DO WINTERING CONDITIONS DRIVE POPULATION TRENDS IN SEMIPALMATED SANDPIPERS (*CALIDRIS PUSILLA*)?

EVIDENCE FROM A CORTICOSTERONE BIOMARKER

By

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Abstract

Some of the most extreme long-distance migrants, Arctic-breeding shorebirds are disproportionately represented in tallies of declining species worldwide. For many shorebirds, including the semipalmated sandpiper (*Calidris pusilla*), the specific causes and mechanisms behind population declines have not been identified. Stressful conditions affecting birds during wintering are often implicated. Interactions between events and processes occurring in the disparate locations used throughout the annual cycle also may be critical in shaping both individual life histories and population demographics. The main objectives of my graduate research were a) to examine whether semipalmated sandpipers wintering in specific locations incur differential levels of stress; and b) to test whether stressful conditions may carry over between different stages of an individual's life cycle. Using measurements of corticosterone (the primary avian stress hormone) deposited in winter-grown feathers, I examined the contribution of breeding season and fall migration to winter-incurred stress, and looked for evidence of carryover effects from wintering conditions to spring migration and subsequent reproductive performance. In Chapter 1, I compared the levels of stress exposure of 40 semipalmated sandpipers that bred at five Arctic sites and spent the austral summer in distinct regions (identified *via* light-sensing geolocators) across their tropical 'wintering' range. I found stress exposure varied by wintering region, and birds using locations along the Atlantic coast of northeastern South America and the Pacific coast of Central America had the highest feather corticosterone levels. I did not find evidence that carryover effects from the breeding season and/or fall migration influenced birds' physiology during winter. In Chapter 2, I investigated whether greater stress exposure during winter might subsequently affect birds during spring migration and/or breeding. I found that geolocator-tracked birds with increased stress levels delayed spring migration and initiated nests later. However, results for a larger dataset (including 254 birds breeding at seven sites across the North American Arctic) suggested low-stress birds nested later. It is possible the larger dataset included replacement clutches that could have confounded relationships with feather corticosterone, as only birds in better condition are likely to re-nest after clutch failure. In addition, I found evidence that stressful wintering conditions carryover to affect reproductive performance: females that accrued high levels of stress during wintering subsequently laid fewer eggs. In confirmed first nests, we found evidence for a clutch size–egg volume tradeoff, with high-stress females producing fewer offspring but potentially investing more in individual offspring. This research represents the first instance of the feather corticosterone technique being used to compare conditions across the wintering range of a calidrid shorebird and reveals specific wintering locations with high levels of stress exposure. This is also the first research that provides a mechanistic perspective on carryover effects between the wintering and breeding stages in a shorebird, through measurements of feather corticosterone. Finally, by showing that poor environmental conditions at wintering sites far from Arctic breeding areas may be detrimental to the reproductive performance of a species with declining populations, this research emphasizes the importance of considering full annual cycles in conservation and research efforts for migratory species.

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Acknowledgments

It takes a village to raise a graduate student, and never is that more apparent than when graduate work relies on data collected by a network of collaborators, and includes running a remote field camp. I owe much to committee member Dr. Richard Lanctot, who invited me to carry out my research as part of the Arctic Shorebird Demographics Network. Rick entrusted me with the Cape Krusenstern National Monument field site and provided critical support, patient oversight, and sound advice on everything from permitting, to bear safety concerns, to managing a field crew. I am most grateful to you, Rick, for pointing me toward a large catalogue of feather samples, and toward semipalmated sandpipers. You consequently sparked a research question and a passion that have propelled me forward throughout my time as a graduate student.

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General Introduction

Globally, over 40% of bird species are believed to be in decline (Vié et al. 2009), with long-distance migrants particularly vulnerable to habitat degradation or loss, direct exploitation, and/or climate change (Kirby et al. 2008, Newton 2008, Wilcove and Wikelski 2008). Arctic-breeding shorebirds, which connect hemispheres through their migrations, are among the most extreme long-distance migrants. For example, the red knot (*Calidris canutus*) migrates 15,000 km one-way between its High Arctic breeding grounds and its wintering areas as far south as Tierra del Fuego in Argentina. Arctic-breeding species encounter diverse conditions and events in the disparate geographic areas used throughout the course of their annual cycles, and are disproportionately represented in the tally of declining shorebird populations worldwide (IWSG 2003, CHASM 2004, Lanctot 2006). Even some of the more abundant shorebirds, such as the semipalmated sandpiper (*Calidris pusilla*), are considered species of conservation concern. Despite a recent population estimate of 2.25 million (Andres et al. 2012a), this species was recently upgraded to Near Threatened on the International Union for the Conservation of Nature Red List (BirdLife International 2016).

The semipalmated sandpiper breeds across the North American Arctic and winters in coastal areas of Central America, the Caribbean Basin, and South America (to southern Peru and Brazil; Hicklin and Gratto-Trevor 2010). There are three recognized breeding populations (Hicklin and Gratto-Trevor 2010, Gratto-Trevor et al. 2012a), which appear to have experienced different trajectories since at least the 1980s. The western population breeds in Alaska and appears to be stable or increasing; the central population breeds in the western Canadian Arctic, with its eastern limit at Hudson Bay, and appears to have recently become stable; and the eastern population breeds in the eastern Canadian Arctic and has experienced a pronounced decline over the past three generations (Andres et al. 2012b, Hicklin and Chardine 2012, Smith et al. 2012). The eastern population's decline is one of the primary reasons for the species' current

population breeds in the eastern Canadian Arctic and has experienced a pronounced decline over the past three generations (Andres et al. 2012b, Hicklin and Chardine 2012, Smith et al. 2012). The eastern population's decline is one of the primary reasons for the species' current

conservation status (BirdLife International 2016). Additionally, declines have been documented along migration routes (Gratto-Trevor et al. 2012b); and a dramatic reduction in semipalmated sandpiper numbers, amounting to approximately 79% over thirty years, was documented in a major 'wintering' area along the coast of northeastern South America (Morrison et al. 2012). (Note that throughout my thesis, 'winter' is defined as boreal winter/austral summer, which for semipalmated sandpipers is approximately mid-September – February.) This decline is larger than can be explained by a loss of individuals from the eastern breeding population alone.

The specific causes of observed declines in this species are not known; but, as for other shorebirds (IWSG 2003, Baker et al. 2004, Morrison et al. 2004, Rogers et al. 2010), conditions encountered during the non-breeding portion of the annual cycle, including on the wintering range and at key migratory stopover sites, have been implicated (Jehl 2007, Mizrahi et al. 2012, Morrison et al. 2012, Watts et al. 2015, BirdLife International 2016, Brown et al. 2017). During the conceptual stages of my research, the three breeding populations of semipalmated sandpiper were thought to remain somewhat segregated on the wintering areas. There appeared to be a clear connection between the declining eastern population (Andres et al. 2012b, Smith et al. 2012) and the wintering in French Guiana and Suriname, where a population-level decline was documented between 1982 and 2010 (Morrison et al. 2012). The central breeding population, for which trends are unclear (Andres et al. 2012b, Smith et al. 2012), also used this wintering area to some extent. Birds from the western breeding population, which is stable or even increasing (Andres et al. 2012b, Smith et al. 2012), could also be found here; but in general, the western breeding population seemed to mostly winter farther west. This picture of migratory connectivity (i.e. connections between the geographic areas used by individuals or populations during one phase of the annual cycle), given by Gratto-Trevor et al. (2012a), was based on very few birds but suggested the eastern breeding population might be limited by factors encountered during winter (Morrison et al. 2012).

However, because all three breeding populations are known to mix in the wintering region where dramatic declines have been documented (Gratto-Trevor et al. 2012a, Brown et al. 2017), and evidence that the central and western populations have been impacted is lacking, some focus was directed toward factors that might be encountered exclusively by eastern breeders. Recent work has considered the role that changes to breeding habitat in the eastern portion of the range (Smith et al. 2012, Kwon 2016) and factors limiting other species along the eastern breeding population's migratory route (Mizrahi et al. 2012, Brown et al. 2017) might play in observed population declines.

Still, suboptimal conditions in the wintering areas have the potential to contribute inordinately to population demographics, as the wintering period comprises up to nine months of the annual cycle (Hicklin and Gratto-Trevor 2010). While efforts have been made to estimate overwinter survival in semipalmated sandpipers (e.g. Sandercock and Gratto-Trevor 1997, Gratto-Trevor and Vacek 2001, Rice et al. 2007), there has been little prior work examining the negative but nonfatal effects experienced by semipalmated sandpipers during the winter season, and whether such residual effects carry forward to affect individual birds or populations in subsequent seasons. Studies specifically comparing the wintering physiology of birds using locations in northeastern South America, the region where major declines had been documented, versus other regions are lacking. Further, wintering condition has not been measured in birds from known breeding locations, making a direct assessment of how environmental conditions in the wintering areas might impact breeding populations difficult.

Lack of a method to reliably track small-bodied birds through space and time means researchers have generally been unable to investigate connections among the processes and events during an individual's full annual cycle. Indeed, most prior research on semipalmated sandpipers, and on shorebirds in general, has focused on a single season because devices that would allow individuals to be tracked during their long-distance migrations (in semipalmated sandpipers, approximately 8 – 12,000 km, one-way; Brown et al. 2017) have traditionally been too large or heavy for small-bodied birds to carry. To follow individuals, researchers relied on marking birds with unique combinations of colored and metal bands to follow their movements. The probability of resighting a bird marked in one location during subsequent stages of the annual cycle was low (for shorebirds, there is a < 2% overall rate of resighting, according to USGS Bird Banding Lab records: https://www.pwrc.usgs.gov/BBL/homepage/howmany.cfm; accessed 25 January 2018). Very recently, advances in miniaturization technology have resulted in devices, including light-level sensing geolocators (hereafter, 'gls'), that are small enough to deploy on semipalmated sandpipers and can track a bird through a full annual cycle. Researchers in the Arctic Shorebird Demographics Network (ASDN), the umbrella organization for my own graduate work, used gls to gain a better picture of migratory connectivity between breeding populations of semipalmated sandpipers and wintering areas spanning most of the previously identified tropical range (Brown et al. 2017).

Using the gls-derived data (approximately one year of data for each tracked bird), together with reproductive data collected by the ASDN at breeding sites across the Arctic, I attempted to address the following major objectives with my graduate research: (1) How can we mechanistically assess whether wintering conditions impose negative effects in semipalmated sandpipers? (2) Do such sublethal effects influence other stages of the annual cycle? I looked to biomarkers (i.e. biologically-derived indicators of a process), which link individual condition to the environment (Ricklefs and Wikelski 2002), and specifically to the endocrine system, as potential tools to explore these questions. The endocrine system modulates a suite of behavioral and physiological changes, known collectively as the 'stress response', that allow individuals to respond to environmental changes or perturbations within their environment (e.g. predator activity, inclement weather, reduced food availability; Wingfield et al. 1998, Sapolsky et al. 2000, Ricklefs and Wikelski 2002). The stress response activates the hypothalamicpituitaryadrenal axis, increasing secretion of stress hormones (i.e. glucocorticoids) into the general blood circulation. Corticosterone (CORT), the primary avian glucocorticoid, is passively deposited in feather keratin while the growing feather is connected to the bloodstream (Bortolotti et al. 2008). Because feather CORT (fCORT) reflects CORT secretion at the time of feather growth and is stable through time, it provides a retroactive measurement of a bird's exposure to stressful conditions (Bortolotti et al. 2008,2009) and can be used as an indirect assessment of habitat and other environmental conditions (Fairhurst et al. 2011,2013).

The overall goal of my research was to determine whether fCORT could be used as an informative biomarker regarding the effect of poor wintering conditions on individual semipalmated sandpipers throughout their annual cycle. In Chapter 1, I evaluated the relative stress level imposed on individual birds wintering across the tropical range. I measured fCORT in tenth secondary feathers, grown on the wintering areas between November and January (Pyle 2008, Laguna et al. 2012, Tavera et al. 2016), and tested whether fCORT level varied with wintering location. Further, because events and conditions encountered throughout a bird's annual cycle can influence individual condition and fitness (Alves et al. 2013, Rushing et al. 2016), I tested whether the variation I observed in winter-incurred fCORT was related to the residual effects of breeding location, breeding effort, and aspects of southward migration in the season prior to feather growth. Birds included in these analyses wintered across the tropical range and bred at five sites distributed across the Alaskan Arctic.

In Chapter 2, I evaluated whether the physiological condition of overwintering semipalmated sandpipers, as marked by their winter-incurred stress levels, carried over to affect processes during the subsequent migration and breeding seasons. Using data from the same gls-equipped birds, I tested for the influence of winter-incurred fCORT on aspects of northward migration and reproductive performance in the season following feather growth. Because fCORT provides a relative comparison of stress imposed during molt, whether wintering location is known or not, I also included reproductive performance data from non-gls birds (i.e. birds without known wintering locations or migration data). The analyses of reproductive performance used a multiyear dataset that included birds breeding at seven sites across the North American Arctic.

Here, I evaluate the use of a relatively novel technique to determine whether limiting factors occur during the wintering stage of a long-distance migrant. This study is the first mechanistic assessment of the physiological condition of overwintering semipalmated sandpipers across the species' tropical range. It provides key information about whether conditions in a major wintering area along the northeast coast of South America (where a population-level decline has been observed) are stressful, information that may be applicable to the conservation of other shorebird species wintering in this region. This study also demonstrates the potential for poor wintering conditions to impact semipalmated sandpiper populations through methods other than reduced survival (i.e. through residual effects that carryover to subsequent seasons). My study makes an important contribution to shorebird research in general, as fCORT has previously been measured to my knowledge in only one other shorebird species (Aharon-Rotman et al. 2016) and never in a calidrid shorebird. Studies that use fCORT to distinguish between quality of wintering sites in avian taxa are rare (Bourgeon et al. 2014, Aharon-Rotman et al. 2016), and the results of my study could have broad application to other migratory birds that are difficult to track throughout their annual cycle.

References

Aharon-Rotman Y, Buchanan KL, Clark NJ, Klaassen M, Buttemer WA. 2016.Why fly the extra mile? Using stress biomarkers to assess wintering habitat quality in migratory shorebirds. Oecologia 182:385-395.

Alves JA, Gunnarsson TG, Hayhow DB, Appleton GF, Potts PM, Sutherland WJ, Gill JA. 2013. Costs, benefits, and fitness consequences of different migratory strategies. Ecology 94:11–17.

Andres BA, Smith PA, Morrison RIG, Gratto-Trevor CL, Brown SC, Friis CA. 2012a. Population estimates of North American shorebirds, 2012. Wader Study Group Bull. 119:178–194.

Andres BA, Gratto-Trevor C, Hicklin P, Mizrahi D, Morrison RIG, Smith PA. 2012b. Status of

Baker AJ, González P, Piersma T, Niles LJ, de Lima Serrano do Nascimento I, Atkinson PW, Clark NA, Minton CDT, Peck MK, Aarts G. 2004. Rapid population decline in red knots: fitness consequences of decreased refuelling rates and late arrival in Delaware Bay. Proc R Soc Lond B 271:875-882.

BirdLife International. 2016. *Calidris pusilla.* The IUCN Red List of Threatened Species 2016: e.T22693373A93400702.

Bortolotti GR, Marchant TA, Blas J, German T. 2008. Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. Funct Ecol. 22:494–500.

Bortolotti, GR, Marchant T, Blas J, Cabezas S. 2009. Tracking stress: localisation, deposition and stability of corticosterone in feathers. J Exp Biol. 212:1477–1482.

Bourgeon S, Leat EHK, Magnusdóttir E, Furness RW, Strøm H, Petersen A, Gabrielsen GW, Hanssen SA, Bustnes JO. 2014. Feather corticosterone levels on wintering grounds have no carry-over effects on breeding among three populations of great skuas (*Stercorarius skua*). PLoS ONE 9(6): e100439.

Brown S, Gratto-Trevor C, Porter R, Weiser EL, Mizrahi D, Bentzen R, Boldenow M, Clay R, Freeman S, Giroux M-A, et al. 2017. Migratory connectivity of semipalmated sandpipers and implications for conservation. Condor 119:207–224.

CHASM (Committee for Holarctic Shorebird Monitoring). 2004. Shorebirds expert network monitoring plan. Monitoring Arctic-nesting shorebirds: an international vision for the future. Conclusions from the pan-Arctic shorebird/wader monitoring and research workshop, Denmark, 3–6 Dec 2003. Supporting publication to the CAFF Circumpolar Biodiversity Monitoring Program – framework document, CAFF CBMP Report No. 4. Akureyri (Iceland): CAFF International Secretariat. 10 p.

Fairhurst GD, Frey MD, Reichert JF, Szelest I, Kelly DM, Bortolotti GR. 2011. Does environmental enrichment reduce stress? An integrated measure of corticosterone from feathers provides a novel perspective. PLoS ONE 6:1–10.

Fairhurst GD, Vogeli M, Serrano D, Delgado A, Tella JL, Bortolotti GR. 2013. Can synchronizing feather-based measures of corticosterone and stable isotopes help us better understand habitat-physiology relationships? Oecologia 173:731–743.

Gratto-Trevor CL, Vacek CM. 2001. Longevity record and annual adult survival of semipalmated sandpipers. Wilson Bull. 113:348–350.

Gratto-Trevor C, Morrison RIG, Mizrahi D, Lank DB, Hicklin P, Spaans AL. 2012a. Migratory connectivity of semipalmated sandpipers: winter distribution and migration routes of breeding populations. Waterbirds 35:83–95.

Gratto-Trevor C, Smith PA, Morrison RIG, Aubry Y, and Cotter R. 2012b. Population trends in semipalmated sandpipers from migration counts. Waterbirds 35:96–105.

Hicklin P, Gratto-Trevo CL. 2010. Semipalmated sandpiper (*Calidris pusilla*), version 2.0. In: Rodewald PG, editor. The birds of North America online. Ithaca (NY): Cornell Lab of Ornithology.

Hicklin PW, Chardine JW. 2012. The morphometrics of migrant semipalmated sandpipers in the Bay of Fundy: evidence for declines in the eastern breeding population. Waterbirds 35:74–82.

IWSG (International Wader Study Group). 2003. Waders are declining worldwide. Conclusions from the 2003 International Wader Study Group conference, Cadiz, Spain. Wader Study Group Bull. 101/102:8–12.

Jehl JR Jr. 2007. Disappearance of breeding semipalmated sandpipers from Churchill, Manitoba: more than a local phenomenon. Condor 109:351–360.

Kirby JS, Stattersfield AJ, Butchart SHM, Evans MI, Grimmett RFA, Jones VR, O'Sullivan J, Tucker GM, Newton I. 2008. Key conservation issues for migratory land- and waterbird species on the world's major flyways. Bird Cons Intern. 18:S49–S73.

Kwon E. 2016. Effects of climate change on the breeding ecology and trophic interactions of Arctic-breeding shorebirds. Ph.D. dissertation. Manhattan (KS): Kansas State University. 188 p.

Laguna MP, Maillé S, Uriot S, Bocher P, Duzont F, and Delcroix E. 2012. Suivi des populations de limicoles migrateurs en Guadeloupe et Guyane, mise en relation avec le dispositif de suivi régional "Pan American Shorebird Program" (PASP). France: l'Office National de la Chasse et de la Faune Sauvage, Programme Européen Interregional Caraïbes [cited 2016 Sep 09). Available from: https://www.documentation.eauetbiodiversite.fr/notice/interreg-iv-caraibes-suivi-des-populations-de-limicoles-migrateurs-en-guadeloupe-et-guyane-mise-en-r0

Lanctot RB. 2006. Monitoring Arctic-nesting shorebirds: an international vision for the future. In: Boere GC, Stroud DA. Waterbirds around the world: a global overview of the conservation, management and research of the world's waterbird flyways. Edinburgh: The Stationary Office. p. 127-130.

Mizrahi DS, Peters KA, Hodgetts PA. 2012. Energetic condition of semipalmated and least sandpipers during northbound migration staging periods in Delaware Bay. Waterbirds 35:135–145.

Morrison RIG, Ross RK, Niles LJ. 2004. Declines in wintering populations of red knots in southern South America. Condor 106:60-70.

Morrison RIG, Mizrahi DS, Ross RK, Ottema OH, de Pracontal N, Narine A. 2012. Dramatic declines of semipalmated sandpipers on their major wintering areas in the Guianas, northern South America. Waterbirds 35:120–134.

Newton I. 2008. The migration ecology of birds. London: Academic Press. 984 p.

Parks MA, Collazo JA, Colón JA, Ramos Álvarez KR, Díaz O. 2016. Change in numbers of resident and migratory shorebirds at the Cabo Rojo Salt Flats, Puerto Rico, USA (1985–2014). Waterbirds 39:209–214.

Pyle P. 2008. Identification guide to North American birds, part II. Point Reyes Station (CA): Slate Creek Press. 835 p.

Rice SM, Collazo JA, Alldredge MW, Harrington BA, Lewis AR. 2007. Local annual survival and seasonal residency rates of semipalmated sandpipers (*Calidris pusilla*) in Puerto Rico. Auk 124:1397–1406.

Rogers DI, Yang H-Y, Hassell CJ, Boyle AN, Rogers KG, Chen B, Zhang Z-W, Piersma T. 2010. Red knots (*Calidris canutus piersmai and C. c. rogersi*) depend on a small threatened staging area in Bohai Bay, China. Emu 110(4): 307-315.

Rushing CS, Ryder TB, Marra PP. 2016. Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. Proc R Soc Lond B Biol Sci.: 283:20152846.

Sandercock BK, Gratto-Trevor CL. 1997. Local survival in semipalmated sandpipers *Calidris pusilla* breeding at La Pérouse Bay, Canada. Ibis 139:305–312.

Sapolsky RM, Romero ML, Munck A. 2000. How do glucocorticoids influence the stress response? Endoc Rev. 21:55–89.

Smith PA, Gratto-Trevor CL, Collins BT, Fellows SD, Lanctot RB, Liebezeit J, McCaffery BJ, Tracy D, Rausch J, Kendall S, et al. 2012. Trends in abundance of semipalmated sandpipers: evidence from the Arctic. Waterbirds 35:106–119.

Tavera EA, Lank DB, González PM. 2016. Effects of migration distance on life history strategies of western and semipalmated sandpipers in Perú. J Field Ornith. 87:293–308.

Vié J-C, Hilton-Taylor C, Stuart SN, editors. 2009. Wildlife in a changing world – an analysis of the 2008 IUCN Red List of Threatened Species. Gland, Switzerland: IUCN. 180 p.

Watts BD, Reed ET, Turrin C. 2015. Estimating sustainable mortality limits for shorebirds using the Western Atlantic Flyway. Wader Study 122(1): 37-53.

Wilcove DS, Wikelski M. 2008. Going, going, gone: is animal migration disappearing? PLoS Biol. 6:e188.

Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson RD. 1998. Ecological bases of hormone-behavior interactions: the "emergency life history stage." Am Zool. 38:191–206.

Chapter 1: Wintering in Atlantic South America imposes stress on a migratory sandpiper[1]

1.1 Abstract

Worldwide, migratory bird species are experiencing declines. Stressful conditions in non-breeding areas are suspected as a primary cause of declines in many species, but direct evidence is often lacking. We used movement data from 40 semipalmated sandpipers (*Calidris pusilla*), equipped with light-sensing geolocators at five breeding sites, to determine their wintering locations. We then measured levels of corticosterone in their winter-grown feathers. We tested 1) whether individuals using four distinct regions across the wintering range, including those wintering in a region undergoing a population-level decline, incurred different levels of stress; and 2) whether breeding site and effort may have influenced stress incurred during winter months. We found stress varied significantly with wintering region; and birds wintering in Atlantic South America, where a dramatic decline has been documented, had relatively high stress levels. Unexpectedly, birds that incubated clutches longer had lower stress during the subsequent winter than birds whose nests failed early. As stress did not vary with breeding site, this suggests individual quality or other unmeasured factors mediated an individual's response to stressful conditions during winter. Our results provide the first direct evidence that semipalmated sandpipers overwintering in a region experiencing a major decline had high levels of winter-incurred stress. Specific environmental causes of stress during winter remain unknown.

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[1] Boldenow ML, Powell AN, Lanctot RB, Porter R, Brown S, Bentzen R, Cunningham J, English W, Freeman S, Grond K, Kwon E, Lank DB, Latty C, Lovarti V, Payer D, Saalfeld S, Sandercock BK, Kitaysky AS. Wintering in Atlantic South America imposes stress on a migratory sandpiper. Prepared for submission in Biology Letters.

1.2 Introduction

In migratory species, conditions and events experienced in disparate locations accumulate across the annual cycle, influencing fitness and driving population trends [1,2]. Declines documented in migratory birds globally [3] are especially prevalent in Arctic-breeding shorebirds [4,5]. These species undertake extreme migrations between their tropical non-breeding (hereafter 'wintering') grounds and the Arctic, encountering diverse threats along the way [6]. In the semipalmated sandpiper (*Calidris pusilla*), a significant decline has been documented in recent decades in the eastern breeding population, whereas the western and central populations appear stable [7,8]. During the austral summer (or 'wintering' season), birds from all three populations mix along the Atlantic coast of northeastern South America (hereafter 'Atlantic South America', see [9–11]). Dramatic declines of overwintering birds have occurred here [12,13], the causes of which are unknown.

In long-distance migrants, wintering location may be one of the most important contributions to population dynamics [2,14,15]. Across a species' wintering range, individual physiological condition and fitness can be affected by large-scale variation in ecological factors (e.g. climate and weather patterns, food resource quality and availability, predator and disease prevalence) and anthropogenic impacts [2,16–19], especially in site-faithful species (such as the semipalmated sandpiper [9]) that remain within the same general location during the entire wintering period. Poor wintering conditions in Atlantic South America are suspected as a primary cause of the eastern population's decline [7,13], but studies directly comparing physiological condition of birds wintering in this region relative to other regions have been lacking.

We assessed how levels of the primary avian stress hormone (corticosterone, hereafter 'CORT') varied in winter-grown feathers of semipalmated sandpipers with known wintering locations. CORT is released by the hypothalamic-pituitary-adrenal axis when adverse environmental conditions are encountered [20,21]. While a temporary increase in CORT levels may be beneficial, helping an individual overcome a stressor, chronically elevated CORT can affect fitness [20–22], including survival [20]. CORT deposited in feathers (fCORT) reflects CORT secretion at the time of feather growth [23,24] and can be used to assess the influence of prolonged exposure to stress (e.g. living in poor habitat conditions [25]) on individual condition and fitness [23,26–29]. We thus predicted exposure to stress would vary with wintering region, and semipalmated sandpipers wintering where population-level declines have been observed would have higher fCORT levels resulting from exposure to poorer wintering conditions. We evaluated this 'winter conditions' hypothesis using feathers from individual birds with known wintering locations spanning the species' wintering range [30].

Wintering and breeding seasons, through their influence on individuals, are likely linked in driving population trends [1,2,31–34]. For example, conditions encountered during the breeding season can carry forward to affect individual physiology and fitness during subsequent seasons [15,31,35,36]. Environmental conditions across the Arctic are likely determined at a local scale [37,38]; consequently, birds' physiological condition during breeding and subsequent seasons might vary by breeding location. Because carryover effects from the breeding season have been linked to fCORT [39,40], we assessed whether winter-deposited fCORT varied with factors experienced during the breeding season prior to feather growth. We predicted that winter-deposited fCORT would vary significantly in birds breeding at geographically disparate sites across the range, due to carryover effects from conditions experienced during the breeding season ('breeding conditions' hypothesis).

Further, the short breeding season could have a disproportionate effect on other components of the annual cycle because reproduction itself is costly [41-44], and might be more so in Arctic-breeding migratory species [43,45–49]. Physiological costs to parents may increase with increased breeding effort [50,51], and costs related to reproductive effort can carry over to influence physiological condition and processes in subsequent seasons [51–56]. Because prior studies demonstrated fCORT can reflect breeding effort [24,53], we predicted birds that successfully hatched chicks (or, those that incubated to hatch or near-hatch) would have higher fCORT, compared to birds whose nests failed early ('breeding effort' hypothesis).

In this study, we looked for direct evidence as to whether observed declines in this species are a likely product of poor conditions in the wintering areas, as previously suggested, by measuring physiological condition of birds using known wintering and breeding locations. We evaluated whether fCORT deposited in winter-grown feathers of semipalmated sandpipers varied with wintering location, or was related to carryover effects from where a bird bred and/or reproductive effort expended during the prior breeding season. Wintering locations were previously identified using light-sensing geolocators, which enabled tracking this small-bodied species throughout the annual cycle [9].

1.3 Methods

1.3.1 Determining wintering location with geolocators

To determine wintering locations for individual birds (Figure 1.1.a inset), we used movement data from semipalmated sandpipers equipped with light-sensing geolocators (gls) at five breeding sites in the Alaskan Arctic (Figure 1.1.b inset). Gls were deployed at Nome during 2011-2013, and all other locations in 2013. See Brown *et al.* [9] for methods on capturing and marking breeding adults, deploying and retrieving gls, and for detailed information on data processing methods used to generate track lines of individual birds. This study has been conducted under all required scientific collection and Institutional Animal Care and Use Committee (IACUC) permits, including UAF IACUC Protocol #454359 (Appendix C).

Wintering locations were defined by the geographic coordinates of an individual once its southward movement ended in fall and before it began northward movement in spring (with birds wintering during ~ mid-September through February). Of the 40 gls-carrying birds, wintering locations could be identified for 36 (additional sample size information included in supplementary materials, Table A-1). Wintering locations clustered into four distinct regions (Figure 1.1.a inset). Each bird used a single region during the wintering period.

1.3.2 Feather collection

When birds were recaptured to retrieve their gls (a year after deployment), we collected the right and left tenth secondary feathers and used one for fCORT analyses (available for all gls-equipped birds). These feathers are molted and regrown on the wintering areas, between November and February [12,57,58].

1.3.3 Determining breeding effort

Breeding effort was recorded in the same season as gls deployment. We determined nest initiation date either by 1) documenting clutch completion for nests found during lay, and back-casting initiation date by assuming one egg was laid per day, or 2) calculating initiation date for nests found with complete clutches by measuring the angle and location of eggs floated in water and applying a species-specific egg flotation curve [59]. Clutch completion, length of incubation, and nest fate (available for 37 and 26 birds, respectively; see supplementary materials, Table A-2) were documented through repeated visits. Field methods are detailed in Brown *et al.* 2014 [60].

