UNIVERSITY OF CALIFORNIA, SAN DIEGO

The foraging ecology, diet, and mass estimation of an apex predator, the leopard seal (*Hydrurga leptonyx*), at Livingston Island, Antarctic Peninsula.

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Oceanography

by

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2016

The Dissertation of Douglas John Krause is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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DEDICATION

To the two most brilliant women I have ever met: My mother, Joan, who stirred a lifelong passion by encouraging me to investigate the curious patterns we found in nature. And, my wife Rachel whose love, patience, and encouragement made this work possible. That Oxford comma was for you.

EPIGRAPH

“We defend the places that we love, we love the places that we understand, and we have to experience these places, see them, feel them, touch them, smell them and then think about them very holistically to understand them.

This has to be done in nature. It is the only way to develop the sense of place so important to our sense of self and to our sense of stewardship of our environment.”

Paul K. Dayton

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ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to my advisors, Paul Dayton and Lisa Ballance, for their belief, encouragement, and mentoring. Lisa always cut time into an impressively full calendar to meet, review, and to challenge me. Our independent study and subsequent discussions on predator-prey dynamics set the stage for what we've accomplished here, and more. She is a natural teacher, a community builder (viva la SWAG), and a dedicated mentor. Paul set an example for me as a consummate naturalist in the classroom, in lab meetings, and especially in the field. He is incredibly knowledgeable, but always ready to learn. He always knows where to find interesting things, but is prepared for the long, careful observation it sometimes takes to see them. He showed me that passion, good ecology, and effective conservation biology are inextricably linked. And, none of them should be kept indoors for very long. Paul, I am so glad you made it out of that outhouse before my snowball hit.

I'd also like to thank my committee: Ryan Kastner, Paul Ponganis, Carolyn Kurle, Mike Goebel, and George Watters. Ryan provided a much needed new perspective on our UAS approach on several levels, and he brought me into his student group (E4E) which has led to some great conversations and potential collaborations. I am grateful to Paul P. for his physiological-ecology perspective and shockingly rapid (and thoughtful) feedback. Carolyn has been open with her lab, with her students, and with consistent and crucial guidance as I moved into the world of stable isotope biochemistry. Her excitement and commitment are infectious. I began learning about field and wildlife biology from Mike years ago, and it continues today. His technical skill and facility for informative, minimally-invasive pinniped behavioral studies have been truly inspiring. His training and his openness to my interest in leopard seals paved the way for this work. Finally, a big thank you to George for supporting this look up the food web, and for a long string of valuable advise inside and outside of this dissertation.

Thank you to the faculty of Biological Oceanography (BO) as well. Particularly, Lisa Levin, Mark Ohman, Peter Franks, Jim Leichter (and, of course Paul Dayton and Lisa Ballance). I came to SIO in search of a comprehensive understanding of the marine environment that surrounds and controls much of what we see at the marine mammal population level. Y'all did not disappoint.

My coauthors on these papers, Gregory Marshall, Kyler Abernathy, Mike Goebel, Carolyn Kurle, Jefferson Hinke, Wayne Perryman and Don LeRoi. You have been incredible resources for technical background, data analysis, experimental design, discussion, and revisions. I am thankful for your essential contributions and look forward to continuing to work with you in the future.

Thank you to the SIO graduate department for their excellent administrative, and sometimes moral, support as I have navigated the Ph.D. process. Especially, Gilbert Bretado, Joshua Reeves, Adam Peterson, Denise Darling, and the Maureens McGreevy and Mccormack.

It is not without sadness that I express my deep gratitude to the former staff of the Scripps Institution of Oceanography Library. It was the finest marine science library in the world for good reason. Its closure was an ill-conceived loss of crucial resources, community, and scholarship. The quite study space, the always-helpful librarians, the conference rooms (where do students meet to study and collaborate now anyway?), and the books, oh the books! A particular thanks to Peter Bruggeman who helped me dig back into history with volumes on early Antarctic exploration, and trusted me to take them back to my office. And, to Amy Butros who has helped me track down so many things, and/or fix so many problems I can't begin to list them. Thank you, as well, to Debra Losey and Robin Schnug at the SWFSC library for support, and for tolerating our clickety-clackity writing groups.

There are so many people who supported both the data collection for this dissertation, and certainly my spirits over the years in the Antarctic. It takes a special kind of person to want to be wet and cold-to-the-bone for hours and days and weeks and months for a few moments of working with wild animals in the hope of making a difference. Thank you to Birgitte MacDonald, Scott Freeman, Ryan Burner, Ray Buchheit, Nicola Pussini, Kevin Pietrzak, McKenzie Mudge, Jay Wright, Michelle Goh, Nicole Cook, Trevor Joyce, and Jefferson Hinke. The Antarctic is not an easy place to get to; therefore, I am grateful as well for the dedicated logistical support that we received from Instituto Antarctico Chileno (INACH), the officers and crew of the *R/V* Yuzhmorgeologiya, the *R/V* Moana Wave, the National Geographic/Lindblad *M/V* Explorer, and the *R/V* L.M. Gould.

Moreover, thank you to my friends and colleagues within the Antarctic Ecosystem Research Division (AERD) at NOAA Fisheries. This group of intelligent, hardworking people regularly does more with less than any I have seen. George Watters, Jeremy Rusin, Stephanie Sexton, Christian Reiss, Christopher Jones, Wayne Trivelpiece, Doug Kinzey, Mike Goebel, Jefferson Hinke, Tony Cossio, Jen Walsh, Jessica Senzer, and particularly, Rennie Holt who did so much to guide my early career (and BBQ skills).

Thank you for the support, all of the things I have learned from you over the years and the levity along the way. New Orleans will never be the same.

To the Dayton lab including, but not limited to, Ed Parnell, Kristin Riser, Brenna Bulach, Shannon Jarrell, Ryan Darrow, Marco Hatch, Talina Konotchick, Eric Keen, Trevor Joyce, and others over the years: thank you for welcoming me in, sharing wine, absurd stories and more than a few laughs.

I have also been fortunate to meet, learn with and from, and relax with an amazing group of people throughout graduate school. In no particular order they include: Cotton Rockwood, Summer Martin, Alyson Fleming, Liz vu, Anne Simonis, Amy Van Cise, A.J. Schlenger, Cali Turner, Eiren Jacobson, Carolina Bonin, Kerri Seger, Levi Lewis, (Tomato crew!) Emily Kelly, Noelle Bowlin, Jill Harris, and Matt Leslie. And, especially, my cohort who somehow made the first, stressful periods of graduate school interesting and fun: Trevor Joyce, Charles Perretti, Noah Ben-Aderet, Sara Walkup/Shen, Amanda Netburn, Stephanie Snyder, Neal Arakawa, Raffaela Abbriano, Lani Gleeson. And, one fellow New Englander who was always ready with a smile, or a pie, or some cheese, Rachel Morrison. We all miss you very much.

Thank you to my original family, the Krauses – Pops (Richard), Will, Dave, and Roy, your lovely wives and my many nieces and nephews; And, to my new family, the Kyles (and Malones) – Will, Carol, Lauren, Jarid, Caroline, and John. You have all been an enormous source of love, encouragement, and levity during my life, and especially during this dissertation process. I look forward to seeing you all, and talking to you all much more often in the future.

Finally, I am okay on my worst days and better on my best days because of one person, my wife Rachel. Thank you for your love, support, understanding and uplifting presence through these long years of writing, data analysis, lost nights and weekends, and months-long absences. “What? Take care of the house, our yard, our finances, our pets, my 220 English high school students, my 120 Speech and Debate team members, without weekends, for 5 months?....No problem. And, yes, I’ll email you that dessert recipe…” Your patience and skill in these endeavors have not been lost on me. This seemingly unending dissertation process has covered six out of the seven years of our marriage, and I am so excited to start our next (non-dissertation) chapter together.

MATERIAL PUBLISHED/PREPARED FOR PUBLICATION IN THE DISSERTATION

Chapter 1, in full, is a reprint of the material as it appears in Animal Biotelemetry 2015. Krause, Douglas J.; Goebel, Michael E.; Marshall, Gregory J.; Abernathy, Kyler. The dissertation author was the primary investigator and author of this material.

Chapter 2, in full, is a reprint of the material as it appears in Marine Mammal Science 2016. Krause, Douglas J.; Goebel, Michael E.; Marshall, Gregory J.; Abernathy, Kyler. The dissertation author was the primary investigator and author of this material.

Chapter 4, in part, is currently being prepared for submission for publication of the material. Krause, Douglas J.; Hinke, Jefferson T.; Perryman, Wayne L.; Goebel, Michael E.; LeRoi, Donald J. The dissertation author was the primary investigator and author of this material.

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Krause, Douglas J., Michael E. Goebel, Gregroy J. Marshall, and Kyler Abernathy "Novel Foraging Strategies Observed in a Growing Leopard Seal (*Hydrurga leptonyx*) Population at Livingston Island, Antarctic Peninsula" Animal Biotelemetry, vol. 3, 2015

Krause, Douglas J., Michael E. Goebel, Gregroy J. Marshall, and Kyler Abernathy "Summer Diving and Haul-out Behavior of Leopard Seals (*Hydrurga leptonyx*) Near Mesopredator Breeding Colonies at Livingston Island, Antarctic Peninsula" Marine Mammal Science, Early view: DOI: 10.1111/mms.12309, 2016

Goebel, M., W. Perryman, J. Hinke, D.J. Krause, N. Hann, S. Gardner, and D. LeRoi "A small unmanned aerial system for estimating abundance and size of Antarctic predators" Polar Biology, vol. 38, 2015

Goebel, M.E., Pussini, N., Buchheit, R., Pietrzak, K., Krause, D.J., and Walsh, J. "Pinniped Research at Cape Shirreff, Livingston Island, Antarctica, 2010/2011" In: AMLR 2010/2011 Field Season Report: Objectives, Accomplishments and Tentative Conclusions, Ed. Walsh, J. NOAA-TM-NMFS-SWFSC-524, 2014

Loeb, V., Dietrich, K., Driscoll, R., Fry, J., Krause, D.J., Sweeney, J., Sanchez, N.P., Martinez, M.A., Ligon, A., Van Cise, A. "Distribution, Abundance, and Demography of Krill" In: AMLR 2008/2009 Field Season Report: Objectives, Accomplishments and Tentative Conclusions, Ed. Amy Van Cise, NOAA-TM-NMFS-SWFSC-445, 2009

FIELDS OF STUDY

Major Field: Biological Oceanography (Marine Ecology)

Studies in Field Ecology
Studies in Animal Behavior
Professor Paul Dayton

Studies in Predator Prey Dynamics
Studies in Marine Mammal Biology
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Studies in Biologging and Biotelemetry
Studies in Animal Movement/Spatial Analysis
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ABSTRACT OF THE DISSERTATION

The foraging ecology, diet, and mass estimation of an apex predator, the leopard seal (*Hydrurga leptonyx*), at Livingston Island, Antarctic Peninsula

by

Douglas John Krause

Doctor of Philosophy in Oceanography

University of California, San Diego, 2016

Professor Lisa Ballance, Co-Chair
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Describing the foraging dynamics of apex predators is crucial to understanding ecosystem function and to effective conservation and management. Leopard seals are conspicuous apex predators in Antarctic coastal ecosystems; however, their foraging ecology is poorly understood. Likely due to a geographical redistribution driven by pack-ice habitat reduction in the western Antarctic Peninsula, leopard seals have been hauling out at Cape Shirreff with increasing frequency in recent years. Utilizing that rare access we implemented an integrated sampling design including morphometrics, biological samples, and bio-logger deployments in January and February between 2008 and 2014. Subsequently, we quantified foraging behavior using: k-means cluster (diving), time-local convex hulls (movement), Bayesian stable isotope mixing models (diet), and linear regression (mass estimation) analyses. While they are typically described as generalist apex predators, video, dive, and movement data suggest they employ specialized foraging patterns. They affect coastal ecosystems through pathways beyond direct predation, including intraspecific kleptoparasitism, predator-induced stress effects, facultative scavenging and food caching. Leopard seal diving behavior is concentrated at night, is both shallow and coastal, and is composed of four distinct dive types. Haul-out probabilities were highest near midday and were positively correlated with available daylight. Video, scat and stable isotope analyses indicate that their summer diet contains four prey groups: Antarctic fur seals, pygoscelid penguins, krill, and demersal notothen fishes. Finally, measurements of body size and mass are fundamental to pinniped population management and research. The recent proliferation of unmanned aerial systems (UAS) in wildlife monitoring has provided a promising new platform for the photogrammetry of free-ranging pinnipeds. Photogrammetric measurements from a single, vertical image obtained using UAS were as accurate as ground measures, and provide a noninvasive approach for estimating the mass and body condition of pinnipeds. This dissertation provides substantial insight into the hunting tactics, foraging behavior, and diet of large adult female leopard seals and provides a viable option for future monitoring.

