies. Our main overall result for annual survivorship showed that the IDF model does not apply in these systems, instead the Time Allocation and the Physiological Tolerance models with the migration distance theory provide a better understanding of the high annual survival estimates obtained. Likewise, ‘oversummering’ as a life-history trade-off hypothesis was validated specifically by juvenile Western Sandpipers, showing a sharp survival benefit relative to migration by deferring migration in the first year of life. Regarding the age effect, we found no evidence to support the inexperience or competitive subordination by adults, but instead juvenile survival from both species indicate a strong selection force by first year birds over adults. The sex term and wing length as a morphology effect didn’t produce any substantial outcome to help us understand differences between populations or species. However, El Niño seasonal effect in our survivorship estimates exposed a specific pattern related only to a specific species, pointing out a probable consequence related to the Pacific flyway. Last, we confirm that survival of migrant birds is distance-dependent, using culmen length as a proxy for migration distance.

Chapter 5.

General Conclusions

5.1. Migration and Life History Strategies

This thesis explores how interrelated components of life history strategies are linked to migration distance and survivorship of Western and Semipalmated Sandpiper populations in an important non-breeding site in Perú. Specifically, I explored how annual and non-breeding survival, moult strategy, and migratory decisions, varied respect to age classes and sex, populations within a species, and the two taxa. The patterns found bear on our understanding of the relative strengths of selective forces shaping these life history attributes.

Chapter 2 focused on how migration distance correlated with the propensity for migration of Western *(Calidris mauri)* and Semipalmated *(Calidris pusilla)* Sandpipers based on a set of pre-migratory indices. In Chapter 3 I assessed the cost of migration again with mark-resighting data between migrant and resident (oversummering) birds in Semipalmated Sandpipers and in Chapter 4 I used mark-resighting data to generate survival estimates in relation to life history strategies, morphology, and an environmental variable, for both species. Across all my chapters, I found differences in characteristics associated with migratory behavior by age class and by population.

Paracas is at the southerly edge of the non-breeding ranges for both Semipalmated and Western Sandpipers. The Time Allocation and the Physiological Tolerance models of migration distance predict higher seasonal survivorship rates for birds migrating further south, I found higher annual survivorship rates than those estimated from more northerly non-breeding sites, and my estimates approached those based on breeding grounds studies, which are the closest available estimates of true annual survivorship. The higher rates at Paracas are attributable to higher rates during the non-breeding season, assuming that there are no major differences in breeding survivorship (e.g. no major carryover effects) and that shorter distance migrations, to northerly sites, are not more costly than longer ones. Thus, greater survivorship appears to be a payoff for spending the non-breeding season further south. This supports the conceptual lines for a negative relationship between annual survival and migration distance shown in Chapter 1, Fig. 1.1.

Semipalmated Sandpipers came to Paracas from across the full breeding range, as assessed by variation in bill lengths. Birds from the eastern population migrate shorter distances than the western breeding conspecifics and Western Sandpipers. The life history strategy of eastern birds centered around a great propensity for a ‘fast’ juvenile life history strategy involving northward migration in the first year. Based on three years of earlier data, about 31% of juvenile Semipalmated Sandpipers gained weighted, molted to breeding plumage and renewed some primary feathers to attempt to migrate, and based on bill lengths, these were biased towards eastern birds (Chapter 2). The model in chapter 3 based on 5 years including later data, suggests that up to 70% of juveniles migrated, Although eastern Semipalmated Sandpipers also had a lower annual survivorship in general than western-breeding Semipalmated Sandpipers or Western Sandpipers (Chapter 4), consistent with previous population level census and demographic data (Morrison et al 2001, Morrison et al 2012), but inconsistent with the negative relationship between migration distance and annual survivorship. When differences in oversummering proportions were taken into account we found the predicted relationship with higher survivorship for the eastern (long-billed) Semipalmated Sandpipers. To generate specific survival estimates for each group of oversummering (resident) and migrant birds from Semipalmated Sandpipers, I used data from all birds observed at Paracas the full year-round and created a specific multi-state model (Chapter 3). This direct test of the cost of migration showed a substantial one. Migrant juveniles had an 11% lower probability of survivorship than oversummering juveniles (0.61 vs. 0.55), while migrant adults had a 24% lower rate (0.82 vs. 0.62). These results support the hypothesis that oversummering can compensate for the loss of breeding opportunities.

In contrast, no juvenile Western Sandpipers prepared for northward migration and breeding by fattening up or moulting into breeding plumages (Chapter 2). All opted for a high survivorship ‘oversummering’ slow life history strategy, as expected based on patterns from other southerly non-breeding populations. The annual survivorship rates of juvenile Western Sandpipers were 0.83, the highest of the age classes/tax/populations studied, and higher than recent spatially-explicit estimates made from breeding ground data, where site fidelity is high (Weiser, in prep). The estimates were 0.13 higher than that of migratory Western adults (Chapter 4). More northerly Western Sandpiper populations follow the fast life history strategy, implicating the difference in migration distance as a potential causal factor. Annual survivorship of Western Sandpipers was negatively related to higher ENSO index conditions, which are associated with higher ocean temperatures and presumably lower upwelling and ocean productivity. No such relationship occurred for Semipalmated Sandpipers. The difference may result from Western Sandpipers at Paracas' year-round association with the Pacific migratory flyway, contrasting with a non-breeding season only relationship for most Semipalmated Sandpipers.