1.3.4 Feather corticosterone assay

Feathers were prepared for hormone analysis according to Will *et al.* 2014 [61], following Bortolotti *et al.* 2008 [24]. Feathers were washed with distilled water and air-dried. After calamus removal, feathers were measured (nearest mm) and clipped to a standard length (30 mm from natural tip to clipped base). Each 30-mm fragment was weighed to the nearest 0.0001g. Feathers were individually extracted in 7mL methanol (HPLC-grade, Fisher Scientific, Waltham, MA). Dried extracts were reconstituted in PBSG buffer and analyzed in a single radioimmunoassay [24], using a Sigma-Aldrich antibody (C 8784, St Louis, MO, USA). To control for loss of fCORT during extraction, 2000 cpm of H^3-labeled CORT (PerkinElmer NET399, Boston, MA, USA) was added to each feather sample, and final fCORT titers were adjusted for % recovery (mean 95.2% ± 2.6%). Assay results were normalized by converting to pg mm^{-1} [25], detrended for feather mass [61], and reported here as $\log_{10}$ fCORT.

1.3.5 Data analysis

To test the winter conditions hypothesis, we compared fCORT values for birds in each pair of wintering regions (e.g. Atlantic South America versus Pacific South America), using Wilcoxon rank sum tests in package ‘coin’ [62], Program R version 3.2.4 [63]. We derived non-parametric bootstrapped mean fCORT and percentile-based confidence intervals (1000 iterations) for each region in package ‘boot’ [64]. Bootstrapping gives more robust estimates than can be obtained by deriving estimates using parametric statistics with small sample sizes, and better approximates true distribution in the population [65]. We excluded birds with unknown wintering locations and the single birds wintering in the Panama and Dominican Republic locations. Males and females were analyzed as one group ($n = 36$), as sex appeared not to affect fCORT (see supplementary material, Appendix A).

We used these same statistical tests for our 'breeding conditions' and 'breeding effort' hypotheses, comparing winter-deposited fCORT of birds using different breeding sites and evaluating whether fCORT varied significantly with prior season's breeding effort, using nest fate (i.e. hatch *versus* fail) and length of incubation (eggs < 7 days, mid 7 – 14 days, and late 14 – 22 days). Length of incubation provided similar information to nest fate but was available for more birds. We used a 90% significance level for all tests, given our sample sizes [66,67].

1.4 Results

1.4.1 Winter conditions hypothesis

Overall, log fCORT levels ranged from 0.709 to 1.171 [pg mm^{-1}] for all birds in our study and differed significantly for semipalmated sandpipers using different wintering regions (Fig. 1.1.a; Table 1.1.a). Wilcoxon rank sum tests revealed birds had higher fCORT levels in two regions and lower levels in two regions. Birds in the lower-stress regions did not differ significantly in fCORT levels (Pacific South America v. Caribbean South America: $W = 30, p = 1.00$) but had lower fCORT than birds wintering in the Atlantic South America ($W = 35, p = 0.04$ and $W = 67, p = 0.04$) and Pacific Central America ($W = 3, p = 0.01$ and $W = 3, p = 0.07$) regions. Birds wintering in the higher-stress regions did not differ significantly in their fCORT levels ($W = 12, p = 0.10$).

1.4.2 Breeding conditions hypotheses

When birds were grouped by breeding site, we observed an extensive overlap in fCORT levels (Fig. 1.1.b; Table 1.1.b). Differences between any pair of breeding sites were not significant, including sites with the lowest and highest fCORT levels (e.g. Point Barrow, hereafter 'Barrow') v. Cape Krusenstern: W = 14, *p* = 0.12).

We found fCORT levels were negatively related to both measures of breeding effort (i.e. nest fate and length of incubation, Figs. 1.1.c and 1.1.d; Table 1.2). Birds that hatched nests tended to have lower fCORT levels than birds whose nests failed (W = 41, *p* = 0.09), and birds that incubated their nests to a late stage had lower levels than birds that stopped incubating at early- (W = 74, *p* = 0.06) or mid-stages (W = 176, *p* = 0.05). In birds ending incubation at early- and mid-stages, fCORT levels were not significantly different (W = 31, *p* = 0.92).

1.5 Discussion

Our results demonstrate regions across the wintering range do not provide equal conditions for overwintering semipalmated sandpipers. Birds using locations in Pacific and Caribbean South America had significantly lower fCORT levels than those wintering in Atlantic South America, the wintering region where a drastic decline in semipalmated sandpipers has been observed [12,13]. Our results support prior studies' suggestions that poor wintering conditions might contribute to declining numbers of birds in this region, which is the primary overwintering area for the eastern breeding population [9–11]. Although our analysis represents a one-time 'snapshot' of wintering conditions in each region, these results suggest high stress as a mechanism by which poor wintering conditions might contribute to declining trends in the eastern breeding population.

However, the potential contribution of wintering conditions to declining trends in semipalmated sandpipers is made less clear by the higher stress levels we unexpectedly found in the small number of birds that wintered in Pacific Central America. In general, birds wintering in this region belong predominantly to the western breeding population [9–11], which is thought to be stable [7,8]. We cannot assess whether the higher stress measured in birds using this region was likely caused by a poor or typical year. Unfortunately, unlike for Atlantic South America, trend data for overwintering shorebirds are lacking for Pacific Central America. If representative of typical conditions, our data may signal a potential area of concern for a portion of the western breeding population. Possibly, some portion of the western breeding population is also declining, but prior population trend analyses were too course to detect this.

Whether wintering conditions contribute to declining breeding populations might depend on the extent to which each population is connected to poor- versus high-quality wintering areas [68,69]. Prior gls and marking analyses indicate the eastern population of semipalmated sandpiper has strong connectivity to wintering areas in Atlantic South America, while the western population has diffuse connectivity and uses the entire wintering range [9–11]. Therefore, the western breeding population might not be declining overall because, unlike eastern breeders, western breeders also use wintering regions associated with lower stress. Similarly, some breeding sites in this study showed strong migratory connectivity with certain wintering regions; others showed diffuse connectivity, with birds breeding in one location using several wintering regions across the species' range. For example, the easternmost breeding site, Canning River, showed strong connectivity to Atlantic South America (Fig. 1.2), while Barrow was only moderately connected with this high-stress region. Because a large proportion of birds breeding at Barrow overwintered in lower-stress regions, they tended toward lower fCORT levels than birds breeding at Canning River (Fig. 1.1.b), although this difference was not significant. Our result showed that breeding site alone did not drive differences winter-incurred fCORT levels, but our limited sample size did not allow us to mechanistically assess whether individual stress loads might be determined by interactions between breeding site and wintering region (i.e. by individual migratory connectivity). Similar to our results, in a study of great skuas (*Stercorarius skua*), fCORT varied by wintering area but not by breeding colony. However, in this species, significant differences were also found in the fCORT levels of females sharing common wintering areas, and these differences appeared to depend on the breeding colony from which birds originated [70].

The potential for an individual's reproductive effort to carry forward to affect events and processes in subsequent seasons has been described in theory [15,35,36] and sometimes demonstrated through direct measures [41,52-55]. However only a few previous studies have directly assessed the relationship of breeding effort to fCORT levels in subsequent seasons [24,27], as we have done here. Contrary to our prediction, our results showed individuals with greater breeding effort (i.e. those incubated to a late stage and/or hatched chicks) incurred lower stress during the subsequent winter. Perhaps some birds experienced adverse breeding conditions that led both to early nest failure [71] and lower physiological condition. These birds may have been unable to recover, and remained in lower condition on the wintering grounds [21,72,73]. However, in this scenario, we should have found support for our breeding conditions hypothesis. Intrinsic quality, not directly assessed here, might also mediate an individual's response to stressful conditions [20,74,75] and confound relationships among breeding site, breeding effort, and subsequent fCORT. For example, higher quality individuals might overcome adverse environmental conditions to successfully reproduce, while poorer quality individuals might fail regardless of local conditions. Indeed, the effect of intrinsic quality on the stress response has important consequences to reproductive success. For example, a bird with up-regulated adrenal function might more readily enter an emergency life history state, redirecting from parental duties to self-maintenance [21,22] and resulting in clutch abandonment. This link between intrinsic quality, stress physiology, and behavior might explain the relationship we found between our measures of breeding effort and fCORT. The influence of intrinsic quality and other factors (e.g. age, pairing history; [76,77]) on both breeding effort and winter stress loads warrants future, focused investigation.

Birds in lower physiological condition may shorten their season in the Arctic to prolong their time in the wintering areas, as suggested in black-legged kittiwakes (*Rissa tridactyla* [40]). In that study, females with experimentally induced stress departed their breeding colonies earlier than controls, and increased their wintering time [40]. We also found semipalmated sandpipers that experienced nest failures started their southward migration earlier compared to birds that incubated longer and/or hatched chicks (see supplementary material, Appendix A). These birds also arrived earlier at their wintering areas. While the winter season may offer an opportunity to recover from the energetically demanding breeding season and costly southward migration, semipalmated sandpipers with nest failures subsequently had higher fCORT. If failed breeders winter in suboptimal conditions [52,54], the consequences of increased exposure to stressors might compound during an individual's annual cycle and result in reduced lifetime fitness. Whether intrinsic quality or other untested factors that may affect individual condition played a role in the winter distribution of semipalmated sandpipers could not be tested here.

The lack of support for our breeding condition and breeding effort hypotheses does not mean carryover effects from the breeding season do not occur in this species. Such carryover effects might have gone undetected due to our small sample size, or some other bias or limitation in our data. For example, we did not assess whether the demands of brood-rearing carryover to influence physiological condition of wintering semipalmated sandpipers, but attending young might have the highest energetic demands ([78], but see [79]). Additionally, while a disproportionate number of our sampled birds were male (see Table A-2), females might incur higher breeding costs [78], such that a relationship between breeding effort and subsequent winter stress might be easier to detect in females (but see also [80,81]). We also assessed fCORT in only one year for each bird, which might cause carryover effects to go undetected [27,82,83], particularly if significant differences in ecological conditions occur among years. Our snapshot assessment could have followed a summer of sufficiently good conditions that negative carry-over effects could be not detected in the following winter. Indeed, in prior studies, end-of-incubation energy deficits have been documented in semipalmated sandpipers in Barrow (name recently changed to Utqiaġvik), Alaska [78] but appear to occur at lower latitudes only during years with challenging environmental conditions [84].

While wintering in higher stress regions might impact survival and/or performance in subsequent seasons, the quantity of fCORT that signals negative but nonfatal (i.e. sublethal) effects in semipalmated sandpipers is unknown, and we lack a reference value for this species to confirm whether the high fCORT values measured here equate to high or 'normal' levels of stress. Notably all birds included in our study were in sufficient condition to complete migrations from the wintering to the breeding areas, and most successfully obtained a mate and produced a clutch (i.e. they were in good enough condition to breed). Assessing fCORT in birds that do not survive the winter season and thus do not return to the breeding areas (e.g. by collecting feathers from birds across the wintering range while they are overwintering) could provide important context regarding the biological significance of the range in fCORT measured in this study. Additionally, because wintering in poor conditions might negatively affect a bird's physiological condition throughout the annual cycle [32,85,86], we might examine the presence of carryover effects from winter to subsequent seasons to determine the potential fitness consequences of wintering in poor conditions.

1.6 Conclusion

Our ability to determine the factors that influence population trends in migratory species is often constrained by an inability to connect the different phases of their annual cycle [36]. Our results address this problem in semipalmated sandpipers, combining a relatively recent geolocator technology with a biomarker of environmental conditions experienced during the wintering stage of their annual cycle. We measured fCORT in winter-grown feathers as a mechanistic assessment of conditions experienced by individuals from known wintering locations. Prior studies that distinguish between quality of migratory birds' wintering sites, using fCORT as a biomarker, are rare; we know of only two (see [16,70]). Our study contributes to this literature and provides the first evidence that stress recorded in winter-grown feathers is an informative biomarker regarding the individual costs and benefits of living conditions encountered by semipalmated sandpipers across their wintering range. Birds wintering in Pacific Central America and Atlantic South America, the latter a region where population-level declines have been observed, were among the most highly stressed in our study. Based on evidence from a small number of birds, our study suggests current environmental conditions in these regions might be detrimental to individual fitness.

Continued research is needed to determine the primary stressor or set of stressors affecting individuals, and possibly populations, especially in 'high-stress' wintering regions used by semipalmated sandpipers. Importantly, habitat quality is likely to vary at finer spatial scales, and we would expect some good quality habitats occur in all regions. We recommend conducting additional studies across the wintering range, increasing coverage and allowing an assessment of birds using a range of environmental conditions at finer spatial scales. Such effort might enable identification of the scale(s) at which stressors occur, and possibly identification of the stressors themselves. We did not determine the biological significance of the range of fCORT levels we observed (i.e. whether semipalmated sandpipers with high stress levels experienced fitness consequences). Sampling birds in the wintering areas would also allow assessment of the physiological condition of birds that do not subsequently return to the breeding areas. Future work should evaluate factors, such as intrinsic quality, that might influence stress in overwintering semipalmated sandpipers; and explore potential carryover effects of winter-incurred stress to other stages of the annual cycle.

1.7 References

1. Rushing CS, Ryder TB, Marra PP. 2016 Quantifying drivers of population dynamics for a migratory bird throughout the annual cycle. *Proc R Soc. B* **283**(1823):20152846. (doi: 10.1098/rspb.2015.2846)

2. Alves JA, Gunnarsson TG, Hayhow DB, Appleton GF, Potts PM, Sutherland WJ, Gill, JA. 2013 Costs, benefits, and fitness consequences of different migratory strategies. *Ecology* **94**(1), 11–7. (doi: 10.1890/12-0737.1)
3. Kirby JS, Stattersfield AJ, Butchart SHM, Evans MI, Grimmett RFA, Jones VR, O'Sullivan J, Tucker GM, Newton I. 2008 Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conserv Int.* **18**(S1), S49–S73. (doi: 10.1017/S0959270908000439)
4. Lanctot RB. 2006 Monitoring Arctic-nesting shorebirds: an international vision for the future. In *Waterbirds around the world: A global overview of the conservation, management and research of the world's waterbird flyways (*eds GC Boere, DA Stroud), pp. 127-130. Edinburgh, UK: The Stationary Office.
5. International Wader Study Group. 2003 Waders are declining worldwide. Conclusions from the 2003 International Wader Study Group Conference, Cadiz, Spain. *Wader Study Group Bull.* **101/102**, 8-12.
6. Munro M. 2017 What's killing the world's shorebirds? *Nature* **541**, 16–20. (doi: 10.1038/541016a)
7. Andres BA, Gratto-Trevor C, Hicklin P, Mizrahi D, Morrison RIG, Smith PA. 2012 Status of the semipalmated sandpiper. *Waterbirds* **35**(1), 146–148. (doi: 10.1675/063.035.0114)
8. Smith PA *et al.* 2012 Trends in abundance of Semipalmated Sandpipers: evidence from the Arctic. *Waterbirds* **35**(1), 106–119. (doi: 10.1675/063.035.0111)
9. Brown S *et al.* 2017 Migratory connectivity of semipalmated sandpipers and implications for conservation. *Condor* **119**(2), 207–224. (doi: 10.1650/CONDOR-16-55.1)

10. Gratto-Trevor C, Morrison RIG, Mizrahi D, Lank DB, Hicklin P, Spaans AL. 2012 Migratory connectivity of semipalmated sandpipers: winter distribution and migration routes of breeding populations. *Waterbirds* **35**(1), 83–95. (doi: 10.1675/063.035.0109)

11. Lank DB. 1983 Migratory behavior of semipalmated sandpipers at inland and coastal staging areas. PhD dissertation, Cornell University. 302 p.

12. Laguna MP, Maillé S, Uriot S, Bocher P, Duzont F, Delcroix E. Suivi des populations de limicoles migrateurs en Guadeloupe et Guyane, mise en relation avec le dispositif de suivi régional “Pan American Shorebird Program” (PASP), pp. 102–116. *Unpubl.* Available from: https://www.documentation.eauetbiodiversite.fr/notice/interreg-iv-caraibes-suivi-des-populations-de-limicoles-migrateurs-en-guadeloupe-et-guyane-mise-en-r0

13. Morrison RIG, Mizrahi DS, Ross RK, Ottema OH, de Pracontal N, Narine A. 2012 Dramatic declines of semipalmated sandpipers on their major wintering areas in the Guianas, northern South America. *Waterbirds* **35**(1), 120-134. (doi: 10.1675/063.035.0112)

14. Marra PP, Holmes RT. 2001 Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. *Auk* **118**(1), 92-104. (doi: 10.1642/0004-8038(2001)118[0092:CODMHS]2.0.CO;2)

15. Fretwell SD. 1972 Populations in a Seasonal Environment. *Monogr Popul Biol.* **5**. Princeton, New Jersey: Princeton University Press. 224 pp.

16. Aharon-Rotman Y, Buchanan KL, Clark NJ, Klaassen M, Buttemer WA. 2016 Why fly the extra mile? Using stress biomarkers to assess wintering habitat quality in migratory shorebirds. *Oecologia* **182**, 385–395. (doi: 10.1007/s00442-016-3679-1)

17. Wikelski M, Cooke SJ. 2006 Conservation physiology. *Trends Ecol Evol.* **21**(2), 38–46. (doi: 10.1016/j.tree.2005.10.018)

18. Piersma T, Rogers DI, González PM, Zwarts L, Niles LJ, de Lima Serrano do Nascimento I, Minton CDT, Baker AJ. 2005 Fuel storage rates before northward flights in red knots worldwide. In *Birds of Two Worlds: The Ecology and Evolution of Migration* (eds. R Greenberg, PP Marra), pp. 262–273. Baltimore, MD: The Johns Hopkins University Press.

19. Castro G, Myers J, Ricklefs R. 1992 Ecology and energetics of sanderlings migrating to four latitudes. *Ecology* **73**(3), 833–844. (doi: 10.2307/1940161)

20. Sapolsky RM, Romero ML, Munck A. 2000 How do glucocorticoids influence the stress response? *Endocr Rev.* **21**(1), 55–89. (doi: 10.1210/er.21.1.55)

21. Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson RD. 1998 Ecological bases of hormone-behavior interactions: the "emergency life history stage." *Am Zool.* **38**(1), 191–206. (doi: 10.1093/icb/38.1.191)

22. Wingfield JC, Kitaysky AS. 2002. Endocrine responses to unpredictable environmental events: stress or anti-stress hormones? *Integr Comp Biol.* **42**(3), 600–609. (doi: 10.1093/icb/42.3.600)

23. Bortolotti GR, Marchant T, Blas J, Cabezas S. 2009 Tracking stress: localisation, deposition and stability of corticosterone in feathers. *J Exp Biol.* **212**, 1477–1482. (doi: 10.1242/jeb.022152)

24. Bortolotti GR, Marchant TA, Blas J, German T. 2008 Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. *Funct Ecol.* **22**, 494–500. (doi: 10.1111/j.1365-2435.2008.01387.x)

25. Fairhurst GD, Vogeli M, Serrano D, Delgado A, Tella JL, Bortolotti GR. 2013 Can synchronizing feather-based measures of corticosterone and stable isotopes help us better understand habitat-physiology relationships? *Oecologia* **173**(3), 731–743. (doi: 10.1007/s00442-013-2678-8)

26. Harms NJ, Legagneux P, Gilchrist HG, Bêty J, Love OP, Forbes MR, Bortolotti GR, Soos C. 2014 Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird. *Proc R Soc B* **282**:20142085. (doi:10.1098/rspb.2014.2085)

27. Legagneux P, Harms NJ, Gauthier G, Chastel O, Gilchrist HG, Bortolotti G, Bêty J, Soos C. 2013 Does feather corticosterone reflect individual quality or external stress in Arctic-nesting migratory birds? *PLoS One* **8**(12), 6–13. (doi: 10.1371/journal.pone.0082644)

28. Koren L, Nakagawa S, Burke T, Soma KK, Wynne-Edwards KE, Geffen E. 2012 Non-breeding feather concentrations of testosterone, corticosterone and cortisol are associated with subsequent survival in wild house sparrows. *Proc R Soc B* **279**(1733), 1560–1566. (doi: 10.1098/rspb.2011.2062)

29. Fairhurst GD, Frey MD, Reichert JF, Szelest I, Kelly DM, Bortolotti GR. 2011 Does environmental enrichment reduce stress? An integrated measure of corticosterone from feathers provides a novel perspective. *PLoS One* **6**(3), 1–10. (doi: 10.1371/journal.pone.0017663)

30. Hicklin P, Gratto-Trevor CL. 2010 Semipalmated Sandpiper (*Calidris pusilla*). In *The Birds of North America Online* (ed. PG Rodewald). Ithaca, NY: Cornell Lab of Ornithology. (doi: 10.2173/bna.6)

31. Gunnarsson TG, Gill JA, Newton J, Potts PM, Sutherland WJ. 2005 Seasonal matching of habitat quality and fitness in a migratory bird. *Proc R Soc B* **272**(1578), 2319–2323. (doi: 10.1111/j.1365-2656.2005.00994.x)

32. Runge MC, Marra PP. 2005 Modeling seasonal interactions in the population dynamics of migratory birds. In *Birds of Two Worlds: The Ecology and Evolution of Migration* (eds. R Greenberg, PP Marra), pp. 375–389. Baltimore, MD: The Johns Hopkins University Press.

33. Sillett TS, Holmes RT, Sherry TW. 2000 Impacts of a global climate cycle on population dynamics of a migratory songbird. *Science* **288**(5473), 2040–2042. (doi: 10.1126/science.288.5473.2040)

34. Sherry TW, Holmes RT. 1995 Summer versus winter limitation of populations: what are the issues and what is the evidence? In *Ecology and Management of Neotropical Migratory Birds* (eds. TE Finch, DM Martin), pp. 85–120. New York/Oxford: Oxford University Press.

35. Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. 2011 Carry-over effects as drivers of fitness differences in animals. *J Anim Ecol* **80**, 4–18. (doi: 10.1111/j.1365-2656.2010.01740.x)

36. Norris DR. 2005 Carry-over effects and habitat quality in migratory populations. *Oikos* **109**(1), 178–186. (doi: 10.1111/j.0030-1299.2005.13671.x)

37. Meltofte H *et al.* 2007 Effects of climate variation on the breeding ecology of Arctic shorebirds. In *Meddelelser om Grønland Bioscience* **59**. Copenhagen: Danish Polar Center. 48 pp.

38. Tulp I. 2007 *The Arctic pulse: timing of breeding in long-distance migrant shorebirds.* PhD dissertation, University of Groningen. 110 pp.

39. Latta SC, Cabezas S, Mejia DA, Paulino MM, Almonte H, Miller-Butterworth CM, Bortolotti GR. 2016 Carry-over effects provide linkages across the annual cycle of a Neotropical migratory bird, the Louisiana waterthrush *Parkesia motacilla*. *Ibis* **158**, 395–406. (doi: 10.1111/ibi.12344)

40. Schultner J, Moe B, Chastel O, Tartu S, Bech C, Kitaysky AS. 2014 Corticosterone mediates carry-over effects between breeding and migration in the kittiwake *Rissa tridactyla*. *Mar Ecol Prog Ser.* **496**, 125–133. (doi: 10.3354/meps10603)

41. Golet GH, Irons DB, Estes JA. 1998 Survival costs of chick rearing in black-legged kittiwakes. *J Anim Ecol.* **67**, 827–841. (doi: 10.1046/j.1365-2656.1998.00233.x)

42. Heaney V, Monaghan P. 1996 Optimal allocation of effort between reproductive phases: the trade-off between incubation costs and subsequent brood rearing capacity. *Proc R Soc B* **263**, 1719–1724. (doi: 10.1098/rspb.1996.0251)

43. Tatner P, Bryant DM. 1993 Interspecific variation in daily energy expenditure during avian incubation. *J Zool.* **231**, 215–232. (doi: 10.1111/j.1469-7998.1993.b01913.x)

44. Drent R, Daan S. 1980 The prudent parent: Energetic adjustments in avian breeding. *Ardea* **68**, 225–252. (doi: 10.5253/arde.v68.p225)

45. Hanssen SA, Hasselquist D, Folstad I, Erikstad KE. 2005 Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proc R Soc B* **272**, 1039–1046.

46. Piersma T, Lindström Å, Drent RH, Tulp I, Jukema J, Morrison RIG, Reneerkens J, Schekkerman H, Visser GH. 2003 High daily energy expenditure of incubating shorebirds on high Arctic tundra: a circumpolar study. *Funct Ecol.* **17**(3), 356–362. (doi: 10.1046/j.1365-2435.2003.00741.x)

47. Piersma T, Morrison RIG. 1994 Energy expenditure and water turnover of incubating ruddy turnstones: high costs under high Arctic climatic conditions. *Auk* **111**(2), 366–376. (doi: 10.2307/4088600)

48. Bókony V, Lendvai AZ, Liker A, Angelier F, Wingfield JC, Chastel O. 2009 Stress response and the value of reproduction: are birds prudent parents? *Am Nat.* **173**(5), 589–598. (doi: 10.1086/597610)

49. Jönsson KI, Tuomi J, Järemo J. 1998 Pre- and postbreeding costs of parental investment. *Oikos* **83**(3), 424–431. (doi: 10.2307/3546670)

50. Ouyang JQ, Sharp PJ, Dawson A, Quetting M, Hau M. 2011 Hormone levels predict individual differences in reproductive success in a passerine bird. *Proc R Soc B* **278**, 2537–2545. (doi: 10.1098/rspb.2010.2490)

51. Gustafsson L, Nordling D, Andersson MS, Sheldon BC, Qvarnström A. 1994 Infectious diseases, reproductive effort and the cost of reproduction in birds. *Philos Trans Biol Sci.* **346**(1317), 323–331. (doi: 10.1098/rstb.1994.0149)

52. Catry P, Dias MP, Phillips RA, Granadeiro JP. 2013 Carry-over effects from breeding modulate the annual cycle of a long-distance migrant: an experimental demonstration. *Ecology* **94**(6), 1230–1235. (doi: 10.1890/12-2177.1)

53. Crossin GT, Phillips RA, Lattin CR, Romero LM, Williams TD. 2013 Corticosterone mediated costs of reproduction link current to future breeding. *Gen Comp Endocrinol.* **193**, 112–120. (doi: 10.1016/j.ygcen.2013.07.011)

54. Bogdanova MI, Daunt F, Newell M, Phillips R a, Harris MP, Wanless S. 2011 Seasonal interactions in the black-legged kittiwake, *Rissa tridactyla*: links between breeding performance and winter distribution. *Proc R Soc. B* **278**(1717), 2412–2418. (doi: 10.1098/rspb.2010.2601)

55. Inger R, Harrison XA, Graeme DR, Newton J, Colhoun K, Gudmundsson GA, McElwaine G, Pickford M, Hodgson, Bearhop S. 2010 Carry-over effects reveal reproductive costs in a long distance migrant. *J Anim Ecol.* **79**(5), 974–982. (doi: 10.1111/j.1365-2656.2010.01712.x)

56. Nilsson J-A, Svensson E. 1996 The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proc R Soc B* **263**, 711–714. (doi: doi:10.1086/303379)

57. Tavera EA, Lank DB, González PM. 2016 Effects of migration distance on life history strategies of western and semipalmated sandpipers in Perú. *J F Ornithol.* **87**(3), 293–308. (doi: 10.1111/jofo.12164)

58. Pyle P. 2008 *Identification Guide to North American Birds, Part II*. Point Reyes Station, California: Slate Creek Press. 835 pp.

59. Liebezeit JR, *et al*. 2007 Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. *Condor* **109**(1), 32–47. (doi: 10.1650/0010-5422(2007)109[32:ATDOSE]2.0.CO;2)

60. Brown SC, Gates HR, Liebezeit JR, Smith PA, Hill BL, Lanctot RB. *Arctic Shorebird Demographics Network Breeding Camp Protocol.* 2014. U.S. Fish and Wildlife Service and Manomet Center for Conservation Sciences. *Unpubl.* Available from: https://www.manomet.org/sites/default/files/publications_and_tools/ASDN_Protocol_V5_20Apr2014.pdf 118 pp.

61. Will AP, Suzuki Y, Elliott KH, Hatch SA, Watanuki Y, Kitaysky AS. 2014 Feather corticosterone reveals developmental stress in seabirds. *J Exp Biol.* **217**, 2371–2376. (doi: 10.1242/jeb.098533)

62. Hothorn T, Hornik K, van de Wiel MA, Winell H, Zeileis A. 2015 *Package "coin": Conditional Inference Procedure in a Permutation Test Framework.* See http://coin.r-forge.r-project.org

63. R Core Team. 2016 *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing.

64. Canty A, Ripley B. 2016 *boot: Bootstrap R (S-Plus) Functions.* See https://cran.r-project.org/web/packages/boot/index.html

65. Davison AC, Hinkley DV. 1997. *Bootstrap methods and their application.* New York: Cambridge University Press.

66. Greenland S, Senn SJ, Rothman KJ, Carlin JB, Poole C, Goodman SN, Altman DG. 2016 Statistical tests, *P* values, confidence intervals, and power: a guide to misinterpretations. *Eur J Epidemiol.* **31**(4), 337–350. (doi: 10.1007/s10654-016-0149-3)

67. Wasserstein RL, Lazar NA. 2016 The ASA's Statement on *p*-Values: Context, Process, and Purpose. *Am Stat.* **70**(2), 129–133. (doi: 10.1080/00031305.2016.1154108)

68. Wilson S, Ladeau SL, Toøttrup AP, Marra PP. 2011 Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. *Ecology* **92**(9), 1789–1798. (doi: 10.1890/10-1757.1)

69. Webster MS, Marra PP. 2005 The importance of understanding migratory connectivity and seasonal interactions. In *Birds of Two Worlds: The Ecology and Evolution of Migration* (eds. R Greenberg, PP Marra), pp. 199-209. Baltimore, MD: The Johns Hopkins University Press.