INTRODUCTION

The sudden introduction of a predator to a new environment can fundamentally alter prey population dynamics and ecosystem function (Spencer and Thompson 2005, Pitt and Witmer 2007, Albins and Hixon 2008, Dorcas et al. 2012). Similarly, induced shifts to the foraging behavior of marine apex predators can alter coastal ecosystems over large geographical areas through direct and cascading effects (Estes et al. 1998, Springer et al. 2003, Williams et al. 2004). Therefore, describing the foraging dynamics of marine apex predators is crucial to understanding ecosystem function (Estes et al. 2011) and to the effective management of marine resources (Boyd et al. 2006, Springer et al. 2008), particularly in rapidly changing systems (Massom and Stammerjohn 2010).

The marine ecosystem in the Antarctic Peninsula region is highly productive (Dayton 1990, Ducklow et al. 2007), and as such, it has a long history of large scale resource extraction by humans. From its discovery in the early nineteenth century the APR experienced waves of harvesting which sequentially depleted stocks of seals (Weddell 1970), whales (Ballance et al. 2006), fish (Kock 1992), and most recently, Antarctic krill (*Euphausia superba*) (Nicol et al. 2012). Krill are probably one of the most important zooplankton species in the Southern Ocean. Along with the tunicate *Salpa thompsoni*, they are the primary phytoplankton grazer (Marr 1962) and are the dominant link to higher trophic levels (Loeb et al. 1997). The abatement of harvesting has led to recoveries in stocks of large whales, which has likely increased resource competition between populations of krill predators (Laws 1977, Trivelpiece et al. 2011).

Therefore, competition for krill as a resource has been elevated in a region facing climate change, another form of anthropogenic stress.

Over the last 60 years the Antarctic Peninsula region (APR) has been warming at one of the fastest rates on earth (Folland et al. 2002, Vaughan et al. 2003, Clarke et al. 2007). Annual surface air temperatures have risen between 3^{o} and 6^{o} C since 1951 (King 1994, Turner et al. 2005). Most glaciers in the region are in retreat (Cook et al. 2005), and average sea surface temperatures (<100 m) have increased by 1^{o}C since 1975 (Gille 2002, Meredith and King 2005). One of the consequences of this climate shift is the substantial loss of annual sea-ice throughout the region both temporally (Stammerjohn et al. 2008) and spatially (Ducklow et al. 2013). Among the many physical and biological impacts of sea-ice reduction (Massom and Stammerjohn 2010) is a foreboding combination of decreases in krill stocks (Atkinson et al. 2004) and increases in krill fishing (Nicol et al. 2012).

Additionally, since 1979 there has been a 21-28% decrease in habitat for millions of Antarctic ice seals (Forcada et al. 2012). Such dramatic habitat changes have likely cascaded through ice seal populations in the APR, however, population trends are not available due to infrequent regional censuses and methodological differences between historical surveys (Forcada and Trathan 2008, Southwell et al. 2012). Nevertheless, climate related changes in leopard seal (*Hydrurga leptonyx*) distribution have been observed. Leopard seals depend on sea-ice as a platform for resting (Rogers and Bryden 1997, Rogers et al. 2013) and breeding (Southwell et al. 2003). Sea-ice retreat to the south and toward the coastline in the APR was correlated with reduced leopard seal foraging range, and increased proximity to the coast (Meade et al. 2015). In concert such trends necessarily concentrate these normally solitary (Wilson 1905, Southwell et al. 2008) apex predators into higher densities and bring them closer to coastal mesopredator (e.g., seal, penguin) colonies and shallow water ecosystems.

Despite the potentially substantial impacts that leopard seals may be having on coastal ecosystems in the APR, they have been difficult to quantify because so little is known about their foraging ecology. They are the largest Antarctic ice seal (Wilson 1902) with the largest gape of any phocid (Ray 1966). They are paradoxically reported as both as krill-dependent (Siniff and Stone 1985), and apex predators (Boveng et al. 1998). However, due to a host of environmental and logistical challenges focal studies of leopard seals have been difficult. Their foraging tactics, preferred prey, consumption rates, habitat use and other basic aspects of foraging ecology are poorly known. Therefore, they are widely referred to as generalist predators.

Trophic dynamics theory predicts that predators will be less diet specialized than their prey (Elton 1927, Lindeman 1942). By extension, apex predators should be generalists to hedge against the risk of periodically unavailable prey. At the population level that theory may hold, but it does not take into account the presence or importance of individual specialization (Van Valen 1965, Roughgarden 1972). In fact, individual foraging specialization is taxonomically widespread, and can have substantial impacts on the accuracy of ecological modeling (Goss-Custard and Durell 1983, Bolnick et al. 2003). In many species individuals with an effective search image for a single prey type develop more efficient foraging strategies (e.g., Werner et al. 1981, Persson 1985). The prevalence of individual specialization tends to be understudied in natural systems

(Bolnick et al. 2003); however, it has been seen in marine apex predators (Pitman and Durban 2012, Pitman et al. 2015).

Foraging specialization may also be driven by intraspecific competition (Linnell and Strand 2000), which has been observed in marine carnivores (Estes et al. 2003, Staniland et al. 2004, Weise et al. 2010). In general, competition for limited resources results from an overlap in target prey, space use, and time (Trivelpiece et al. 1987, Townsend et al. 2008). Populations tend to alleviate competitive pressure by expanding their niche width through individual specialization for alternative prey, expanded habitat use, and temporal access to resources (Palomares and Caro 1999, Svanbäck and Bolnick 2005, 2007). The learning capacity of any animal is limited, so the efficiency gains of specializing necessitate decreased success for alternate prey (Hoelzel et al. 1989, Kato et al. 2000). Therefore, if competition within a specialization increases, for example due to reduced ice habitat, the conflict will be particularly intense due to restricted alternatives (Goss-Custard et al. 1984). And, indeed, intra-guild carnivore competition is characterized by aggressive behavior (Ballard et al. 2003). For leopard seals, though, agonistic interactions, specialization, and other social behaviors have been difficult to describe and confirm (Hiruki et al. 1999).

Study Site

In the midst of this complex and rapidly changing marine ecosystem, the U.S. Antarctic Marine Living Resources (US AMLR) Program has been conducting a suite of long term ecological monitoring projects for over 30 years. Under NOAA Fisheries they are gathering data to inform fisheries management through the Antarctic Treaty System.

US AMLR operates both at sea, and land-based surveys annually, including a field camp at Cape Shirreff, Livingston Island, Antarctica (Figure 1-1).

This low-lying peninsula is seasonally ice free allowing access to sandy and rocky beaches ideal for pinniped and seabird breeding. Hemmed in by glaciers, the Cape is approximately 3 km long and 1.5 km wide. There are seasonal breeding populations of Gentoo (*Pygoscelis papua*) and chinstrap penguins (*Pygoscelis antarcticus*), brown skuas (*Stercorarius antarcticus),* Antarctic terns (*Sterna vittata*), kelp gulls (*Larus dominicanus)*, Wilson’s storm petrels (*Oceanites oceanicus),* Antarctic fur seals, Weddell seals (*Leptonychotes weddellii*) and southern elephant seals (*Mirounga leonina*). Non-breeding seasonal residents include southern giant petrels (*Macronectes giganteus*), crabeater seals (*Lobodon carcinophaga*), and leopard seals.

The local offshore geography features a submarine canyon, and the bathymetry slopes down to a typically narrow, deep continental shelf break (Dayton et al. 1994) approximately 50 km to the north. The shelf break is historically associated with the southern boundary of the Antarctic Circumpolar Current (Orsi et al. 1995), which is a key oceanographic boundary for krill (Atkinson et al. 2009). Both the canyon and the shelf break are periodically mesopredator foraging hot spots (Santora and Veit 2013). Within 50 km of the Cape wind mixing and deep water canyon intrusions keep the water column well mixed (Needham et al. 2010).

This highly productive marine environment in close proximity to the ice-free Cape Shirreff supports abundant populations of krill-dependent predators as well as a krill fishery. The ALMR field camp at Cape Shirreff serves as a base for a multi-species program focused on using brush-tailed penguins and Antarctic fur seals as indicator species. These studies are designed to provide indices used to inform management of the regional krill fishery (CCAMLR Ecosystem Monitoring Program (CEMP); (Agnew 1997)).

Over the last 20 years, perhaps driven by the regional reduction of pack-ice habitat, adult female leopard seals have been hauling out with increasing frequency near mesopredator breeding colonies near the Cape Shirreff field camp. During this period, the gentoo penguin population remains level despite large regional increases, and the steady 60-year recovery of the Antarctic fur seal has shifted to a steep decline (US AMLR unpublished data).

Objectives

Rapid climate change in the APR and its follow-on effects are placing increasing levels of stress on krill and krill-dependent predators. Leopard seals are likely impacting both groups through direct predation and resource competition, yet we lack resolved information about their foraging ecology. Our objectives are to leverage our unique access to leopard seals at Cape Shirreff and a suite of innovative bio-logging instruments and novel analyses to study:

1) Hunting tactics, preferred prey items, foraging success rates
2) Diving and foraging behavior, temporal activity, haul-out patterns
3) Diet components and proportions and trophic position within the known food web

At each stage we will examine the Cape Shirreff population as a whole, but also test for differences between individuals at appropriate time and spatial scales. And, finally, we will explore new:

4) Methods for tracking and monitoring the nutritive condition of leopard seals that could be scaled up to gather information at a regional level.

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CHAPTER 1:

Novel foraging strategies observed in a growing leopard seal (*Hydrurga leptonyx*) population at Livingston Island, Antarctic Peninsula

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Abstract

Leopard seals are apex predators that can alter the community structure of Antarctic coastal ecosystems. Previous behavioral studies were limited to land-based, daytime observations of foraging leopard seals. Consequently, foraging tactics, social behaviors, and indirect ecosystem impacts are poorly understood. Here we present the first analysis of animal-borne HD video footage for foraging leopard seals. Each CRITTERCAM was deployed with Fastloc GPS and time-depth-recorder instruments providing fine-scale habitat context for observed foraging behavior. We analyzed seven deployments obtained in January and February of 2013 and 2014 from adult female leopard seals near mesopredator breeding colonies on Livingston Island, Antarctica. The average deployment length was 4.80 ± 2.45 (range: 0.86 - 9.12) days, which covered a total of 16 foraging trips. Habitat use, along with 39 prey capture attempts, and 11 leopard seal social encounters were scored from 50.3 hours of video data. We obtained 3,833 post-filter GPS positions, accurate to within 70 m, and the mean dive depth was 14.84 ± 8.98 m. Leopard seal foraging focused on four prey items: Antarctic fur seals, Antarctic fur seal pups, pygoscelid penguins, and demersal notothen fishes. Ambush tactics used only by a subset of leopard seals drove high capture success rates of fur seal pups. We identified novel prey-specific foraging tactics including stalking and flushing notothen fishes. Leopard seals have been described as generalist apex predators; however, video and movement data suggest that leopard seals employ specialized prey-specific hunting tactics. Although preliminary, our findings indicate that leopard seals can affect coastal ecosystems through pathways beyond direct predation, including intraspecific kleptoparasitism and facultative scavenging/food caching. Our results

suggest that position-integrated video data will be vital in quantifying the ecological impact of this abundant and versatile apex predator.

Introduction

The foraging behavior of apex predators can alter marine coastal ecosystems through direct and indirect pathways of predation (Estes et al. 1998, Williams et al. 2004, Estes et al. 2011). Leopard seals (*Hydrurga leptonyx*) are large, abundant, top-predators with a circum-Antarctic distribution (Laws 1984). They can directly reduce Antarctic fur seal (*Arctocephalus gazella*) population abundance through predation of pups (Boveng et al. 1998, Schwarz et al. 2013). Intense predation has also been reported at some penguin breeding colonies (Kooyman et al. 1990, Ainley et al. 2005). Though not examined to date, leopard seals likely affect coastal ecosystems through pathways other than direct predation as well (Ballard et al. 2003). For example, leopard seals may compete with sympatric mesopredators (e.g., penguins or fur seals) for common prey resources, or perceived predation risk may reduce mesopredator fitness (Creel et al. 2007, Creel and Christianson 2008, Wirsing et al. 2008). Despite the potential for leopard seals to control prey populations and affect trophic pathways through top-down forcing, their prey and non-prey interactions are not well studied.