Western-breeding Semipalmated Sandpiper juveniles were more likely to oversummer than eastern juveniles, and these short-billed birds obtained higher survivorship rates than migrant Semipalmated Sandpipers by remaining in Perú (Chapters 3, 4). Therefore, one of my general findings is that oversummering propensity of Semipalmated Sandpipers is lower than of Western Sandpipers. But, the western Semipalmated Sandpiper population thus match the strategies of sympatric breeding Western Sandpipers, suggesting a common or more factors are involved. My first suggestion sets migration distance as a strong candidate, with the longer distances traveled by western birds of both species favouring delayed migration and breeding, thus oversummering and higher annual survivorship rates. Another way to explain this would be that the Pacific flyway is more dangerous in terms of the predator landscape. Juvenile Western Sandpiper southern migration is almost consistent with the migration pattern of western population of Peregrine falcon, same for the western and central populations of Semipalmated Sandpipers (Lank et al 2003). This higher mass-dependent predation danger scenario could have also favored this extra oversummering behavior. Also, western juvenile Semipalmated Sandpipers (short-billed birds) had less probability to do PPW (Chapter 2, Addendum), similar to Western Sandpipers where juveniles don't perform that molt at all, suggesting another similarity in juvenile wing-molt strategy by these two sympatric breeding populations of birds.

My findings are generally consistent with the hypothesis that birds obtain higher annual survivorship when traveling further migration distances, and that when this combines with slower life histories, the higher survivorship can offset the fitness cost of a lost reproductive opportunity. Under reasonable assumptions about small carryover effects, the numbers do not suggest that an ideal-free distribution of fitness occurs across the non-breeding range, which was also recently suggested by Reneerkens et al (2019) for sanderlings along the East Atlantic coast of Africa and Europe. In general, the survivorship rates of juveniles were lower than those of adults, but less so than some might predict. All the juveniles in this study had completed a southward migration, and a higher relative mortality may have occurred further north.

5.2. Significance and Implications for Conservation

Migratory shorebirds can be guides pointing to environmental change. As worldwide travelers choosing the strategy “travel to reproduce”, they are subject to being affected by the events occurring at all stages and locations of their annual life cycle (González 2006). Understanding the patterns that drive life history strategies and how these are related to population survivorship and growth rates is fundamental to conservation practices. Understanding changes in demographic rates, and potential causes of variation in avian populations, can greatly aid the design and development of conservation strategies in the face of environmental changes. Comparing species’ survivorship rates across large spatial scales can help to identify habitats and populations under threat before detectable abundance declines occur (Piersma et al 2016). The worldwide decline of current many long-distance migrating shorebirds is an alarming threat and reported across all the main migratory flyways (Morrison et al 2001, Conklin et al 2014, Hansen et al 2015). Plentiful shorebird species are classified to be of conservation concern worldwide (Zöckler et al 2003). Some identified causes are habitat loss in critical foraging stop-over sites like in the East Asian-Australian Flyway (Murray et al 2014, Hua et al 2015), habitat degradation (Balachandran 2006, Piersma et al 2016, Studds et al 2017), hunting pressure (Zöckler et al 2010), human-induced food depletion in key foraging migratory sites (Gonzalez et al 2006) and physiological or ecological stressors on tropical non-breeding grounds before northward migration (Leyrer et al 2013, Reneerkens et al 2019).

Despite the fact there is true evidence of population decline worldwide, most of the real causes at the western hemisphere remain elusive. Much of the concern comes from declines observed in indices of population abundance calculated from data collected at migratory stopover sites (NABCI 2012; 2016), comparisons between data gathered 30 years ago and recent aerial surveys at non-breeding sites (Morrison et al 2012), and probably mislead interpretations from morphometric data variation through an specific length of time (Hicklin and Chardine 2012). Some hypothesis had been tested to determine the cause of shorebird population decline in the Americas, still with little support but suggesting for a possible shift in distribution or a reduction in size of the breeding population (Bart et al 2007). Determining when and where mortality occurs within the annual life cycle and the plausible causes of it is important for understanding population dynamics, the evolutionary drivers of long-distance migration and a contribution for shorebird conservation and management policies.

My thesis contributes with novel information about current population demographic trends and its relationship to life history strategies of two species of migratory shorebirds in the Americas. I emphasize results from my survival studies (Chapter 3 and 4), as comparative analyses of shorebird survival rates at non-breeding sites are scarce, they vary across flyways and tend to be underestimated (Méndez et al 2018). As a first step I chose a site where the last attempt to gather general information about shorebirds was 30 years ago. Reinforcing the importance of studies at non-breeding sites where site-fidelity is mostly determined by ecological factors is being suggested as a priority (Sandercock and Jaramillo 2002). Especially when these ecosystems are currently among the most severely affected by environmental change, through processes such as global warming, sea level rise and land claim (Sutherland et al 2012). As a second step I selected two shorebird species which are globally distributed in the western hemisphere, but the lack of information about their non-breeding population dynamics is greatly disproportionate with respect to other shorebird species in the region. Here I showed how survivorship can vary depending on the species, population, age class and other factors associated with life history strategies and migration distance (Chapter 3). I took a more specific approach on Chapter 4 focused only in one shorebird species to deepen more into the cost of migration and how this can affect migratory strategies and population survivorship.

5.3. Conclusions

My analysis suggests that mortality rates were fairly constant for resident birds at Paracas throughout the year but drop substantially during migration and breeding seasons (Chapter 3, Table 3.3). This suggests that sandpipers experience greater difficulties at those stages than on overwintering grounds. This conclusion differs from a widespread view among songbird biologists of the previous generation, which emphasized the potential driving role of habitat conversion in tropical areas to avian population declines, rather than problems on migration or on breeding grounds (González-Prieto 2018, Bayly et al 2019). Shorebird biologists have generally left open many possible scenarios. Compelling cases have been made for negative population level effects of human harvest of shorebird prey at specific on wintering grounds (e.g. mussels in the Dutch Wadden Sea (Beukema and Cadée 1996) or at migration stopover sites (e.g. Horseshoe crabs at Delaware Bay (González et al 2006). There is a substantial current controversy about the magnitude and reality of globally higher levels of nest predation in arctic-breeding shorebirds (Kubelka et al 2018, Bulla et al 2019, Kubelka et al 2019).