70. Bourgeon S, Leat EHK, Magnusdóttir E, Furness RW, Strøm H, Petersen A, Gabrielsen GW, Hanssen SA, Bustnes JO. 2014 Feather corticosterone levels on wintering grounds have no carry-over effects on breeding among three populations of great skuas (*Stercorarius skua*). *PLoS One* **9**(6), 1–6. (doi: 10.1371/journal.pone.0100439)

71. Silverin B. 1986 Corticosterone-binding proteins and behavioral effects of high plasma levels of corticosterone during the breeding period in the pied flycatcher. *Gen Comp Endocrinol.* **64**(1), 67–74. (doi: 10.1016/0016-6480(86)90029-8)

72. Breuner CW, Patterson SH, Hahn TP. 2008 In search of relationships between the acute adrenocortical response and fitness. *Gen Comp Endocrinol.* **157**(3), 288–295. (doi: 10.1016/j.ygcen.2008.05.017)

73. Wingfield JC, Sapolsky RM. 2003 Reproduction and resistance to stress: when and how. *J Neuroendocrinol.* **15**(8), 711–724. (doi: 10.1046/j.1365-2826.2003.01033.x)

74. Angelier FF, Wingfield JC, Weimerskirch H, Chastel O. 2010 Hormonal correlates of individual quality in a long-lived bird: a test of the "corticosterone-fitness hypothesis". *Biol Lett.* **6**(6), 846–849. (doi: 10.1098/rsbl.2010.0376)

75. Ricklefs RE, Wikelski M. 2002 The physiology / life-history nexus. *Trends Ecol Evol.* **17**(10), 462–468. (doi: 10.1016/S0169-5347(02)02578-8)

76. Angelier F, Weimerskirch H, Dano S, Chastel O. 2007 Age, experience and reproductive performance in a long-lived bird: a hormonal perspective. *Behav Ecol Sociobiol.* **61**, 611–621. (doi: 10.1007/s00265-006-0290-1)

77. Heidinger BJ, Nisbet ICT, Ketterson ED. 2006 Older parents are less responsive to a stressor in a long-lived seabird: a mechanism for increased reproductive performance with age? *Proc R Soc B* **273**, 2227–2231. (doi: 10.1098/rspb.2006.3557)

78. Ashkenazie S, Safriel UN. 1979 Time-energy budget of the semipalmated sandpiper *Calidris pusilla* at Barrow, Alaska. *Ecology* **60**(4),783–799. (doi: 10.2307/1936615)

79. Tulp I, Schekkerman H, Bruinzeel LW, Jukema J, Visser GH, Piersma T. 2009 Energetic demands during incubation and chick rearing in a uniparental and a biparental shorebird breeding in the high Arctic. *Auk* **126**(1), 155–164. (doi: 10.1525/auk.2009.07181)

80. Bulla M, Valcu M, Rutten AL, Kempenaers B. 2014 Biparental incubation patterns in a high-Arctic breeding shorebird: How do pairs divide their duties? *Behav Ecol.* **25**(1), 152–164. (doi: 10.1093/beheco/art098)

81. Cresswell W, Holt S, Reid JM, Whitfield DP, Mellanby RJ. 2003 Do energetic demands constrain incubation scheduling in a biparental species? *Behav Ecol.* **14**(1), 97–102. (doi: 10.1093/beheco/14.1.97)

82. Williams CT, Kitaysky AS, Kettle AB, Buck CL. 2008 Corticosterone levels of tufted puffins vary with breeding stage, body condition index, and reproductive performance. *Gen Comp Endocrinol.* **158**:29–35. (doi: 10.1016/j.ygcen.2008.04.018)

83. Kitaysky AS, Piatt JF, Wingfield JC. 2007 Stress hormones link food availability and population processes in seabirds. *Mar Ecol Prog Ser.* **352**, 245–258. (doi: 10.3354/meps07074)

84. Gratto-Trevor C. 1991 Parental care in semipalmated sandpipers *Calidris pusilla*: brood desertion by females. *Ibis* **133**, 394–399.

85. Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2003 Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. *Proc R Soc B* **03pb0683.1**, 1–6. (doi: 10.1098/rspb.2003.2569)

86. Marra P, Hobson KA, Holmes RT. 1998 Linking winter and summer events in a migratory bird by sing stable-carbon isotopes. *Science* **282**, 1884–1886. (doi: 10.1126/science.282.5395.1884)

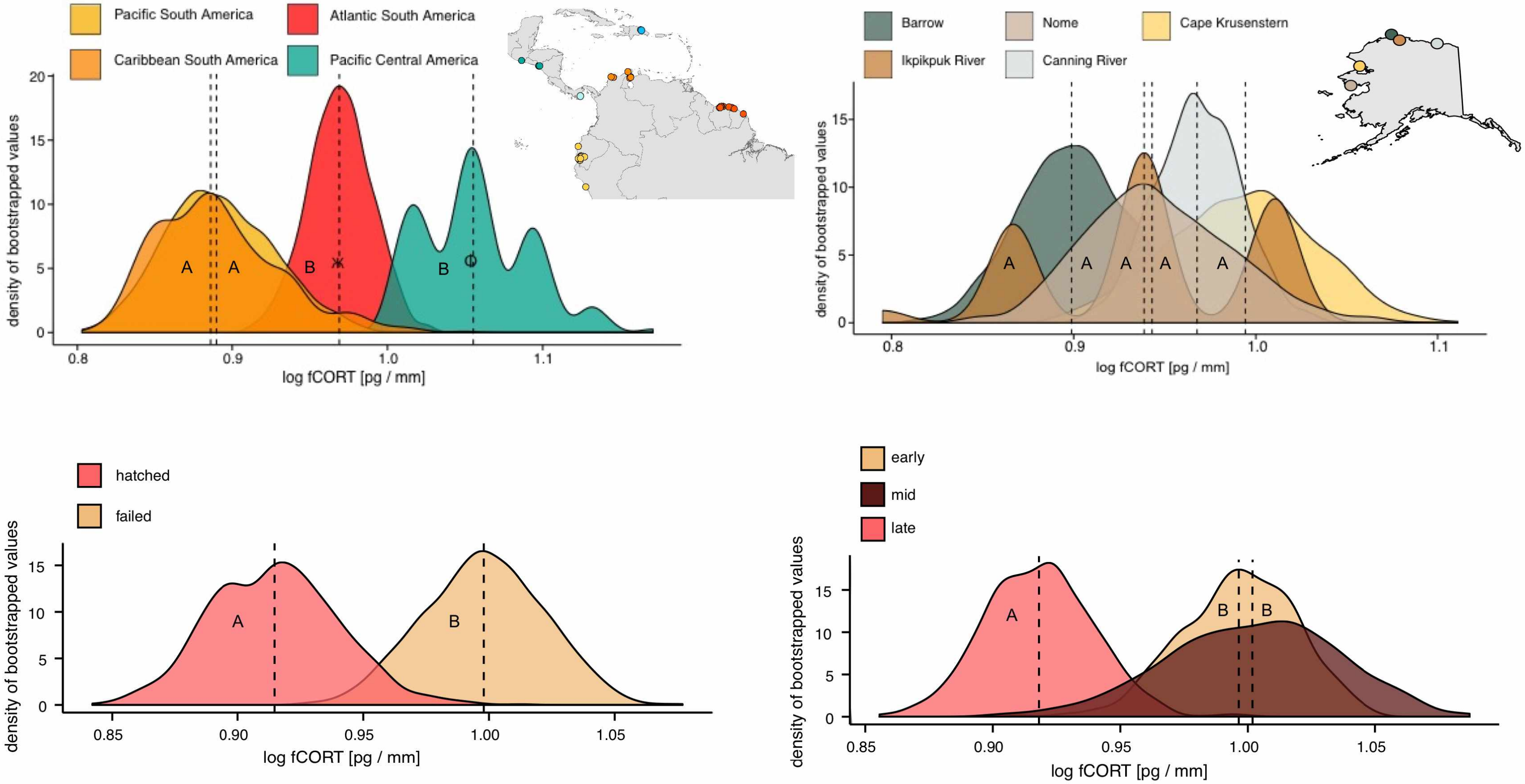

Figure 1.1. Bootstrapped mean corticosterone (log fCORT [pg mm^{-1}]) in winter-grown feathers of semipalmated sandpipers. Dashed lines indicate means. Different letters (A – B) denote significant differences, based on pairwise comparisons of wintering regions, breeding sites, nest fate, or length of incubation ($p \leq 0.10$). a) fCORT differed significantly between wintering regions. Two birds, wintering in Panama (lt. blue dot, ϕ) and Dominican Republic (dk. blue dot, ж; n = 1 ea.), were not included in bootstrap analyses or pairwise comparisons. b) fCORT was not significantly different between birds breeding at different sites. **c)** fCORT was significantly lower in birds that hatched nests than those whose nests failed in the previous season, and in birds that incubated to a late stage (14-22 days) versus those whose nests failed at early (< 7 days) and mid (7 – 14 days) incubation.

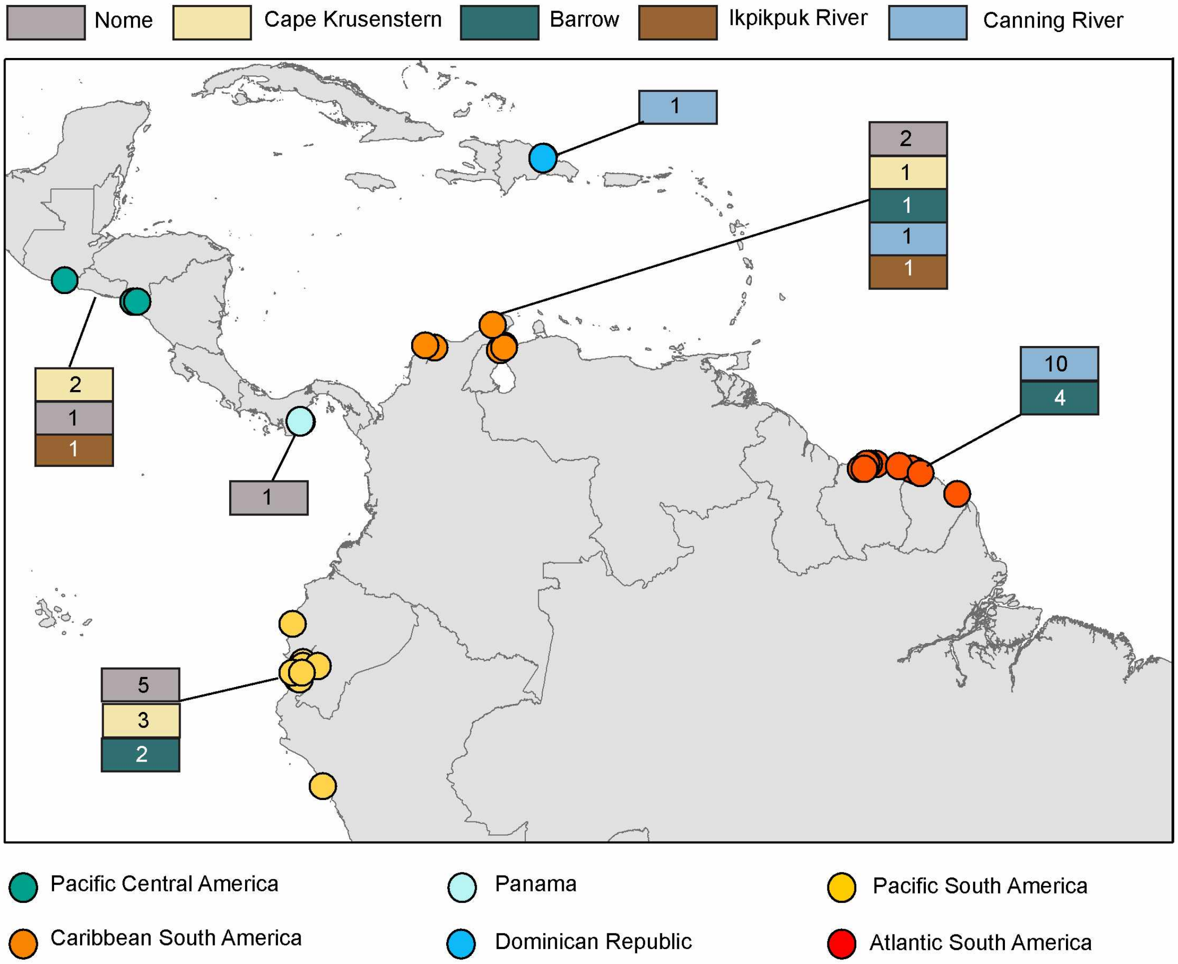

Figure 1.2 Migratory connectivity of 36 semipalmated sandpipers. GIs were placed on individual birds (circles) from five breeding sites (Nome, Cape Krusenstern, Point Barrow, Ikpikpuk River, and Canning River; see Fig. 1.1.b inset). Birds used four main wintering regions (Pacific Central America, Pacific South America, Caribbean South America, and Atlantic South America), plus Panama and Dominican Republic. Four birds with unassigned wintering regions are not depicted.

Table 1.1. Relationship between wintering and breeding locations and log fCORT [pg mm^{-1}] in winter-grown feathers of semipalmated sandpipers. Unique letters (i.e. A-E) denote groups with significant ($p \leq 0.10$) differences in fCORT, based on Wilcoxon rank sum tests. Bootstrapped confidence intervals for the mean derived from percentiles, based on 1000 replicates.

a) Wintering Region	***Range***	***Sample Mean***	***Wilcoxon Differences***[a]	***Bootstrapped 90% CI***
Atlantic South America (*n* = 14)	0.856 – 1.117	0.970	B	0.935, 1.003
Caribbean South America (*n* = 6)	0.795 – 1.091	0.892	A	0.836, 0.970
Dominican Republic (*n* = 1)	0.942	n/a[b]	n/a	n/a
Pacific South America (*n* = 10)	0.756 – 1.137	0.892	A*	0.837, 0.951
Pacific Central America (*n* = 4)	1.002 – 1.171	1.057	B*	1.005, 1.129
Panama (*n* = 1)	1.048	n/a	n/a	n/a
b) Breeding Site	***Range***	***Sample Mean***	***Wilcoxon Differences***[c]	***Bootstrapped 90% CI***
Canning River (*n* = 12)	0.844 – 1.117	0.969	A	0.929, 1.006
Ikpikpuk (*n* = 3)	0.795 – 1.013	0.939	B	0.795, 1.013
Barrow (n = 8)	0.756 – 1.026	0.898	C	0.843, 0.953
Cape Krusenstern *(n* = 7)	0.842 – 1.137	0.990	D	0.914, 1.067
Nome (*n* = 10)	0.778 – 1.171	0.948	E	0.876, 1.034

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[a] **90% CIs for Wilcoxon-based difference in location between wintering regions:** A:A* = (-0.087, 0.086), A:B = (0.156, -0.016), A:B* = (-0.298, -0.080), A*:B = (-0.152, -0.022), A*:B* = (-0.273, -0.045), B:B* = (-0.164, 0.014)

[b] **n/a = not applicable**

[c] **90% Cis for Wilcoxon-based difference in location between breeding sites:** A:B = (-0.126, 0.180), A:C = (-0.002, 0.134), A:D = (-0.119, 0.074), A:E = (-0.054, 0.117), B:C = (-0.125, 0.185), B:D = (-0.251, 0.162), B:E = (-0.163, 0.166), C:D = (-0.190, 0.005), C:E = (-0.142, 0.062), D:E = (-0.056, 0.173)

Table 1.2. Relationship between breeding effort and log fCORT [pg mm^{-1}] in winter-grown feathers of semipalmated sandpipers. Unique letters (i.e. A-B) denote groups with significant ($p \leq 0.10$) differences in fCORT, based on Wilcoxon rank sum tests. Bootstrapped confidence intervals for the mean derived from percentiles, based on 1000 replicates.

a) Nest Fate	***Range***	***Sample Mean***	***Wilcoxon Differences***[ab]	***Bootstrapped 90% CI***
Hatched (n = 8)	0.815 – 1.062	0.914	A	0.867, 0.965
Failed (n = 18)	0.788 – 1.158	0.997	B	0.788, 1.158
b) Last Known Incubation Stage				
Early (<7 days, n = 5)	0.910 – 1.062	0.997	B	0.953, 1.038
Mid (7 – 14 days, n = 13)	0.788 – 1.158	1.002	B*	0.932, 1.063
Late (14 – 22 days, n = 19)	0.748 – 1.136	0.919	A	0.878, 0.961

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[a] **90% CIs for Wilcoxon-based difference in location based on breeding effort (nest fate):** A:B = (-0.162, 0.000)

[b] **90% CIs for Wilcoxon-based difference in location based on breeding effort (length of incubation):** A:B = (0.015, 0.152), A:B* = (0.017, 0.162), B:B* 90% CI for diff. in location = (-0.101, 0.105)

Chapter 2: Stress incurred during winter delays start of spring migration and affects reproductive performance in semipalmated sandpipers (*Calidris pusilla*)[2]

2.1 Abstract

In semipalmated sandpipers (*Calidris pusilla*), poor environmental conditions on wintering grounds have likely contributed to observed population declines, although the mechanisms behind the declines are not well known. In other migratory birds, wintering conditions are known to affect migration behavior and future reproductive performance. Here, we combined data from light-sensing geolocators (gls) with a biomarker of stress exposure to examine the carryover effects of wintering conditions on subsequent stages of the annual cycle. First, we tested whether winter-incurred stress, as deposited in winter-grown feathers (fCORT), was related to timing of spring migration and date of nest initiation. For timing of migration, we used data collected with gls deployed on 24 semipalmated sandpipers at five breeding sites in the Arctic. For timing of nest initiation, we used data from gls-equipped birds and also assessed timing for birds not tracked with gls (254 birds at seven sites). Second, we tested whether winter-incurred stress levels of female birds affected clutch size (156 nests at six sites) and egg volume (101 nests at four sites). We found that start date of spring migration (but not migration rate or arrival date) had a positive relationship with fCORT: for birds wintering at the same longitude, migration was delayed up to 15 days with an increase in their fCORT levels. In the confirmed first nests of gls-

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[2] Boldenow, ML, Powell AN, Lanctot RB, Porter R, Bentzen R, Cunningham J, English W, Freeman S, Gates HR, Giroux, M-A, Grond K, Hill B, Kwon E, Lank DB, Latty C, Lecomte N, Lovarti V, Payer D, Rausch J, Saalfeld S, Sandercock BK, Woodard P, Kitaysky AS. Stress incurred during wintering delays start of spring migration and affects reproductive performance in semipalmated sandpipers (*Calidris pusilla*). Prepared for submission in Behavioral Ecology.

equipped birds, nest initiation was delayed up to five days with an increase in fCORT. In the larger dataset, fCORT was negatively related to nest initiation dates, likely reflecting initiation of second clutches after failure of undetected first nests. There was a negative relationship between clutch size and fCORT, although the threshold at which females laid fewer eggs also depended on breeding site and reflected a seasonal decline in clutch size. Contrary to our prediction, egg volume had a positive relationship with fCORT, but we found evidence (in confirmed first nests only) that females exposed to higher levels of stress during the winter may engage in a clutch size-egg volume tradeoff, reducing the number of eggs laid while investing more in each individual egg/offspring. Overall, our results suggested semipalmated sandpipers wintering in regions associated with higher exposure to stress experienced direct and indirect carryover effects to the timing and behavior of spring migration timing and to subsequent reproductive performance.

2.2 Introduction

Migratory animals experience complex, and often poorly understood, interactions between the events and processes taking place in the disparate locations used during their annual cycles (Norris 2005, Webster and Marra 2005, Runge et al. 2014). In long-distance migrants, wintering location can be one of the most important factors determining population dynamics (Marra and Holmes 2001, Alves et al. 2013), as the wide range of environmental conditions encountered across a wintering range can influence birds' physiological condition and affect fitness (Castro et al. 1992, Marra et al. 1998, Marra and Holmes 2001, Alves et al. 2013, Clark et al. 2016). In the Arctic-breeding semipalmated sandpiper (*Calidris pusilla*), concerns have been raised (Smith et al. 2012, BirdLife International 2016) due to population declines at some breeding sites and migratory stopover locations (Gratto-Trevor et al. 2012, Hicklin and Chardine 2012), as well as a dramatic decline at a major ‘wintering’ area, used during the austral summer, along the Atlantic coast of northeastern South America (Morrison et al. 2012). Poor wintering conditions are believed to contribute to these population-level declines (Harrington 2003, Andres et al. 2012, Hicklin and Chardine 2012, Morrison et al. 2012, Brown et al. 2017), but the specific causes and mechanisms behind them are not known. Although efforts have been made to estimate overwinter survival in semipalmated sandpipers (e.g. Sandercock and Gratto-Trevor 1997, Gratto-Trevor and Vacek 2001, Rice et al. 2007), there has been little work on the potential carryover effects of wintering conditions on reproduction. Most prior research on semipalmated sandpipers has focused on within-season effects because small body size and hemispheric migrations make individual birds difficult to track through space and time. However, seasonal interactions (i.e. carryover effects from one stage of the annual cycle to another) may have important consequences to individual fitness, and population dynamics.

The wintering conditions experienced by individual birds have been shown to carry forward to affect migration and breeding phenology in a variety of migratory species. For example, individuals using poorer quality wintering habitats have been shown to have delayed spring departure from the wintering areas and delayed arrival on breeding grounds, and to initiate nests later (Marra et al. 1998, Gill et al. 2001, Studds and Marra 2005, Gunnarsson et al. 2006, Guillemain et al. 2008, Sorensen et al. 2009). In many taxa, including shorebirds (Sandercock 1998a, Schroeder et al. 2007), birds that lay eggs earlier generally experience higher reproductive success (Lepage et al. 2000, Norris et al. 2003, Sorensen et al. 2009, Harms et al. 2014). In addition, chicks that hatch earlier may be larger at hatch (Schroeder et al. 2007) and subsequently experience faster growth rates (Tulp and Schekkerman 2001, Ritz et al. 2005, McKinnon et al. 2012), an extended period of parental care (Ashkenazie and Safriel 1979, Gratto-Trevor 1991, Ruthrauff et al. 2009, Jamieson et al. 2014), and higher survival (Soikkeli 1967, Amat et al. 2001, Ruthrauff and McCaffery 2005, Hill 2012). To some extent, earlier hatching may also allow juveniles to take advantage of the peak of ephemeral insect food resources (Lank et al. 1985, Schekkerman et al. 2003, Meltofte et al. 2007a, McKinnon et al. 2012), allowing them to achieve full growth potential and accumulate the energy reserves needed to successfully migrate south and survive the winter (Dawson et al. 2000, Lepage et al. 2000, Ruthrauff and McCaffery 2005, Meltofte et al. 2007b, Newton 2008, Harrison et al. 2011). Delays in timing of migration and commencement of breeding can thus have important consequences for reproductive performance (Lack 1950, Perrins 1970, Price et al. 1988, Kokko 1999, Williams 2005, Drent 2006).

In addition, wintering in poor conditions may limit the ability of females to invest in their reproductive success. Although shorebirds are generally categorized as income breeders (using locally-derived food resources to fuel their reproduction; Klaassen et al. 2001), the extent to which individuals use exogenous resources versus endogenous reserves for egg formation can vary (Martin 1987, Meijer and Drent 1999, Morrison and Hobson 2004, Hobson and Jehl 2010, Jaatinen et al. 2016). When local conditions are not amenable to egg production (e.g. in harsh springs), the endogenous reserves of females may be especially important (Nol et al. 1997, Morrison and Hobson 2004, Morrison et al. 2005). Resource-limited females can reduce their reproductive investment by laying clutches with fewer eggs, or eggs of smaller volume (Martin 1987, Bernardo 1996, Christians 2002. Although egg size clines may be related to geographic gradients in productivity (Meltofte et al. 2007b), in several bird species, including shorebirds, smaller clutches are associated with poorer pre-breeding body condition of females (Winkler and

Walters 1983, Blomqvist et al. 1997, Nol et al. 1997, Reynolds et al. 2003, Lehikoinen et al. 2006). Producing smaller eggs can also have negative fitness consequences (Martin 1987, Williams 1994, Bernardo 1996). Larger eggs tend to result in chicks with larger body size, faster growth rate, and higher survival (Ricklefs 1984, Blomqvist et al. 1997, Amat et al. 2001, Christians 2002, O'Dwyer 2004, Schroeder et al. 2007, Gladbach et al. 2010, Krist 2011). Thus, if overwintering under sub-optimal conditions limits female endogenous energy stores, it could manifest as a relationship between clutch parameters (e.g. number and size of eggs laid) and conditions encountered in the prior winter. In other words, we might see a carryover effect to female reproductive performance in the subsequent breeding season, and possibly overall fitness.

In semipalmated sandpipers, an effect of wintering condition on the timing of migration and breeding, or reproductive performance through breeding investment, has not been demonstrated. However wintering conditions may inordinately affect other stages of the annual cycle because individuals of this species spend much of the year (approximately seven months; Hicklin and Gratto-Trevor 2010) at single wintering location (Brown et al. 2017). To directly assess the environmental conditions experienced by individual birds during the winter months, we used a biomarker (i.e. a biologically derived indicator; Ricklefs and Wikelski 2002) that has been shown to link individual condition to the environment. Specifically, we measured corticosterone (CORT, the primary avian stress hormone) in winter-grown feathers. Feather corticosterone (hereafter, 'fCORT') provides a measurement of a bird's exposure to stressful conditions at the time of feather growth (Bortolotti et al. 2008,2009). CORT secretion into the general blood circulation increases when the adrenocortical function is activated in response to adverse conditions (e.g. predator activity, inclement weather, reduced food availability; (Sapolsky et al. 2000, Ricklefs and Wikelski 2002). Because CORT is passively deposited in growing feather tissues (Bortolotti et al. 2008), fCORT measurements provide an indirect assessment of environmental conditions encountered during molt (Fairhurst et al. 2011). Further, because fCORT is stable through time (Bortolotti et al. 2009), feathers growing during the wintering season can be collected in the breeding areas, and exposure to stress assessed retroactively. Chronically elevated CORT is related, and may contribute, to reduced physiological condition and fitness (Sapolsky et al. 2000, Kitaysky et al. 2003, Clinchy et al. 2004, Butler et al. 2010, Schoech et al. 2011, Will et al. 2015, Latta et al. 2016) and provides a link between environmental conditions experienced outside the breeding season and future reproductive performance (Marra et al. 1998, Legagneux et al. 2013, Harms et al. 2014, Schultner et al. 2014).

In Chapter 1, we showed that semipalmated sandpipers using locations along the northeast coast of South America, where population declines have previously been identified (Morrison et al. 2012), had significantly higher fCORT levels than birds using locations along the coast of northwest South America. While assessing fCORT levels in winter-grown feathers may provide valuable information regarding the quality of their wintering habitat, it was not known whether these differences in stress among birds using disparate locations had carryover effects that may influence semipalmated sandpiper populations through mechanisms other than reduced survival. Here, we combined movement data obtained from light-sensing geolocators (hereafter, 'gls') with this biomarker of stress exposure, to examine whether poor environmental conditions experienced by overwintering semipalmated sandpipers carried over to affect processes during the following spring migration and breeding seasons. We also used data from non-tracked birds, assuming high fCORT levels equated to relatively poorer wintering conditions, regardless of location.

We tested the predictions of two major study hypotheses. First, we evaluated whether differences in wintering conditions (as reflected in fCORT) affected the timing of spring migration and breeding. For the ‘breeding phenology’ hypothesis, we predicted birds with higher fCORT would have later dates of departure from the wintering areas, arrival at breeding sites, and nest initiation. Because there is strong selection acting on arrival time (Bêty et al. 2004, Drent 2006), birds that depart later might increase their rate of migration to reach the breeding areas ‘on time’ (Gunnarsson et al. 2006); however, birds in poorer physiological condition may be unable to ‘make up for’ a delayed start by increasing flight speeds or reducing time spent refueling. Given equivalent start dates, we predicted birds with higher fCORT levels would migrate more slowly. Second, we evaluated whether females wintering in poor conditions would invest less in reproduction. Under our ‘breeding investment’ hypothesis, we predicted females with higher winter-incurred fCORT levels would have smaller clutches and/or would lay smaller eggs.

2.3 Methods

2.3.1 Field data collection: breeding phenology and clutch characteristics

Data were collected at seven sites in the Alaska and Canadian Arctic, as part of the Arctic Shorebird Demographics Network (ASDN): Igloolik (69.399°N, -81.544°W), Mackenzie Delta (69.373°N, -134.893°W), Canning River (70.118°N, -145.851°W), Ikpikpuk River (70.553°N, -154.735°W), Point Barrow (hereafter, ‘Barrow’; 71.302°N, -156.760°W), Cape Krusenstern (67.114°N, -163.496°W), and Nome (64.443°N, -164.962°W; Figure 1 in Brown et al. (2017)). These sites extend across a large part of the semipalmated sandpiper breeding range. We located nests during 2012 – 2014 by systematically searching and rope dragging tundra habitats. We determined nest initiation date either by 1) documenting clutch completion for nests found during lay and back-casting initiation date by assuming one egg was laid per day (Brown et al. 2014); or 2) for complete clutches, measuring the angle and location of eggs floated in water and using a species-specific egg flotation curve to calculate initiation date (Liebezeit et al. 2007). Nest initiation date was determined for 254 individuals and final clutch size was available for 145 females. At clutch completion, we measured length and breadth of each egg at the widest point, accurate to the nearest 0.01 mm, and calculated egg volume (Governali et al. 2012). Egg measurements were only available for Igloolik, Barrow, Cape Krusenstern, and Nome.

2.3.2 Collection of feathers and movement data

We captured adults on their nests during incubation using bownets and walk-in traps at five of the seven sites from 2012-2014, and at two sites (Igloolik and Ikpikpuk River) from 2013-2014. We marked adults with unique numbered metal bands and measured their wing, bill, head, and tarsus lengths to the nearest 0.1 mm (detailed methods in Brown et al. 2014). At this time, we collected the right and left tenth secondary feathers for later fCORT analyses. These feathers are molted and regrown during November through February, on the wintering areas (Pyle 2008, Laguna et al. 2012, Tavera et al. 2016). For a subset of birds, which were tracked using gls mounted on leg flags, we also had spring migration movements and winter locations (see Brown et al. 2017). These tracking devices were deployed on breeding birds in 2013 and retrieved in 2014 at five sites (all but Igloolik and Mackenzie River). All data were collected under the required scientific collection and Institutional Animal Care and Use Committee (IACUC) permits, including UAF IACUC Protocol #454359 (Appendix C).

2.3.3 Sex assignment

We determined sex of each bird through field observations of behavior (e.g. territory and mating displays by males) and/or by comparing morphometric measurements of mated individuals, following methods detailed in Brown et al. (2014) and using published information from Sandercock (1998b) and Pyle (2008). When sex could not be determined through these methods, we used blood samples collected at capture. For each bird, we collected blood (≤ 25 μl) and stored it in Longmire buffer solution until analysis. We used Qiagen®'s DNeasy Spin-Column Protocol to extract total DNA (Qiagen 2006) and followed methods from Griffiths et al. (1998) for genetic sex determination.