Leopard seal research has largely focused on identifying top-down ecosystem effects through direct predation. Reports of leopard seal diet in the western Antarctic Peninsula (WAP) indicate that Antarctic krill (*Euphausia superba*), crabeater (*Lobodon carcinophagus*) and fur seal pups, penguins and myctophid fish are key prey items (Siniff and Stone 1985, Green and Williams 1986, Walker et al. 1998, Casaux et al. 2009);

however, observations were often contradictory. Previous studies of leopard seal predation on fur seals (Walker et al. 1998, Hiruki et al. 1999, Vera et al. 2005) and penguins (Kooyman 1965, Penney and Lowry 1967, Müller-Schwarze and Müller-Schwarze 1975, Rogers and Bryden 1995, Ainley et al. 2005) were informative, but limited to opportunistic, land-based, daytime observations. Accordingly, the preferred prey items, hunting tactics and success rates of leopard seals are poorly known.

Describing the social behaviors of predatory carnivores can also be vital to understanding their ecosystem impacts (Bertram 1979, Macdonald 1983, Wilmers et al. 2003). For example, while some carnivores hunt alone, others employ an array of cooperative strategies which can affect prey choice and capture success rates (Kruuk 1975, Gittleman 1989, Creel and Creel 1995, Mech and Peterson 2003). Interference competition can also affect ecosystems by forcing predators to expand their foraging habitat, alter their target prey, or increase their hunting effort (Murphy et al. 1998, Palomares and Caro 1999). Intraspecific competition, in particular, is often intense due to the high likelihood of niche overlap (Schoener 1983, Townsend et al. 2008), and is characterized by aggressive behavior (Ballard et al. 2003). For leopard seals, though, agonistic interactions, evidence of cooperative hunting, and other social behaviors have been difficult to describe and confirm (Hiruki et al. 1999).

Despite their ecological relevance, focal studies on leopard seals have been hindered because the seals are difficult to access and observe. Leopard seals are solitary (Wilson 1905, Southwell et al. 2008) and are typically associated with remote marginal pack ice habitat (Gilbert and Erickson 1977, Rogers and Bryden 1997, Bester et al. 2002, Rogers et al. 2005). The recent loss of sea ice in the WAP, though, due to rapid regional

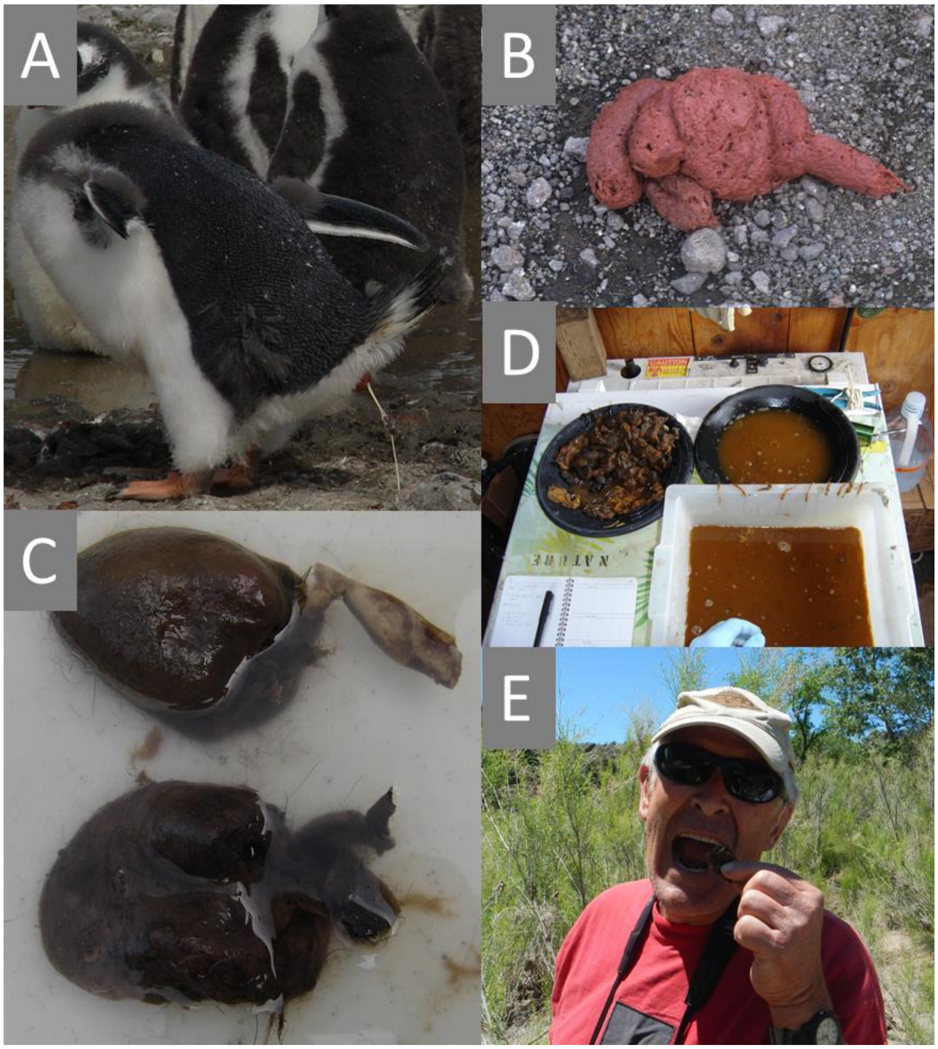

Figure 1-0: Scatology is a powerful, though potentially biased, technique for investigating the diet of marine mammals. While many animals, including birds (A) heavily process their diet before excretion, the feces or "poo" (B) of marine mammals, including pinnipeds, typically retains hard prey parts that allow for the identification of diet items. Occasionally, dense muscle tissue will survive the digestion process as well. Like these two fur seal pup hearts (C) that were found in a leopard seal scat at Cape Shirreff. There are many variants on scat sorting, but they typically involve soaking (D) and sieving scat remains. An important procedural note: make sure the scat is dry before you taste it as demonstrated by Distinguished Professor Dayton (E).

warming (Vaughan et al. 2003, Meredith and King 2005, Vaughan 2006) has forced a redistribution of resident Antarctic ice seals (Forcada et al. 2012). It is likely that these regional movements have driven the growing number of leopard seals to predictably haul out on land at Cape Shirreff, Livingston Island ([a]US-AMLR *unpublished observations*). And, while opportunistic surveillance is temporally restricted, and land-based observations are not well suited to marine predators that are often submerged (Marshall 1990), animal-borne video data has allowed the description of prey selection (Parrish et al. 2005), habitat use (Parrish et al. 2000, Parrish et al. 2002), foraging tactics (Davis et al. 1999, Bowen et al. 2002, Heaslip et al. 2014) and community interactions (Parrish et al. 2008) for predatory phocids. Predictable haul outs and animal-borne video have allowed unprecedented access to free-ranging, adult leopard seals.

The integration of high resolution animal-borne GPS, time-depth, and video instruments provides an opportunity to describe the hunting and social behaviors of vertebrates. Historically, utilization density maps of low-accuracy animal movement data have been helpful in identifying key foraging habitat (Worton 1989) and time-at-location or movement-based models have identified foraging strategies (e.g., Austin et al. 2004, Freitas et al. 2008, McClintock et al. 2012). Overwhelmingly, though, movement models and home range estimators have considered foraging area, spatiotemporal interactions, and animal movement separately (Lyons et al. 2013). Fortunately, Fastloc GPS technology integrated into animal-borne tags (Rutz and Hays 2009) has facilitated the collection of accurate at-sea positions (Costa et al. 2010) collected at regular, frequent intervals (Dujon et al. 2014). These time-integrated, GPS data sets (Tomkiewicz et al. 2010) motivated the creation of analytical techniques (Kie et al. 2010), such as the nonparametric Time Local Convex Hull (T-LoCoH) kernel approach, that can simultaneously address area use and movement on ecologically relevant time scales (Getz and Wilmers 2004, Lyons et al. 2013).

We use this integrated video and spatial approach to quantify and describe leopard seal prey selection, foraging tactics, habitat use, and ecologically relevant intraspecific social interactions.

Methods

Research was conducted at Cape Shirreff (62.47^o S, 60.77^o W) on the north shore of Livingston Island (Figure 1-1). Bounded by glaciers to the south, the Cape is approximately 3 km long and 1.5 km wide. Within 2 nautical miles (nm) of the shoreline the bathymetry is shallow (< 100m). Offshore it slopes down to a characteristically narrow, deep (> 400m) continental shelf break (Dayton et al. 1994) approximately 50 km to the north. The shelf break is historically associated with the southern boundary of the southern Antarctic Circumpolar Current front (Orsi et al. 1995), which concentrates Antarctic krill (Atkinson et al. 2009). Access to these reliably productive foraging grounds and the Cape’s ice-free beaches have facilitated abundant, krill-dependent pinniped and seabird breeding populations (Figure 1-1). The U.S. Antarctic Marine Living Resources Program (US-AMLR) field camp at Cape Shirreff serves as a base for a multi-species, long-term ecological monitoring program focused on using Antarctic fur seals and gentoo (*Pygoscelis papua*) and chinstrap penguins (*Pygoscelis antarctica*) as indicator species. These studies are designed to provide indices which inform management of the regional krill fishery through the Antarctic Treaty system (CCAMLR Ecosystem Monitoring Program (CEMP); (Agnew 1997).

Despite this concentration of multiple potential prey resources, regular surveys never reported seeing more than two leopard seals at Cape Shirreff before 1996 (Boveng et al. 1998). However, the number of leopard seals has been steadily increasing since that time (Goebel et al. 2014). Leopard seals haul out on Cape Shirreff beaches annually between December and June with peak densities in January (range: 22.7 – 54.5 seals/nautical mile (nm)^2) and February (range: 20.5 – 38.7 seals/nm^2) (US-AMLR *unpublished observations*). While haul out densities may underrepresent the number of leopard seals present within a survey area (Rogers et al. 2013), they do provide a minimum reference estimate. The densities of adult female leopard seals hauling out at Cape Shirreff are two orders of magnitude higher than reported elsewhere in the Antarctic (range: 0.01 – 0.521 seals/nm^2) (Rogers and Bryden 1997 and references therein, Erickson and Hofman 1974, Bester et al. 2002). Based on incidental observations and scat analysis, leopard seal predation on fur seal pups and penguins is common between December and March (Vera et al. 2005, US-AMLR *unpublished observations*), but it has been difficult to quantify.

Healthy, adult, female leopard seals were selected for this study in January and February of 2013 and 2014 (Table 1-1). A National Geographic CRITTERCAM video instrument (Generation VI, or Micro-marine, settings in Figure S1-1, 720x1280/30 frames per second (fps), color video, (Marshall et al. 2007), a time-depth-recorder (Mk9 (67 x 17 x 17 mm, 30g), Wildlife Computers, Redmond WA, USA, sample rate: 60 samples/min; or National Geographic CRITTERCAM VI, Washington D.C., sample rate:

60 samples/min; or DST-Milli-TD/100,Star Oddi, Gardabaer, Iceland, sample rate: 12 samples/min), a Fast-loc GPS instrument (SPLASH 10-AF-297A (86 x 55 x 26 mm, 130g), Wildlife Computers, Redmond WA, USA; or F2G134A (58 x 35 x 18 mm, 38g), Sirtrack Ltd., Havelock North, New Zealand) set at the maximum acquisition rate, and a VHF transmitter (Advanced Telemetry Systems, Isanti, MN, USA) were attached to the forward-dorsal mid-line pelage using Devcon 5-minute epoxy. All deployments and recoveries were conducted on chemically immobilized seals.