A growing literature shows that steadily increasing raptor populations over the past 30 years are altering habitat selection, migration tactics, and potentially even the morphology of small shorebirds (e.g. Ydenberg et al 2004, 2017, Pomeroy et al 2006, Van Den Hout et al 2008, Lank et al 2017), but translation of this into population level consequences, considering both direct mortality and indirect effects has not yet been attempted. While at Paracas, annual apparent survivorship rates were on the order of 0.81 for adults and 0.64 for juvenile Semipalmated Sandpipers (Chapter 3, Table 3.4). The annual survivorship estimates for adults from Chapter 4 were 0.70 and 0.71. Weiser et al in prep, and Hitchcock and Gratto-Trevor (1997) showed that that population growth rates over 1.0 could be achieved with annual survivorships of ca. 0.75 for adults and 0.44 for juveniles. My estimates a minimum with respect to true survivorship, since permanent emigration cannot be factored out. I conclude that shorebirds at Paracas are doing well, and the area deserves protection to allow local shorebirds to continue to survive.

My results contribute novel knowledge of non-breeding shorebird population dynamics and offer a broad understanding of the patterns that drive avian life history strategies and how these are related to population survivorship, which is fundamental for conservation practices.

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Appendix A

Contour plot showing the relationship between culmen length, day of the year and weight during the pre-migratory season in juvenile Semipalmated Sandpipers.

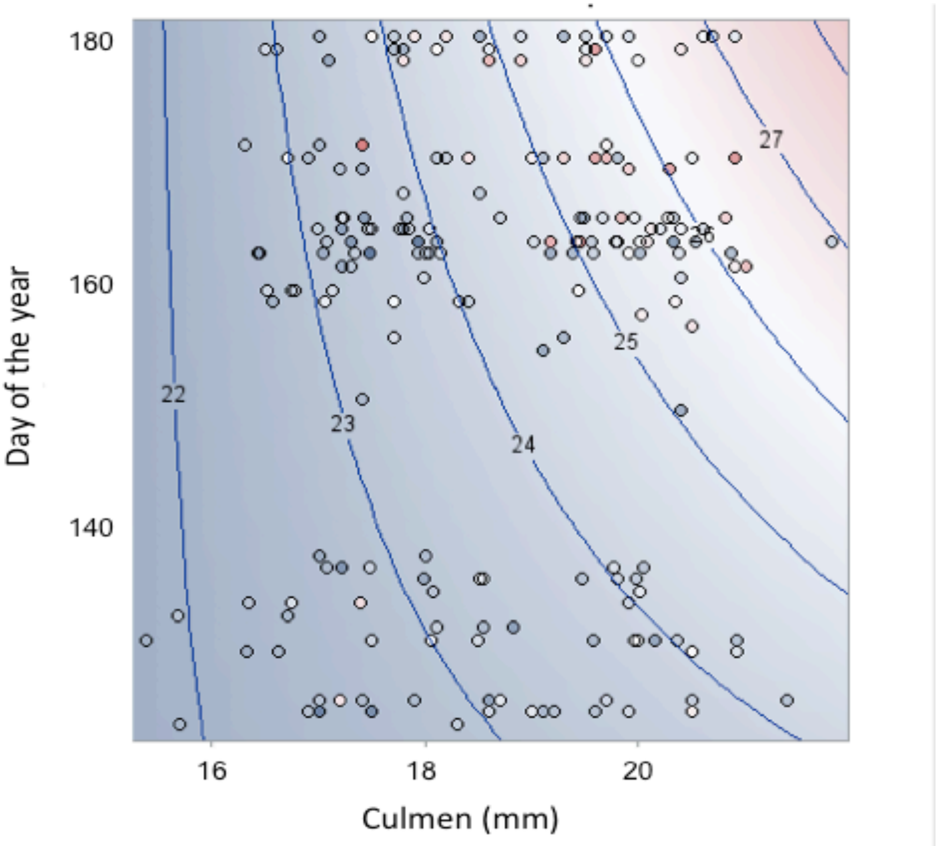

Figure A1. **Model of analysis of variance of mass as a function of culmen and day of the year and their interaction (culmen*dayoftheyear) in juvenile Semipalmated Sandpipers.**