2.3.4 Collection of migration data and identification of wintering location

The gls-equipped semipalmated sandpipers in our study wintered throughout the species' range (see Chapter 1, Fig. 1.2). We defined wintering locations by the approximate gls-derived geographic coordinates of an individual, once directional movement ended in fall and before movement began in spring (~ mid-September through February). Gls settings and data processing methods (e.g. methods used to refine longitude and latitude) are detailed in Brown et al. (2017). We determined start and end dates of northbound migration at a 0.5 – 1 day resolution by identifying consistent, directional movement and distances between position fixes of over 200 km. We calculated migration rate (km/day) using approximate distances migrated between breeding and wintering locations, based on track lines, divided by total duration of spring migration.

Gls also recorded patterns in daily light readings indicative of incubation, and we used these patterns to confirm whether nest initiation dates determined through systematic searches and field observations (i.e. as described above) were in fact a bird's first nesting attempt. This was true in all cases but two, where light data indicated an earlier nest had been initiated prior to the nest being located through field observations. In both cases, involving male birds, we used the nest initiation date determined by the light patterns for the breeding phenology analyses.

2.3.5 Feather corticosterone assay

We prepared feathers for stress hormone assay according to Will et al. (2014), following Bortolotti et al. (2008). Feathers were washed with distilled water and air-dried. After calamus removal, feathers were measured (nearest mm) and clipped to a standard length (30 mm from natural tip to clipped base). We weighed each 30-mm fragment to the nearest 0.0001g. Feathers were individually extracted in 7mL methanol (HPLC-grade, Fisher Scientific, Waltham, MA). Dried extracts were reconstituted in PBSG buffer and analyzed by radioimmunoassay (Bortolotti et al. 2008), using a Sigma-Aldrich antibody (C 8784, St Louis, MO, USA). Samples were analyzed in three assays; intra- and inter-assay CV(s) were less than 3%. To control for loss of fCORT during extraction, 2000 cpm of H^3-labeled CORT (PerkinElmer NET399, Boston, MA, USA) was added to each feather, and final fCORT titers were adjusted for % recovery (mean 95.6% ± 3.6%). Assay results were normalized by converting fCORT concentrations to pg mm^{-1} (Bortolotti et al. 2008), detrended for feather mass (Will et al. 2014), and $\log_{10}$-transformed.

2.3.6 Data analysis

2.3.6.1 Breeding phenology: gls-equipped birds

To examine whether winter stress levels (i.e. fCORT) were related to the timing of spring migration and nest initiation (breeding phenology hypothesis), we fit generalized linear regressions, with start of spring migration (*n* = 24), migration rate (*n* = 21), date of breeding site arrival (*n* = 21), and nest initiation date (*n* = 19) of gls-equipped birds as response variables. Sample sizes decreased through time due to gls failures (i.e. dead batteries) or failure of gls-equipped birds to nest (or failure of observers to find nests). Only data from the 2014 spring migration and breeding season were included in these analyses.

The phenology-related response variables were fit to generalized linear regressions with fCORT, our main explanatory variable of interest, and other factors that could influence migration and breeding phenology in gls-equipped birds (Tables B-1 – B-4). When examining the effects of breeding and wintering location, we used the approximate longitude of the breeding site or wintering location, as these reflected east-west trends (and to some extent, north-south trends for breeding sites). We used generalized linear regressions to examine how start date of spring migration and migration rate explained variation in breeding site arrival, and how start date of migration and date of breeding site arrival explained variation in migration rate and date of nest initiation. Candidate models included additive effects and/or two-way interactions and, given limitations of our small sample sizes, were constrained to those with two or fewer variables. We considered only interactive effects for which we could develop *a priori* hypotheses (described in Tables B-1 – B-4). Models were fit in Program R version 3.2.4 (R Core Team 2016), and we selected the best models for inference using Akaike's information criterion corrected for small sample size (AICc). As determined with package 'glmulti' (Calcagno 2013), models with ΔAICc < 2 were considered as equally parsimonious. Of these, we retained only models in which all terms were statistically significant. We used a 90% significance level for all tests, given our sample sizes (Greenland et al. 2016, Wasserstein and Lazar 2016).

2.3.6.2 Breeding phenology: all birds

We also examined whether fCORT levels affect breeding phenology using a dataset that included non-tracked birds (*n* = 254, including birds with and without gls). These data were collected during 2012 – 2014 at all sites except Igloolik and Ikpikpuk River, where we had data only for 2013 and 2014. At some nests both mates were sampled, so we used a mixed-effects model (package 'lme4' (Bates et al. 2015) with nest ID included as a random effect. Nest ID did not have an important influence (variance < 0.0001). Therefore, we used a modeling process with fixed effects only, fitting nest initiation date to generalized linear regressions with our main explanatory variable of interest, fCORT, and other factors that could influence breeding phenology in this larger dataset (Table B-5). The set of explanatory variables we used for the larger dataset was not identical to the set used for gls birds. For example, data on spring migration were not available for non-tracked birds, and we also included gls deployment as an explanatory variable because there is evidence that carrying a gls has negative effects on the reproductive success of semipalmated sandpipers (Weiser et al. 2016). We used categorical breeding site as a proxy for effect of relative location, environmental conditions (e.g. timing of snow melt, peak insect abundance), and/or other site-specific but unmeasured factors that could influence breeding activities in our analyses for timing of nest initiation. Candidate models included additive effects and/or two-way interactions. We included only those interactions for which we determined, *a priori*, plausible biological explanations (described in Table B-5). We selected the best models for inference, based on the methods described herein for gls-equipped birds. Because gls deployment did not appear in top models explaining variation in nest initiation date, we removed this variable and refit nest initiation date using all individuals (regardless of gls presence or absence). We selected the best models for inference, following the methods outlined above for gls-equipped birds.

2.3.6.3 Breeding investment: females

To determine the relationships between fCORT level and breeding investment, we restricted our dataset to only females, as female condition is likely to directly affect clutch characteristics. Clutch size (number of eggs in a complete clutch) was available for 156 females breeding at 6 sites (all except Ikpikpuk River) and mean egg volume was available for 108 females breeding at Igloolik, Barrow, Cape Krusenstern, and Nome. Clutch size and mean egg volume (cm^3) of each nest were fit to generalized linear regressions that included fCORT, our main explanatory variable of interest. We also included presence of a gls and within-season factors that may affect clutch characteristics of female semipalmated sandpipers (Tables B-6 & B-7). Competing models included additive and two-way interactive effects for which we determined, *a priori*, plausible biological explanations (described in Tables B-6 & B-7). We selected the best models for inference following the methods outlined to test our breeding phenology hypothesis.

2.4 Results

2.4.1 Breeding phenology: geolocator-equipped birds

2.4.1.1 Start of spring migration

Semipalmated sandpipers equipped with gls initiated spring migration over a two-month period, ranging from 11 March – 7 May (mean = 18 April). Our top models (Table 2.1.a) showed birds returning to the more eastern breeding sites (also the farther north sites in this study) beginning migration later than birds breeding farther west (and at lower latitudes). Top models also showed birds wintering farther west beginning migration later, with wintering area departure up to 27 days later for birds wintering at western versus eastern longitudes. Regressing individual start dates on fCORT alone revealed migration was delayed by ~ 1 day for each 0.02 pg mm^{-1} increase of fCORT ($\beta = 52.94$, $p = 0.08$; Fig. 2.1.a); and, although a model including fCORT as the sole explanatory variable was not selected, fCORT appeared in three of the five top models. In all three models, birds with higher fCORT levels began migration later. For birds wintering at the same longitude, those with the highest fCORT levels started spring migration up to 15 days later compared to those with the lowest fCORT levels.

2.4.1.2 Migration rate

Migration rates of semipalmated sandpipers carrying geolocators ranged from 142 – 458 km/day (mean = 254 km/day). Based on AICc values, there was one top model (Table 2.1.b). This model showed a seasonal effect on migration rate: birds increased their rate of migration with later migration start dates, except those birds wintering farthest west. These birds had slower migration rates with increasingly later start dates.

2.4.1.3 Breeding site arrival date

Timing of arrival on the breeding grounds was more contracted than initiation of spring migration and ranged from 24 May – 7 June (mean = 1 June). When individual arrival dates were regressed on fCORT alone, the relationship was not significant ($p = 0.8$; Fig. 2.1.b); and fCORT was not included as an explanatory variable in top models. There were two top models explaining timing of arrival (Table 2.1.c), showing birds breeding farther to the west were earliest to arrive, regardless of their wintering location. Our best-supported model included only breeding site longitude. A parsimonious set of models also included sex and the interaction of sex with breeding site longitude. In addition to the geographic trend described above, this model showed males arriving earlier than females. The effect of breeding site longitude on arrival date was more pronounced for males than females. For males, arrival was up to 9 days earlier for birds breeding at western versus eastern sites, whereas for females the difference was 1 – 2 days.

2.4.1.4 Nest initiation date

In gls-equipped birds, nest initiation occurred over 28 days (28 May – 25 June, mean = 8 June) across all sites; but at any given site, nest initiation took place over less than one week. The exception was Canning River, where nest initiation occurred over 21 days (4 – 25 June; mean = 12 June, $n = 12$). Our top model was that in which timing of nest initiation was regressed only on date of arrival at the breeding site (Table 2.1.d); across all parsimonious models, timing of nest initiation showed a delay in nesting of ~ 1 – 1.5 days for each day of delayed arrival. When individual nest initiation dates were regressed on fCORT alone, the relationship was not significant ($p = 0.4$; Fig. 2.1.c). However, fCORT was included in one model competing with the "arrival only" model; birds with higher fCORT levels tend to nest later, given equal dates of arrival (p-value of the interaction fCORT x arrival date = 0.004). This model showed a 1-day delay in nest initiation for every 0.2 pg mm^{-1} increase in fCORT at early arrival dates. At later arrival dates, the influence of fCORT was stronger (early *versus* late arrival: $\beta = 1.76$ *versus* 6.26, p = 0.05; see Fig. 2.2), such that nest initiation was delayed 1 day for every 0.06 pg mm^{-1} increase in fCORT by the last day of arrival.

2.4.2 Breeding phenology: all birds

For all birds in all years, nest initiation occurred over a 46-day period (15 May – 30 June; mean = 9 June). There were four top models that explained variation in nest initiation dates among our larger sample of birds (Table 2.2). The model with the lowest AICc value included only breeding site; and all four models included breeding site as a factor, showing birds breeding at Nome initiating nests the earliest, and Igloolik birds initiating nests the latest. Models showed a difference of ~ 2 – 4 weeks between these two sites. Mean nesting dates at the other sites were closer together; and although there was not a strict longitudinal trend across all sites, birds generally nested earlier (~1 to 5 days) at more westerly sites compared to easterly sites. Year-specific effects were included in two competing models, with year changing nest initiation dates within a given site by < 1 day to 4 days. A model including only fCORT was not supported, but fCORT did appear in the one competing model. In this model, nest initiation date had a negative relationship with fCORT level, such that (at each breeding site) birds with the highest levels of fCORT nested up to 2 weeks earlier than birds with the lowest levels of fCORT.

2.4.3 Breeding investment: females

For the females in our study, we documented clutch sizes below the modal size (three instead of four eggs) in 15% of nests. From our candidate models, sixteen parsimonious models explained variation in clutch size (Table 2.3). Although each left a large proportion of variation (> 75%) unexplained, within our model set, breeding site and interactions with breeding site appeared in all models and consistently explained the highest proportion of clutch size variation. Additionally, models consistently showed three-egg clutches increased in prevalence with later dates of nest initiation, in both gls and non-gls birds; and at later dates, clutch size had a negative relationship with fCORT. Year was also included in top models; three-egg clutches were more prevalent in some years than others, but other patterns remained the same regardless of year. Finally, three-egg clutches were more prevalent in gls-equipped females (33% of nests) than non-gls females (12% of nests).

Mean volume of a single egg, calculated from all eggs across all clutches of non-gls females with nests, was 6.40 cm^3 (range: 5.30 – 7.62 cm^3). From our candidate models, six parsimonious models of similar weight explained mean egg volume within a clutch (Table 2.4). Breeding site and the interactions of nest initiation date or fCORT with breeding site consistently explained the most variation in mean egg volume. Females nesting at Igloolik laid the largest eggs, and those at Cape Krusenstern the smallest, with mean volume of eggs at 7 – 14% larger than eggs at Cape Krusenstern. The relationship between fCORT and mean egg volume was not as predicted; birds with lower fCORT levels laid smaller eggs at all sites. For example, at Barrow mean egg volume increased 0.01 – 0.02 cm^3 for each increase of 0.20 pg mm^{-1} of fCORT. At each site, mean egg volume decreased with progressively later dates of nest initiation. At Barrow, models showed mean egg volume decreased 0.02 – 0.05 cm^3 for each five days of delayed nest initiation. At all sites, mean egg volume was negatively related to clutch size in gls-equipped females, but there was no relationship between clutch size and mean egg volume in non-gls females. At Barrow, the eggs of gls-equipped females were 10 – 12% larger in three-egg clutches than in four-egg clutches. Given equivalent nest initiation dates, mean egg volume in four-egg clutches was lower for gls-equipped females compared to non-gls females; for females at Barrow, the difference was 1 – 2%. The opposite relationship was seen in three-egg clutches, with the eggs of gls-equipped females 9 – 10% larger than those of non-gls females.

2.5. Discussion

Poor wintering conditions are believed to contribute to population-level declines in semipalmated sandpipers (Morrison et al. 2012, BirdLife International 2016, Brown et al. 2017), and fCORT measurements, used as a biomarker of birds' exposure to stressors, confirmed that some regions across the wintering range provide suboptimal environmental conditions (see Chapter 1). Here, we considered whether differences in stress exposure carried over to directly and/or indirectly affect individuals during subsequent stages of the annual cycle. Under our breeding phenology hypothesis, we predicted birds with higher fCORT would have later dates of departure from the wintering areas, later arrival at their breeding sites, and later initiation of nests. However, because of strong selective pressure on breeding phenology during the short Arctic summer, birds that depart the wintering areas late might increase their rate of migration in order to arrive and breed 'on time'. We further hypothesized that birds in poorer physiological condition (i.e. with higher fCORT) may be unable to manipulate their arrival time through faster migrations. Under our breeding investment hypothesis, we predicted females that experienced poorer wintering conditions (and therefore had higher fCORT levels) would subsequently be limited in their ability to lay full clutches and/or would lay smaller eggs. Our analyses provided mixed support for our predictions under both hypotheses but suggest overall that semipalmated sandpipers wintering in regions associated with higher exposure to stress may experience negative carryover effects to the timing of spring migration and breeding, as well as reproductive performance.

2.5.1 Breeding phenology hypothesis

2.5.1.1 Spring migration

In long-distance migrants, and perhaps especially in Arctic-breeding species, the advantages of early arrival at breeding areas (Kokko 1999, Both and Visser 2001, Meltofte et al. 2007a, McKinnon et al. 2012) result in strong selective pressure on the timing of spring migration (Bêty et al. 2004, Drent 2006, Gunnarsson et al. 2006). Thus, spring departures from wintering areas tend to be highly synchronized (e.g. Dick et al. 1997 *in* Piersma 2005), with birds wintering farther from their breeding areas generally beginning northward migration earlier in order to reach the breeding areas 'on time' (Gunnarsson et al. 2006, Newton 2008). This is the general pattern we detected for semipalmated sandpipers. Birds wintering closest to the breeding areas, along the Pacific coast of Central America, tended to begin spring migration later; and birds wintering along the Pacific coast of South America departed earlier. However, in any given wintering area, start of spring migration was delayed in birds with higher winter-incurred fCORT (*a.k.a.*, 'high-stress birds'). Further, departure dates for birds wintering along the Atlantic coast of South America, one of the wintering regions most distant to the breeding areas, did not align with distance-based patterns. These birds, wintering at approximately the same distance as birds in 'Pacific South America', also began spring migration later. Possibly poor wintering conditions delayed departure for individuals from this wintering area, compared to individuals wintering in less stressful regions, as birds wintering in 'Pacific Central America' and 'Atlantic South America' were exposed to higher levels of stress (Chapter 1). Breeding site longitude was also included in one top model, suggesting birds may respond to annual cues or 'typical' breeding site conditions and vary their departure dates to arrive early, but not so early as to encounter detrimental conditions (Morton 2002).

Birds may also vary their migration rate to reach the breeding areas ‘on time’, maximizing their reproductive success by ensuring their breeding cycle remains in tune with climatic conditions and the phenology of prey species (Meltofte et al. 2007a, Tulp and Schekkerman 2008, McNamara et al. 2011, McKinnon et al. 2012, Kwon 2016). It follows logically that the semipalmated sandpipers with later departures tended to migrate at a faster rate, catching up with those departing earlier so that arrival dates were more contracted than start dates. Additionally, the birds in our study that wintered farther from the breeding areas undertook more rapid migrations than those using locations in closer proximity. Such an influence of distance on migration rate has also been documented in the Icelandic black-tailed godwit (*Limosa limosa islandica*; Gunnarsson et al. 2006). However, we did not find the predicted relationship between migration rate and winter exposure to stress. Of individuals using the same wintering region, those with higher fCORT levels migrated faster, which suggests the residual effects of poor wintering conditions did not limit birds’ abilities to ‘catch up’. However, because the rate at which birds migrated during spring appeared to be largely influenced by the date at which they departed the wintering areas, our models suggest a potential path for carryover effects from wintering conditions to the breeding season through migratory behavior. If birds in better condition depart the wintering areas earlier and migrate at a slower pace (stopping more frequently or more often), they may have increased opportunity to rest and refuel along their migration routes, maintaining better body condition as they progress northward and giving them an advantage at arrival (Tulp 2007). For birds in poorer wintering condition that depart later, ‘making up for’ a delayed start may itself have consequences (Alerstam and Lindström 1991), through greater energy expenditure on faster speed migrations and/or decreased refueling opportunities. Thus, stressful wintering conditions may indirectly influence migratory behavior, and there is potential for negative effects to compound across seasons.

2.5.1.2 Nest initiation

The breeding phenology of arctic shorebirds typically shows a strong relationship with local environmental conditions (Gratto and Cooke 1987, Hannon et al. 1988, Liebezeit et al. 2014), and we might expect to find temporal or geographic variance in conditions amenable to breeding activities (Meltofte et al. 2007b, Kwon 2018). A separate study at our focal breeding sites, overlapping with the years in our study, found mean daily temperature and timing of peak insect emergence varied by site, although there were not strict latitudinal or longitudinal patterns (Kwon 2016). In top models for our larger dataset, birds tended to nest earlier at lower-latitude, western breeding sites (i.e. Nome and Cape Krusenstern), although timing of nest initiation also did not show a strict geographic pattern. Birds might delay reproductive activities during a year with particularly inclement weather (Nol et al. 1997, Klaassen et al. 2001), or advance activities during years of high predator abundance (Smith et al. 2010); and we found that year explained some variation in nest initiation date in our inclusive dataset.

Nest initiation date may be tightly coupled with arrival date (Schamel and Tracy 1987, Schekkerman et al. 2004, Gunnarsson et al. 2006), resulting from the short window during which conditions in the Arctic are amenable to breeding. Indeed, for gls-equipped birds with movement data, we found birds that arrived later at the breeding sites nested later. However, while shorebirds typically lay eggs five to eight days after arrival (Meltofte et al. 2007b), the range in dates over which birds initiated nests was twice as long as the range in birds' arrival dates in our study. This deviation from the 'normal' interval between arrival and nesting suggests some birds in our study required additional time to transition from migration to breeding states (Morrison et al. 2005). In other taxa, poor pre-breeding physiological condition is known to delay nest initiation (Bêty et al. 2003, Schroeder et al. 2007, Sorensen et al. 2009, Harms et al. 2014), and we found that gls-equipped birds with higher levels of fCORT initiated nests up to 4.5 days later. Such a delay could significantly impact reproductive success in a compressed breeding schedule (Kokko 1999, Meltofte et al. 2007a, Schekkerman et al. 2003, McKinnon et al. 2012). Conversely, when we included non-gls birds in our analysis, birds exposed to more stressful wintering conditions nested earlier. This negative relationship between nest initiation and fCORT was more pronounced for birds breeding at western sites compared to eastern sites.

Explanations for the apparent difference in the relationship of fCORT to nest initiation between the larger dataset and the gls-only birds may be attributable to data structure, including differences in the numbers of birds and breeding sites, and model inputs. For example, we considered whether the difference could be attributed to a year effect, since data for gls-equipped birds were from a single year. However, when we ran our models using all birds nesting only in 2014 (*n* = 73), nest initiation dates were earlier for birds with higher fCORT (see supplementary materials, Appendix B). A key difference between the two datasets is the larger dataset included birds with and without gls, and date of arrival (an important driver of nesting date) was unknown for non-tracked birds. Further, while we could be certain nest initiation dates for gls-equipped birds represented only first nest attempts (as verified by patterns in the light data), our larger dataset likely contained second nest attempts (following failure of undetected, first nests). Renesting is not uncommon in arctic-breeding shorebirds (although rates are highly variable; (McCaffery & Ruthrauff 2004, Naves et al. 2008, Meltofte et al. 2007b, Ruthrauff et al. 2009, Gates et al. 2013, Weiser et al. 2018a). Because only birds in good condition should be able to invest in a replacement clutch (Hegyi and Sasvari 1998, Hipfner et al. 1999, Gates et al. 2013), and second nests would have a later mean initiation date than first nests within a given breeding site, the presence of replacement clutches within the larger dataset could confound the relationship between nest initiation date and fCORT. We were not able to determine what proportion of the larger dataset was comprised of replacement clutches, or separate first from second nest attempts to control for this effect.

2.5.2 Breeding investment hypothesis

While the typical and/or maximum size of a species' clutch (four eggs in semipalmated sandpipers) is determined by life history characteristics (Lack 1947, Winkler and Walters 1983, Walters 1984, Starck and Ricklefs 1998), deviations in egg number are often attributed to environmental conditions and/or physiological condition of parents (Winkler and Walters 1983). Many of these same factors also influence avian egg size, including parental characteristics (such as size and physiological condition) and quantity and quality of food resources (Ricklefs 1984, Martin 1987, Bernardo 1996, Perrins 1996, Christians 2002, Michel et al. 2003). Within our candidate models breeding site best explained deviation from a full clutch; and our models showed breeding site was also an important predictor of mean volume of a female's eggs, with larger-volume eggs found at Igloolik and smaller-volume eggs found at Nome and Cape Krusenstern. However, this relationship could have been a product of geographically driven female size differences, rather than variation in environmental conditions. In general, larger females of a species tend to lay larger eggs (Ricklefs 1984, Michel et al. 2003), and semipalmated sandpipers at eastern Arctic sites are larger than those at western sites (Hicklin and Gratto-Trevor 2010). Date of nest initiation, which is tied to within-season environmental conditions, was also an important predictor of both clutch size and mean egg volume. Female semipalmated sandpipers in our study tended to lay smaller clutches at later nest initiation dates, in keeping with a pervasive trend documented across avian taxa (Winkler and Walters 1983) and in other studies with our focal species (Sandercock et al. 1999, Kwon et. al 2018, Weiser et al. 2018a). Females in our study that nested later also tended to lay smaller-volume eggs, a trend that has been documented in other studies of shorebirds (Tulp and Schekkerman 2001, Meltofte et al. 2007b, Kwon et al. 2018, Weiser et al. 2018a). Seasonal declines in egg number and size may be related to within-season deterioration in environmental conditions during the short Arctic summer. For clutch size, there may be increased costs and/or diminished returns on breeding investment for females that initiate clutches later (Rowe et al. 1994, Kwon et al. 2018, Weiser et al. 2018a). Presence of replacement clutches in the dataset may have also contributed toward prevalence of smaller clutches at later nest dates (Amat 1999, Gates et al. 2013, Weiser et al. 2018a). However, a seasonal decline in clutch size was found in the confirmed first nests of glsequipped birds in this study and in other studies that excluded replacement clutches (Winkler and Walters 1983).

Exposure to high-stress wintering conditions appeared to contribute to delayed initiation of confirmed first nests, showing the potential that wintering conditions indirectly influence female investment in individual offspring. Additionally, 'lower-quality' individuals and/or individuals in poorer condition often reproduce later (Drent and Daan 1980, Price et al. 1988, Hochachka 1990, Rowe et al. 1994, Christians et al. 2001). Accordingly, Sandercock et al. (1999) hypothesized an increased prevalence of smaller clutches produced later in the season might be related to parental quality in semipalmated sandpipers; similarly, Weiser et al. (2018a) hypothesized a seasonal decline in egg volume was caused by among-individual variation, with lower female quality constraining egg size at later nesting dates. Our models explaining clutch size variation provided some evidence in support of this hypothesis; we found later in the breeding season, high-stress females were more likely to lay smaller clutches than low-stress females initiating nests on the same day. The ‘fCORT threshold’ at which clutch sizes were reduced was breeding site-specific, suggesting birds might make up for winter deficits and produce a full clutch if they encounter favorable conditions during the breeding season.

Females faced with resource limitations and/or reduced physiological condition might reduce egg volume before reducing number of eggs, due to lesser instantaneous fitness consequences (Martin 1987). However, contrary to our expectations, we found a positive relationship between egg volume and fCORT, with high-stress females laying larger eggs than low-stress females nesting on the same day. We posit two potential explanations for the observed relationship between mean egg volume and fCORT. Because birds at Igloolik tended toward higher-stress than birds at other breeding sites in our study (Fig. 2.3), their larger size, and the concomitant influence on egg size, might have confounded our results. The models may also reflect a true relationship between egg volume and fCORT and show a carryover effect of wintering conditions to female breeding investment, with resource-limited females laying fewer but larger eggs. While not widely demonstrated in shorebirds (Olsen et al. 1994), a clutch size–egg volume tradeoff may be adaptive, with females decreasing the number of eggs laid but increasing their investment in individual eggs, to improve the quality and chances of survival of individual offspring (Monaghan et al. 1995, Williams 2005). Indeed, we found support for a clutch size–egg volume tradeoff in our dataset. Models showed smaller clutches contained larger eggs, but only if females were equipped with gls (i.e. this relationship occurred only in confirmed first nests); clutch size did not influence egg volume in non-gls females.

The lack of evidence for a clutch size–egg volume tradeoff in non-gls females could be have been caused by inclusion of egg volume measurements from replacement clutches, as eggs in replacement clutches tend to be smaller in volume (Hipfner et al. 1999, Gates et al. 2013, Weiser et al. 2018a). On the other hand, carrying a gls may have affected female reproductive performance. Carrying a tracking device has been shown to significantly and negatively affect a variety of avian taxa, through measures such as body condition and reproductive performance, including clutch size (Barron et al. 2010). External tracking devices, such as gls, may result in higher energy expenditures due to flight drag and reduce the post-migration energy reserves available to be invested in egg formation (Pennycuick et al. 2012). We found gls-equipped females had an increased prevalence of smaller clutches and slightly smaller eggs, and fCORT levels were significantly higher in females wearing geolocators than females without ($\beta = 0.113$, $p = 0.0007$, $n = 156$). Carrying a gls may have affected female condition throughout the one-year tracking period; and the extra stress incurred may have tipped females over some condition threshold, contributing toward the observed clutch size–egg volume tradeoff.

A large proportion of clutch size variation in semipalmated sandpipers remained unexplained in our top models, and we expect factors not evaluated here may be more determinant of whether female semipalmated sandpipers lay modal or reduced clutches. In shorebirds, conditions encountered during the breeding season often determine female ability to lay a full clutch (Nol et al. 1997, Sandercock et al.1999, Weiser et al. 2018b). Timing of snow melt, temperatures experienced early in the breeding season, and abundance of arvicoline rodents (an alternative prey resource for shorebird predators) may all be important factors in female decisions to lay full clutches (Kwon 2018, Weiser et al. 2018b), and the spatial and temporal explanatory variables we included may not have captured these drivers. Partial depredation of nests, or removal of damaged eggs by parents following other disturbance events, may also have caused the maximum number of eggs to be recorded below what was laid by the female (but see Sandercock et al. 1999, Weiser et al. 2018a). Finally, female characteristics, such as body condition at egg laying or age and experience (Houston et al. 1983, Winkler and Walters 1983, Bolton et al. 1992) were not captured in our models but may also be important determinants of clutch size. While our models examining mean intra-clutch egg volume better explained variation, some of these same unexplored factors may also play a role in egg size. Despite these limitations, our results provide evidence that wintering conditions may impose negative carryover effects on reproductive performance in semipalmated sandpipers. We were not able to determine whether these apparent changes in female breeding investment ultimately reduced the number of offspring that successfully hatched, nor how these carryover effects impacted survival of young and their eventual recruitment into the breeding population.

2.6 Conclusion

Our study, the first research using fCORT to assess carryover effects between the wintering and breeding stages in a shorebird, demonstrates that fCORT can be useful in discerning whether limiting factors might occur during the wintering stage of a migratory species' annual cycle. We found semipalmated sandpipers in relatively poorer physiological condition during their wintering period experienced carryover effects to spring migration, and may have also experienced delays to breeding and a reduction in overall breeding investment. We also found evidence that high-stress females may have adaptively engaged in a clutch size–egg volume tradeoff. In confirmed first nests, females laid fewer but larger-volume eggs, thus increasing their investment in individual offspring and potentially improving offspring quality and survival. This research provides new insight, as clutch size-egg volume tradeoffs have not been widely demonstrated in shorebirds or other species with determinate clutch sizes and precocial young.

Whether the direct and indirect carryover effects documented here ultimately reduced the number of offspring parents successfully hatched and fledged, or that eventually recruited into breeding populations, was beyond the scope of this study. Very few studies follow shorebird chicks to fledge, and fewer still beyond the first summer. Examining the role of parental stress in the growth and survival of offspring may be warranted, to determine whether the delays to spring migration and breeding and changes in breeding investment identified here could scale up to affect population demographics. The role of intrinsic quality and other factors (such as age and pairing history; Heidinger et al. 2006, Angelier et al. 2010) in determining individual winter stress loads and reproductive performance should also be investigated.

This research emphasizes the importance of considering full annual cycles in conservation and research efforts for migratory species, showing that poor environmental conditions at wintering sites far from Arctic breeding areas may be detrimental to the reproductive performance of a species with declining populations. Programs targeting the conservation of semipalmated sandpipers should continue research into the role of wintering conditions in life cycle processes. Increasing feather tissue samples from central and eastern breeders might help demonstrate whether effects of poor wintering conditions carryover to contribute to population dynamics in this species.

2.7 References

Alerstam T, Lindström Å. 1991. Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E, editor. Bird migration: physiology and ecophysiology. Berlin: Springer-Verlag. p. 331-351.