During the 2013 and 2014 seasons these seven study animals were each captured twice (N=14) using the midazolam-butorphanol sedation protocol established by Pussini and Goebel (Pussini and Goebel 2015). The duration of these captures ranged between 37 and 91 minutes. All pharmaceuticals and doses fell within the reported safe ranges (Pussini and Goebel 2015). Prior to release each animal was weighed in a sling using a tripod, hand winch, and a tensionometer (MSI-7300 Dyna-Link 2, capacity 1,000 ± 0.5 kg).

All target animals were successfully sedated. Each animal's recovery was visually monitored until it recovered to a mobile state. The average recovery time was 7.17 ± 6.20 (range: 1 – 19) min. No tachycardia or respiratory distress was observed during captures. All animals in this study were re-sighted at least once within two weeks of capture, in a healthy state. No reduced motor function or infection was observed.

Data analysis

TDR data were downloaded using software provided by the manufacturer (Wildlife Computers (WC): Mk9 Host v1.09, Mk10 Host v1.26; National Geographic

Remote Imaging: Crittercam GUI; Star Oddi: SeaStar v5.24). All dive records were zero-offset corrected (ZOC) for pressure transducer calibration drift (WC Instrument Helper, ZOC method = “automatic”, or [diveMove (Luque 2007)] ZOC method = “visual”). Utilizing time-date stamps, and instrument ‘dry’ periods (salt water switch was dry continuously for > 2.4 hours (h)), dive and foraging variables were calculated using a customized Excel form including: number and length of foraging trips, the number and length of haul out periods, number of dives/ foraging trip, and mean max depth/per foraging trip. The haul out periods during which instruments were deployed or recovered were excluded from analysis because total lengths were unknown.

High definition CRITTERCAM video data were reviewed using Quicktime Player v.7.7.4. Using the definitions listed in Figure S1-2, three independent observers each scored 50.3 h of video footage by time of day, habitat type (shallow, coastal, deep), behavior (hauled out, resting, traveling, searching, waiting, breath stop, non-feeding event [inter or intra specific]), feeding event (target prey, pursuit tactic (Table 1-2) [ambush, stalk, chase, flush, incidental, handling, processing]), capture success and consumption success. A foraging attempt was any detectable movement in pursuit of an identifiable prey item, while a non-feeding event described the presence of any animal that was not pursued. The definitions of large carnivore hunting tactics vary across studies based on the terrain, target prey, and hunter morphology (Kruuk 1972a, Schaller 1972, Bertram 1979, Van Orsdol 1984, Taylor 1989, Davis et al. 1999, Caro and Fitzgibbon 2009, Hilborn et al. 2012). The descriptions in Table 1-2 attempt to distill the fundamental aspects of these terms common across carnivore systems. Observations were entered into a time-linked database. Fish were identified to species by an Antarctic fish specialist (^{b}Jones *Personal communication*) and confirmed with identification keys (Gon and Heemstra 1990). Leopard seals observed during social encounters were identified, when possible, by comparing video segments to US-AMLR tag and photo-ID catalogs; identifications were verified by three independent observers.

Fastloc GPS data were downloaded and surface position locations were calculated using manufacturer software (DAP Processor (WC); Sirtrack and Pathtrack archival GPS Ver. 1.11). Solved positions based on fewer than 6 satellites (Dujon et al. 2014), residual error > 15.0 (WC), or with a Pathtrack LocSolve accuracy indicator < 30 were removed. All subsequent data analysis was conducted using R (R-Core-Team 2014); all relevant R packages are listed in brackets with citations. Remaining GPS positions were passed through a filter to remove positions requiring travel speeds > 4 m/s [argosfilter (Freitas 2012)].

In order to link video-observed behaviors with foraging habitat, post-filter GPS data was further analyzed, and animations and behavior maps were created [tlocoh (Lyons and Getz 2014)]. Each GPS data set per individual leopard seal was reviewed to ensure even time-sampling-interval of locations; all temporally concentrated location ‘burst’ segments were removed to reduce bias (Lyons 2014). Time Local Convex Hulls (T-LoCoH) are essentially minimum convex polygons created for each GPS location based on a given number of nearest neighbor points which are local in space and time. Nearest neighbors were selected using the adaptive (‘a’) method (Getz et al. 2007). Each hull (e.g., Figure S1-3) has several characteristics by which an individual animal’s movement can be described: (1) elongation (eccentricity,‘ecc’) which is a basic measure of directionality (indicated by the red oval in Figure S1-3). Sorting the hulls by ecc produces a color-coded behavior map of movement, or elongation distribution. The color scale ranges from red (likely transit behavior) to light blue (little or no directionality) (2) re-visitation (number of separate visits to a given hull, 'nsv') which provides a metric for how often an animal re-visited a given area, and (3) duration (mean length of visit, 'mnlv') which indicates how long an individual spent in a given hull per visit (Lyons et al. 2013). Separate visits were defined by an inter-visit gap period of ≥ 3 h.

Plots of position color-coded by foraging trip, elongation distributions, and position maps color-coded by duration and re-visitation rates were created for each animal (Lyons 2014). Duplicate points (two GPS positions in the exact same location) were offset by 1 meter. All T-LoCoH map locations were plotted in a Universal Transverse Mercator (UTM) zone 20 projection. The x-axis (easting) and y-axis (northing) were plotted in meters.

Area maps were created using Antarctic coastline data from the SCAR Antarctic Digital Database. [ggplot2 (Wickham 2009)]. All values are listed as mean ($\bar{X}$) ± standard deviation (SD) unless otherwise indicated. Antarctic fur seal processing times per individual leopard seal were compared using Welch's two-sample t-tests, with a level of significance of $p \leq 0.05$.

Results

The average deployment length was 4.80 ± 2.45 (range: 0.86 - 9.12) days (d), which cumulatively covered 16 leopard seal foraging trips (Table 1-1). Thirty-nine prey capture attempts and 11 leopard seal social encounters were scored from 50.3 h of video data. We obtained 3,833 post-filter GPS positions (Figure S1-1), accurate to within 70 m

(Dujon et al. 2014). The mean dive depth was 14.84 ± 8.98 m (Table 1-1) and the mean maximum depth was 62.0 ± 15.3 m (range: 47 – 84 m). On average leopard seals spent 58.2 ± 22.6 (range: 40.3 – 72.2) % of deployment time hauled out on land. Despite variance between individual seals in the percent time they spent in each behavioral state (Figure S1-4), leopard seals consistently spent most of their in-water time searching for prey (50.4 ± 26.9 %) or immobile and resting (23.2 ± 21.1 %, Figure 1-2). Feeding behavior was focused on four prey items: Antarctic fur seals, Antarctic fur seal pups, demersal notothen fishes, and *Pygoscelid* penguins (Figure 1-3). The key targets were Antarctic fur seal pups, successfully captured in 76.5% of attempts, and notothen fishes, captured in 64.3% of attempts.

Hunting tactics

At Cape Shirreff five of the seven leopard seals targeted Antarctic fur seals (Table 1-1). Adult female or juvenile male fur seals (N=3) were pursued using a chase tactic, and none were captured. Four leopard seals attempted to capture at least one fur seal pup, but the high capture success rates were driven by three individuals (422Y, 406Y & 397G) who succeeded in 13 of 14 attempts; all of which used an intertidal ambush technique (Figure S1-5). The other three leopard seals either made no fur seal pup attempt or were unsuccessful using a coursing/chase tactic (Figure 1-4a).

Four of the seven leopard seals attempted to catch a notothen fish. Fish hunting focused on three groups: unidentified demersal notothen fish (N=5), humped rockcod (*Gobionotothen gibberifrons*) (N=6), and black rockcod (*Notothenia coriiceps*) (N=3). As with fur seal pup tactics, the overall capture success rates were driven by a subset of individuals. One leopard seal (401Y) employed either flush or stalk techniques and was 88.9% successful, while the other three individuals used chase tactics and were 20% successful (Figure 1-4b). Additionally, 401Y utilized prey-specific tactics. For all humped rockcod, seal 401Y inverted its body head-down and flushed the fish from rock cover or sponge beds with its snout (Figure S1-6). Black rockcod were observed swimming approximately 2-3 meters above the sea floor. The seal approached these fish from behind and below slowly and then abruptly struck when it was about 1 meter away. Both fish species were taken to the surface to be processed. However, the humped rockcod were eaten whole, while the heads were removed from black rockcod; perhaps to reduce irritation from the black rockcod's prominent opercular spines (Gon and Heemstra 1990).

Foraging specialization

For direct comparison of habitat use and foraging behavior, temporally overlapping deployments were conducted on two leopard seals (401Y and 397G) who hauled-out regularly on the same beach. Leopard seal 401Y targeted only demersal fish and adult fur seals while 397G targeted only fur seal pups, and these prey differences corresponded to distinct habitat use. While they both used the area around Cape Shirreff, 401Y was distinctly off shore (Figure 1-5a), and 397G followed the coastline almost exactly (Figure 1-5b). Seal 401Y had high re-visitation rates to three areas (Figure S1-7) revealed by video data to be fishing grounds. The elongation distribution maps show that 401Y had low directionality within fishing areas but transited directly between them (Figure 1-5c). Seal 397G transited between fur seal breeding beaches and had several rapid transits offshore to process kills (Figure 1-5d). High re-visitation rates seem to correspond to searching effort, which for 397G focused on fur seal breeding beaches (Figure S1-8). Seal 397G searched along all fur seal beaches (purple color, Figure 1-6), but ambush hunting behavior, mostly around the two largest breeding beaches (Figure 1-1), increased her duration per hull (green color, Figure 1-6).

Kleptoparasitism

One of the seven Cape Shirreff CRITTERCAM records (397G) covered three foraging days and contained 10 successful Antarctic fur seal pup captures, six of which were stolen by at least three other adult female leopard seals. Additionally, 397G attempted to steal a pup but was unsuccessful. Two of the kleptoparasitic females were identified from our study population by photo-id, both of which were longer (standard length) and heavier than 397G. These interactions are clearly aggressive (Figure S1-9). Each consisted of a surprise attack while 397G was beginning to process captured, dead pups followed by 19.5 ± 5.2 seconds (s) of open-mouthed head strikes. While 100% (N=7) of leopard seal social interactions were agonistic when one had a captured pup, 0% (N=4) were agonistic when neither had a pup. All interactions were between two individuals, and when mass was known for both, the smaller leopard seal was never successful at defending captured prey.

Scavenging/food caching

Three leopard seals at Cape Shirreff were observed on CRITTERCAM video to discover and consume carcasses (one penguin, and two fur seal) on the sea floor in 18 to

32 meters of water. These scavenged prey items represent 22.2% of all fur seal pups (N=9) and 100% of all penguins (N=1) consumed in the study (Figure 1-7).

Discussion

Large carnivore hunting tactics include one or a combination of sit-and-wait, stalk, flush, ambush, or chase/coursing techniques (Schaller 1972, Van Orsdol 1984, Davis et al. 1999, Caro and Fitzgibbon 2009), which are selected based on prey movement, size, and vulnerabilities (Kruuk 1972a, Bertram 1979, Bowen et al. 2002). Studying the tactics used by carnivores has provided insight into the impact pathways between predators and their ecosystem (Bertram 1979), the influence of environmental factors and terrain (Murray et al. 1995, Hilborn et al. 2012), and the importance of inter- and intraspecific competition (Stirling 1974, Bertram 1979, Parrish et al. 2008, Scantlebury et al. 2014). Although the bulk of this field has been focused on terrestrial systems, the adaptations of marine carnivores should facilitate similar environmental and energetic evolutionary drivers of hunting behavior (Estes 1989).

Hunting tactics

The majority of previous reports on leopard seal hunting tactics were recorded at penguin colonies, and described two approaches: a sit-and-wait technique, used if there was available cover and a reliable procession of penguins (Kooyman 1965, Mader 1998), or an ambush in the water or ice edge (Penney and Lowry 1967, Kooyman et al. 1990, Rogers and Bryden 1995). Chase techniques were rarely reported and were unsuccessful (Rogers and Bryden 1995). One study of hunting tactics on Antarctic fur seals indicated that a small number of leopard seals using an ambush technique in intertidal areas had the biggest impact; while chase techniques were seen, they were rarely successful (Hiruki et al. 1999).

At Cape Shirreff, leopard seals used both chase and ambush tactics when hunting fur seals. As with previous studies, successful hunting was driven by a subset of individuals using an ambush tactic. Chase tactics were used opportunistically by leopard seals, though success rates were low (Table 1-1). The specialized intertidal ambush technique was likely developed because small mesopredators can out-maneuver leopard seals in open water, but in shallow coastal areas leopard seals can use restricted space, cover, and surprise to their advantage (DeLaca et al. 1975).