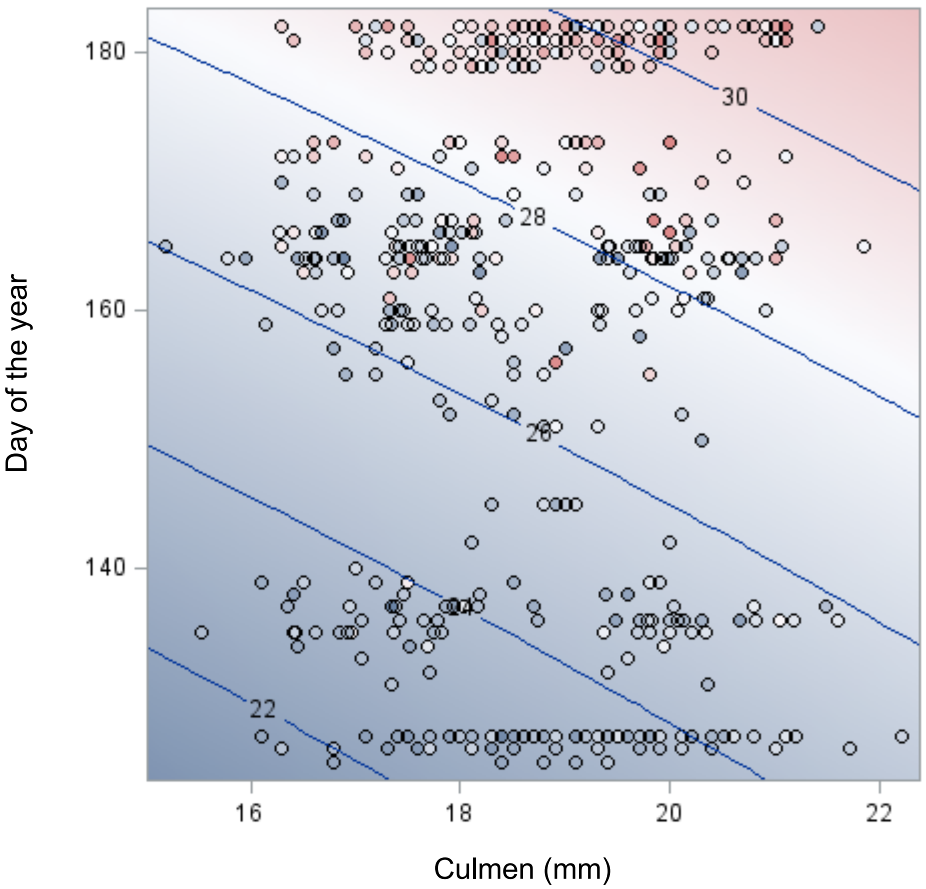

Figure A2. **Model of analysis of variance of mass as a function of culmen and day of the year and their interaction (culmen*dayoftheyear) in adult Semipalmated Sandpipers.**

Appendix B

Detailed annual survival and monthly residency estimates for Semipalmated Sandpipers at Paracas, Perú.

Table B1. **Survival estimates of the best model for Semipalmated Sandpipers at Paracas, Perú.**

Year	Estimate ± SE	LCL	UCL
2011	0.673 ± 0.058	0.551	0.775
2012	0.780 ± 0.028	0.721	0.829
2013	0.693 ± 0.017	0.658	0.725
2014	0.678 ± 0.019	0.64	0.714
2015	0.738 ± 0.026	0.685	0.786

Table B2. **Survival estimates of the second best model (age included) for Semipalmated Sandpipers at Paracas, Perú.**

Year	Estimate ± SE		LCL		UCL	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
2011	0.631 ± 0.066	0.668 ± 0.056	0.496	0.552	0.748	0.767
2012	0.764 ± 0.030	0.792 ± 0.028	0.700	0.733	0.819	0.841
2013	0.661 ± 0.030	0.696 ± 0.017	0.601	0.662	0.716	0.729
2014	0.644 ± 0.032	0.680 ± 0.019	0.578	0.642	0.705	0.716
2015	0.711 ± 0.034	0.743 ± 0.026	0.641	0.690	0.773	0.790

Table B3. **Survival estimates for monthly residency for Semipalmated Sandpipers at Paracas, Perú.**

Month	Estimate ± SE		LCL		UCL	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
October	0.869 ± 0.024	0.830 ± 0.025	0.814	0.775	0.909	0.873
November	0.869 ± 0.022	0.830 ± 0.020	0.819	0.787	0.907	0.866
December	0.828 ± 0.024	0.780 ± 0.023	0.776	0.732	0.870	0.822
January	0.931 ± 0.035	0.908 ± 0.042	0.825	0.788	0.975	0.963
February	0.440 ± 0.037	0.366 ± 0.024	0.369	0.320	0.512	0.414
March	1 ± 0.000	1 ± 0.000	0	0	1	1

Appendix C

Detailed annual survival and monthly residency estimates for Western Sandpipers at Paracas, Perú.

Table C1. Survival estimates of the best model for Western Sandpipers at Paracas, Perú.

Year	Estimate ± SE		LCL		UCL	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
2011	0.848 ± 0.03	0.720 ± 0.012	0.78	0.697	0.898	0.743
2012	0.859 ± 0.029	0.737 ± 0.012	0.793	0.713	0.906	0.760
2013	0.871 ± 0.027	0.757 ± 0.012	0.809	0.733	0.915	0.780
2014	0.82 ± 0.034	0.678 ± 0.011	0.745	0.655	0.877	0.700
2015	0.769 ± 0.04	0.604 ± 0.012	0.682	0.581	0.837	0.627

Table C2. Survival estimates for monthly residency for Western Sandpipers at Paracas, Perú.

Month	Estimate ± SE		LCL		UCL	
	Juveniles	Adults	Juveniles	Adults	Juveniles	Adults
October	0.992 ± 0.004	0.930 ± 0.030	0.98	0.843	0.997	0.971
November	0.991 ± 0.004	0.915 ± 0.026	0.98	0.847	0.996	0.955
December	0.969 ± 0.008	0.763 ± 0.030	0.951	0.698	0.981	0.817
January	0.951 ± 0.013	0.665 ± 0.039	0.92	0.584	0.971	0.737
February	0.741 ± 0.042	0.225 ± 0.022	0.65	0.185	0.816	0.270
March	0.718 ± 0.047	0.205 ± 0.036	0.618	0.143	0.801	0.286

Appendix D

Multiple Simulations to estimate unobservable states for juvenile and adult Semipalmated Sandpipers at Paracas, Perú.