Alves JA, Gunnarsson TG, Hayhow DB, Appleton GF, Potts PM, Sutherland WJ, Gill JA. 2013. Costs, benefits, and fitness consequences of different migratory strategies. Ecology 94(1): 11–17.

Amat JA, Rosendo MF, Gonzalo MA. 1999. Replacement clutches by Kentish plovers. Condor 101(4):746–751.

Amat JA, Rosendo MF, Gonzalo MA. 2001. Intraclutch egg-size variation and offspring survival in the Kentish plover *Charadrius alexandrinus*. Ibis 143(1):17–23.

Andres, BA, Gratto-Trevor C, Hicklin P, Mizrahi D, Morrison RIG, Smith PA. 2012. Status of the semipalmated sandpiper. Waterbirds 35(1):146–148.

Angelier F, Wingfield JC, Weimerskirch H, Chastel O. 2010. Hormonal correlates of individual quality in a long-lived bird: a test of the 'corticosterone–fitness hypothesis'. Biol Lett. 6:846-849.

Ashkenazie S, Safriel UN. 1979. Breeding cycle and behavior of the semipalmated sandpiper at Barrow, Alaska. Auk 96(1):56–67.

Barron DG, Brawn JD, Weatherhead PJ. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. Methods Ecol Evol. 1(2):180–187.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67(1):1-48.

Bernardo J. 1996. The particular maternal effect of propagule size, especially egg size: patterns, models, quality of evidence and interpretations." Am Zool. 36(2): 216–236.

Bêty J, Gauthier G, Giroux JF. 2003. Body condition, migration, and timing of reproduction in snow geese: a test of condition-dependent model of optimal clutch size. Am Nat. 162(1):110–121.

Bêty J, Giroux JF, Gauthier G. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behav Ecol Sociobiol. 57(1): 1–8.

BirdLife International. 2016. *Calidris pusilla*. The IUCN Red List of Threatened Species 2016: e.T22693373A93400702.

Blomqvist D, Johansson OC, Götmark F. 1997. Parental quality and egg size affect chick survival in a precocial bird, the lapwing *Vanellus vanellus*. Oecologia 110(1):18–24.

Bolton M, Houston D, Monaghan P. 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. J Anim Ecol. 61(3):521–532.

Bortolotti GR, Marchant TA, Blas J, German T. 2008. Corticosterone in feathers is a long-term, integrated measure of avian stress physiology. Funct Ecol. 22:494–500.

Bortolotti GR, Marchant T, Blas J, Cabezas S. 2009. Tracking stress: localisation, deposition and stability of corticosterone in feathers. J Exp Biol. 212:1477–1482.

Both C, Visser ME. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411(6835):296–298.

Brown SC, Gates HR, Liebezeit JR, Smith PA, Hill BA, Lanctot RB. 2014. Arctic Shorebird Demographics Network breeding camp protocol. Unpubl. report: U.S. Fish and Wildlife Service and Manomet Center for Conservation Sciences. Available from:

https://www.manomet.org/sites/default/files/publications_and_tools/ASDN_Protocol_V5_20Apr2014.pdf 118 p.

Brown S, Gratto-Trevor C, Porter R, Weiser EL, Mizrahi D, Bentzen R, Boldenow M, Clay R, Freeman S, Giroux M-A, et al. 2017. Migratory connectivity of semipalmated sandpipers and implications for conservation. Condor 119:207–224.

Butler MW, Leppert LL, Dufty AM. 2010. Effects of small increases in corticosterone levels on morphology, immune function, and feather development. Physio Biochem Zool. 83(1): 78–86.

Calcagno V. 2013. glmulti: model selection and multimodel inference made easy. R Package Version 1.0.7. Available from: https://CRAN.R-project.org/package=glmulti

Castro G, Myers JP, Ricklefs RE. 1992. Ecology and energetics of sanderlings migrating to four latitudes. Ecology 73(3):833–844.

Christians JK. 2002. Avian egg size: variation within species and inflexibility within individuals. Biol Rev of the Camb Philos. 77:1–26.

Christians JK, Evanson M, Aiken JJ. 2001. Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. J Anim Ecol. 70:1080–1087.

Clark NJ, Clegg SM, Klaassen M. 2016. Migration strategy and pathogen risk: non-breeding distribution drives malaria prevalence in migratory waders. Oikos 125:1358–1368.

Clinchy M, Zanette LY, Boonstra R, Wingfield JC, Smith JNM. 2004. Balancing food and predator pressure induces chronic stress in songbirds. Proc R Soc B 271(1556):2473–2479.

Dawson A, Hinsley SA, Ferns PN, Bonser RHC, Eccleston L. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proc R Soc B 267(1457):2093–2098.

Drent R, Daan S. 1980. The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252.

Drent RH. 2006. The timing of birds' breeding seasons: the Perrins hypothesis revisited especially for migrants. Ardea 94(3):305–322.

Fairhurst GD, Frey MD, Reichert JF, Szelest I, Kelly DM, Bortolotti GR. 2011. Does environmental enrichment reduce stress? An integrated measure of corticosterone from feathers provides a novel perspective. PLoS ONE 6(3):1–10.

Gates HR, Lanctot RB, Powell AN. 2013. High renesting rates in Arctic-breeding dunlin (*Calidris alpina*): a clutch-removal experiment. Auk 130(2):372–380.

Gill, JA, Norris K, Potts PM, Gunnarsson TG, Atkinson PW, Sutherland WJ. 2001. The buffer effect and large-scale population regulation in migratory birds. Nature 412:436–438.

Gladbach A, Gladbach DJ, Quillfeldt P. 2010. Seasonal clutch size decline and individual variation in the timing of breeding are related to female body condition in a non-migratory species, the upland goose *Chloephaga picta leucoptera*. J Ornithol. 151(4):817–825.

Governali FC, Gates HR, Lanctot RB, Holmes RT. 2012. Egg volume can be accurately and efficiently estimated from linear dimensions for Arctic-breeding shorebirds. Wader Study Group Bull. 119(1):46–51.

Gratto-Trevor CL, Vacek CM. 2001. Longevity record and annual adult survival of semipalmated sandpipers. Wilson Bull. 113(3): 348–350.

Gratto-Trevor C, Smith PA, Morrison RIG, Aubry Y, Cotter R. 2012. Population trends in semipalmated sandpipers from migration counts. Waterbirds 35(1): 96–105.

Gratto-Trevor CL. 1991. Parental care in semipalmated sandpipers *Calidris pusilla*: brood desertion by females. Ibis 133: 394–399.

Gratto CL, Cooke F. 1987. Variation in the breeding biology of the semipalmated sandpiper. Ornis Scand 18(3):233–235.

Greenland S, Senn SJ, Rothman KJ, Carlin JB, Poole C, Goodman SN, Altman DG. 2016. Statistical tests, p values, confidence intervals, and power: a guide to misinterpretations. Eur J Epidemiol. 31(4):337–350.

Griffiths R, Double MC, Orr K, Dawson RJG. 1998. A DNA test to sex most birds. Mol Ecol. 7(8):1071–1075.

Guillemain M, Elmberg J, Arzel C, Johnson AR, Simon G. 2008. The income-capital breeding dichotomy revisited: late winter body condition is related to breeding success in an income breeder. Ibis 150(1):172–176.

Gunnarsson TG, Gill JA, Atkinson PW, Gélinaud G, Potts PM, Croger RE, Gudmundsson GA, Appleton GF, Sutherland WJ. 2006. Population-scale drivers of individual arrival times in migratory birds. J Anim Ecol. 75(5):1119–1127.

Harms NJ, Legagneux P, Gilchrist HG, Bêty J, Love OP, Forbes MR, Bortolotti GR, Soos C. 2014. Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird. Proc R Soc B 282:1–8.

Harrington B. 2003. Shorebird management during the non-breeding season – an overview of needs, opportunities, and management concepts. Wader Study Group Bull. 100:59–66.

Harrison XA, Blount JD, Inger R, Norris DR, Bearhop S. 2011. Carry-over effects as drivers of fitness differences in animals. J Anim Ecol. 80:4–18.

Hegyi Z, Sasvari L. 1998. Parental condition and breeding effort in waders. J Anim Ecol. 67(1): 41–53.

Heidinger BJ, Nisbet ICT, Ketterson ED. 2006. Older parents are less responsive to a stressor in a long-lived seabird: a mechanism for increased reproductive performance with age? Proc R Soc B 273:2227-2231.

Hicklin P, Gratto-Trevo CL. 2010. Semipalmated sandpiper (*Calidris pusilla*), version 2.0. In: Rodewald PG, editor. The birds of North America online. Ithaca (NY): Cornell Lab of Ornithology.

Hicklin PW, Chardine JW. 2012. The morphometrics of migrant semipalmated sandpipers in the Bay of Fundy: evidence for declines in the eastern breeding population. Waterbirds 35:74–82.

Hill B. 2012. Factors affecting survival of dunlin (*Calidris alpina arcticola*) adults and chicks. M.S. thesis. Fairbanks (AK): University of Alaska Fairbanks. 206 p.

Hipfner JM, Gaston AJ, Martin DL, Jones IL. 1999. Seasonal declines in replacement egg-layings in a long-lived, arctic seabird: costs of late breeding or variation in female quality? J Anim Ecol. 68(5):988–998.

Hobson KA, Jehl JR. 2010. Arctic waders and the capital-income continuum: further tests using isotopic contrasts of egg components. J Avian Biol. 41(5):565–572.

Hochachka W. 1990. Seasonal decline in reproductive performance of song sparrows. Ecology 71(4): 1279-1288.

Houston DC, Jones PJ, Sibly RM. 1983. The effect of female body condition on egg laying in lesser black-backed gulls *Larus fuscus*. J Zool Soc Lond. 200:509–520.

Jaatinen K, Öst M, Hobson KA. 2016. State-dependent capital and income breeding: a novel approach to evaluating individual strategies with stable isotopes. Front. Zool. 13:24.

Jamieson SE, Ydenberg RC, Lank DB. 2014. Does predation danger on southward migration curtail parental investment by female western sandpipers? Anim Migr. 2(1):34–43.

Kitaysky AS, Kitaiskaia EV, Piatt JF, Wingfield JC. 2003. Benefits and costs of increased levels of corticosterone in seabird chicks. Horm Behav. 43(1):140–149.

Klaassen M, Lindstrom A, Meltofte H, Piersma T. 2001. Arctic waders are not capital breeders. Nature 413:794.

Kokko H. 1999. Competition for early arrival birds in migratory birds. J Anim Ecol. 68(5):940–950.

Krist M. 2011. Egg size and offspring quality: a meta-analysis in birds. Biol Rev of the Camb Philos. 86:692–716.

Kwon E, English WB, Weiser EL, Franks SE, Hodkinson DJ, Lank DB, Sandercock BK. 2018. Delayed egg-laying and shortened incubation duration of Arctic-breeding shorebirds coincide with climate cooling. Ecol Evol. 8:1339-1351.

Kwon E. 2016. Effects of climate change on the breeding ecology and trophic interactions of Arctic-breeding shorebirds. Ph.D. dissertation. Manhattan (KS): Kansas State University. 188 p.

Lack D. 1947. The significance of clutch-size in the partidge (*Perdix perdix*). J Anim Ecol. 16 (1):19–25.

Lack D. 1950. The breeding seasons of European birds. Ibis 92:288–316.

Laguna MP, Maillé S, Uriot S, Bocher P, Duzont F, and Delcroix E. 2012. Suivi des populations de limicoles migrateurs en Guadeloupe et Guyane, mise en relation avec le dispositif de suivi régional "Pan American Shorebird Program" (PASP). France: l'Office National de la Chasse et de la Faune Sauvage, Programme Européen Interregional Caraïbes [cited 2016 Sep 09). p. 102–116. Available from: https://www.documentation.eauetbiodiversite.fr/notice/interreg-iv-caraibes-suivi-despopulations-de-limicoles-migrateurs-en-guadeloupe-et-guyane-mise-en-r0

Lank DB, Oring LW, Maxson SJ. 1985. Mate and nutrient limitation of egg-laying in a polyandrous shorebird. Ecology 66(5):1513–1524.

Latta SC, Cabezas S, Mejia DA, Paulino MM, Almonte H, Miller-Butterworth CM, Bortolotti GR. 2016. Carry-over effects provide linkages across the annual cycle of a neotropical migratory bird, the Louisiana waterthrush *Parkesia motacilla*. Ibis 158:395–406.

Legagneux P, Harms NJ, Gauthier G, Chastel O, Gilchrist HG, Bortolotti G, Bêty J, Soos C. 2013. Does feather corticosterone reflect individual quality or external stress in Arctic-nesting migratory birds? PLoS ONE 8(12):6–13.

Lehikoinen A, Kilpi M, Öst M. 2006. Winter climate affects subsequent breeding success of common eiders. Global Change Biol. 12(7):1355–1365.

Lepage D, Gauthier G, Menu S. 2000. Reproductive consequences of egg-laying decisions in snow geese. J Anim Ecol. 69:414–427.

Liebezeit JR, Gurney KEB, Budde M, Zack S, Ward D. 2014. Phenological advancement in Arctic bird species: relative importance of snow melt and ecological factors. Polar Biol. 37(9):1309–1320.

Liebezeit JR, Smith PA, Lanctot RB, Schekkerman H, Tulp I, Kendall SJ, Tracy DM, Rodrigues RJ, Meltofte J, Robinson JA, et al. 2007. Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. Condor 109(1):32–47.

Marra P, Hobson KA, Holmes RT. 1998. Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282:1884–1886.

Marra PP, Holmes RT. 2001. Consequences of dominance-mediated habitat segregation in American redstarts during the nonbreeding season. Auk 118(1):92–104.

Martin TE. 1987. Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst. 18(1):453–487.

McCaffery BJ, Ruthrauff DR. 2004. How intensive is intensive enough? Limitations of intensive searching for estimating shorebird nest numbers. Wader Study Group Bull. 103_63-66.

McKinnon L, Picotin M, Bolduc E, Juillet C, Bêty J. 2012. Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. Can J Zool. 90(8):961–971.

McNamara JM, Barta Z, Klaassen M, Bauer S. 2011. Cues and the optimal timing of activities under environmental changes. Ecol Lett. 14(12):1183–1190.

Meijer T, Drent R. 1999. Re-examination of the capital and income dichotomy in breeding birds. Ibis 141:399–414.

Meltofte H, Høye TT, Schmidt NM, Forchhammer MC. 2007a. Differences in food abundance cause inter-anual variation in the breeding phenology of High Arctic waders. Polar Biol. 30(5):601–606.

Meltofte H, Piersma T, Boyd H, McCaffery B, Gantner B, Golovnyuk VV, Graham K, Gratto-Trevor CL, Morrison RIG, Nol E, et al. 2007b. Effects of climate variation on the breeding ecology of Arctic shorebirds. Meddelelser om Grønland Bioscience 59. Copenhagen: Danish Polar Center. 48 p.

Michel P, Ollason JC, Grosbois V, Thompson PM. 2003. The influence of body size, breeding experience and environmental variability on egg size in the northern fulmar (*Fulmarus glacialis*). J Zool. 261(4):S0952836903004291.

Monaghan P, Bolton M, Houston DC. 1995. Egg production constraints and the evolution of avian clutch size. Proc R Soc B 259(1355):189–191.

Morrison RIG, Hobson KA. 2004. Use of body stores in shorebirds after arrival on High-Arctic breeding grounds. Auk 121(2):333–344.

Morrison RIG, Davidson NC, Piersma T. 2005. Transformations at high latitudes: why do red knots bring body stores to the breeding grounds? Condor 107(2):449–457.

Morrison RIG, Mizrahi DS, Ross RK, Ottema OH, de Pracontal N, Narine A. 2012. Dramatic declines of semipalmated sandpipers on their major wintering areas in the Guianas, northern South America. Waterbirds 35(1):120–134.

Morton ML. 2002. The mountain white-crowned sparrow: migration and reproduction at high altitude. Stud Avian Biol-Ser. 24:23-33.

Naves LC, Lanctot RB, Taylor AR, Coutsoubos NP. 2008. How often do Arctic shorebirds lay replacement clutches? Wader Study Group Bull. 115(1):2–9.

Newton I. 2008. The migration ecology of birds. London: Academic Press. 984 p.

Nol E, Blanken MS, Flynn L. 1997. Sources of variation in clutch size, egg size and clutch completion dates of semipalmated plovers in Churchill, Manitoba. Condor 99(2):389–396.

Norris DR. 2005. Carry-over effects and habitat quality in migratory populations. Oikos 109(1):178–186.

Norris DR, Marra PP, Kyser TK, Sherry TW, Ratcliffe LM. 2003. Tropical winter habitat limits reproductive success on the temperate breeding grounds in a migratory bird. Proc R Soc B 03pb0683.1:1–6.

O'Dwyer TW. 2004. Breeding biology of Gould's petrels *Pterodroma leucoptera*: predicting breeding outcomes from a physiological and morphological appraisal of adults. Ph.D. dissertation. Wollongon (Australia): University of Wollongong. 170 p.

Olsen PD, Cunningham RB, Donnelly CF. 1994. Is there a trade-off between egg size and clutch size in altricial and precocial nonpasserines? A test of a model of the relationship between egg and clutch size. Aust J Zool. 42:323–328.

Pennycuick CJ, Fast PLF, Ballerstädt N, Rattenborg N. 2012. The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration. J Ornithol. 153(3):633–644.

Perrins, CM. 1970. The timing of birds' breeding seasons. Ibis 112:242–255.

Perrins CM. 1996. Eggs, egg formation, and the timing of breeding. Ibis 138:2–15.

Price T, Kirkpatrick M, Arnold SJ. 1988. Directional selection and the evolution of breeding date in birds. Science 240(4853):798-799.

Pyle P. 2008. Identification guide to North American birds, part II. Point Reyes Station (CA): Slate Creek Press. 835 p.

Qiagen. 2006. DNeasy ® blood & tissue handbook for purification of total DNA from animal blood and animal tissue. Hilden (Germany): Qiagen Group. p. 28–30

R Core Team. 2016. R: a language and environment for statistical computing–version X [Internet]. Vienna (Austria): R Foundation for Statistical Computing. [cited 14 March 2018]. Available from: http://www.R-project.org/

Reynolds SJ, Schoech SJ, Bowman R. 2003. Nutritional quality of prebreeding diet influences breeding performance of the Florida scrub-jay. Oecologia 134(3):308–316.

Rice SM, Collazo JA, Alldredge MW, Harrington BA, Lewis AR. 2007. Local annual survival and seasonal residency rates of semipalmated sandpipers (*Calidris pusilla*) in Puerto Rico. Auk 124(4):1397–1406.

Ricklefs RE. 1984. Egg dimensions and neonatal mass of shorebirds. Condor 86(1):7–11.

Ricklefs RE, Wikelski M. 2002. The physiology/life-history nexus. Trends Ecol Evol. 17(10):462–468.

Ritz MS, Hahn S, Peter HU. 2005. Factors affecting chick growth in the south polar skua (*Catharacta maccormicki*): food supply, weather and hatching Date. Polar Biol. 29(1):53–60.

Rowe L, Ludwig D, Schluter D. 1994. Time, condition, and the seasonal decline of avian clutch size. Am Nat. 143(4):698–722.

Runge CA, Martin TG, Possingham HP, Willis SG, Fuller RA. 2014. Conserving mobile species. Front Ecol Environ. 12(7):395–402.

Ruthrauff DR, Keller JN, Rizzolo DJ. 2009. Ecological factors regulating brood attendance patterns of the western sandpiper *Calidris mauri*. Ibis 151(3):523–534.

Ruthrauff DR, McCaffery BJ. 2005. Survival of western sandpiper broods on the Yukon-Kuskokwim Delta, Alaska. Condor 107(3):597–604.

Sandercock, BK. 1998a. Chronology of nesting events in western and semipalmated sandpipers near the Arctic Circle. J Field Ornithol. 69(2):235–243.

Sandercock, BK. 1998b. Assortative mating and sexual size dimorphism in western and semipalmated sandpipers. Auk 115(3):786–791.

Sandercock BK, Gratto-Trevor CL. 1997. Local survival in semipalmated sandpipers *Calidris pusilla* breeding at La Pérouse Bay, Canada. Ibis 139:305–312.

Sandercock BK, Lank DB, Cooke F. 1999. Seasonal declines in the fecundity of Arctic-breeding sandpipers: different tactics in two species with an invariant clutch size. J Avian Biol. 30(4):460–468.

Sapolsky RM, Romero ML, Munck A. 2000. How do glucocorticoids influence the stress response? Endocr Rev. 21(1):55–89.

Schamel D, Tracy DM. 1987. Latitudinal trends in breeding red phalaropes. J Field Ornithol. 58(2):126–134.

Schekkerman H, Tulp I, Piersma T, Visser GH. 2003. Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. Oecologia 134(3):332–342.

Schekkerman H, Tulp I, Calf KM, de Leeuw JJ. 2004. Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2002. Alterra-report 922. Wageningen (The Netherlands): Alterra, Green World Research. 110 p.

Schoech SJ, Rensel MA, Heiss RS. 2011. Short- and long-term effects of developmental corticosterone exposure on avian physiology, behavioral phenotype, cognition, and fitness: a review. Curr Zool. 57(4):514–530.

Schroeder J, Hooijmeijer J, Both C, Piersma T. 2007. The importance of early breeding in black-tailed godwits (*Limosa limosa*). Osnabrücker Naturw Mitt. 32:239–241.

Smith PA, Gratto-Trevor CL, Collins BT, Fellows SD, Lanctot RB, Liebezeit J, McCaffery BJ, Tracy D, Rausch J, Kendall S, et al. 2012. Trends in abundance of semipalmated sandpipers: evidence from the Arctic. Waterbirds 35:106–119.

Soikkeli M. 1967. Breeding cycle and population dynamics in the dunlin (*Calidris alpina*). Ann Zool Fenn. 4(2):158–198.

Sorensen MC, Hipfner JM, Kyser TK, Norris DR. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. J Anim Ecol. 78(2):460–467.

Starck JM, Ricklefs RE, editors. 1998. Avian growth and dfevelopment: evolution within the altricial-precocial spectrum. New York (NY): Oxford University Press. 441 p.

Studds CE, Marra PP. 2005. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. Ecology 86(9):2380–2385.

Tavera EA, Lank DB, González PM. 2016. Effects of migration distance on life history strategies of western and semipalmated sandpipers in Perú. J Field Ornith. 87:293–308.

Tulp I. 2007. The Arctic pulse: timing of breeding in long-distance migrant shorebirds. PhD dissertation. Groningen (The Netherlands): University of Groningen. 260 p.

Tulp I, Schekkerman H. 2001. Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2001. Alterra-report 451. Wageningen (The Netherlands): Alterra, Green World Research. 110 p.

Tulp I, Schekkerman H. 2008. Has prey availability for Arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. Arctic 61(1):48-60.

Walters JR. 1984. The evolution of parental behavior and clutch size in shorebirds. In: Burger J, Olla BL, editors. Shorebirds: breeding behavior and populations. New York (NY): Plenum Press. p. 243–287.

Wasserstein RL, Lazar NA. 2016. The ASA's statement on p-values: context, process, and purpose. Am Stat. 70(2):129–33.

Webster MS, Marra PP. 2005. Birds of two worlds: the ecology and evolution of migration. Greenberg R, Marra PP, editors. Batlimore (MD): The Johns Hopkins University Press. p 199-209.

Weiser EL, Brown SC, Lanctot RB, Gates HR, Abraham KF, Bentzen RL, Bêty J, Boldenow ML, Brook RW, Donnelly TF, et al. 2018a. Life-history tradeoffs revealed by seasonal declines in reproductive traits of Arctic-breeding shorebirds. J Avian Biol. 49(2):e01531.

Weiser EL, Brown SC, Lanctot RB, Gates HR, Abraham KF, Bentzen RL, Bêty J, Boldenow ML, Brook RW, TF Donnelly, et al. 2018b. Effects of environmental conditions on reproductive effort and nest success of Arctic-breeding shorebirds. Ibis doi:10.1111/ibi.12571.

Weiser EL, Lanctot RB, Brown SC, Alves JA, Battley PF, Bentzen R, Bêty J, Bishop MA, Boldenow M, Bollache L, et al. 2016. Effects of geolocators on hatching success, return rates, breeding movements, and change in body mass in 16 species of Arctic-breeding shorebirds. Mov Ecol. 4:12.

Will AP, Suzuki Y, Elliott KH, Hatch SA, Watanuki Y, Kitaysky AS. 2014. Feather corticosterone reveals developmental stress in seabirds. J Exp Biol. 217:2371–2376.

Will A, Watanuki Y, Kikuchi DM, Sato N, Ito M, Callahan M, Wynne-Edwards K, Hatch S, Elliott K, Slater L, et al. 2015. Feather corticosterone reveals stress associated with dietary changes in a breeding seabird. Ecol Evol. 5(19):4221–4232.

Williams TD. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. Biol Rev. 69(1):35–59.

Williams TD. 2005. Mechanisms underlying the costs of egg production. BioScience 55(1):39–48.

Winkler DW, Walters JR. 1983. The determination of clutch size in precocial birds. In: Johnston RF, editor. Current ornitholology vol 1. Boston (MA): Springer. p. 33-68

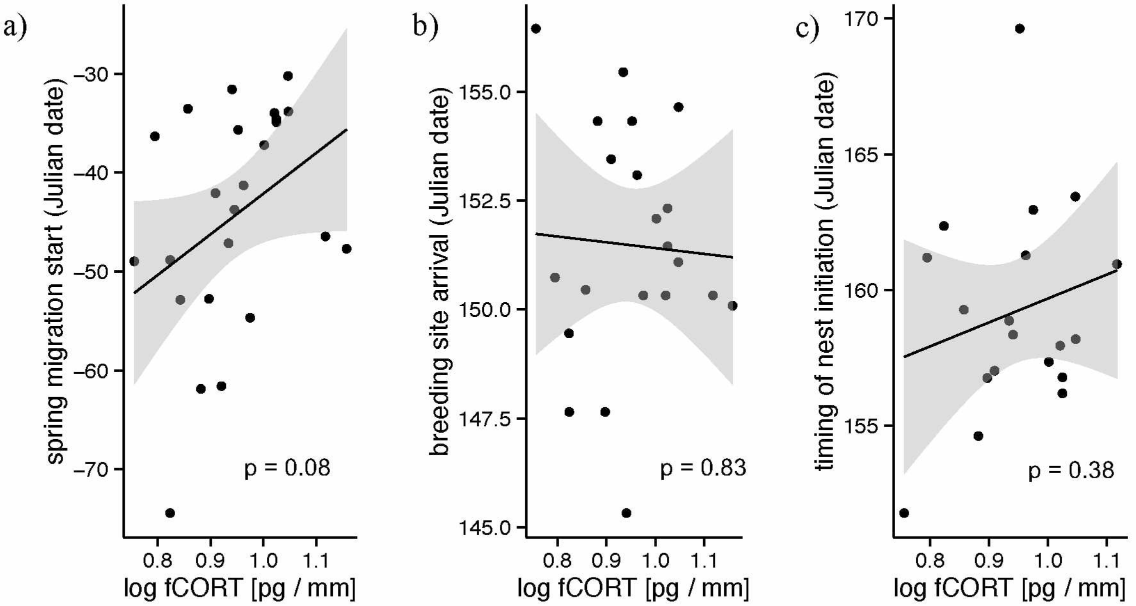

Figure 2.1. Wintering season carry-over effects to timing of spring migration and breeding in gls-equipped semipalmated sandpipers. Dependent variables regressed on winter-incurred log fCORT [pg / mm] are: a) spring migration start, independent of wintering longitude (*n* = 24); b) timing of arrival at breeding sites, independent of breeding longitude (*n* = 21); and c) timing of nest initiation, independent of arrival (*n* = 19). Gray shading depicts 90% confidence intervals around the regression lines.

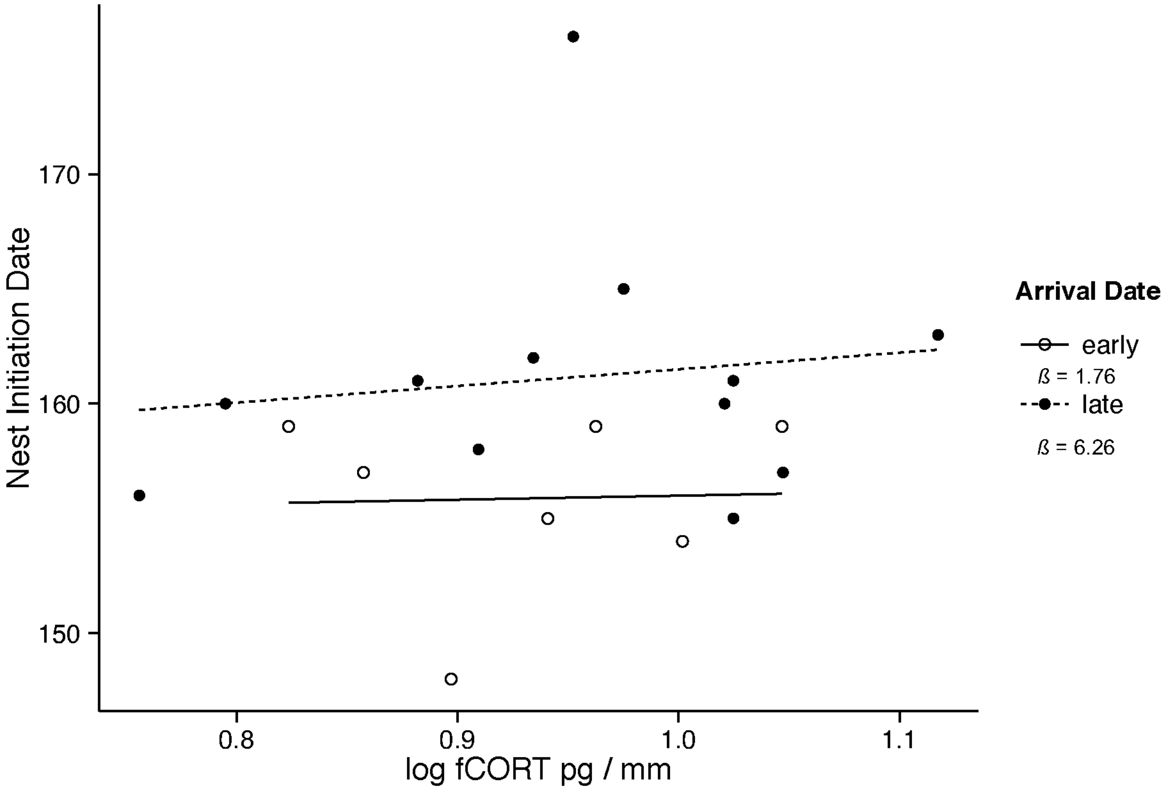

Figure 2.2. Influence of fCORT on nest initiation dates in gls-equipped semipalmated sandpipers (*n* = 19). At later dates of arrival, birds with high fCORT levels appeared to have increasingly delayed nest initiation. Arrival period is displayed as early and late for ease of graphical interpretation (Julian Days 140-149, 150-160, respectively). The overall *p*-value for the interaction of fCORT with arrival date is 0.004.