To our knowledge foraging tactics by free-ranging leopard seals on fish have not previously been reported. A video-based study of Weddell seal foraging behavior identified hunting tactics on two groups of notothen fishes; large benthic Antarctic cod were stalked, while smaller ice-associated fishes were flushed from ice cracks with air bubbles (Davis et al. 1999). The Cape Shirreff population of leopard seals all spent most of their searching effort on the benthos near shore, yet most animals had no or low success capturing demersal fish. One individual (401Y), though, utilized prey-specific stalk and flush techniques to great effect. These initial results of predation on fur seal pups and notothen fish suggest that individual-based hunting specialization is important for this population of leopard seals.

Foraging specialization

Reports based on the diet and morphology of leopard seals describe a generalist apex predator that will readily adjust its foraging effort toward the most available prey resource across a broad spectrum of the Antarctic food web (Laws 1984, Siniff and Stone 1985, Rogers 2009). Their slender body form, and large fore flippers provide speed and maneuverability (Kooyman 1981). Leopard seals have the longest jaws of any seal (Ray 1966). That massive gape contains a combination of carnivorous recurved canines and interlocking tricuspid postcanines (Kooyman 1981, Rogers 2009) that can subdue large-bodied prey, or sieve krill and fish as needed (Hocking et al. 2013). Despite these general traits, whether individual leopard seals readily switch prey across trophic levels or develop specialized foraging strategies is not known.

Many marine predators develop specialized hunting tactics (Pitman and Durban 2012, Pitman et al. 2015), and intraspecific competition can drive the development individual-based specialized foraging strategies in marine carnivores (Estes et al. 2003, Staniland et al. 2004, Weise et al. 2010). Indeed, high leopard seal densities seem to be coincident with prey-specific hunting tactics at Cape Shirreff. Additionally, two study animals (401Y and 397G) with practically identical foraging options employed distinct hunting tactics on different prey in separate areas around Cape Shirreff. Although sample sizes remain small, these prey-specific hunting tactics and distinctive movement patterns, along with previous observations (Rogers and Bryden 1995, Hiruki et al. 1999), suggest that leopard seals concentrated at mesopredator breeding colonies employ specialized foraging techniques.

Kleptoparasitism

Although generally solitary, observations of two or more free-ranging leopard seals interacting have been reported (Hiruki et al. 1999 and references therein). Some of these interactions were attributed to play or cooperative hunting; however, other interactions involving a prey item obtained by one leopard seal and transferred to another were less clear (Hiruki et al. 1999). These and other shore-based reports, which indicated that up to 14.2% of all fur seal pup captures at Cape Shirreff may have been stolen (Vera et al. 2005), could not be confirmed without underwater observations (Hiruki et al. 1999).

Kleptoparasitism is a potentially important competition pathway realized when a parasite steals food from a host (Brockmann and Barnard 1979). Predatory carnivores have high energetic costs due to hunting; therefore kleptoparasitism can affect individual and population viability (Creel and Creel 1996, Gorman et al. 1998, Krofel et al. 2012). Although kleptoparasitism is common across animal taxa, it has rarely been described for mammals in marine systems (Iyengar 2008); with notable exceptions (Riedman and Estes 1988, Parrish et al. 2008). Animal-borne video data from Cape Shirreff confirm that at least some prey exchanges between adult leopard seals are aggressive and kleptoparasitic (Figure S1-9).

In systems where kleptoparasitism is common, hosts develop strategies to build resilience to the loss of energy (Brockmann and Barnard 1979, Creel et al. 2001, Iyengar 2008). Therefore, if kleptoparasitism is persistent for leopard seals at Cape Shirreff, hosts should utilize the most efficient hunting tactics (Scantlebury et al. 2014), have higher prey capture rates (Krofel and Kos 2010), and process their prey more quickly than non-hosts (Krofel et al. 2012). And, indeed, 397G utilized the most successful tactic in the study (ambush), had the highest pup capture rate per foraging time (2.43 pups/hr vs. 1.78 pups/hr [422Y] or 0.18 pups/hr [406Y]), and had the lowest pup processing times ($\bar{X}$ = 10.38 ± 2.03 min, $t = -3.2$, $p \leq 0.01$). Additionally, 397G moved away from the pup-capture location to process prey and, ostensibly, to avoid kleptoparasites (Figure 1-5 b) while other, larger animals (e.g., 422Y, 406Y) did not. Although the sample size is limited, these results suggest that kleptoparasitism is a substantial competitive pathway among adult leopard seals.

Scavenging/food caching

Leopard seals foraging at mesopredator colonies have been reported to kill penguins ([c]Ponganis *personal communication*, [d]Lescroël *personal communication,* Kooyman 1965) or fur seal pups (US-AMLR *unpublished observations*) in excess of what they immediately processed and ate. There is a spectrum in carnivore behavior describing a predator killing prey in excess of its immediate consumption needs. One end of that spectrum is “surplus killing” when a carnivore kills prey items but never consumes them (Kruuk 1972b). On the other end is “food caching” which, for carnivores, describes a satiated predator that continues to kill prey and either store or defend it until it can be consumed later (Vander Wall 1990). Even though no energy is gained, there are advantages to surplus killing, including hunting practice for immature animals (Kruuk 1972b) or in the organization of social structure (Kruuk 1972). Almost all examples of surplus killing involve environmental or pathological factors (e.g., severe weather, disease) that inhibit prey from their natural predator defense mechanisms (Kruuk 1972b). In all known reports of leopard seals killing excess prey, though, there are no such inhibitions to predator defense. Further, the list of potential advantages for surplus killing does not extend to solitary adult leopard seals, implying that reports of excess prey-killing likely lead to food caching.

Food caching is a behavioral hedge against competition for limited resources (Andersson and Krebs 1978) and is associated with variable environments and unpredictable food availability (Smith and Reichman 1984). Although a taxonomically broad spectrum of terrestrial birds and mammals demonstrate food caching (Vander Wall 1990), it has only been reported for two marine mammals to date. Transient killer whales (*Orcinus orca*) in the northeastern Pacific were reported to abandon gray whale (*Eschrichtius robustus*) kills but return to feed on the submerged carcasses (Barrett-Lennard et al. 2011). And, Weddell seals (*Leptonychotes weddellii*) in the Ross Sea region have been observed to cache fish in breathing holes (Kim et al. 2005, Ponganis and Stockard 2007).

A leopard seal at Cape Washington was observed patrolling within 10 meters of a previously killed, partially-stripped emperor penguin in an ice lead. That seal made aggressive movements and vocalizations when researchers approached the penguin carcass, and it eventually consumed the carcass ([c]Ponganis *personal communication*, Figure S1-10). Three of the seven leopard seals at Cape Shirreff consumed mesopredator carcasses in this study. Because there are no other marine apex predators at Cape Shirreff, we can assume that all three scavenged carcasses resulted from previous leopard seal kills. Furthermore, due to rapid processing by shallow water amphipods (*Orchomenella*, US-AMLR *unpublished observations*), the carcasses were no more than a few days old.

A second continuum of behavior exists within the context of carnivore scavenging with “sloppy feeding” at one end and, again, “food caching” on the other. While both refer to a situation in which a predator scavenges a carcass, sloppy feeding applies when the carcass was present through inefficient prey processing by the original predator (Wilson and Wolkovich 2011), and food caching applies when the carcass was killed and stored with the intent of future recovery (Macdonald 1976). The food caching strategy becomes advantageous when an individual can recover its kills, or another’s kills, at a rate consummate with its predatory effort (Vander Wall and Jenkins 2003). Fur seal pup carcass processing by leopard seals is similar to penguin processing (Hamilton 1939, Kooyman 1965). The leopard seal whips the carcass violently back and forth (Figure S1-9) until the skin has been peeled back to expose the viscera and body muscle, which the leopard seal consumes. Three lines of evidence suggest that scavenged carcasses at Cape Shirreff were cached: 1) Mesopredator carcass processing has been observed frequently and does not match the sloppy feeding description (US-AMLR *unpublished observations*) 2) any kill remains left at the surface are immediately consumed by predatory birds including brown skuas (*Stercorarius antarcticus*), giant petrels (*Macronectes giganteus*), and Wilson’s storm petrels (*Oceanites oceanicus*). So for a carcass to survive for later consumption, we suspect that it must be deposited purposefully below its buoyancy composition depth, and 3) the adult leopard seal at Cape Washington was engaged in cache defense, and when one member of a species employs caching behavior, generally all do (Vander Wall and Jenkins 2003).

Irrespective of its label, facultative scavenging of carrion is both present in the behavior of leopard seals at Cape Shirreff and ecologically important. Scavenging is a biologically widespread behavior (DeVault et al. 2003) that can structure communities and stabilize food webs (Wilson and Wolkovich 2011). At Cape Shirreff, scavenging was present in both field seasons. Additionally, leopard seals spent 80.8% of their searching effort scouring the benthos despite a fish capture-attempt rate (0.56/hr) more than an order of magnitude lower than reports for other phocids (9.3/hr, Bowen et al. 2002). This suggests that benthic-oriented searching may not be limited to fish hunting but may also focus on carrion which can provide high quality food at low acquisition cost (Wilson and Wolkovich 2011). Due to its potential importance, we suggest that future predator impact models of Antarctic coastal ecosystems include a scavenging/caching impact pathway.

Conclusions

Leopard seals are probably affecting Antarctic coastal ecosystems through both direct and indirect pathways, several of which have not been studied or discussed to date. Mesopredator breeding colonies, in particular, appear to draw high densities of adult leopard seals that facilitate social interactions (Kooyman 1981, Borsa 1990, Hiruki et al. 1999, Ainley et al. 2005). Social encounters at Cape Shirreff were often aggressive, indicating the influence of intraspecific interference competition. No evidence of cooperative hunting was found. Video and movement data suggest that leopard seals individually employ specialized, prey-specific hunting tactics including ambush tactics on Antarctic fur seal pups and flush and stalking tactics on notothen fishes.

Surprisingly, demersal fishes are a key prey item for leopard seals at Cape Shirreff, which puts them in direct competition with both Gentoo penguins and blue-eyed Antarctic shags (*Phalacrocorax (atriceps) bransfieldensis*) that forage locally to provision their chicks during January and February. We report the first observations of predation attempts by leopard seals on non-pup fur seals in the WAP. These attacks suggest that predator-induced stress effects on fur seal physiology and behavior are likely (Creel and Christianson 2008). The most immediate indirect impacts to mesopredator populations, though, are likely driven by kleptoparasitism which can increase predation rates (Krofel and Kos 2010) and scavenging/caching which is an understudied but ecologically crucial energy pathway (Wilson and Wolkovich 2011).

While these observations are preliminary, the regular occurrence of such novel behaviors within a relatively small sample size indicates that they are not unusual. Our expanded understanding of the importance of intraspecific competition and the indirect effects of leopard seals on Antarctic coastal ecosystems would not have been possible, and often could not have been anticipated, without the use of animal-borne video and Fastloc GPS. Given the potential magnitude of top-down forcing by leopard seals, we suggest expanding current studies to integrate diet and foraging ecology to verify these preliminary results and expand baseline data for future ecosystem models.

Chapter 1, in full (excluding page 18, Figure 1-0 and legend), is a reprint of the material as it appears in Animal Biotelemetry 2015. Krause, Douglas J.; Goebel, Michael E.; Marshall, Gregory J.; Abernathy, Kyler. The dissertation author was the primary investigator and author of this material.

Acknowledgements

This paper was greatly improved by suggestions and comments by L. Ballance, P.

Dayton, J. Hinke and two anonymous reviewers. We are grateful to K. Pietrzak, M. Mudge, J. Wright, N. Cook, M. Zimmerman, M. Goh, T. Joyce, N. Pussini, D. Vejar and J. Hinke for their assistance in the field. We thank L. Rodriguez, S. Pawlak, N. Lyon and K. Searles for scoring video footage. The financial, infrastructure and logistical support of the US-AMLR Program has made this work possible, and George Watters, its Director, is thanked enthusiastically. Funding for instruments and travel was provided by the National Geographic Society (NGS)/Waitt Grant # W256-12, and the Mary Maude Vestal B. Houghes Pay-It-Forward travel grant. Intra-Antarctic transportation was kindly provided by Lindblad/NGS Expeditions, and logistical support by NGS Remote Imaging. Leopard seal interactions and captures were conducted in accordance with Marine Mammal Protection Act Permit No. 16472-02 granted by the Office of Protected Resources, National Marine Fisheries Service, the Antarctic Conservation Act Permit No. 2012-005, and the NMFS-SWFSC Institutional Animal Care and Use Committee Permit No. SWPI2011-02.