In this section I report briefly on a set of simulations where 100 datasets for each of several different scenarios is generated, and fitted them each to 4 different models:

1. S(J,R,M,A)P(dot)Psi(stratum)
2. S(J,R=M,A)P(dot)Psi(stratum)
3. S(J,R,M,A)P(stratum)Psi(stratum)
4. S(J,R=M,A)P(stratum)Psi(stratum)

Thus far I have simulated 4 scenarios, with p=0.8 for all of them:

1. $S^J = 0.7$; $S^R = 0.75$; $S^M = 0.65$; $S^A = 0.8$; migratory transitions in >1 month.
2. $S^J = 0.7$; $S^R = 0.75$; $S^M = 0.60$; $S^A = 0.8$; migratory transitions in >1 month. (greater difference between survival for R and M)
3. $S^J = 0.7$; $S^R = 0.75$; $S^M = 0.75$; $S^A = 0.8$; migratory transitions in >1 month. (Equal survival between R and M)
4. $S^J = 0.7$; $S^R = 0.75$; $S^M = 0.65$; $S^A = 0.8$; migratory transitions deterministic in only 1 month for states A and M.

Scenario 1

In this scenario, generating values for monthly survival (value in parentheses is monthly survival scaled to annual survival – but of course no individuals remain in the same state for a whole year) were: $S^J = (0.55)^{1/12}$; $S^R = (0.75)^{1/12}$; $S^M = (0.65)^{1/12}$; $S^A = (0.8)^{1/12}$. Values for transition probabilities were as follows.

Point estimates for survival probability were largely unbiased for models 2 and 4 (the correct survival generating model), and interestingly, it did not seem to make much difference if p was correctly modelled as constant or incorrectly as state-specific (but I did not yet try a scenarios where it truly differed among states). However, variability in bias was much greater for S^R than for other survival parameters, and standard error for this parameter was an order of magnitude greater than other survival parameters (Figure D2). There was an unexpected jump in SE for S^R, but the probability of remaining in state R was relatively small, so this may be a data scarcity issue.

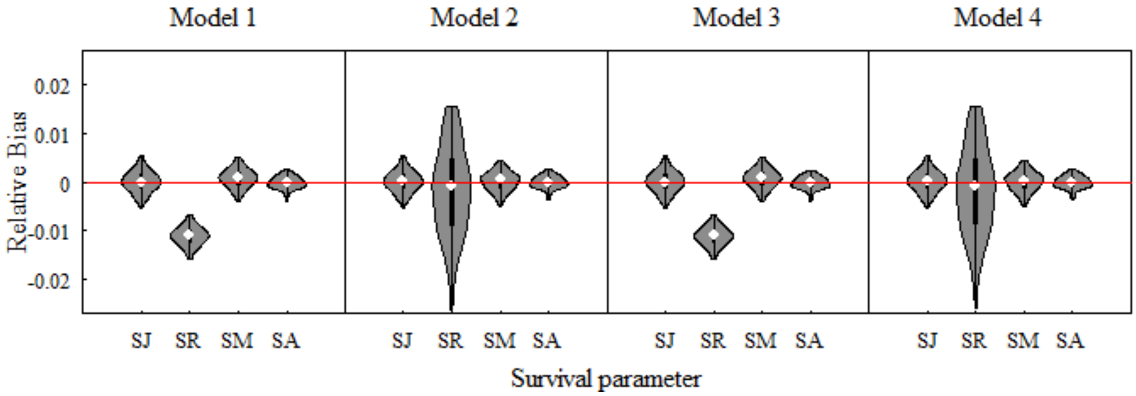

Figure D1. **Violin density plots for relative bias of survival estimates from 100 simulated datasets from Scenario 1. Models are described in the text. For perspective, if monthly survival is 0.97 then negative relative bias of 0.02 translates to monthly survival = 0.951. Over six months, that translates to survival = 0.951^6 = 0.738 rather than 0.97^6 = 0.833.**

The generating model was selected as the lowest AICc model 26% of the time, and model 1 (where $S^R = S^M$) was selected 58% of the time. Thus, with the survival difference only 0.1, and with large SE in one of the survival parameters, the model struggled to differentiate the 2 survival parameters. If $S^R = S^A$, and it were modeled so, then I suspect that model performance would improve markedly.

Scenario 2

This scenario is just like Scenario 1, but with a somewhat larger difference in survival between states R and M. I'd expect that the generating model might be selected more often, but I would not expect improvement in the SE of the estimate for S^R. Indeed, bias and SE results (not shown) look very similar to those from Scenario 1. The generating model was selected as the best model 56% of the time, and Model 1 was selected 32% of the time (models with varying p were selected only 12% of the time).