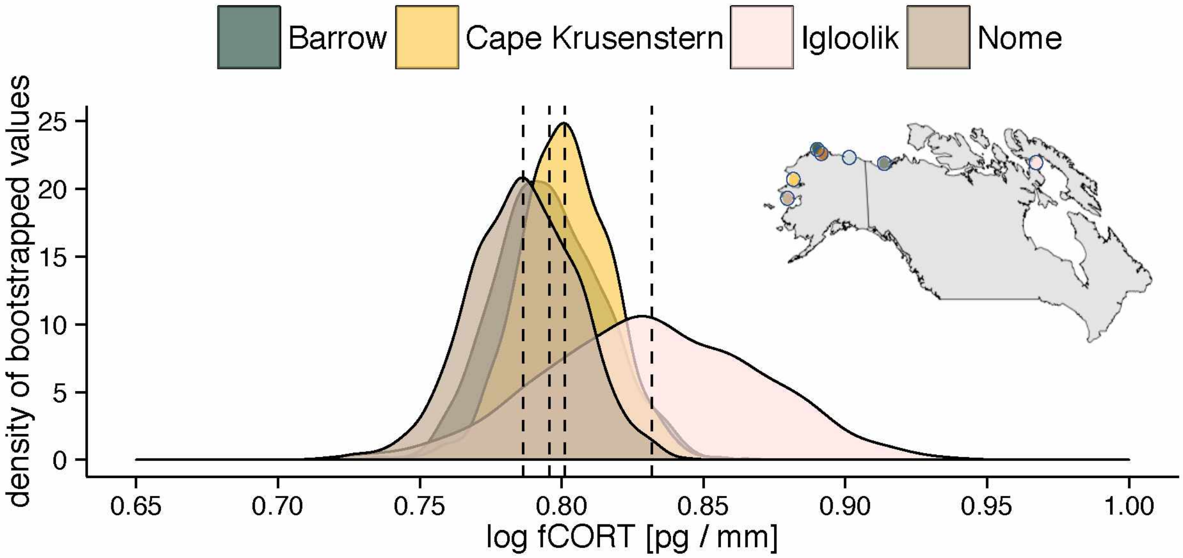

Figure 2.3. Bootstrapped mean corticosterone in winter-grown feathers of female semipalmated sandpipers with mean egg volume measurements, grouped by breeding site. Dashed lines indicate means. Overall log fCORT ranged from 0.536 – 1.153 [pg mm^{-1}] in this subsample (*n* = 108). Wilcoxon rank sum tests showed differences were not significant between any two sites. No egg volume data were available for Ikpikpuk, Canning, or Mackenzie River sites (shown from left to right after Barrow).

Table 2.1. Parsimonious models (Δ $\text{AIC}_c < 2$) explaining a) spring migration start date, b) migration rate, c) breeding site arrival date, and d) nest initiation date of gls-equipped semipalmated sandpipers. A model with fCORT only and the intercept-only model are shown for comparison. Candidate models evaluated and an explanation of terms are in Tables B-1 – B-4.

	a) Migration Start Date (*n* = 24)	**k**	**AIC_c**	**ΔAIC_c**	**w_i**	**deviance explained**
1.	winter long + winter long * fCORT	4	189.70	0	0.164	46%
2.	fCORT + winter long	4	189.80	0.10	0.156	45%
3.	fCORT + winter long * fCORT	4	190.09	0.39	0.135	45%
4.	winter long	3	190.46	0.76	0.112	37%
5.	winter long * breeding long	3	190.49	0.79	0.110	37%
6.	fCORT	3	197.76	8.06	.	14%
7.	intercept	2	198.80	9.10	.	.

	b) Migration Rate (*n* = 21)	**k**	**AIC_c**	**ΔAIC_c**	**w_i**	**deviance explained**
1.	winter long + start date + winter long * migration start	5	223.20	0	0.509	84%
2.	fCORT	3	253.86	30.66	.	4%
3.	intercept	2	251.92	28.72	.	.

	c) Breeding Site Arrival Date (*n* = 21)	**k**	**AICc**	**ΔAICc**	**w_i**	**deviance explained**
1.	breeding long	3	108.76	0.00	0.523	53%
2.	sex + breeding long + sex * breeding long	5	108.94	0.18	0.477	66%
3.	fCORT	3	124.68	15.92	.	<1%
4.	Intercept	2	121.93	21.69	.	.

	d) Nest Initiation Date (*n* = 19)	**k**	**AICc**	**ΔAICc**	**w_i**	**deviance explained**
1.	arrival date	3	111.96	0.00	0.502	51%
2.	fCORT + arrival date * fCORT	4	113.33	1.37	0.252	56%
3.	fCORT	3	125.20	13.24	.	2%
4.	Intercept	2	122.79	10.83	.	.

Table 2.2. Parsimonious models (∆ $AIC_c \le 2$) and all terms significant explaining nest initiation date of semipalmated sandpipers breeding at 7 sites during 2012-2014. A model with fCORT only and the intercept-only model are shown for comparison. Candidate models and an explanation of all terms are in Table B-5.

	Nest Initiation Date (*n* = 254)	**k**	**AIC_c**	**ΔAIC_c**	**w_i**	**deviance explained**
1.	breeding site	8	1534.09	0	0.356	53%
2.	breeding site + year + year * breeding site	15	1534.20	0.11	0.337	56%
3.	year + breeding site * year	9	1535.56	1.47	0.171	53%
4.	fCORT + fCORT * breeding site	9	1536.03	1.94	0.135	53%
5.	fCORT	3	1714.22	180.13	.	<1%
6.	intercept	2	1712.51	178.42	.	.

Table 2.3. Parsimonious models (Δ AIC$_c \leq 2$) explaining variation in clutch size of female semipalmated sandpipers at 6 breeding sites during 2012-2014. The intercept-only model and simplified models including significant relationships between clutch size and fCORT are included for comparison. Single variables and two-way interactions included in candidate models are described in Table B-6. Here, site = breeding site, date = nest initiation date.

	a) Total Clutch Size (*n* = 156)	**k**	**AICc**	**ΔAICc**	**w_i**	**Deviance Explained**
1.	fCORT + date + site + gls + fCORT * date	11	93.09	0.00	0.10	22%
2.	fCORT + site + gls + fCORT * date + date * year	11	93.34	0.25	0.09	22%
3.	fCORT + date + gls + fCORT * date + date * site	11	93.44	0.35	0.09	22%
4.	date + site + gls + fCORT * date + fCORT * year	11	93.45	0.36	0.09	22%
5.	site + gls + fCORT * date + fCORT * year + date * year	11	93.73	0.64	0.08	21%
6.	date +gls + fCORT * date + fCORT * year + date * site	11	93.80	0.71	0.07	22%
7.	fCORT + site + gls + fCORT * date	10	94.41	1.32	0.05	20%
8.	site + gls + fCORT * date + fCORT * year	10	94.50	1.41	0.05	20%
9.	fCORT + year + gls + fCORT * date + date * year + site * year	12	94.62	1.53	0.05	22%
10.	fCORT + date + year + gls + fCORT * date + site * year	12	94.62	1.53	0.05	22%
11.	fCORT + site + year + gls + fCORT * date + date * year	12	94.63	1.54	0.05	22%
12.	year + gls + fCORT * date + fCORT * year + date * year + site * year	12	94.63	1.54	0.05	22%
13.	date + year + gls + fCORT * date + fCORT * year + site * year	12	94.63	1.54	0.05	22%
14.	site + year + gls + fCORT * date + fCORT * year + date * year	12	94.64	1.55	0.05	22%
15.	date + site + year + gls + fCORT * date + fCORT * year	12	94.64	1.55	0.05	22%
16.	date + year + gls + date * site	14	94.78	1.69	0.04	24%
17.	fCORT + date + fCORT * date	5	107.40	16.17	.	6%
18.	fCORT * site	8	111.11	19.88	.	8%
19.	*intercept*	*2*	*111.40*	*20.17*	.	.
20.	fCORT + site + fCORT * site	13	111.60	20.37	.	14%
21.	fCORT	3	113.19	21.96	.	<1%

Table 2.4. Parsimonious models (Δ AIC$_c \leq 2$) explaining the variation in mean egg volume (cm^3) of semipalmated sandpipers at 4 breeding sites during 2012-2014. A model with fCORT only and the intercept model are shown for comparison. The intercept-only model and simplified models including significant relationships between clutch size and fCORT are included for comparison. Single variables and two-way interactions included in candidate models are described in Table B-7. Here, site = breeding site, date = nest initiation date, clutch = clutch size.

	b) Mean Egg Volume (*n* = 108)	**k**	**AICc**	**ΔAICc**	**w_i**	**Deviance Explained**
1.	fCORT + date + gls + date * site + clutch * gls	9	92.92	0.00	0.09	40%
2.	date + gls + fCORT * date + date * site + clutch * gls	9	92.99	0.07	0.09	39%
3.	fCORT + site + gls + clutch * gls	8	93.05	0.13	0.09	38%
4.	date + site + fCORT * date + gls + clutch * gls	9	93.14	0.22	0.09	39%
5.	fCORT + fCORT * site + gls + clutch * gls	8	93.47	0.55	0.07	38%
6.	site + fCORT * date + gls + clutch * gls	8	94.58	1.66	0.04	37%
7.	fCORT * site	6	97.93	5.01	.	32%
8.	fCORT + site + fCORT * site	9	99.74	6.82	.	36%
9.	fCORT + date + fCORT * date	5	107.40	14.48	.	6%
10.	fCORT * date	3	128.98	36.06	.	4%
11.	fCORT	3	130.37	37.45	.	3%
12.	*intercept*	*2*	*131.44*	*38.52*	.	.

General Conclusion

Migratory life histories are widely accepted to have evolved in response to spatiotemporal variation in both resources and risk (as reviewed in Newton 2008, Cresswell et al. 2011). They involve complex, and typically poorly understood, interactions between the events and processes taking place in the disparate locations used during their annual cycles. Gaining a better understanding of these interactions is critical to conservation of migratory species (Norris 2005, Webster and Marra 2005, Runge et al. 2014), including shorebirds. In all the world's flyways, a larger proportion of shorebird populations are declining than not (International Wader Study Group 2003, Stroud et al. 2006).

The work presented in the two chapters of my Master's thesis examined the potential for conditions encountered during winter to impose carryover effects (i.e. negative but nonfatal effects that carry forward to impact later stages of the annual cycle) in a species of migratory shorebird. Each spring, shorebirds travel north to the Arctic from distant wintering areas, nesting and rearing chicks in coastal tundra habitats. At the high latitudes, shorebirds find a seasonal pulse in invertebrate prey that enables them to meet the high energetic demands of reproduction (Meltofte et al. 2007a, Tulp & Schekkerman 2008, Alerstam et al. 2011). In a harsh environment and during a breeding stage that comprises less than one quarter of their annual cycle, adult shorebirds obtain territories and mates and invest in offspring through reproduction, incubation, and eventually rearing of chicks. Birds face selective pressure in the timing of these events in seasonal environments (Drent 2006), and their fitness increases when events are fine-tuned to climatic conditions and the phenology of their prey species (Schekkerman et al. 2003, Meltofte et al. 2007a, Tulp & Schekkerman 2008, McNamara et al. 2011, McKinnon et al. 2012, Kwon 2016). Each fall, because the prospects for survival are increased at southern latitudes (Newton 2008, Cresswell et al. 2011), shorebirds migrate back to the wintering areas. Together, the long-distance spring and fall migrations may comprise one quarter of the annual cycle. The remainder, up to seven months, is spent in the wintering areas.

In my study species, the semipalmated sandpiper (*Calidris pusilla*), the eastern breeding population has been declining since the 1970s/80s (Andres et al. 2012, Hicklin and Chardine 2012, Smith et al. 2012). A population-level decline has also been recorded over a similar time period for birds overwintering along the coast of northeastern South America (Morrison et al. 2012), seeming to suggest limiting factors for this species might be found during winter (Morrison et al. 2012, Watts et al. 2015, BirdLife International 2016, Brown et al. 2017). To better understand how the three breeding populations of semipalmated sandpipers disperse across their wintering areas, Brown et al. (2017) employed a tracking technology only recently available for use with small-bodied birds. Using light-sensing geolocators (hereafter 'gls') to track individual birds over one annual cycle, they uncovered a more complicated pattern of migratory connectivity than was previously understood. This new pattern of migratory connectivity also complicated our understanding of which factors might contribute to declines in semipalmated sandpipers because the western breeding population showed stronger connectivity with wintering areas in French Guiana and Suriname than previously thought (Brown et al. 2017). Although conditions in this region are known to pose problems for shorebirds (Morrison et al. 2012, Watts and Turrin 2016), the western breeding population is considered stable, or possibly increasing (Andres et al. 2012, Smith et al. 2012). Conditions at key habitats used by eastern breeders during their spring or fall migrations could be the underlying cause of decline

(Brown et al. 2017), but the results of my graduate research suggest we should not dismiss the influence of wintering conditions on the population demographics of semipalmated sandpipers.

Previously, studies comparing the wintering physiology of semipalmated sandpipers using locations across the wintering range (including in northeastern South America, the region where major declines had been documented) were lacking. Further, wintering condition had not been measured in birds from known breeding locations, making a direct assessment of how environmental conditions in the wintering areas might impact breeding populations difficult. My research addressed this critical knowledge gap. In Chapter 1, I provided evidence that the physiological condition of semipalmated sandpipers varied with wintering location. I measured feather corticosterone (fCORT) in the winter-grown feathers of 36 semipalmated sandpipers that were tracked to their wintering locations (Brown et al. 2017). These birds came from five breeding sites distributed across Alaska, and their wintering locations clustered into four distinct regions. Location data from gls showed these individuals remained within one region during the wintering period (approximately 7 months). I tested for variation in fCORT among wintering locations and also accounted for variation caused by carryover effects from breeding conditions and breeding effort in the season prior to feather growth. I found birds wintering in Atlantic South America had among the highest levels of winter-incurred stress, suggesting environmental conditions in this region (which encompasses French Guiana and Suriname) could be detrimental to individual fitness. Because I did not find support for a carryover effect from the breeding season to winter, I have increased confidence that the winter-incurred fCORT measured in tenth secondary feathers was truly driven by exposure to stressors in the wintering areas.

In Chapter 2, to determine whether birds wintering in relatively poorer environmental conditions experience effects other than reduced survival, I examined whether winter-incurred stress affected timing of subsequent spring migration or breeding. Using data for the 36 glsequipped birds, I found wintering in relatively poorer conditions delayed departure from the wintering areas but not date of arrival to breeding areas. Despite their later start, semipalmated sandpipers wintering in poorer conditions undertook their northward migrations at a faster rate and tended to arrive ‘on time’, likely due to strong selective pressure for early arrival (Both and Visser 2001, Bêty et al. 2004, Gunnarsson et al. 2006). But ‘making up for’ a delayed start may itself have consequences (Alerstam and Lindström 1991): expending greater energy on faster migrations and/or stopping less often or for shorter periods to rest and refuel might have resulted in birds arriving in lower physiological condition, compared to birds that departed earlier.

Following arrival to their breeding sites, shorebirds typically take five to eight days before commencing egg laying (Meltofte et al. 2007b); but individuals in lower condition may require additional time to transition from a migratory to a breeding state (Morrison et al. 2005). For birds in my study, the range of nest initiation dates was twice the range in arrival dates; and my results showed birds with higher winter stress loads initiated nests later than less-stressed birds arriving on the same date. For the high-stress birds, the time needed to make the transition to a breeding state may have been at least partially caused by a carryover effect of wintering in poor conditions, and resulted in a delay that could significantly impact reproductive success in a compressed breeding schedule (Kokko 1999, Schekkerman et al. 2003, Meltofte et al. 2007a, McKinnon et al. 2012). However, when I tested this same relationship using a larger dataset (which included 218 birds that were not tracked with gls; i.e. with known breeding but not wintering locations), I found conflicting results: nest initiation was up to two weeks later in birds with lower winter-incurred fCORT. One difference between the two datasets, which could have led to these opposing results, is the larger dataset likely included initiation dates of replacement clutches (i.e. second nests) that followed failure of undetected first nests, while the gls-only dataset included only first nests (as verified by patterns in the light data). Because only birds in good condition should be able to re-nest (e.g. Hegyi and Sasvari 1998, Hipfner et al. 1999, Gates et al. 2013, but see also Amat et al. 1999), inclusion of replacement clutches could have confounded the relationship between initiation date and fCORT.

Also in Chapter 2, I more directly examined whether winter-incurred stress carried over to negatively affect breeding investment by female semipalmated sandpipers, while also evaluating within-season factors encountered during breeding. Because prior studies show Arctic-breeding shorebirds, traditionally considered income breeders (Klaassen et al. 2001), also use endogenous reserves to some extent for egg formation (Hobson and Jehl 2010, Jaatinen et al. 2016), I tested for relationships of fCORT in female birds to clutch size and mean intra-clutch egg volume (of 156 females that bred at six sites and 108 females that bred at four sites, respectively). Factors that drive local environmental conditions, including breeding site and year, explained variation in both clutch size and egg volume, and both measures of breeding investment declined with later nest initiation dates. Such seasonal declines could be related to deteriorating environmental conditions during summer in the Arctic, but my study provides evidence that overwintering in poor conditions may also play a role: females with high winter-incurred stress were more likely to lay fewer eggs, including when accounting for nest initiation date. I also found support for a carryover effect of wintering conditions on egg volume, but not in the manner predicted. In confirmed first nests, high-stress females were more likely to lay eggs of larger volume, and mean egg volume was larger in smaller clutches. This suggests resource-limited females might invest less in total number of eggs but increase the volume of individual eggs, which could improve chances for their offspring (Monaghan et al. 1995, Williams 2005). I did not find these relationships in non-gls females, for which some of the egg measurements may have come from replacement clutches; eggs in replacement clutches, laid by birds in better physiological condition, tend to be smaller in volume (Hipfner et al. 1999, Gates et al. 2013, Weiser et al. 2018).

The data available for my study did not allow me to investigate the influence of intrinsic quality and other factors (e.g. age, pairing history; Heidinger et al. 2006, Angelier et al. 2010) on winter stress loads, breeding effort in the season prior to feather growth, or breeding investment in the season following feather growth. However, the results of both chapters suggest intrinsic quality might, to some extent, mediate an individual's response to stressful conditions year-round. Individuals of lower intrinsic quality (and therefore consistently lower condition) might have an up-regulated adrenal function, and therefore higher stress biomarkers, that causes them to more readily enter an emergency life history state and redirect from parental duties to self-maintenance (Wingfield et al. 1998, Wingfield and Kitaysky 2002). This link between intrinsic quality, stress physiology, and behavior might explain why those birds in my study that had higher breeding effort (i.e. incubated to hatch) subsequently had lower fCORT. My models left a large proportion of clutch size variation unexplained, so clearly factors other than wintering conditions or breeding conditions measured on a site-wide scale may be more determinant of whether semipalmated sandpipers lay modal or reduced clutches. Further, because lower-quality individuals often reproduce later in the season (Hochachka 1990, Christians et al. 2001), intrinsic factors may have also played a role in the seasonal declines in female breeding investment observed this study. Future, focused work on this topic is warranted.

Experimentally derived reference values of fCORT are not available in this species to confirm whether birds in my study with higher fCORT levels indeed had high levels of stress compared to the population at large. In addition, I measured fCORT only in semipalmated sandpipers that were in good enough physiological condition to complete their spring migrations to the breeding areas, missing birds for which poor wintering conditions may have been fatal during the energetically taxing spring migration. Thus, while my first chapter showed fCORT measurements can differentiate between the relative quality of wintering sites in this species, it was not clear whether wintering in poorer conditions subsequently imposed negative effects on individual birds. The results of my second chapter help to answer this question, revealing both direct and indirect carryover effects of exposure to stressors during the winter. Winter-incurred stress influenced the timing and behavior of spring migration and may have influenced nest initiation dates, as higher-stressed birds took longer to nest after arriving at their breeding sites. There appeared to be an overall seasonal decline in both clutch size and egg volume. Yet, when accounting for nest initiation date, females with high winter-incurred stress were more likely to lay fewer eggs. Finally, in confirmed first nests, mean egg volume was larger in smaller clutches, and high-stressed females were also more likely to lay eggs of larger volume. This result suggests resource-limited females might make a clutch size-egg volume tradeoff, investing less in total number of eggs but more in each individual offspring. I have not assessed whether migration and breeding delays, or changes in breeding investment, ultimately reduced the number of offspring parents in this study successfully hatched and fledged. Likewise, I do not know how the carryover effects identified here impacted survival of young, and their eventual recruitment into the breeding population. Regardless, my results provide evidence that wintering conditions may have nonfatal but negative carryover effects to semipalmated sandpiper during subsequent seasons. In other words, stressors experienced far from Arctic breeding areas may have fitness consequences, lowering the physiological condition of birds entering the breeding season and reducing their reproductive performance.

Long-distance migrants do not recognize the geopolitical boundaries that separate critical habitats used throughout their annual cycle. While their conservation needs are thus global in scale, and require a good understanding of their full annual cycle, physically following a migrant through space and time is often impractical. For example, shorebirds that breed in the Arctic winter on every continent except Antarctica (Stroud et al. 2006). This study assesses physiological condition of semipalmated sandpipers across the species' wintering range and demonstrates that environmental conditions in a major wintering area along the northeast coast of South America, where a population-level decline has been observed, are stressful. Other studies have shown poor wintering conditions are more likely to have a population-level effect if migratory connectivity with poor-quality areas is strong (Norris 2005, Webster and Marra 2005, Wilson et al. 2011), as for the eastern breeding population with wintering areas in Atlantic South America. While birds in the western population also utilize the higher-stress regions identified in Chapter 1, our results suggest the western population may be stable due to its diffuse patterns of migratory connectivity and a higher proportion of birds wintering in lower-stress regions. However, if western birds shift from lower-stress regions identified in my first chapter toward higher-stress regions, or conditions in these lower-stress wintering regions deteriorate, the western breeding population could experience negative effects as well. Further, my results demonstrate the potential for poor wintering conditions to impact semipalmated sandpiper populations through mechanisms other than reduced survival (i.e. through residual effects that carry over to subsequent seasons). My study thus provides information that could be of key importance to conservation and management efforts for this species and may also be applicable to the conservation and management of other shorebird species wintering in this region.

The research described here makes an important contribution to shorebird research in general, as fCORT has previously been measured in only one other shorebird species to my knowledge (Aharon-Rotman et al. 2016), and never in a calidrid shorebird. My results also show that fCORT can be used to remotely evaluate wintering conditions in migratory birds, and may be useful in discerning whether limiting factors occur during the wintering stage of the annual cycle, and by what mechanisms they impact individual birds. Studies that use fCORT to distinguish between quality of wintering sites in avian taxa are rare (Bourgeon et al. 2014, Aharon-Rotman et al. 2016), and the results of my study could have broad application to other migratory birds that are difficult to track in time and space. However, conducting work in the winter season remains important in research that aims to address conservation and management concerns for long-distance migrants. While my results show wintering conditions may be important to multiple stages of the annual cycle, the specific factors that induced a stress response in the individual birds included in this study are not known. Therefore, while this study provides evidence that population-limiting factors may occur during the winter season, on-the-ground research will likely be needed to identify specific causes.

References

Aharon-Rotman Y, Buchanan KL, Clark NJ, Klaassen M, Buttemer WA. 2016. Why fly the extra mile? Using stress biomarkers to assess wintering habitat quality in migratory shorebirds. Oecologia 182:385–395.

Alerstam T, Lindström Å. 1991. Optimal bird migration: the relative importance of time, energy, and safety. In: Gwinner E, editor. Bird migration: physiology and ecophysiology. Berlin: Springer-Verlag. p. 331-351.

Alerstam T, Hedenström A, Åkesson S. 2011. Long-distance migration: evolution and determinants. Oikos 103:247–260.

Amat JA, Fraga RM, Arroyo GM. 1999. Replacement clutches by Kentish plovers. Condor 101:746–751.

Andres BA, Gratto-Trevor C, Hicklin P, Mizrahi D, Morrison RIG, Smith PA. 2012. Status of the semipalmated sandpiper. Waterbirds 35:146–148.

Angelier FF, Wingfield JC, Weimerskirch H, Chastel O. 2010. Hormonal correlates of individual quality in a long-lived bird: a test of the "corticosterone-fitness hypothesis". Biol Lett. 6:846–849.

Bêty J, Giroux JF, Gauthier G. 2004. Individual variation in timing of migration: causes and reproductive consequences in greater snow geese (*Anser caerulescens atlanticus*). Behav Ecol Sociobiol. 57:1–8.

BirdLife International. 2016. *Calidris pusilla*. The IUCN Red List of Threatened Species 2016: e.T22693373A93400702.

Both C, Visser ME. 2001. Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. Nature 411:296–298.

Bourgeon S, Leat EHK, Magnusdottir E, Furness RW, Strom H, Petersen A, Gabrielsen GW, Hanssen SA, Bustnes JO. 2014. Feather corticosterone levels on wintering grounds have no carry-over effects on breeding among three populations of great skuas (*Stercorarius skua*). PLoS ONE 9:1–6.

Brown S, Gratto-Trevor C, Porter R, Weiser EL, Mizrahi D, Bentzen R, Boldenow M, Clay R, Freeman S, Giroux M-A, et al. 2017. Migratory connectivity of semipalmated sandpipers and implications for conservation. Condor 119:207–224.

Christians JK, Evanson M, Aiken JJ. 2001. Seasonal decline in clutch size in European starlings: a novel randomization test to distinguish between the timing and quality hypotheses. J Anim Ecol. 70:1080–1087.

Cresswell KA, Satterthwaite WH, Sword GA. 2011. Understanding the evolution of migration through empirical examples. In: Milner-Gulland EJ, Fryxell JM, Sinclair AR, editors. Animal Migration – a synthesis. Oxford: Oxford University Press. p. 7-16.

Drent RH. 2006. The timing of birds' breeding seasons: the Perrins hypothesis revisited especially for migrants. Ardea 94:305–322.

Gates HR, Lanctot RB, Powell AN. 2013. High renesting rates in Arctic-breeding dunlin (*Calidris alpina*): a clutch-removal experiment. Auk 130:372–380.

Gunnarsson TG, Gill JA, Atkinson PW, Gélinaud G, Potts PM, Croger RE, Gudmundsson GA, Appleton GF, Sutherland WJ. 2006. Population-scale drivers of individual arrival times in migratory birds. J Anim Ecol. 75:1119–1127.

Hegyi Z, Sasvari L. 1998. Parental condition and breeding effort in waders. J Anim Ecol. 67:41–53.

Heidinger BJ, Nisbet ICT, Ketterson ED. 2006. Older parents are less responsive to a stressor in a long-lived seabird: a mechanism for increased reproductive performance with age? Proc Royal Soc Lond B Biol Sci 273:2227–2231.

Hicklin PW, Chardine JW. 2012. The morphometrics of migrant semipalmated sandpipers in the Bay of Fundy: evidence for declines in the eastern breeding population. Waterbirds 35:74–82.

Hipfner JM, Gaston AJ, Martin DL, Jones IL. 1999. Seasonal declines in replacement egg-layings in a long-lived, arctic seabird: costs of late breeding or variation in female quality? J Anim Ecol. 68:988–998.

Hobson KA, Jehl JR. 2010. Arctic waders and the capital-income continuum: further tests using isotopic contrasts of egg components. J Avian Biol. 41:565–572.

Hochachka W. 1990. Seasonal decline in reproductive performance of song sparrows. Ecology 71(4):1279-1288.

International Wader Study Group. 2003. Waders are declining worldwide. Conclusions from the 2003 International Wader Study Group conference, Cadiz, Spain. Wader Study Group Bull. 101/102:8–12.

Jaatinen K, Öst M, Hobson KA. 2016. State-dependent capital and income breeding: a novel approach to evaluating individual strategies with stable isotopes. Front Zool. 13:24.

Klaassen M, Lindstrom A, Meltofte H, Piersma. 2001. Arctic waders are not capital breeders. Nature 413:794–794.

Kokko H. 1999. Competition for early arrival birds in migratory birds. J Anim Ecol. 68:940–950.

Kwon E. 2016. Effects of climate change on the breeding ecology and trophic interactions of Arctic-breeding shorebirds. Ph.D. dissertation. Manhattan (KS): Kansas State University. 188 p.

McKinnon L, Picotin M, Bolduc E, Juillet C, Bêty J. 2012. Timing of breeding, peak food availability, and effects of mismatch on chick growth in birds nesting in the High Arctic. Can J Zool. 90:961–971.

McNamara JM, Barta Z, Klaassen M, Bauer S. 2011. Cues and the optimal timing of activities under environmental changes. Ecol Lett. 14:1183–1190.

Meltofte H, Høye TT, Schmidt NM, Forchhammer MC. 2007a. Differences in food abundance cause inter-anual variation in the breeding phenology of High Arctic waders. Polar Biol. 30(5):601–606.

Meltofte H, Piersma T, Boyd H, McCaffery B, Gantner B, Golovnyuk VV, Graham K, Gratto-Trevor CL, Morrison RIG, Nol E, et al. 2007b. Effects of climate variation on the breeding ecology of Arctic shorebirds. Meddelelser om Grønland Bioscience 59. Copenhagen: Danish Polar Center. 48 p.

Monaghan P, Bolton M, Houston DC. 1995. Egg production constraints and the evolution of avian clutch size. Proc Roy Soc Lond B. 259:189–191.

Morrison RIG, Davidson NC, Piersma T. 2005. Transformations at high latitudes: why do red knots bring body stores to the breeding grounds? Condor 107:449–457.

Morrison RIG, Mizrahi DS, Ross RK, Ottema OH, de Pracontal N, Narine A. 2012. Dramatic declines of semipalmated sandpipers on their major wintering areas in the Guianas, northern South America. Waterbirds 35:120–134.

Newton I 2008. The migration ecology of birds. London: Academic Press. 984 p.

Nol E, Blanken MS, Flynn L. 1997. Sources of variation in clutch size, egg size and clutch completion dates of semipalmated plovers in Churchill, Manitoba. Condor 99:389–396.