Endnotes

[a] United States Antarctic Marine Living Resources Program (US-AMLR) is administered by the NOAA Fisheries Antarctic Ecosystem Research Division (AERD), SWFSC La Jolla, CA, USA. [b] Jones, C.D. *Personal Communication*. Dr. Christopher Jones provided assistance in identifying two species of notothen fish. AERD, SWFSC, La Jolla, CA 92037. November, 2014. [c] Ponganis, P. *Personal Communication*. Dr. Paul Ponganis and his field crew at Cape Washington 2011 (B. McDonald, M. Tift, G. Marshall and M. Fowler) provided field observations, photos, and video of a probable

leopard seal caching event. The video was supported by NSF grant 0944220 to P. Ponganis. MMPA Permit 15261. Scripps Institution of Oceanography, UCSD, La Jolla, CA 92037. August, 2014. [d]Lescroël, A. *Personal Communication*. Dr. Amélie Lescroël shared observations of leopard seal predation on Adélie penguins at Cape Crozier during the Fifth International Bio-logging Conference, Strasbourg France. September, 2014.

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Tables

Table 1-1: Individual leopard seal deployment details and hunting tactics. Deployment dates, lengths and the number of foraging trips are listed per individual. Dive depth is mean ($\bar{X}$) ± standard deviation (SD). Listed mass obtained during recovery capture. Target prey: 1 = Antarctic fur seal adult, 2 = Antarctic fur seal pup, 3 = notothen fish, 4 = penguin. Carcass indicates the consumption of a scavenged/cached carcass within an individual's video record. Seal 394Y made no capture attempts within the video record. Hunting tactics that were successful > 50% of the time are highlighted in bold.

Animal ID	Deployment Date	Deployment Length (d)	Dive Depth (m)	No. Trips	Mass (kg)	Standard Length (cm)	Carcass	Target Prey - Hunting Tactics
406Y	January 8, 2013	9.12	12.2 ± 8.2	4	498	312	4	**2 - ambush**, 4 - chase, 3 - chase
394Y	February 1, 2013	4.69	13.1 ± 6.5	2	416	285	--	--
422Y	January 12, 2013	0.86	14.1 ± 9.3	1	416	293	2	**2 - ambush**, 3 - chase
397G	January 16, 2014	5.82	14.6 ± 10.5	3	385	289	--	**2 - ambush**
16OR	February 12, 2014	4.65	17.7 ± 12.2	1	494	311	--	1 - chase, 2 - chase
401Y	January 14, 2014	4.12	16.1 ± 8.6	2	485	301	2	1 - chase, **3 - flush & stalk**
37OR	January 23, 2014	4.30	15.0 ± 8.8	3	406	298	--	3 - chase

Table 1-2: Definitions based on a literature review of carnivore hunting tactics.

Hunting Tactic	Definition
Ambush	Moving, usually slowly, into an advantageous position and using surprise to capture prey with a rush or quick grasp.
Stalk	Actively tracking, and moving slowly to close the distance to prey while avoiding detection, typically ending in a rush to capture.
Chase	Any accelerated swim or maneuver to pursue prey; chases tend to be longer than the 'burst rushes' of ambush or stalk techniques.
Flush	Using a body part, vocalization, or other means to move prey away from shelter.
Incidental	An interaction with a potential prey that was not precipitated by any notable pursuit effort; includes scavenging.

Figures

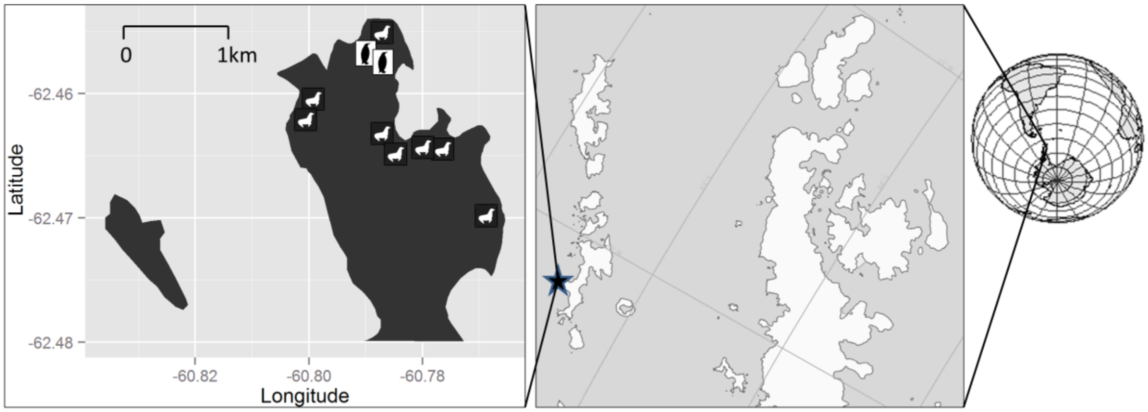

Figure 1-1: A Map of the US-AMLR study area. The black star marks the location of Cape Shirreff on Livingston Island near the Antarctic Peninsula. Seal and penguin symbols have been added to indicate the location of major breeding areas for Antarctic fur seals, and *Pygoscelid* penguins; symbols are not scaled directly to population size.

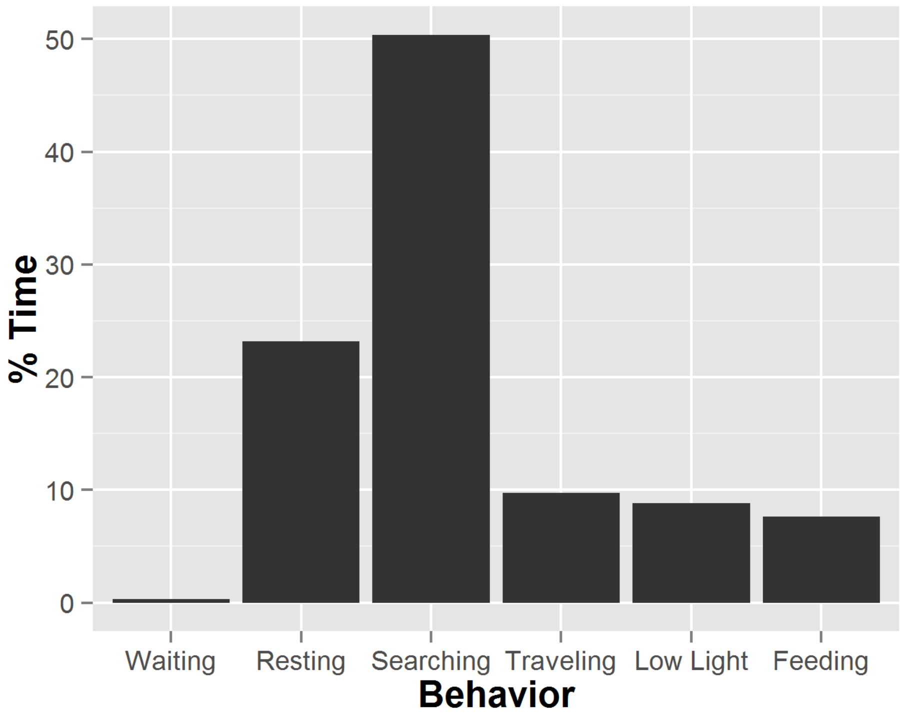

Figure 1-2: Percent of total time per behavior, based on scored CRITTERCAM video. “Low Light” refers to any video segment that was too dark, or obscured to reliably identify behavior.

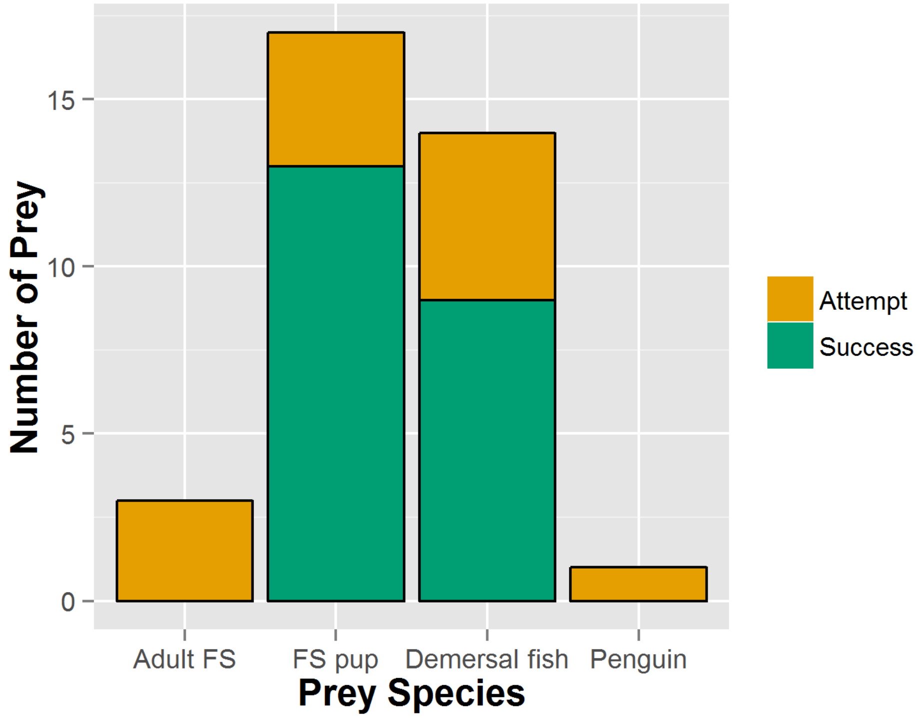

Figure 1-3: Number of attempts and captures per target prey species. Adult and juvenile Antarctic fur seals, "Adult FS" (N=3), Antarctic fur seal pups, "FS pup" (N=17), demersal notothen fishes, "Demersal fish" (N=14), and penguins (N=1). A "Capture" occurs when a leopard seal obtains a prey item and successfully handles it until the prey is dead.

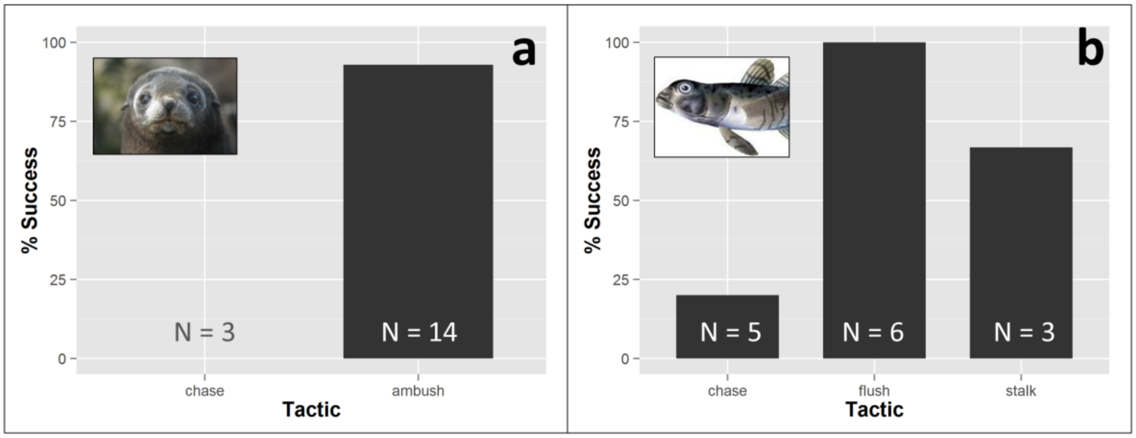

Figure 1-4: Prey capture success rates by hunting tactic. Target prey were: a) Antarctic fur seal pups and b) notothen fishes.