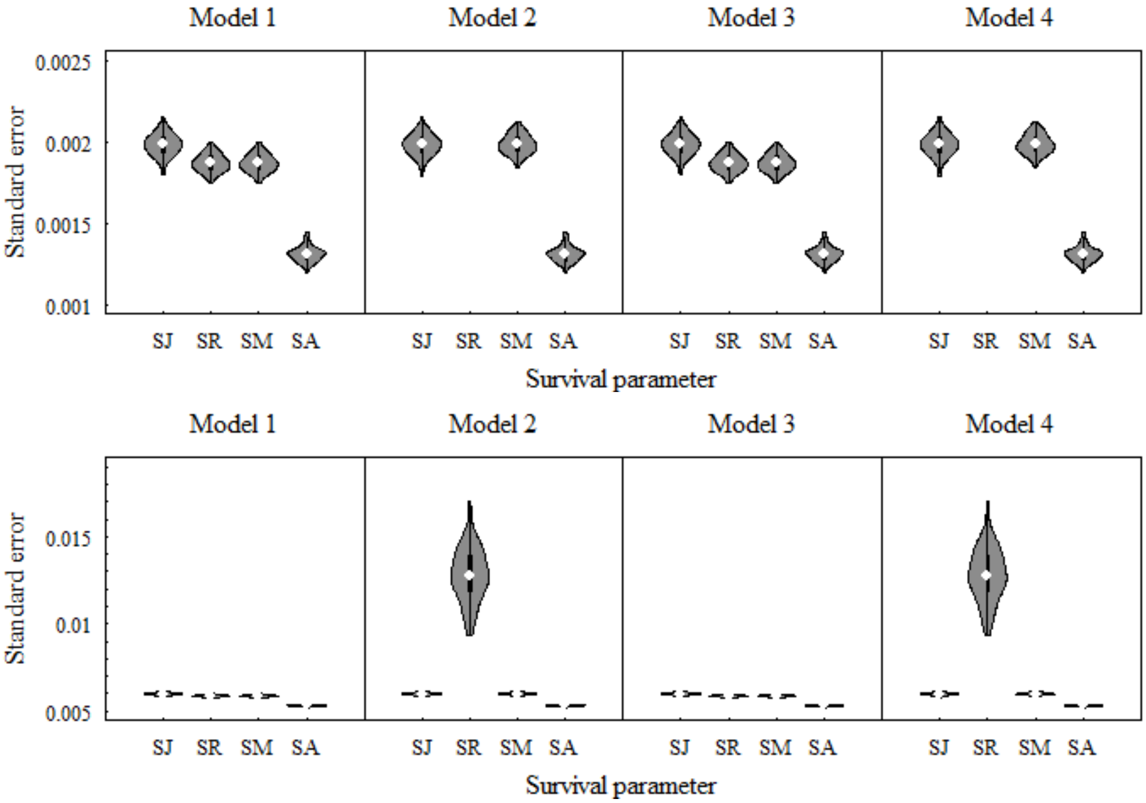

Figure D2. **Violin density plots for standard error of survival estimates from 100 simulated datasets of scenario 1, at two different scales. Models are described in the text.**

Scenario 3

This scenario was like scenario 1, except that $S^R = S^M = 0.75$. The modest negative bias seen in S^R in Figure 1 disappeared in this scenario (Figure 3). Estimates were precise, but again SEs are very large for S^R for Model 2 and Model 4 (not shown – look very similar to Figure 2). The generating model (here with $S^R = S^M$) was selected 66% of the time, and model 3 same as model 1, but with state-specific p) was selected an additional 13% of the time. Model 2 (with $S^R \neq S^M$) was selected 19% of the time.

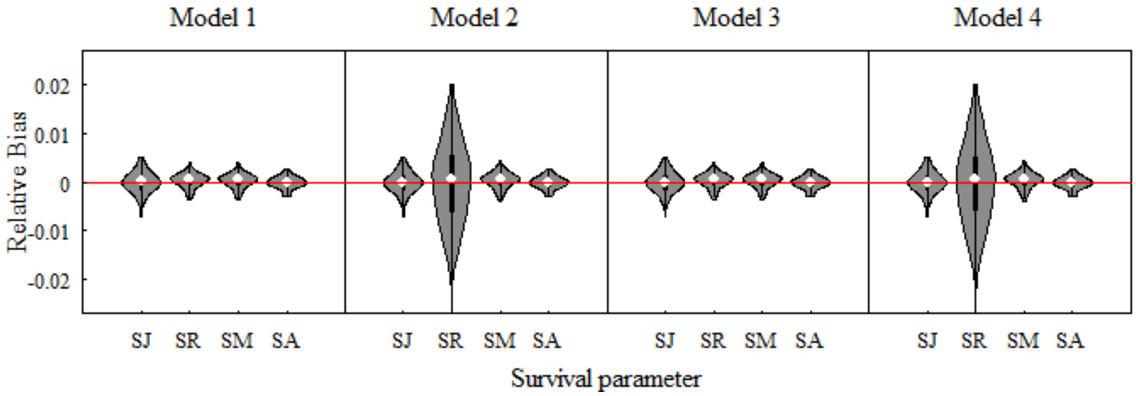

Figure D3. **Violin density plots for relative bias of survival estimates from 100 simulated datasets from Scenario 3. Models are described in the text.**

Scenario 4

This scenario was the same as scenario 1, but with migratory transitions deterministic within a single transition period. For example, all individuals in state A deterministically migrate in April, rather than probabilistically migrating in April, with remaining M than deterministically migrating in May (as in Scenario 1).

In the section above where only a single dataset was fitted, there was a suggestion that precision of the S^R estimate was better when transitions were more deterministic, and that conclusion is confirmed here. Relative bias was low for Models 2 and 4 (Figure D4), and although the SE for S^R was still much greater than for the other survival parameters, it was much reduced from Scenario 1 (Figure D5).

Also, the correct model (Model 2 with $S^R \neq S^M$) was selected 74% of the time, and Model 4 (also with $S^R \neq S^M$, but also with state-specific p) was selected an additional 17% of the time. Models 1 and 3 (with $S^R = S^M$) were selected cumulatively only 9% of the time.

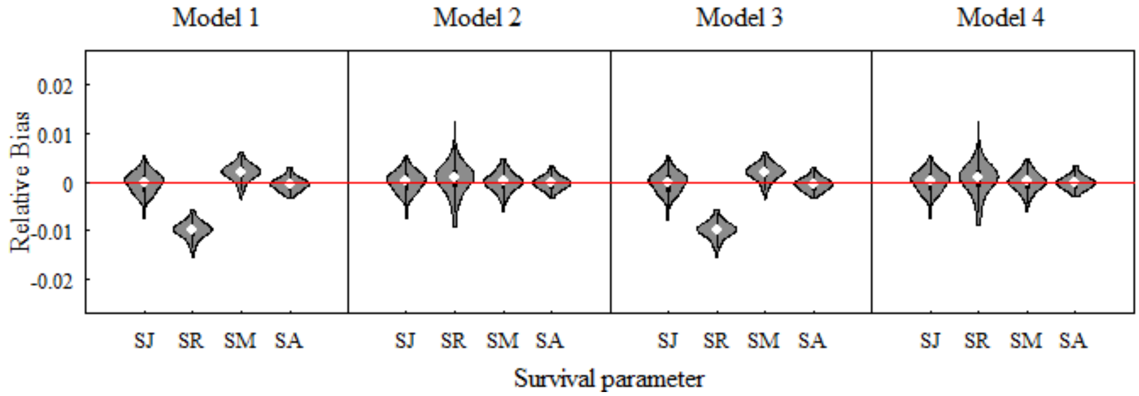

Figure D4. **Violin density plots for relative bias of survival estimates from 100 simulated datasets from Scenario 4. Models are described in the text.**