Norris DR. 2005. Carry-over effects and habitat quality in migratory populations. Oikos 109:178–186.

Runge CA, Martin TG, Possingham HP, Willis SG, Fuller RA. 2014. Conserving mobile species. Front Ecol Environ. 12:395–402.

Schekkerman H, Tulp I, Piersma T, Visser GH. 2003. Mechanisms promoting higher growth rate in arctic than in temperate shorebirds. Oecologia 134(3):332–342.

Smith PA, Gratto-Trevor CL, Collins BT, Fellows SD, Lanctot RB, Liebezeit J, McCaffery BJ, Tracy D, Rausch J, Kendall S, et al. 2012. Trends in abundance of semipalmated sandpipers: evidence from the Arctic. Waterbirds 35:106–119.

Stroud DA, Baker A, Blanco DE, Davidson NC, Delany S, Ganter B, Gill R, Gonzalez P, Haanstra L, Morrison RIG, et al. 2006. The conservation and population status of the world's waders at the turn of the millenium. In: Boere GC, Galbraith CA, Stroud DA, editors. Waterbirds around the world: a global overview of the conservation, management and research of the world's waterbird flyways. Edinburgh: The Stationary Office. p. 643-648.

Tulp I, Schekkerman H. 2008. Has prey availability for Arctic birds advanced with climate change? Hindcasting the abundance of tundra arthropods using weather and seasonal variation. Arctic 61(1):48-60.

Watts B, Reed E, Turrin C. 2015. Estimating sustainable mortality limits for shorebirds using the Western Atlantic Flyway. Wader Study 122:37–53.

Watts BD, Turrin C. 2016. Assessing hunting policies for migratory shorebirds throughout the Western Hemisphere. Wader Study 123:6–15.

Webster MS, Marra PP. 2005. The importance of understanding migratory connectivity and seasonal interactions. In: Greenberg R, Marra PP, editors. Birds of two worlds: the ecology and evolution of migration. Baltimore (MD): The Johns Hopkins University Press. p. 199–209.

Weiser EL, Brown SC, Lanctot RB, Gates HR, Abraham KF, Bentzen RL, Bêty J, Boldenow ML, Brook RW, Donnelly TF, et al. 2018a. Life-history tradeoffs revealed by seasonal declines in reproductive traits of Arctic-breeding shorebirds. J Avian Biol. 49(2):e01531.

Williams TD. 2005. Mechanisms underlying the costs of egg production. BioScience 55:39–48.

Wilson S, Ladeau SL, Tøttrup AP, Marra PP. 2011. Range-wide effects of breeding- and nonbreeding-season climate on the abundance of a Neotropical migrant songbird. Ecology 92:1789–1798.

Wingfield JC, Kitaysky AS. 2002. Endocrine responses to unpredictable environmental events: Stress or anti-stress hormones? Integr Comp Biol 42:600–609.

Wingfield JC, Maney DL, Breuner CW, Jacobs JD, Lynn S, Ramenofsky M, Richardson RD. 1998. Ecological bases of hormone-behavior interactions: the "emergency life history stage." Am Zool. 38:191–206.

APPENDIX A

Supplementary Material for Chapter 1

A.1 Data used to test main Chapter 1 hypotheses

Table A-1. Semipalmated sandpipers used to test the ‘wintering conditions’ (*n* = 36) and ‘breeding conditions’ (*n* = 40) hypotheses. Birds with ‘unknown’ wintering assignments were not used for the ‘wintering conditions’ analyses.

Wintering Region	Breeding Site										
	Canning River		**Ikpikpuk River**		**Barrow**		**Cape Krusenstern**		**Nome**		**Wintering Region TOTAL**
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
Pacific Central America				1			2		1		**4**
Pacific South America						2	2	1	4	1	**10**
Caribbean South America		1	1		1		1			2	**6**
Atlantic South America	7	3			4						**14**
Panama										1	**1**
Dominican Republic		1									**1**
Unknown			1		1		1		1		**4**
Breeding Site TOTAL	**12**		**3**		**8**		**7**		**10**		

Table A-2. Semipalmated sandpipers used to test the 'breeding effort' hypothesis. Measurements of breeding effort included nest fate (NF: fail (F) v hatch (H); n = 26) and incubation stage (IS: early (E), mid (M), and late (L); n = 37). Males (m) and females (f) were included in this dataset.

Wintering Region	Breeding Site																									Wintering Region TOTAL
	Canning River m = 7, f = 5					**Ikpikpuk River** m = 2, f = 1					**Barrow** m = 4, f = 1					**Cape Krusenstern** m = 6, f = 1					**Nome** m = 6, f = 4					
	Nest Fate		Incubation Stage			Nest Fate		Incubation Stage			Nest Fate		Incubation Stage			Nest Fate		Incubation Stage			Nest Fate		Incubation Stage			
	F	H	E	M	L	F	H	E	M	L	F	H	E	M	L	F	H	E	M	L	F	H	E	M	L	
Pacific Central America m = 3, f = 1						1			1							1	1		1	1	1			1		**NF = 4** **IS = 4**
Pacific S. America m = 6, f = 3															1	1	1		1	2	3	2	1	1	3	**NF = 7** **IS = 9**
Caribbean S. America m = 3, f = 3	1			1		1			1						1	1			1			2			2	**NF = 5** **IS = 6**
Atlantic S. America m = 10, f = 3	6		3	4	3							1		1	2											**NF = 7** **IS = 12**
Panama m = 0, f = 1																					1				1	**NF = 1** **IS = 1**
Dom. Republic m = 0, f = 1	1		1																							**NF = 1** **IS = 1**
Unknown m = 3, f = 0							1			1										1					1	**NF = 1** **IS = 3**
Breeding Site TOTAL	**NF = 8** **IS = 12**					**NF = 3** **IS = 3**					**NF = 1** **IS = 5**					**NF = 5** **IS = 7**					**NF = 9** **IS = 10**					

A.2 Additional hypothesis testing

A.2.1. Introduction to migration timing and effort

In addition to examining the potential for carryover effects from breeding effort to winter-incurred stress levels, we assessed whether factors from southward migration carry forward to affect the condition of wintering birds. The 'migration timing' hypothesis suggests individuals that remain longer in the Arctic might experience increased costs and, due to carryover effects, incur higher stress levels on the wintering grounds (measured as higher fCORT). Carryover effects to winter could occur as a result of deteriorating weather conditions or decreased food resources [1], seasonally increased exposure to avian predators along their migration routes [2,3], and/or depletion of food resources at key staging areas [4,5].

If shorebirds do not acquire sufficient energy reserves to fuel their long-distance flights [6], they might arrive at wintering areas late and/or in poor condition and not compete successfully for high quality territories [7–9]. Therefore, we also evaluated a second aspect of this hypothesis, namely that poorer physiological condition (i.e. higher fCORT levels) might be related to delayed arrival on the wintering areas. Shorebirds are expected to distribute themselves on the local landscape where food is most abundant [10,11], and food-based territoriality is known to occur in shorebirds during the non-breeding season [12, Myers 1984 *in* 13]. These behaviors are especially prevalent in calidrid shorebirds [12,14]. We therefore predicted birds with later breeding site departures and/or later wintering area arrivals would have decreased access to high-quality wintering habitats (e.g. those with the highest prey densities) and would subsequently have higher fCORT levels in winter-grown feathers.

We also evaluated a 'migration effort' hypothesis, which suggests differences among individuals in the physiological and energetic costs incurred during migration (here, fall) might influence their physiological condition during the subsequent season (here, winter; [15–18]). We predicted birds migrating faster and longer distances between breeding and wintering locations would incur greater costs, and these would carry over to result in higher fCORT levels in winter-grown feathers.

A.2.2. Supplemental Methods

To address the migration timing and migration effort hypotheses, we used the same individuals with which we addressed the wintering conditions hypothesis in the main text. We included data for those birds with known length of incubation, complete southward migration tracks, and known wintering region assignments (*n* = 32; Table A-3).

A.2.2.1 Sex assignment

We determined sex of each bird through field observations of behavior (e.g. territory and mating displays by males) and/or by comparing morphometric measurements of mated individuals, following methods detailed in Brown *et al.* [19] and using published information from Pyle [20] and Sandercock [21]. When sex could not be determined through these methods, we used blood samples collected at capture. For each bird, we drew blood (≤ 25 μl) into a plain capillary tube and stored it in Longmire buffer solution until analysis. We used Qiagen®'s DNeasy Spin-Column Protocol to extract total DNA [22] and followed methods from Griffiths *et al.* [23] for genetic sex determination.

A.2.2.2 Identification of migration parameters

We identified dates of departure from breeding sites and arrival at wintering areas for individual birds, using data from light-sensing geolocators. Periods of travel were identified by consistent, directional movement and distances between position fixes of over 200 km. This approach allowed us to identify start and end of southward migration at a 0.5 to 1 day resolution. We used departure and arrival dates to calculate approximate migration rate (total km traveled / total # of days), and determined approximate distance migrated by connecting known stopover sites using straight track lines.

A.2.2.3 Data analysis

To examine the migration timing and migration effort hypotheses, we fit our response variable, log fCORT (pg mm^{-1}, detrended for feather mass), using generalized linear regressions to each of our explanatory variables individually. These were date of southward migration start or wintering area arrival, migration rate (km / day), and migration distance (km). We also fit models with wintering latitude, breeding site, incubation stage (early, middle, or late), and sex as explanatory covariates. We did not include nest fate as explanatory variables in models, as it covaried with incubation stage (see main text Figs. 1.1.c and 1.1.d) but had a more restricted sample size.

We also fit models that included combinations of the above explanatory variables, including additive and two-way interactions (Table A-4). We considered only those interactive effects for which we could determine *a priori* hypotheses that made biological sense. Given limitations of our small sample sizes, candidate models were constrained to those with three or fewer variables. Models were fit in Program R version 3.2.4 [24]. From the candidate models, we selected the best models for inference using Akaike's information criterion corrected for small sample size (AICc), using package 'glmulti' [25]. Models with ΔAICc < 2 were considered as equally parsimonious; and of these, we retained only models in which all terms were statistically significant.

Table A-3. Semipalmated sandpipers used to test the 'migration timing' and 'migration effort' hypotheses (*n* = 32). Birds included in this dataset had different levels of breeding effort (i.e. incubating to early (E), mid (M), and late (L) stages). This dataset included both males (m) and females (f).

Wintering Region	Breeding Site															
	Canning River			**Ikpikpuk River**			**Barrow**			**Cape Krusenstern**			**Nome**			**Wintering Region TOTAL**
	Incubation Stage			Incubation Stage			Incubation Stage			Incubation Stage			Incubation Stage			
	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	
Pacific Central America					1						1	1		1		**4 (m = 3, f = 1)**
Pacific S. America									1		1	2	1	1	3	**9 (m = 6, f = 3)**
Caribbean S. America		1			1				1		1				2	**6 (m = 3, f = 3)**
Atlantic S. America	3	4	3					1	2							**13 (m = 10, f = 3)**
Breeding Site TOTAL	**11 (m = 7, f = 4)**			**2 (m = 1, f = 1)**			**5 (m = 4, f = 1)**			**6 (m = 5, f = 1)**			**8 (m = 5, f = 3)**			

Table A-4. Explanatory variables included in candidate models used to assess the 'migration timing' and 'migration effort' hypotheses. Using generalized linear regressions, we tested whether breeding site, incubation stage (incubation), start date of southward migration (start), migration rate (rate; km / day), migration distance (distance; km), wintering area arrival date (arrival), wintering region (WRegion), and sex contributed to winter-incurred fCORT levels in semipalmated sandpipers.

fCORT ~	Included in Top Models?	Rationale	Predicted Response
1. WRegion	Y	Variable environmental conditions across the wintering range might differentially affect individual condition (here, fCORT).	+ / -
2. Breeding Site	N	Variable environmental conditions across the breeding range might differentially affect individual condition, carrying over to nfluence winter fCORT.	+ / -
3. Breeding Site * WRegion	N	Carryover effects that result from conditions encountered at the breeding sites might affect individuals wintering in poorer environmental conditions but be offset in regions with better conditions. Such differences might be reflected in fCORT.	+ / -
4. Start	N	Birds starting migration later might encounter factors (e.g. food shortages, increased predator encounters, inclement weather) that affect them physiologically and carryover to increase winter-incurred fCORT. Higher fCORT might also be associated with later migration start if birds in poorer condition require longer preparation time before tsouthbound departures, and are unable to offset their poorer condition prior to the wintering period.	+
5. Start * WRegion	N	Birds starting migration later might be in poorer physiological condition, which might be offset or not depending on environmental conditions encountered in the wintering areas. In poorer-quality wintering regions, we might expect costs would not be offset; thus there would be higher fCORT in birds that start migration later (assuming later start incurs costs such as those described above).	+ / -
6. Arrival	Y	If high-quality habitats are limited, we expect birds arriving late to wintering areas would incur higher fCORT than earlier-arrivals with better access to higher quality or more abundant resources.	+
7. Arrival * WRegion	N	High-quality habitats might not be limited in all wintering regions. In regions with less overall high-quality habitat, late-arriving birds might not be able to sufficiently meet their needs and could incur higher fCORT. In regions where high-quality habitats are not limited, this relationship may not occur.	+ / -
8. Distance	N	Birds migrating over longer distances might incur greater physiological cost, which might carryover to affect them during the wintering period and be recorded through higher fCORT.	+
9. Distance * WRegion	N	Physiological costs might increase with distance migrated, but relationship between distance and fCORT might depend on whether environmental conditions are sufficient to offset costs of migration.	+ / -

Table A-4. Continued

fCORT ~	Included in Top Models?	Rationale	Predicted Response
10. Rate	Y	Physiological costs might increase with increasing rate of migration, and these costs might carryover to affect birds during the wintering period (and be reflected as higher fCORT). Alternatively, birds migrating at a faster rate might gain access to better territories in the wintering areas, which could offset physiological costs incurred during migration and result in reduced fCORT.	+ / -
11. Rate * WRegion	Y	Birds migrating more quickly might incur higher physiological costs, but whether these costs carryover to influence winter-incurred fCORT might depend on region. Carryover effects (reflected as higher fCORT) might occur in birds wintering in regions with more adverse environmental conditions, while wintering in good environmental conditions might offset migratory costs and result in lower fCORT. Alternatively, if higher-quality habitats are more limited in a given wintering region, birds that migrate at a faster rate might gain better territories and therefore have reduced fCORT levels.	+ / -
12. Sex	N	Sex-specific differences in physiological costs could be reflected in fCORT levels.	+ / -
13. Sex * WRegion	N	If high quality habitats are limited in a given wintering region, there might be differences in the quality of habitats used by the sexes, if access to choice habitats is sex-driven. We would expect such differences could be reflected in fCORT levels. However if high quality habitats are not limited, there might be no difference in how the sexes segregate on the wintering grounds.	+ / -
14. Incubation	Y	Birds that incubate longer might incur greater physiological cost through the energetic demands of incubation; and, if they successfully hatch a clutch, costs associated with brood attendance. Increased effort might result in carryover effects to birds during the wintering period (higher fCORT).	+
15. Incubation * WRegion	N	Physiological costs of incubation might increase as the incubation period progresses, but any carryover effects associated with breeding effort might be offset in high quality wintering regions. In regions with more adverse conditions, carryover effects might be reflected as higher fCORT).	+ / -
16. Start * Breeding Site	N	Birds starting migration later might incur physiological effects that carryover to cause higher fCORT. This might depend on the location at which they begin migration.	+ / -
17. Arrival * Breeding Site	N	If there is a cost to arriving late on the wintering area, we would expect birds arriving later to have higher fCORT. However, even late arrivals might be able to compete for higher-quality territories if they are in good physiological condition. Breeding in less adverse environmental conditions might influence ability to obtain high-quality wintering territory (and thus winter-incurred fCORT levels).	+ / -

Table A-4. Continued

fCORT ~	Included in Top Models?	Rationale	Predicted Response
18. Distance * Breeding Site	N	Physiological costs might increase with increasing distance migrated. However, if birds encounter better environmental conditions prior to migration, they might be in sufficient physiological condition to offset some of the costs of longer-distance migrations (and have lower fCORT expected based on only distance). Similarly, birds in poorer pre-migratory condition might experience greater carryover effects (and thus have higher fCORT than we might expect based on only distance).	+ / -
19. Rate * Breeding Site	N	Physiological costs might increase with increasing rates of migration. However, if birds encounter better environmental conditions prior to migration, they might be in sufficient physiological condition to offset costs of faster migrations (and have lower fCORT). Similarly, birds in poorer pre-migratory condition might experience higher costs of faster migrations, and thus have higher fCORT.	+ / -
20. Sex * Breeding Site	N	The sexes might experience different effects from challenging environmental conditions encountered in breeding areas, based on their different reproductive roles. However, sex-specific costs might be less apparent in birds breeding in benign locations. The costs of breeding in adverse conditions might carryover to affect the sexes differently in the winter (and be reflected in fCORT).	+ / -
21. Incubation * Breeding Site	N	Carryover effects related to the physiological costs of incubation might only be apparent in birds that experience adverse environmental conditions at their breeding site. For these birds, the costs of breeding might carryover to affect them during winter (and be reflected in fCORT).	+ / -
22. Distance * Start	N	The costs of delaying migration might depend on the distance traveled between breeding and wintering areas. There might be greater costs for birds undertaking longer migrations, and these costs might be reflected in fCORT.	+
23. Rate * Start	N	Birds starting migration later might be forced to migrate more quickly, leading to higher migration costs that carryover to affect birds during the wintering period (reflected as higher fCORT).	+ / -
24. Sex * Start	N	If there is a cost to starting migration later, the sexes might not be affected equally. Or, average start date of southward migration might be sex-specific, and we might see higher fCORT in one sex versus the other that cannot be explained by start date.	+ / -
25. Distance * Arrival	N	If there are costs to longer migrations, they might depend to some extent on arrival time (and whether distance-related costs can be offset by being early). If arriving earlier can offset some of the costs of migrating farther, than earlier-arriving birds might have lower fCORT than we would expect.	+

Table A-4. Continued

fCORT ~	Included in Top Models?	Rationale	Predicted Response
26. Rate * Arrival	N	Birds that migrate more slowly and arrive later in wintering areas might obtain lower quality habitats and have higher fCORT levels. Conversely, birds that migrate more quickly and arrive earlier might obtain better quality habitats and have lower fCORT levels.	+
27. Sex * Arrival	N	If there is a cost to arriving at the wintering areas later, the sexes might not be affected equally. If later-arriving males have better access to high quality territories than females arriving at the same time, we might see higher fCORT in females than can be explained based on arrival date alone.	+ / -
28. Distance * Rate	N	Birds migrating more quickly over equal distances might incur greater physiological costs (reflected as higher fCORT).	-
29. Distance * Sex	N	If there is a cost to migrating over longer distances, the sexes might not be affected equally.	+ / -
30. Distance * Incubation	N	The cost of migration distance might have more affect in birds that incurred the costs of longer incubations, such that birds incubating longer would have higher fCORT than birds that incubated for a shorter period but traveled the same distance.	+
31. Rate * Sex	N	The costs of faster migrations might not be the same for both sexes. If females incur greater costs of faster migrations, perhaps due to in lower pre-migratory condition, we might they would have higher fCORT than males migrating at an equivalent rate.	+ / -
32. Rate * Incubation	N	The cost of faster migrations might have more affect in birds that also incur costs of longer incubations (reflected as higher fCORT).	+

A.2.3. Supplemental results for 'migration timing' and 'migration effort' hypotheses

Migration start date ranged from 26 June – 19 July (mean = 9 July), winter arrival date ranged from 27 July – 14 October (mean = 27 August), and speed of migration ranged from 99 – 373 km / day (mean = 228 km / day). The range of distances traveled from breeding areas varied by wintering destination: 1) Pacific Central America: 8450 – 10,600 km; 2) Pacific South America: 9700 – 11,050 km; 3) Caribbean South America: 8700 – 10,250 km; and 4) Atlantic South America: 9900 – 11,250 km.

Consistent with results from Wilcoxon rank sum tests (see results in main text), when fCORT was regressed on individual variables, we found it decreased with progressively later stages of incubation ($p = 0.03$) and varied with wintering region ($p = 0.01$) but not with breeding site ($p = 0.2$). In addition, generalized linear regressions revealed fCORT tended to decrease with distance migrated ($\beta < 0.001, p = 0.09$); but there was no relationship between fCORT and start of migration ($p = 0.9$), date of arrival in the wintering areas ($p = 0.5$), or migration rate ($p = 0.6$).

Similarly, our top models (Table A-5) confirmed the patterns revealed through Wilcoxon rank sum tests (see results in main text). Models showed fCORT would be highest in birds wintering in Pacific Central America and Atlantic South America, and lower in birds using the other wintering regions. Models also showed fCORT levels would be lowest in birds that incubated all or most of the way to hatch. In addition to these patterns, we found a negative relationship between fCORT and rate of migration for birds in each wintering region, except Pacific Central America. In this region, birds with the highest fCORT levels also had traveled at the slowest rates during their southward migration. Finally, models showed, regardless of wintering region, birds arriving progressively later to the wintering areas would have increasingly lower levels of fCORT. Top models explained 28 – 52% of the variation in fCORT levels, with wintering region and incubation stage explaining the largest percent. Sex, breeding site, and migration start date did not appear in top models.

Table A-5. Parsimonious models (Δ $AIC_c \leq 2$ and all terms significant) explaining variation in winter-deposited fCORT in semipalmated sandpipers. Explanatory variables appearing in top models were southward migration rate (km / day), wintering area arrival date, incubation stage, and wintering region (WRegion). The intercept-only model, not included in the set of top models, is shown for comparison. Other explanatory variables that were included in candidate models were sex, breeding site, and migration start date.

fCORT ~	k	AICc	ΔAICc	w_i	deviance explained
WRegion + Incubation Stage	8	-55.701	0.00	0.331	47%
Incubation Stage + Rate + WRegion * Rate	9	-55.040	0.661	0.238	52%
Incubation Stage	4	-55.032	0.669	0.237	28%
Arrival Date + Rate + WRegion * Rate	7	-54.627	1.074	0.194	45%
Intercept	2	-51.967	7.25	.	.

A.2.4. 'Migration timing' and 'migration effort' hypotheses discussion

It appears winter-incurred stress loads in semipalmated sandpipers in this study did not relate directly to timing of southward migration as predicted. Migration start date did not appear in our top models; and although winter arrival date appeared in one top model, opposite our predictions, birds with higher winter-incurred fCORT levels were those that arrived earlier at the wintering areas. These results suggest late arrival to wintering areas may not limit semipalmated sandpipers' access to higher quality habitats (e.g. those with adequate food resources). While competition for food resources has been documented in the tropics [26], territory defense in small-bodied shorebirds may be driven by more ephemeral habitat changes (e.g. tidal cycles, prevailing wind speed and direction, see [13,14,26,27]) and not seasonally, negating the influence of arrival date. However, during years with exceptionally adverse conditions, competitive interactions may increase [28]. Because successful establishment and maintenance of territories over longer durations have been documented for some territorial individuals [14], late arrival may have a negative effect during harsher winters. A positive relationship between arrival date and fCORT levels could exist in such years but might not have been revealed by our dataset, if the fCORT levels we measured were incurred during a more typical winter. Alternatively, our results might reveal birds that increase their time in the wintering areas (through earlier arrivals) have increased exposure to stressors.

Our migration effort hypothesis also was not well supported. Although fCORT tended to decrease with increasing migration distance, this relationship was likely a product of wintering region. Migration distance did not appear in our top models explaining variation in fCORT. While birds wintering in Pacific Central America had the shortest migrations, they had consistently higher fCORT than birds in other regions (although not significantly higher than in birds wintering in Atlantic South America; see results in main text). Our results suggest the higher costs of migrating to more distant areas might be offset by the benefits of wintering in higher quality habitats or regions with more benign conditions. This has been documented in other species; e.g. ruddy turnstones (*Arenaria interpres*) wintering farther south in Australia have lower blood parasite loads than those wintering farther north [29]; Icelandic black-tailed godwits (*Limosa limosa islandica*) and red knots (*Calidris canutus islandica*), occupying more southerly wintering sites incur lower net costs, despite longer migrations, than those occupying more northerly wintering sites [15,30]; and sanderlings (*Calidris alba*) expended more energy and had lower body fat, despite greater time spent foraging, at northern sites than at southern sites [31]. However, the highly stressed birds wintering in Atlantic South America had among the longest migrations.

Also contrary to our predictions, we only found a positive relationship between rate of southward migration and subsequent fCORT levels and in birds that wintered in Pacific Central America. For birds wintering in all other regions, those with higher winter-incurred fCORT tended to have a slower rate of migration during the previous fall. We speculated, generally, birds that migrated more slowly might have been in poorer condition before or during southward migration, causing them to stop more frequently or for longer duration to rest. Our dataset did not allow us to explore this potential relationship between fCORT and number or mean duration of migratory stopovers. The relationship found for birds in Pacific Central America might indicate overwintering semipalmated sandpipers do retain the effects of energy expended for southward migration under some circumstances. Pacific Central America is at the northern edge of the semipalmated sandpiper wintering range [32], suggesting it might have marginal habitat for this species, or harsher conditions compared to more southerly regions. This region experiences weather and climate extremes, including hurricanes and floods, and has been undergoing a prolonged period of drought [33–35]. While birds might generally recover from the physiological costs of migration prior to growing tenth secondary feathers, they might not be able to offset migration costs in wintering areas with poor conditions (e.g. Pacific Central America). However, we would again expect to see this same relationship for birds wintering in Atlantic South America, where stress levels were not significantly different from those in Pacific Central America. An alternative explanation is the small number of birds using Pacific Central America might have biased our results, and there might not be a true difference in the relationship between migration rate and subsequent fCORT.

A.3 References

1. Elkins N. 2004 *Weather and Bird Behavior*. London: A & C Black. 276 pp.
2. Jamieson SE, Ydenberg RC, Lank DB. 2014 Does predation danger on southward migration curtail parental investment by female western sandpipers? *Anim Migr.* **2**(1), 34–43. (doi: 10.2478/ami-2014-0004)
3. Lank DB, Butler RW, Ireland J, Ydenberg RC. 2003 Effects of predation danger on migration strategies of sandpipers. *Oikos* **103**(2), 303–319. (doi: 10.1034/j.1600-0706.2003.12314.x)
4. Boates JS, Smith PC. 1989 Crawling behaviour of the amphipod *Corophium volutator* and foraging by semipalmated sandpipers, *Calidris pusilla*. *Can J Zool.* **67**, 457–462. (doi: 10.1139/z96-162)
5. Schneider DC, Harrington BA. 1981 Timing of shorebird migration in relation to prey depletion. *Auk* **98**(4), 801–811.

6. Hope DD, Lank DB, Smith BD, Ydenberg RC. 2011 Migration of two calidrid sandpiper species on the predator landscape: how stopover time and hence migration speed vary with geographical proximity to danger. *J Avian Biol.* **42**(6), 522–529. (doi: 10.1111/j.1600-048X.2011.05347.x)

7. McKinnon EA, Stanley CQ, Stutchbury BJM. 2015 Carry-over effects of nonbreeding habitat on start-to-finish spring migration performance of a songbird. *PLoS One* **10**(11): e0141580. (doi: 10.1371/journal.pone.0141580)

8. Stutchbury BJM, Gow EA, Done T, MacPherson M, Fox JW, Afanasyev V. 2011 Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proc R Soc B* **278**, 131–137. (doi: 10.1098/rspb.2010.1220)

9. Kokko H. 1999 Competition for early arrival birds in migratory birds. *J Anim Ecol.* **68**(5), 940–950. (doi: 10.1046/j.1365-2656.1999.00343.x)

10. Hicklin PW, Smith PC. 1984 Selection of foraging sites and invertebrate prey by migrant semipalmated sandpipers, *Calidris pusilla*, in Minas Basin, Bay of Fundy. *Can J Zool.* **62**, 2201–2210. (doi: 10.1139/z84-321)

11. Churchwell RT, Kendall S, Brown SC, Blanchard AL, Hollmen TE, Powell AN. 2017 The first hop: use of Beaufort Sea deltas by hatch-year semipalmated sandpipers. *Estuar Coast.* **41**(1), 280-292. (doi: 10.1007/s12237-017-0272-8)

12. Colwell MA. 2000 A review of territoriality in non-breeding shorebirds (*Charadrii*). *Wader Study Group Bull.* **93**, 58–66.

13. Colwell MA. 2010 *Shorebird Ecology, Conservation, and Management.* Berkeley, CA: University of California Press. 344 pp.

14. Recher HF, Recher JA. 1969 Some aspects of the ecology of migrant shorebirds. II. Aggression. *Wilson Bull.* **81**(2), 140–154. (doi: 10.2307/1932979)

15. Alves JA, Gunnarsson TG, Hayhow DB, Appleton GF, Potts PM, Sutherland WJ, Gill JA. 2013 Costs, benefits, and fitness consequences of different migratory strategies. *Ecology* **94**(1), 11–17. (doi: 10.1890/12-0737.1)

16. Newton I. 2008 *The Migration Ecology of Birds.* London: Academic Press.

17. Drent R, Piersma T. 1990 An exploration of the energetics of leap-frog migration in Arctic breeding waders. In *Bird Migration* (ed E. Gwinner), pp. 399–412. Berlin: Springer.

18. Myers JP, Maron JL, Sallaberry M. 1985 Going to extremes: why do sanderlings migrate to the Neotropics? *Ornithol Monogr.* **36**, 520–535. (doi: 10.2307/40168302)

19. Brown SC, Gates HR, Liebezeit JR, Smith PA, Hill BL, Lanctot RB. Arctic Shorebird Demographics Network Breeding Camp Protocol. 2014. *Unpubl.* report from U.S. Fish and Wildlife Services and Manomet Center for Conservation Sciences. Available from: https://www.manomet.org/sites/default/files/publications_and_tools/ASDN_Protocol_V5_20Apr2014.pdf 118 pp.

20. Pyle P. 2008 *Identification Guide to North American Birds, Part II.* Point Reyes Station, California: Slate Creek Press. 835 pp.