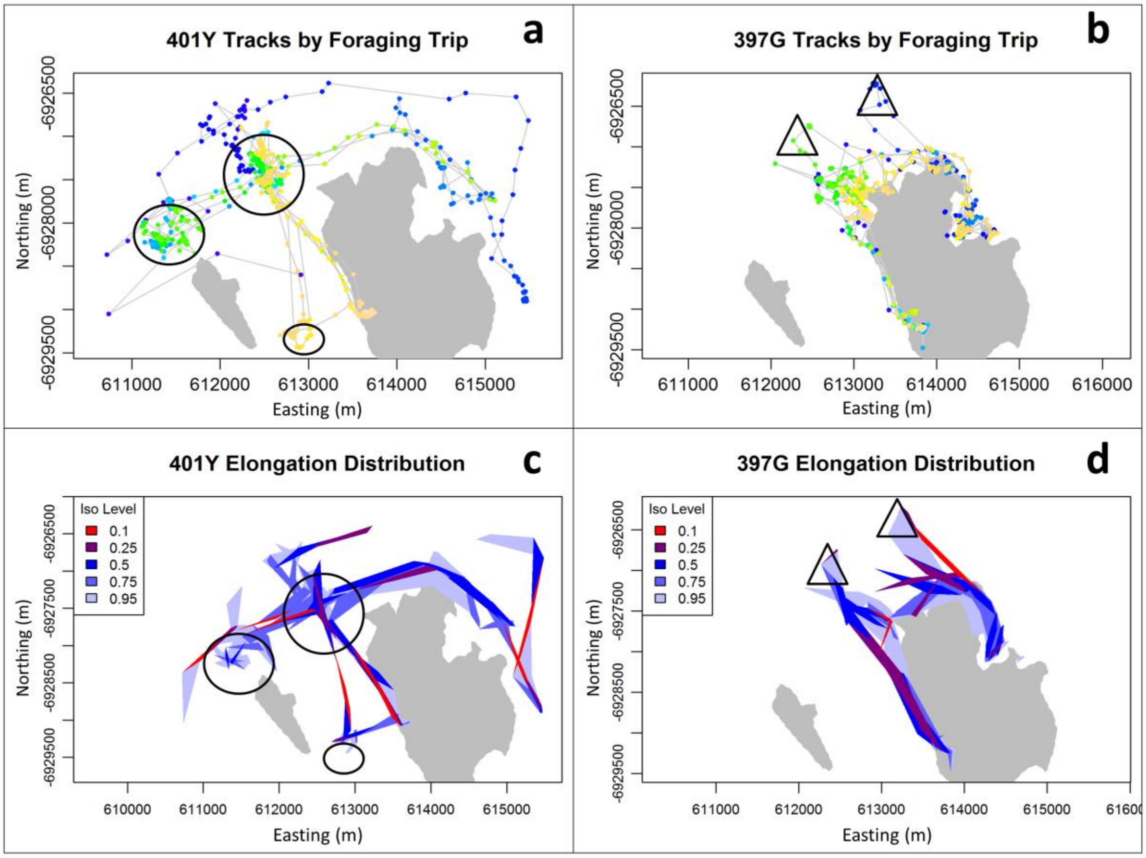

Figure 1-5: Foraging locations and elongation distributions for 401Y and 397G. a & c) Post-filter GPS positions (N=574) for leopard seal 401Y. Black circles indicate areas associated with benthic foraging for fish as identified by video and dive data. a) A map of all movement tracks with points color coded by foraging trip. c) An elongation distribution map which plots the isopleths sorted by descending elongation (‘ecc’). Hulls were created using the fixed ‘a’ method (a=2000, s=0.06). b & d) Post-filter GPS positions (N=768) for leopard seal 397G. Black triangles indicate areas associated with Antarctic fur seal pup processing as identified by video data. b) A map of all movement tracks with points color coded by foraging trip. d) An elongation distribution map which plots the isopleths sorted by descending elongation (‘ecc’). Hulls were created using the fixed ‘a’ method (a=2250, s=0.04).

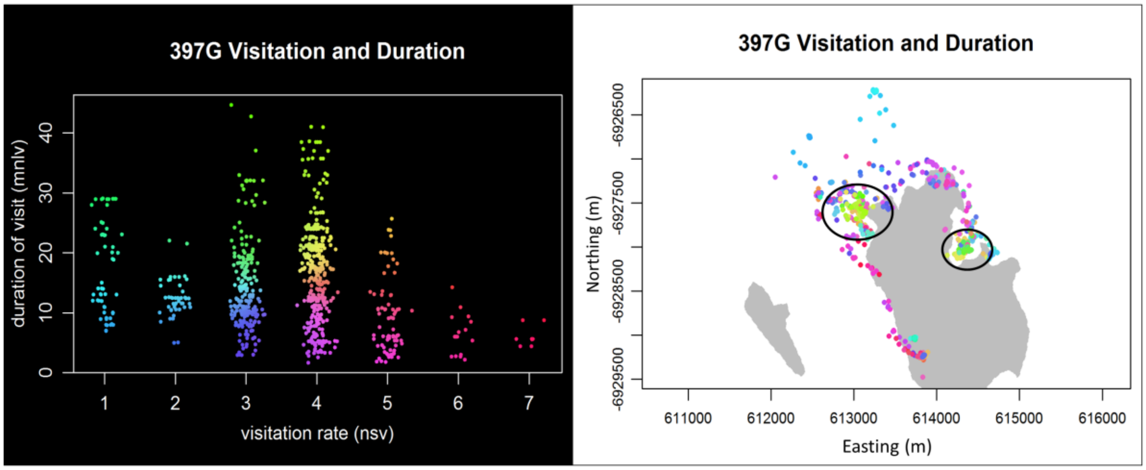

Figure 1-6: Re-visitation and duration behavior plots for 397G. Hulls were created using the fixed ‘a’ method (a=2250, s=0.04). Left pane - a scatterplot where each point represents a hull color-coded by location duration (“mnlv”) and re-visitation (“nsv”) (N=768). Points were each jiggled (by 0.1 on x-axis, by 0.05 on y-axis) to better see point density. Right pane – Animal location hulls colored based on their position in mnlv-nsv space. Active ambush hunting behavior areas are denoted by black ovals.

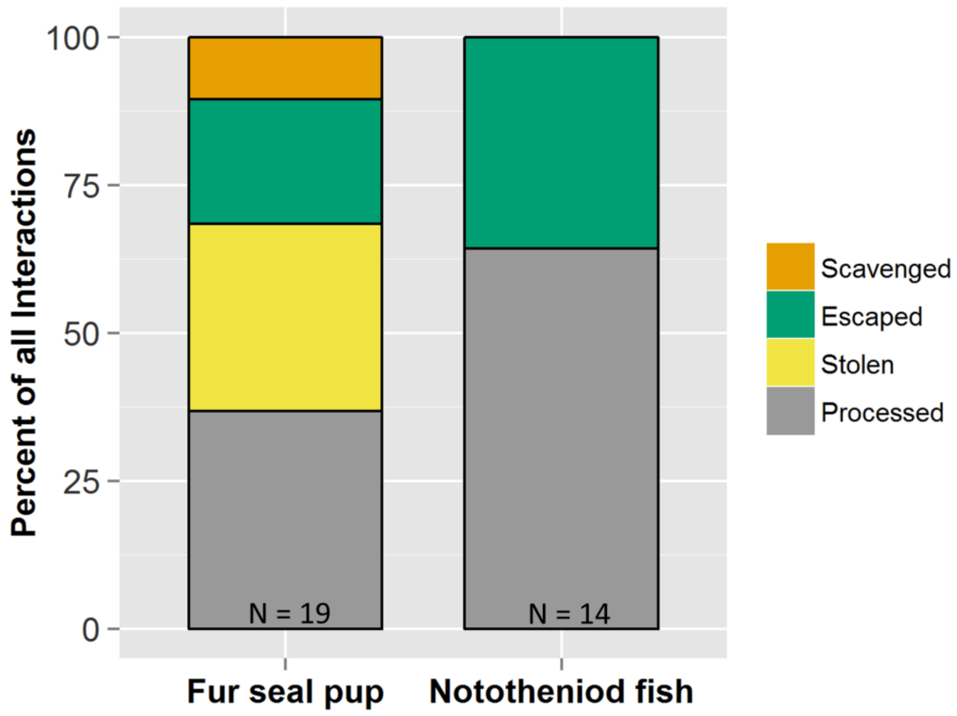

Figure 1-7: Fate of all prey interactions by species. A proportional stacked plot indicating the outcomes for each leopard seal encounter with Antarctic fur seal pups and notothen fishes.

CHAPTER 2:

Summer diving and haul-out behavior of leopard seals (*Hydrurga leptonyx*) near mesopredator breeding colonies at Livingston Island, Antarctic Peninsula

Douglas J. Krause, Michael E. Goebel, Gregory J. Marshall, Kyler Abernathy

Abstract

Leopard seals are conspicuous apex predators in Antarctic coastal ecosystems, yet their foraging ecology is poorly understood. Historically, the ecology of diving vertebrates has been studied using high-resolution time-depth records; however, to date such data have not been available for leopard seals. Twenty-one time-depth recorders were deployed on seasonally resident adult females in January and February between 2008 and 2014. The average deployment length was 13.65 ± 11.45 d and 40,308 postfilter dives were recorded on 229 foraging trips. Dive durations averaged 2.20 ± 1.23 min. Dives were shallow with 90.1% measuring 30 m or less, and a mean maximum dive depth of 16.60 ± 10.99 m. Four dive types were classified using a k-means cluster analysis and compared with corresponding animal-borne video data. Dive activity (number of dives/h) was concentrated at night, including crepuscular periods. Haul-out probabilities were highest near midday and were positively correlated with available daylight. Visual observations and comparisons of diving activity between and within years suggest individual-based differences of foraging effort by time of day. Finally, dive and video data indicate that in addition to at-surface hunting, benthic searching and facultative scavenging are important foraging strategies for leopard seals near coastal mesopredator breeding colonies.

Introduction

Leopard seals (*Hydrurga leptonyx*) are a conspicuous yet cryptic component of Antarctic coastal ecosystems. Although they are widely distributed around the Antarctic (Laws 1984, Rogers 2009), they are not well studied. Their population has been estimated at 300,000 (Erikson and Hanson 1990) and that figure may be negatively biased (Southwell *et al.* 2012). Leopard seals are the largest Antarctic ice seal (Wilson 1902, Bonner 1994), with the longest phocid jaw (Ray 1966). Leopard seal teeth consist of carnivorous recurved canines and plankton-sieving tricuspid molars (Hamilton 1939, Kooyman 1981). Their large size and gape, maneuverability, broad distribution, and dual-purpose dentition enable them to exploit a wide range of prey from Antarctic krill (*Euphausia superba*) to seabirds, otariids, and phocids (Siniff and Stone 1985, Boveng *et al.* 1998, Hall-Aspland and Rogers 2004). Yet, despite the potential ecological importance of leopard seals, their impact on marine ecosystems is not well understood.

Leopard seals are typically solitary (Wilson 1905, Southwell *et al.* 2008) and associated with marginal pack ice habitat (Gilbert and Erickson 1977, Rogers and Bryden 1997, Bester *et al.* 2002, Rogers *et al.* 2005). However, some leopard seals congregate seasonally in higher densities near mesopredator (*e.g.*, penguin and Antarctic fur seal (*Arctocephalus gazella*) colonies (Hofman *et al.* 1977, Kooyman *et al.* 1990, Hiruki *et al.* 1999). The demographics of such leopard seals are not well known, but seem to vary by location, season (Borsa 1990, Walker *et al.* 1998) and regional winter sea-ice extent (Jessopp *et al.* 2004, Forcada and Robinson 2006). And, while winter (April-October) predation by transient leopard seals likely has a limited effect on mesopredator populations (Forcada *et al.* 2009), summer (December-March) predation by seasonally resident leopard seals has been shown to reduce Antarctic fur seal abundance (Boveng *et al.* 1998). Such summer hunting of mesopredators seems to be dominated by resident females (Rogers and Bryden 1995, Hiruki *et al.* 1999, Vera *et al.* 2005).