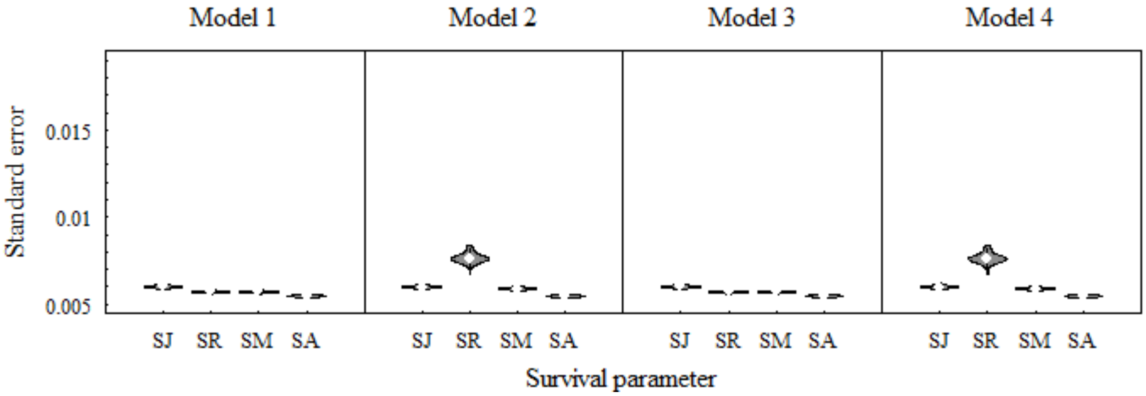

Figure D5. **Violin density plots for standard error of survival estimates from 100 simulated datasets of scenario 4, at two different scales. Models are described in the text.**

Conclusions

It seems clear form the simulations that the model works better (meaning better able to differentiate S^R and S^M, when they are in fact different), when migratory transitions are deterministic.

It also seems clear that when migratory transitions are *not* deterministic, then, even if the $S^R \neq S^M$ model is selected, it might be difficult to draw meaningful inference about the effect size of differences in survival.

Appendix E

Metrics of total reencounters by year for MSMR model in Semipalmated Sandpipers at Paracas, Perú (Chapter 3).

Table E1. **Number time birds were encountered (captures and resightings) including initial banding occasion and subsequent occasions by year for Semipalmated Sandpipers at Paracas, Perú.**

Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
2014	309	247	119	96	71	48	20	24	19	18	6	9	4	2	1	1	994
2015	196	100	54	32	20	16	7	10	4	4	2	.	.	.	.	.	445
2016	117	38	25	11	7	5	5	1	1	.	.	.	.	.	.	.	210
2017	68	38	14	12	6	7	4	.	.	.	.	.	.	.	.	.	149
2018	165	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	165
Total	855	423	212	151	104	76	36	35	24	22	8	9	4	2	1	1	1963

Table E2. **Total reencounters after banding week per year (left side) and number of subsequent years encountered (right side) for Semipalmated Sandpipers at Paracas, Perú.**

	Number of Reencounters				Number of Years			
	Mean	SD	Range	N	Mean	SD	Range	N
2014	3.15	2.62	14	685	1.208	1.57	5	725
2015	2.67	2.08	9	249	0.654	1.18	4	344
2016	2.35	1.65	7	93	0.354	0.83	3	164
2017	2.28	1.56	5	81	0.523	0.88	2	107
2018	.	.	.	.	.	.	.	124
Total	2.91	2.39	14	1108	0.83	1.36	5	1464

Appendix F

Metrics of total reencounters by year for ORDMS model in Semipalmated and Western Sandpipers at Paracas, Perú (Chapter 4).

Table F1. **Number time birds were encountered (captures and resightings) including initial banding occasion and subsequent occasions by year for Semipalmated Sandpipers at Paracas, Perú.**

Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total
2011	162	44	21	5	7	4	2	5	.	2	2	.	1	.	.	.	.	1	.	1	.	.	257
2012	371	175	108	49	39	26	18	10	12	4	4	6	4	2	3	4	1	.	1	.	1	.	838
2013	456	262	144	87	62	47	33	20	24	22	11	7	7	6	2	2	.	.	2	1	.	2	1197
2014	49	39	28	13	18	11	10	7	4	5	2	1	.	.	1	.	.	.	.	.	.	.	188
2015	119	68	35	26	20	8	9	2	2	4	1	4	.	.	.	.	.	.	.	.	.	.	298
2016	84	33	7	4	4	9	2	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	146
2017	45	16	2	8	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	75
Total	1286	637	345	192	154	105	74	46	43	37	20	18	12	8	6	6	1	1	3	2	1	2	2999

Table F2. **Total reencounters after banding week per year (left side) and number of subsequent years encountered (right side) after year of banding for Semipalmated Sandpipers at Paracas, Perú.**

	Number of Reencounters				Number of Years			
	Mean	SD	Range	N	Mean	SD	Range	N
2011	2.97	3.30	18.00	95	1.82	1.09	4.00	95
2012	3.15	3.08	19.00	467	1.90	1.11	4.00	459
2013	3.41	3.15	20.00	741	1.73	0.85	3.00	669
2014	3.54	2.65	13.00	139	1.58	0.63	2.00	118
2015	2.85	2.33	10.00	179	1.18	0.38	1.00	159
2016	2.48	1.97	7.00	62	1	0	0	40
2017	2.00	1.17	3.00	30	.	.	.	0
Total	3.21	2.98	20.00	1713	1.70	0.92	4.00	1540

Table F3. **Number of years encountered (resightings) including banding year for Semipalmated Sandpipers at Paracas, Perú.**

	Banding year only	**2**	**3**	**4**	**5**	**6**
2011	162	51	22	13	6	3
2012	379	225	120	64	35	15
2013	528	340	190	120	19	.
2014	70	59	50	9	.	.
2015	139	131	28	.	.	.
2016	106	40	.	.	.	.
2017	75	.	.	.	.	.