21. Sandercock BK. 1998 Assortative mating and sexual size dimorphism in western and semipalmated sandpipers. *Auk* **115**(3), 786–791. (doi: 10.2307/4089430)

22. Qiagen. 2006 *DNeasy ® Blood & Tissue Handbook For purification of total DNA from animal blood animal tissue. DNeasy ® Blood & Tissue Handbook.* Hilden, Germany: Qiagen Group. pp. 28–30. See http://diagnostics1.com/MANUAL/General_Qiagen.pdf

23. Griffiths R, Double MC, Orr K, Dawson RJG. 1998 A DNA test to sex most birds. *Mol Ecol.* 78, 1071–1075.

24. R Core Team. 2016 *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. Available from: http://www.R-project.org/

25. Calcagno V. 2013 *glmulti: model selection and multimodel inference made easy*. R Package Version 1.0.7. Available from: https://CRAN.R-project.org/package=glmulti

26. Tripp KJ, Collazo JA. 1997 Non-breeding territoriality of semipalmated sandpipers. *Wilson Bull.* **109**(4), 630–642.

27. Connors PG, Myers JP, Connors CW, Pitelka FA. 1981 Interhabitat movements by sanderlings in relation to foraging profitability and the tidal cycle. *Auk* **98**:49–64.

28. Duffy DC, Atkins N, Schneider DC. 1981 Do shorebirds compete on their wintering grounds? *Auk* **98**(2), 215–229.

29. Aharon-Rotman Y, Buchanan KL, Clark NJ, Klaassen M, Buttemer WA. 2016 Why fly the extra mile? Using stress biomarkers to assess wintering habitat quality in migratory shorebirds. *Oecologia* **182**, 385–395. (doi: 10.1007/s00442-016-3679-1)

30. Wiersma P, Piersma T. 1994 Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of red knots. *Condor* **96**(2), 257–279. (doi: 10.2307/1369313)

31. Castro G, Myers J, Ricklefs R. 1992 Ecology and energetics of sanderlings migrating to four latitudes. *Ecology* **73**(3), 833–844. (doi: 10.2307/1940161)

32. Hicklin P, Gratto-Trevor CL. 2010 Semipalmated Sandpiper (*Calidris pusilla*). In *The Birds of North America Online* (ed. PG Rodewald). Ithaca, NY: Cornell Lab of Ornithology. (doi: 10.2173/bna.6)

33. United Nations Development Programme. 2013 Nicaragua Project Document: Strengthening the resilience of multiple-use protected areas to deliver multiple global environmental benefits. *Unpubl. report*.

34. Benessaiah K. 2008 Mangroves, shrimp aquaculture and coastal livelihoods in the Estero Real, Gulf of Fonseca, Nicaragua. Senior thesis, McGill University. 154 pp.

35. Eisermann K. 2006 Evaluation of waterbird populations and their conservation in Guatemala. In *Important Bird Areas Americas, Priority Sites for Biodiversity Conservation* (eds. C Devenish, DF Diaz Fernández, RP Clay, I Davidson, IY Zabala), pp. 235-242. Quito, Ecuador: Birdlife International.

APPENDIX B

Supplementary Material for Chapter 2

B.1 Components of candidate models

Table B-1. Explanatory variables included in candidate models to explain start of spring migration in gls-equipped semipalmated sandpipers: wintering longitude ('wintering long'), breeding site longitude ('breeding long'), winter-incurred fCORT (in pg mm^{-1}), sex, and two-way interactive effects. The candidate model set was constrained to models with two or fewer explanatory variables.

Start of spring migration (*n* = 24)	**Included in Top Models?**	**Rationale**	**Predicted Response**
1. wintering long	Y	Start of spring migration could be driven by a bird's wintering location, resulting from factors such as distance from breeding areas, environmental conditions encountered over winter and/or just prior to migration, and social cues received from other birds overwintering in the same location.	+ / -
2. breeding long	N	Start of spring migration could depend on a bird's ultimate destination in the breeding range, as a product of distance or site-specific spring phenology. Birds breeding farther from the wintering areas might be pressured to begin migration earlier (here, the farthest east sites were also farthest north), or birds breeding at sites with later spring phenology might begin migration later (the farther west).	+ / -
3. fCORT	Y	A bird's overwintering physiological condition could determine start of spring migration, and e might expect those in poorer condition (i.e. with higher fCORT) would require a longer period of preparation before undertaking long distance migrations, and would therefore begin migration later.	+
4. sex	N	Given that males establish territories, they may be adaptively driven to begin spring migration earlier.	+ / -
5. fCORT * wintering long	Y	While the overwintering physiological condition of birds is expected to relate to environmental conditions, we would expect for birds wintering in the same approximate location, those in poorer condition (i.e. with higher fCORT) would require longer preparation time before migrating.	+
6. fCORT * breeding long	N	If start of spring migration is driven in part by breeding site, for birds breeding at the same sites, we would expect those in poorer condition (i.e. with higher fCORT) would require longer preparation time before undertaking spring migration.	+
7. fCORT * sex	N	For one or both sexes, physiological condition of an individual (i.e. fCORT level) could determine start date of spring migration. We expect birds in poorer condition (i.e. with higher fCORT) would have delayed migration, but the influence of fCORT might be different for the sexes.	+
8. wintering long * breeding long	Y	Start date of spring migration could depend on the interaction of departure point with destination. For example, start date could be driven by factors such as distance between wintering and breeding areas, or environmental factors encountered along the migration route between the two points.	+ / -
9. sex * wintering long	N	If the sexes segregate on the wintering areas (e.g. at smaller scales than previous studies could detect), in wintering areas with limited high-quality territories, one sex might typically obtain inferior territories. The sex using inferior territories might experience physiological effects (i.e. higher fCORT) that cause delayed start of migration, but only in areas lacking high-quality territories.	+ / -
10. sex * breeding long	N	Males may be adaptively driven to begin spring migration as early as possible, to establish good territories in the breeding areas. However females might delay on the wintering areas, so as not to arrive in the breeding areas until conditions are more likely to be amenable for nesting. The timing of departure might be driven by ultimate destination but be sex-dependent.	+ / -

Table B-2. Explanatory variables included in candidate models to explain migration rate in gls-equipped semipalmated sandpipers: wintering longitude (‘wintering long’), breeding site longitude (‘breeding long’), migration start date, breeding site arrival date (‘arrival date’), winter-incurred fCORT (in pg mm^{-1}), sex, and two-way interactive effects. The candidate model set was constrained to models with two or fewer explanatory variables.

Migration rate (*n* = 21)	**Included in Top Models?**	**Rationale**	**Predicted Response**
8. fCORT * breeding long	N	Timely arrivals could be breeding site-specific. For birds breeding at the same site, those in better condition (i.e. with lower fCORT) might be better able to speed up their migrations to arrive “on time”.	-
9. fCORT * migration start	N	How quickly a bird must migrate to have a timely arrival on the breeding areas may depend on when it starts migrating. For birds beginning migration on the same date, those in poorer physiological condition (i.e. with higher fCORT) might be expected to migrate more slowly.	-
10. fCORT * sex	N	Within a given sex, we might expect birds in poorer condition (e.g. with higher fCORT) to migrate more slowly, although the rate of influence might be different between the sexes.	+ / -
11. wintering long * breeding long	N	Migration rate could depend on the interaction of departure point with destination (e.g. due to distance, or environmental factors encountered along the migration route between the two points).	+ / -
12. wintering long * start date	Y	If migration rate is driven by departure point, for birds wintering at approximately the same location, we might expect those departing later would need to undertake faster migrations to arrive “on time”.	+
13. breeding long * start date	N	If migration rate is driven by destination, for birds breeding at approximately the same location, we might expect those departing later would need to undertake faster migrations to arrive “on time”.	+

Table B-2. Continued.

Migration rate (*n* = 21)	**Included in Top Models?**	**Rationale**	**Predicted Response**
8. fCORT * breeding long	N	Timely arrivals could be breeding site-specific. For birds breeding at the same site, those in better condition (i.e. with lower fCORT) might be better able to speed up their migrations to arrive “on time”.	-
9. fCORT * migration start	N	How quickly a bird must migrate to have a timely arrival on the breeding areas may depend on when it starts migrating. For birds beginning migration on the same date, those in poorer physiological condition (i.e. with higher fCORT) might be expected to migrate more slowly.	-
10. fCORT * sex	N	Within a given sex, we might expect birds in poorer condition (e.g. with higher fCORT) to migrate more slowly, although the rate of influence might be different between the sexes.	+ / -
11. wintering long * breeding long	N	Migration rate could depend on the interaction of departure point with destination (e.g. due to distance, or environmental factors encountered along the migration route between the two points).	+ / -
12. wintering long * start date	Y	If migration rate is driven by departure point, for birds wintering at approximately the same location, we might expect those departing later would need to undertake faster migrations to arrive “on time”.	+
13. breeding long * start date	N	If migration rate is driven by destination, for birds breeding at approximately the same location, we might expect those departing later would need to undertake faster migrations to arrive “on time”.	+

Table B-3. Explanatory variables included in candidate models to explain date of breeding site arrival in gls-equipped semipalmated sandpipers: breeding site longitude (‘breeding long’), wintering longitude (‘wintering long’), migration start date (‘migration start’), migration rate (km / day), winter-incurred fCORT (in pg mm^{-1}), sex, and two-way interactive effects. The candidate model set was constrained to models with two or fewer explanatory variables.

Breeding site arrival (*n* = 21)	**Included in Top Models?**	**Rationale**	**Predicted Response**
1. wintering long	N	Breeding site arrival date could be influenced by where a bird spent the winter, resulting from factors such as distance from breeding areas, environmental conditions encountered over winter and/or just prior to migration, and social cues received from other birds overwintering in the same location.	+ / -
2. breeding long	Y	Breeding site arrival date could be determined by a bird’s ultimate destination, resulting from factors such as distance from wintering areas, or environmental conditions encountered along the migration route. As birds travel north, spring phenology might provide information as to whether conditions in the Arctic are likely to be amendable to breeding, and birds might hold at some point along the way.	+ / -
3. migration start	N	How early a bird arrives at the breeding area may depend on how early it left the wintering area.	+
4. migration rate	N	Date of arrival at the breeding areas might be influenced by how rapidly a bird undertakes migration.	-
5. fCORT	N	A bird’s overwintering physiological condition could determine arrival date, with birds in poorer condition (i.e. with higher fCORT) arriving later at the breeding areas (e.g. because they left later, had slower flight speeds, or required more stopovers to rest and refuel).	+
6. sex	Y	Males establish breeding territories and may be adaptively driven to arrive earlier at breeding areas.	+ / -
7. fCORT * wintering long	N	While the overwintering physiological condition of individual birds is expected to relate to environmental conditions, for birds wintering in the same approximate location, we would expect those in poorer condition (i.e. with higher fCORT) might arrive later at the breeding areas.	+ / -
8. fCORT * breeding long	N	If spring migration is driven in part by breeding site, for birds breeding at the same sites, we would expect those in poorer condition (i.e. with higher fCORT) might have delayed arrival.	+ / -
9. fCORT * migration start	N	There may be an effect of physiological condition on how well timing of breeding site arrival corresponds with timing of departure from the wintering areas. For birds departing on the same day, those in poorer physiological condition (i.e. with higher fCORT) might be expected to arrive later.	+
10. fCORT * sex	N	For one or both sexes, physiological condition of an individual could determine date of arrival at the breeding areas, and the rate of influence may be different for the sexes.	+ / -
11. wintering long * breeding long	N	Breeding site arrival date could depend on the interaction of departure point with destination (e.g. due to distance, or environmental factors encountered along the migration route between the two points).	+ / -
12. sex * wintering long	N	If sex segregation occurs on the wintering areas, in areas with limited high-quality territories, one sex might typically obtain inferior territories and experience physiological effects (i.e. higher fCORT) that cause birds to arrive later at the breeding areas. In wintering areas with abundant high quality territories, an effect of sex on arrival date might not occur.	+ / -
13. sex * breeding long	Y	Males may be adaptively driven to arrive at the breeding sites as soon as environmental conditions enable foraging. Females might delay their arrival until conditions are more amenable for nesting. Thus site-specific conditions might drive the timing of arrival, but sex might also play a role.	+ / -

Table B-4. Explanatory variables included in candidate models to explain nest initiation date in gls-equipped semipalmated sandpipers: wintering longitude ('wintering long'), categorical breeding site ('breeding site'), migration start date ('migration start'), breeding site arrival date ('arrival date'), winter-incurred fCORT (in pg mm^{-1}), sex, and two-way interactive effects. The candidate model set was constrained to two or fewer explanatory variables and two or fewer terms.

Nest initiation date (*n* = 19)	**Included in Top Models?**	**Rationale**	**Predicted Response**
1. wintering long	N	The date at which a bird initiates its first nest could be determined by where it spent the winter, and subsequently how ready the bird is for the breeding season, or due to an effect of distance between wintering location and the breeding area.	+ / -
2. breeding site	N	The date at which a bird initiates its first nest could depend on where it breeds. We would expect site-specific conditions would result in differences in when conditions become amenable for breeding.	+ / -
3. migration start	N	How early a bird begins nesting may depend on how early it leaves the wintering area.	+
4. arrival date	Y	The date at which a bird initiates its first nest may be coupled with its date of breeding site arrival.	+
5. fCORT	Y	A bird's overwintering physiological condition could determine how quickly it is ready to undertake breeding.. Birds in poorer condition (i.e. with higher fCORT) might initiate first nests later.	-
6. sex	Y	The date at which a bird is ready to begin nesting may vary in some sex-specifc fashion.	+ / -
7. fCORT * winter long	N	The overwintering physiological condition of individual birds is expected to relate to environmental conditions; however, in birds wintering in the same approximate location, we would expect those in poorer condition (i.e. with higher fCORT) to initiate nests later.	-
8. fCORT * breeding site	N	While breeding site might determine how early a bird can initiate a nest, for birds breeding at the same site, those in better condition (i.e. with lower fCORT) might be better able to nest earlier.	-
9. fCORT * migration start	N	How early a bird initiates its first nest may depend on when it starts migrating, and a bird's overwintering physiological condition might influence migration start. For those that begin migration on the same date, those in poorer physiological condition might be expected to initiate nests later.	-
10. fCORT * arrival date	Y	The date at which a bird initiates its first nest may be coupled with its date of arrival on the breeding grounds. However birds in poorer physiological condition (i.e. with higher fCORT) may require a longer period between migration and breeding and may initiate first nests later.	-

Table B-4. Continued.

Nest initiation date (*n* = 19)	**Included in Top Models?**	**Rationale**	**Predicted Response**
11. fCORT * sex	N	Within a given sex, we might expect birds in poorer condition (e.g. with higher fCORT) would initiate nests later, although the rate of influence might be sex-specific.	+ / -
12. sex * arrival date	Y	Males arriving on the same day as females may begin nesting earlier, since they are not egg-laying. Or, females might choose a mate with an established territory, and begin nesting earlier than males.	+ / -
13. sex * wintering long	N	In some species, sexes segregate on the wintering areas. If this occurred, one sex might obtain inferior territories in wintering areas with limited high-quality territories. In birds that wintered in such areas, one sex might thus be delayed in readiness for breeding activities.	+/ -
14. wintering long * breeding site	N	Date of nest initiation could depend on the interaction of departure point with destination (e.g. due to distance, environmental factors encountered along the migration route, or how conditions encountered in the wintering areas interact with conditions encountered in the breeding areas).	+ / -
15. wintering long * start date	N	How soon a bird must depart a wintering area to be "on time" for breeding activities might depend on where it winters. For those birds wintering in approximately the same location, we might expect those that begin migration sooner would be able to initiate nests sooner.	+
16. breeding site * arrival date	N	For birds breeding in the same location, those arriving earlier should be able to initiate nests sooner.	+

Table B-5. Explanatory variables included in candidate models to explain nest initiation date in a larger dataset of semipalmated sandpipers, including those with and without gls: categorical breeding site, year, winter-incurred fCORT (in pg mm^{-1}), sex, presence of gls, and two-way interactive effects.

Nest initiation date (*n* = 254)	**Included in Top Models?**	**Rationale**	**Predicted Response**
1. breeding site	Y	The date at which a bird initiates a nest could be determined by its breeding location, due to the site-specific differences in environmental conditions that are amenable to breeding.	+ / -
2. year	Y	The date at which environmental conditions are amenable to breeding might vary annually, and thus date of nest initiation might also be expected to vary annually.	+ / -
3. fCORT	Y	The pre-breeding physiological condition of a bird might determine how early a bird begins its breeding activities. Here, we expect birds with higher fCORT would be in poorer condition and thus begin breeding, and initiate nests, later.	+
4. gls	N	Birds may experience an effect of wearing a gls that causes them to delay breeding activities compared to non-tracked birds.	+
5. fCORT * site	Y	Date at which conditions are amenable to breeding might be site-specific, and birds in better pre-breeding condition might be better able to begin breeding as soon as conditions allow. In this case, birds in better physiological condition at the same breeding site (i.e. those with lower fCORT) would be expected to initiate nests earlier.	+
6. fCORT * year	N	The importance of pre-breeding condition to the onset of breeding activities might vary annually. In years with harsh springs, pre-breeding condition might be more important. In these years, we might expect birds with higher fCORT would initiate nests later. The effect of fCORT might be negligible during years with benign environmental conditions.	+ / -
7. fCORT * sex	N	Within a given sex, we might expect birds in poorer condition (i.e. with higher fCORT) to nest later, although the influence of pre-breeding condition might be different between the sexes.	+
8. site * year	Y	The date at which a bird initiates a nest could be determined by spatial and temporal interactions (i.e. nest date might vary annually at any given breeding site).	+ / -

Table B-6. Explanatory variables included in candidate models to explain clutch size in female semipalmated sandpipers: categorical breeding site, year, nest initiation date, winter-incurred fCORT (in pg mm^{-1}), and two-way interactive effects.

Clutch size (*n* = 156)	**Included in Top Models?**	**Rationale**	**Predicted Response**
1. breeding site	Y	Site-specific environmental conditions might determine likelihood of a female laying a four- *versus* three-egg clutch.	+ / -
2. year	N	Environmental conditions might vary annually, and in harsher years clutches of reduced size might be more common.	+ / -
3. nest date	Y	Changes in within-season environmental conditions might increase the likelihood of laying reduced clutch sizes at later dates. Further, declining survival rates of chicks hatched too late might result in pressure for females to truncate their clutch sizes at later dates, to begin incubation earlier.	-
4. fCORT	Y	Females in poorer pre-breeding condition (i.e. those with higher fCORT) might have fewer endogenous resources for egg formation and thus increased likelihood of laying smaller clutches.	-
5. gls	Y	Females equipped with gls might experience increased stress and lay fewer eggs. Nests for gls-equipped females are known to be first nests, which might also influence relationships (but not because the bird is wearing a tracking device).	
6. fCORT * site	Y	The importance of pre-breeding condition to clutch size might vary with breeding site. At sites with harsher environmental conditions, pre-breeding condition might be more important to female ability to lay a full clutch, and birds with higher fCORT might therefore lay clutches of reduced size.	+ / -
7. fCORT * year	N	The importance of pre-breeding condition to clutch size might vary with year. During years with harsher environmental conditions, pre-breeding condition might be more important to female ability to lay a full clutch, and birds with higher fCORT might lay clutches of reduced size.	+ / -
8. fCORT * date	Y	Given equivalent dates of nest initiation, females in poorer condition (here, with higher fCORT) might be more likely to lay clutches of reduced size.	-
9. site * year	N	Prevalence of three-egg clutches at any given breeding site may depend on harshness of the year.	+ / -
10. date * site	N	Prevalence of three-egg clutches at later nest initiation dates may depend on relative harshness of within-season environmental conditions at a given breeding site.	+ / -
11. date * year	Y	Females might have an increased likelihood of laying reduced clutches at later nest initiation dates in years with harsh environmental conditions, but years with benign environmental conditions might not see a seasonal decline in clutch size.	+ / -

Table B-7. Explanatory variables included in candidate models to explain mean egg volume of individual clutches laid by female semipalmated sandpipers: categorical breeding site, year, nest initiation date ('nest date'), winter-incurred fCORT (in pg mm^{-1}), clutch size, and two-way interactive effects. The candidate model set was constrained to models with only additive effects or two-way interactions.

Mean egg volume (*n* = 108)	**Included in Top Models?**	**Rationale**	**Predicted Response**
1. breeding site	Y	Site-specific environmental conditions might influence egg volume, with females experiencing harsher conditions and/or limited food resources laying smaller eggs.	+ / -
2. year	N	Females might lay smaller eggs in harsher years and/or years with limited food resources.	+ / -
3. nest date	Y	Changes in within-season environmental conditions might result smaller eggs at later nest dates.	-
4. fCORT	Y	Females in poorer pre-breeding condition (i.e. with higher fCORT) might have fewer endogenous resources to invest in egg formation and thus an increased likelihood of laying smaller-volume eggs.	-
5. clutch size	N	Because females must limit their investment in egg formation, there might be a tradeoff between number and size of eggs. In this case, we might expect females that lay a four-egg clutch would have smaller eggs than females that lay smaller clutches.	-
6. gls	Y	Females equipped with gls might experience increased stress and lay lower-volume eggs. Nests for gls-equipped females are known to be first nests, which might also influence relationships (but not because the bird is wearing a tracking device).	+ / -
7. fCORT * site	N	The importance of pre-breeding condition to egg size might vary with breeding site. At sites with harsher environmental conditions, pre-breeding condition might be more important, and we might expect females with higher fCORT would lay smaller eggs at these sites.	+ / -
8. fCORT * year	N	The importance of pre-breeding condition to egg size might vary with year. During years with harsher environmental conditions, pre-breeding condition might be more important, and we might expect birds with higher fCORT would lay smaller eggs.	+ / -

Table B-7. Continued.

Mean egg volume (*n* = 108)	**Included in Top Models?**	**Rationale**	**Predicted Response**
9. fCORT * date	Y	Given equivalent dates of nest initiation, females in poorer condition (here, with higher fCORT) might be more likely to lay smaller eggs.	-
10. site * year	N	The likelihood of females laying smaller eggs might change with both spatial and temporal variation in environmental conditions. Egg size at any given breeding site may depend on harshness of the year.	+ / -
11. date * site	Y	Prevalence of smaller-volume eggs at later nest initiation dates may depend on relative harshness of environmental conditions at a given breeding site.	+ / -
12. date * year	Y	Females might have an increased likelihood of laying smaller eggs at later nest initiation dates only in years with harsh environmental conditions.	+ / -
13. date * clutch size	N	If conditions at later nest dates are limiting, they might result in a tradeoff between laying a full clutch and laying larger-volume eggs.	-
14. year * clutch size	N	If conditions are limiting in any given year, they might result in a tradeoff between laying a full clutch and laying larger-volume eggs.	+ / -
15. clutch size * gls	N	Females equipped with gls might experience effects that result in smaller eggs laid in larger clutches. We may also see a clutch size-egg volume tradeoff only in confirmed first nests.	+ / -

B.2. Supplemental Analyses and Discussions

B.2.1 'Breeding phenology': 2014 birds only

B.2.1.1 Data analysis

As discussed in the main text, we found opposite relationships between nest initiation dates and fCORT for gls-equipped birds and birds in in a larger dataset that included both gls- and non-gls birds. Birds wore gls at nest initiation during 2014 only, and the larger dataset included nest dates for 2012–2014. Thus, in our main results, we could not separate out the effect of gls versus year on nest initiation date. To determine whether the difference was related to a year effect, we fit generalized linear regressions for all birds ($n = 73$) breeding in 2014, following methods outlined in the main text. Our candidate models included the same explanatory variables as our models for the larger dataset (i.e. fCORT, sex, categorical breeding site, fCORT x site, and fCORT x sex), except year. Additionally, we included presence of a gls as an explanatory variable.

B.2.1.2 Results and Discussion

For all birds breeding in 2014, including those with and without gls, nest initiation occurred over a 42-day period (15 May – 26 June; mean = 9 June). Based on AICc values, there were two competing models (Δ AICc ≤ 2; Table B-8). Both models showed birds breeding at the farthest west site, Nome, had the earliest nest initiation dates; and at the farthest east site, Igloolik, birds nested the latest. Between these two sites, models suggested a difference in nest initiation date of ~ 3 weeks (as an effect of breeding site alone) or ~ 3 to 4 weeks (as an effect of the interaction of fCORT with breeding site). There was a consistent, negative effect of fCORT on nest initiation date at all sites (i.e. birds with higher winter-incurred fCORT nested earlier), excepting in birds breeding at Igloolik. For these birds, those with higher winter-incurred fCORT nested later. The rate at which nest date changed with increasing fCORT was site-specific: at some sites, models showed nest initiation date would only change by ~ 1 day over the full range of fCORT levels (0.30 pg mm^{-1}). At Nome, the model suggested nest date would change by ~ 4 days over the full range of fCORT levels (or be ~1 day earlier for every increase of 0.08 pg mm^{-1}).

These modeled relationships are based on birds breeding only in 2014, but are similar to findings reported in the main text. Thus, the opposite relationships modeled for nest initiation dates ~ fCORT for gls-equipped birds and the larger dataset, which included non-gls birds, does not appear to simply be a year effect. Alternative explanations for these opposite relationships are discussed in the main text.

Table B-8. Parsimonious models (Δ $AIC_c \leq 2$ and all terms significant) explaining timing of nest initiation in semipalmated sandpipers breeding at 7 sites, in 2014 only.

Nest initiation date (*n* = 73) ~	df	AIC_c	ΔAIC_c	w_i	deviance explained
1. breeding site	8	475.75	0	0.715	50%
2. fCORT + fCORT * breeding site	9	477.59	1.84	0.285	51%
3. intercept	2	512.62	36.87	.	.

APPENDIX C

Approval letter for project 454359 from the University of Alaska Fairbanks Institutional Animal Care and Use Committee (IACUC)

Animal handling, marking, and monitoring procedures were approved by animal care and use committees and permitting agencies at Environment and Climate Change Canada, Kansas State University, National Park Service, University of Alaska Fairbanks, U.S. Fish & Wildlife Service, and U.S. Geological Survey – Alaska Science Center. The approval letter to Dr. Abby Powell for project 454359 from the University of Alaska Institutional Animal Care and Use Committee (covering the Cape Krusenstern breeding site during M.L. Boldenow Mater's Research, 2013–2014) is included herein.

UNIVERSITY OF ALASKA FAIRBANKS

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Institutional Animal Care and Use Committee

909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

June 20, 2014

To:	Abby Powell Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[454359-9] Beringian Shorebirds

The IACUC reviewed and approved the Amendment/Modification to the Protocol referenced above by Designated Member Review.

Received:	June 19, 2014
Approval Date:	June 20, 2014
Initial Approval Date:	May 1, 2013
Expiration Date:	May 1, 2015

This action is included on the July 10, 2014 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

(The following information is also available in a printable format in the IRBNet Forms and Templates)

HOW DO I REPORT CONCERNS ABOUT ANIMALS IN A UAF RESEARCH FACILITY?

- All "live" animal concerns related to care and use should be reported to the IACUC
- Email: uaf-iacuc@alaska.edu Phone: 474-7800
- Report form: www.uaf.edu/iacuc/report-concerns/
- IACUC Committee Members: www.uaf.edu/iacuc/iacuc-info/
- Additional information: www.uaf.edu/ori/responsible-conduct/research-misconduct/ and www.uaf.edu/ori/responsible-conduct/conflict-of-interest/

WHAT SHOULD I DO IF AN ACCIDENT OR INCIDENT OCCURS IN AN UAF ANIMAL FACILITY?

- **For all immediate *human* emergencies call 911** or UAF Dispatch at 474-7721 for less immediate emergencies.
- If you have **suffered an animal bite or other injury**, complete an "Accident/Incident Investigation form" (personal injury) form available at www.uaf.edu/safety/incidentreport-2012.pdf.
- If an accident such as a **chemical spill** occurs, contact the Environmental Health, Safety, and Risk Management (EHS&RM) Supervisor at 474-5617 or the Hazmat Coordinator at 474-7889.

WHO DO I CONTACT IF I FIND A DEAD, INJURED, OR DISTRESSED ANIMAL IN A UAF RESEARCH FACILITY?

- During regular business hours, immediately contact facility staff and/or Veterinary Services Staff at 474-7020.
- After hours or on weekends, immediately contact facility staff and/or Veterinary Services Staff using the contact numbers posted on the "Emergency Contact Information" in the facility or call UAF Dispatch at 474-7721.
- Contact the IACUC at 474-7800 or uaf-iacuc@alaska.edu if an "Emergency Contact Information" sign is NOT posted in the facility.
- Contact the IACUC if you are not satisfied with the response from Vet Services.

HOW DO I REPORT ANY CONCERNS REGARDING WORK HAZARDS OR ANY GENERAL UNSAFE CONDITIONS?

- Complete an "Unsafe Condition Reporting Program" form, available at the EHS&RM website: www.uaf.edu/safety/unsafe-condition/

WHERE CAN I OBTAIN GENERAL OCCUPATIONAL SAFETY INFORMATION?

- www.uaf.edu/iacuc/occupational-health/

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

May 1, 2013

To:	Abby Powell Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[454359-2] Beringian Shorebirds

The IACUC reviewed and approved the Amendment/Modification to the Protocol documents referenced above by Designated Member Review.

Received:	April 25, 2013
Approval Date:	May 1, 2013
Initial Approval Date:	May 1, 2013
Expiration Date:	May 1, 2014

This action is included on the May 16, 2013 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
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- IACUC Committee Members: www.uaf.edu/iacuc/iacuc-info/
- Additional information: www.uaf.edu/ori/responsible-conduct/research-misconduct/ and www.uaf.edu/ori/responsible-conduct/conflict-of-interest/

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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 24, 2013

To: Abby Powell
Principal Investigator

From: University of Alaska Fairbanks IACUC

Re: [454359-1] Beringian Shorebirds

The IACUC has reviewed the Protocol referenced above by Full Committee Review and requires modifications and/or clarifications to the submitted materials. The IACUC has determined that your revised materials can be handled by designated member review rather than being deferred to the next committee meeting. No animal activities may be initiated until the IACUC has reviewed and approved your revised documents.

Received:	April 11, 2013
Reviewed:	April 18, 2013

Required Modifications/Clarifications:

The committee discussed this submission and is requesting the following revisions:

1. Describe the process for adding personnel to the banding permit and explain when banding permit is expected to be modified

2. In the literature search, please provide the keywords and database(s) searched.

3. In the animal use table in Tagging and Marking, please describe the geolocators; size, weight, placement, affect on animal, etc.

4. Describe net dragging method; include rope gauge, potential for nest damage and how damage wil be assessed and procedures modified if damage occurs.

5. Describe the "bander hold" referenced in protocol.

This action is recorded in the minutes from the IACUC meeting on April 18, 2013.

If you have any questions about how to submit the required information through IRBNet please contact the Office of Research Integrity for assistance (email fyori@uaf.edu or call x7800/x7832).