Table F4. Number time birds were encountered (captures and resightings) including initial banding occasion and subsequent occasions by year for Western Sandpipers at Paracas, Perú.

Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Total
2011	92	39	23	8	4	6	2	.	3	.	1	1	.	.	.	179
2012	68	32	18	10	11	4	5	3	3	2	.	1	.	.	.	157
2013	97	59	49	36	22	23	12	13	8	6	5	1	1	1	1	334
2014	22	25	18	13	14	12	11	10	3	5	4	1	.	.	1	139
2015	28	29	21	17	6	9	7	3	1	2	.	.	.	.	.	123
2016	65	51	23	15	10	12	12	5	2	2	.	.	.	.	.	197
2017	18	6	4	5	.	.	.	.	.	.	.	.	.	.	.	33
Total	390	241	156	104	67	66	49	34	20	17	10	4	1	1	2	1162

Table F5. Total reencounters after banding week per year (left side) and number of subsequent years encountered (right side) after year of banding for Western Sandpipers at Paracas, Perú.

	Number of Reencounters				Number of Years			
	Mean	**SD**	**Range**	**N**	**Mean**	**SD**	**Range**	**N**
2011	2.44	2.12	10.00	87	0.81	0.98	3.00	84
2012	2.99	2.33	10.00	89	1.97	1.05	4.00	86
2013	3.58	2.65	13.00	237	1.80	0.87	3.00	228
2014	4.15	2.82	13.00	117	1.66	0.69	2.00	99
2015	2.95	2.03	8.00	95	1.23	0.42	1.00	78
2016	2.90	2.13	8.00	132	1	0	0	63
2017	1.93	0.88	2.00	15	.	.	.	0
Total	3.24	2.46	13.00	772	1.65	0.85	4.00	638

Table F6. **Number of years encountered (resightings) including banding year for Western Sandpipers at Paracas, Perú.**

	Banding year only	2	3	4	5	6
2011	95	42	23	12	7	.
2012	71	36	28	12	9	1
2013	106	104	74	41	9	.
2014	40	46	41	12	.	.
2015	45	60	18	.	.	.
2016	134	63	.	.	.	.
2017	33	.	.	.	.	.

Appendix G

Parameter structures of ORDMS model for Semipalmated and Western Sandpipers in Paracas, Perú.

Table G1. Parameter structures for Semipalmated Sandpipers. Annual survival S with 21 options, monthly residency ϕ with 7 options, new arrival probability $p$ent with 3 options, resighting probability p with 6 options and transitiion probability ψ with the 3 fixed parameters.

Parameters				
Annual survival	**Monthly Residency**	**New arrival probability**	**Resighting probability**	**Transition probability**
S(year)	ϕ(age)	pent(month)	p(year+month)	ψ(.)
S(year+age)	ϕ(culmen)	pent(.)	p(year)	
S(age)	ϕ(.)	pent(year)	p(.)	
S(culmen)	ϕ(year)		p(effort.resights)	
S(year+culmen)	ϕ(month)		p(effort.captures)	
S(age+culmen)	ϕ(year+age)		p(effort.all.ocassions)	
S(year+age+culmen)	ϕ(month+age)			
S(.)				
S(year+ala)				
S(enso)				
S(year+enso)				
S(enso+culmen)				
S(year+enso+culmen)				
S(enso+age)				
S(enso+age+culmen)				
S(enso+enso^2)				
S(year+enso+enso^2)				
S(enso+enso^2+culmen)				
S(year+enso+enso^2+culmen)				
S(enso+enso^2+age)				
S(enso+enso^2+age+culmen)				

Table G2. **Parameter structures for Western Sandpipers. Annual survival S with 29 options, monthly residency ϕ with 9 options, new arrival probability $p$ent with 3 options, resighting probability p with 6 options and transitiion probability ψ with the 3 fixed parameters.**

Parameters				
Annual survival	Monthly Residency	New arrival probability	Resighting probability	Transition probability
S(year)	ϕ(age)	pent(month)	p(year+month)	ψ(.)
S(year+age)	ϕ(culmen)	pent(.)	p(year)	
S(age)	ϕ(.)	pent(year)	p(.)	
S(culmen)	ϕ(year)		p(effort.resights)	
S(year+culmen)	ϕ(month)		p(effort.captures)	
S(age+culmen)	ϕ(year+age)		p(effort.all.ocassions)	
S(year+age+culmen)	ϕ(month+age)			
S(.)	ϕ(sex)			
S(year+ala)	ϕ(month+sex)			
S(enso)				
S(year+enso)				
S(enso+culmen)				
S(year+enso+culmen)				
S(enso+age)				
S(enso+age+culmen)				
S(enso+enso^2)				
S(year+enso+enso^2)				
S(enso+enso^2+culmen)				
S(year+enso+enso^2+culmen)				
S(enso+enso^2+age)				
S(enso+enso^2+age+culmen)				
S(enso+enso^2+sex)				
S(year+enso+enso^2+sex)				
S(enso+enso^2+age+sex)				
S(enso+sex)				
S(year+enso+sex)				
S(enso+age+sex)				
S(sex)				
S(year+sex)				