Tracking known leopard seals foraging near penguin colonies revealed that while hunting grounds were accessed only by a few individuals at a time, those seals came and went from a much larger population within the area (Kooyman 1981, Rogers and Bryden 1995). This dynamic is consistent with observations from Cape Shirreff, Antarctic Peninsula (Vera *et al.* 2005), suggesting the pattern is not rare and that mesopredator-hunting leopard seals are more numerous than previously thought (Penney and Lowry 1967, Müller-Schwarze 1984). With more predators than available space, access to hunting grounds must be regulated, but the associated mechanisms are not known. As with other apex carnivores, access may be determined by intraspecific competition based on a hierarchy of dominance (Revilla and Palomares 2001). The number of leopard seals actively hunting at a given colony is likely related to colony size (Ainley *et al.* 2005), but if Kooyman (1981) and Rogers and Bryden (1995) are correct, any static census of those animals will underestimate leopard seal abundance in the area. Poor access and logistical challenges have limited previous studies to land-based, daytime observations of leopard seals targeting mesopredator prey (*e.g.*, Kooyman 1965, Penney and Lowry 1967, Rogers and Bryden 1995, Walker *et al.* 1998, Hiruki *et al.* 1999), which has left mechanisms of intraspecific competition, daily patterns of foraging, haul-out, and diving behavior poorly understood.

Advances in satellite-linked time depth recorders (SLDRs) have facilitated the collection of summarized leopard seal diving behavior. One juvenile male was tracked near Adelaide Island (Kuhn *et al.* 2006) and two adult females were instrumented off Queen Maud Land (Nordøy and Blix 2009). These studies corroborated previous assumptions, based on physiology, that the leopard seal dive repertoire would be shallow and brief compared to other phocids (Drabek 1975, Williams and Bryden 1993). Nordøy and Blix (2009) also supported previous, shore-based observations that indicated leopard seals generally haul-out at midday during the summer (Gilbert and Erickson 1977, Rogers and Bryden 1997). The sample sizes were small (*n*≤2), though, and dive data resolution was restricted by satellite transmission bandwidths. The resultant depth-binned histograms did not allow for a detailed study of diving behavior.

Analysis of full resolution time-depth-recorder (TDR) dive profiles has been crucial to understanding the foraging ecology of diving vertebrates (Schreer *et al.* 2001, Kooyman 2004). Initially, studies of pinniped TDR profiles utilized manual classification of putative foraging behavior based on dive shape and summaries of key dive variables (*e.g*., Kooyman 1966, Le Boeuf *et al.* 1988, Hindell *et al.* 1991, McConnell *et al.* 1992, Lydersen and Kovacs 1993, Crocker *et al.* 1997). More recent automated statistical approaches are better suited to large, high-resolution data sets and reduce the potential biases of manual classification (*e.g*., Schreer and Testa 1996, Burns *et al.* 1997, Tinker *et al.* 2007, Thums *et al.* 2008, Weise *et al.* 2010, Villegas-Amtmann *et al.* 2013). The k-means cluster analysis, in particular, can be applied to populations, like the leopard seal, where *a priori* knowledge of diving behavior is lacking (Schreer and Testa 1995).

A comprehensive understanding of marine vertebrate diving behavior is usually not possible with dive profiles alone (Simpkins *et al.* 2001, Watanabe and Takahashi 2013, Viviant *et al.* 2014). Dive data should be augmented, when possible, with other ecological, physiological, or behavioral data in order to maximize confidence in any biological conclusions (Hooker *et al.* 2002). The integration of photographic and video data from animal-borne video systems (*e.g*., CRITTERCAM) has been shown to increase the predictive power of dive data in pinniped systems (Davis *et al.* 2013). Animal-borne video data has improved the classification of vertebrate dive profiles (Baechler *et al.* 2002, Madden *et al.* 2008), and the identification of foraging success (Bowen *et al.* 2002, Davis *et al.* 2003, Parrish *et al.* 2008, Watanabe and Takahashi 2013).

Adult female leopard seals have recently been hauling out with increasing frequency near mesopredator breeding colonies at Cape Shirreff in densities (>20 seals/nautical mile^2, Krause *et al.* 2015) two orders of magnitude higher than those reported by regional surveys (Erickson and Hofman 1974, Forcada and Trathan 2008). The local increase in leopard seal abundance may be part of a geographical redistribution driven by the substantial reduction of pack-ice habitat in the western Antarctic Peninsula (Massom and Stammerjohn 2010, Forcada *et al.* 2012). Reduced sea ice tends to concentrate leopard seals (Bester *et al.* 1995, Meade *et al.* 2015); therefore, the loss of sea ice near Cape Shirreff may have further increased leopard seal density by limiting available haul-outs to coastal beaches.

The summer population of leopard seals at Cape Shirreff is dominated by seasonally-resident adult females that haul-out predictably on land (U.S. AMLR[1] *unpublished data*). Footage of foraging leopard seals from animal-borne video and GPS bio-loggers have expanded land-based observations of predation upon mesopredators to reveal novel foraging strategies including hunting demersal fish, and facultative scavenging (Krause *et al.* 2015). There were also indications of intraspecific competition amongst leopard seals resulting in prey specialization and kleptoparasitism (Krause *et al.*

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[1] The United States Antarctic Marine Living Resources (U.S. AMLR) Program is administered by NOAA Fisheries through the Antarctic Ecosystem Research Division (AERD), SWFSC La Jolla, CA, USA.

2015). Estimating the extent of facultative scavenging (Wilson and Wolkovich 2011) and intraspecific competition (Linnell and Strand 2000, Svanbäck and Bolnick 2005), as well as mesopredator predation, will be important to understanding the ecosystem-level impacts of leopard seals.

Female leopard seals that forage near mesopredator breeding colonies may play a distinct and important role in coastal Antarctic ecosystems. Full-resolution diving records from January and February at Cape Shirreff were examined to describe the foraging behavior of these apex predators. We established basic biological patterns such as: (1) activity budgets and (2) daily haul-out patterns. We also assessed the potential influence of environmental covariates on haul-out behavior. Subsequently, we applied a k-means cluster analysis to our multiyear TDR data and: (3) summarized robust groupings of diving behavior (dive types), and (4) compared results with a subset of video data to test the accuracy of common foraging effort estimators. Finally, recent reports of shared foraging areas, and hunting-tactic specialization in leopard seals suggest that competition may control foraging effort in some areas. To test these assertions, we examined differences in the proportion of dive type, and variability of dive activity by time of day for evidence of individual specialization.

Methods

Research was conducted within the U.S. AMLR Program study area at Cape Shirreff (62.47^{o} S, 60.77^{o} W) on Livingston Island (Figure 2-1). Cape Shirreff holds the largest breeding colony of Antarctic fur seals in the Antarctic Peninsula region along with breeding colonies of chinstrap (*Pygoscelis antarctica*) and Gentoo (*P. papua*) penguins

(ATCM 2011). Leopard seals haul-out on Cape Shirreff beaches, with peak densities occurring in January and February (Krause *et al.* 2015).

Healthy adult female leopard seals known to be seasonal residents were selected for this study during the course of seven consecutive field seasons between 2008 and 2014 in January and February. We recovered 21 high-resolution TDRs from 16 individuals (Table 2-1). Five seals (with tags numbered 422Y, 04OR, 09OR, 390G, and 406Y) were sampled during multiple field seasons. Each TDR was set to record pressure (depth), wet-dry state, and time.

During January and February adult female leopard seals molt their fur, which can limit instrument deployments attached to their pelage. Hence, from 2008 through 2011 seven TDRs (Mk9 (67 x 17 x 17 mm, 30 g),Wildlife Computers (WC), Redmond, WA; sample rate: 30 samples/min) were attached to Global Super Maxi Allflex cattle tags and applied through the interdigital webbing of the hind flippers. These instruments were deployed by stealth without capture, or in conjunction with a single manual intra-muscular (IM) injection of the sedative Midazolam (0.1 – 0.2 mg/kg). Instruments were retrieved without capture, by clipping the Allflex tag mount while the animal slept. While these deployments achieved extended deployment times (Table 2-1), recoveries were difficult and instruments were often lost when the tags pulled free from the flipper (seven recoveries from fourteen deployments).

In order to increase our instrument recovery success and include additional bio-loggers, all instruments after 2011 were glued to chemically immobilized seals. During the 2012 through 2014 seasons fourteen TDRs (Mk9, WC, sample rate: 60 samples/min (*n*=11); or National Geographic CRITTERCAM VI, Washington D.C., sample rate: 60

samples/min (*n*=1); or DST-Milli-TD/100,Star Oddi, Gardabaer, Iceland, sample rate: 12 samples/min (*n*=2)), and VHF transmitters (Advanced Telemetry Systems, Isanti, MN, USA (*n*=14)) were attached to the forward-dorsal midline pelage using Devcon 5-minute epoxy. Each of these fourteen deployments involved two chemical immobilizations per study animal, one for deployment and one for recovery (*n*=28).

Midazolam-Butorphanol Capture Protocol

Leopard seal immobilization captures were completed using a midazolam-butorphanol sedation protocol (Pussini and Goebel 2015). We defined two target levels of chemical induction: 1) preliminary induction, when the animal could safely be approached to set the spinal needle; typically defined by reduced mobility, closed eyes, and toleration of palpitation at the spinal site, and 2) complete induction, when researchers could safely take samples, measurements and attach instruments to the leopard seal; defined by cessation of mobility, and no reaction to palpitation, pain stimulus, or sound. Three captures were omitted from dosage and recovery time calculations due to dart malfunctions, which prevented an accurate estimation of dose.

An initial mean dose of 0.170 ± 0.021 (range: 0.119 – 0.225) mg/kg butorphanol (butorphanol tartarate, 50 mg/mL, Zoopharm, Windsor, CO) and 0.226 ± 0.057 (range: 0.152 – 0.385) mg/kg midazolam (Midazolam HCL C-IV 50 mg/mL, Zoopharm) was administered intramuscularly (IM) *via* a pressurized 5cc pistol dart using an air-compressed compensated dart gun (Dan-inject, Denmark) chosen to minimize disturbance (Higgins *et al.* 2002). The 2 mm x 60 mm collared dart injection needle was selected to provide rapid delivery and to penetrate through the blubber layer without causing undue trauma (Gales 1989). Darted seals were monitored visually for signs of preliminary induction for approximately 10 min. Upon preliminary induction (17.68 ± 6.59 (range: 12 – 38) min), a spinal needle was set in the intervertebral extradural vein of the lumbar region (Sweeney 1974, Hubbard 1968). Additional doses of 0.0026 ± 0.0012 (range: 0.000 – 0.004) mg/kg/min midazolam were administered intravenously (IV) to maintain complete induction. The mean time from dart to complete induction was 29.56 ± 10.12 (range: 15 – 54) min.

All target animals were successfully sedated, and all deployed instruments were recovered. Prior to release each animal was weighed in a sling using a tripod, hand winch, and a tensionometer (MSI-7300 Dyna-Link 2, capacity 1,000 ± 0.5 kg). Postcapture, sedation reversal doses of 0.114 ± 0.014 (range: 0.094 – 0.150) mg/kg naltrexone (50 mg/mL, Zoopharm), and 0.0025 ± 0.0007 (range: 0.0 – 0.0036) mg/kg flumazenil (0.1 mg/ML, Victor Medical, Irvine, CA) were delivered IV. Each animal's recovery was visually monitored until it reached a mobile state. The average recovery time (from reversal injection until recovered) was 4.30 ± 4.27 (range: 1 – 15) min. Excessive mucous production was noted in seal airways during three captures, however, no respiratory distress or tachycardia were observed.

The total duration of these captures (time from initial dart to recovery) ranged from 44 to 108 min depending on the combination of desired tasks (including: deployment and recovery of TDRs, other instruments, morphometrics, and biological samples). After handling, all animals in this study were re-sighted at least once within two weeks of capture in a healthy state. No reduced motor function or infection was observed.

Data Analysis

TDR data were downloaded using software provided by the manufacturer (Wildlife Computers (WC): Mk9 Host v1.09, Mk10 Host v1.26; National Geographic Remote Imaging: Crittercam GUI; Star Oddi: SeaStar v5.24). All dive records were zero-offset corrected (ZOC) for pressure transducer calibration drift (WC Instrument Helper, ZOC method = “automatic”, or R package diveMove (Luque 2007), ZOC method = “visual”). Dives were defined as being ≥6 m (Kuhn *et al.* 2006). Summary files were created (Instrument Helper, WC) by calculating the following variables for each dive: maximum depth, dive duration, bottom time (cumulative time spent below ‘bottom’ portion of the dive calculated from the inflection points on a histogram distribution of time at depth for each dive), wiggle count (the number of ascent-to-descent diversions during the bottom of the dive >1 m), mean wiggle distance, and mean ascent and descent rates.

Haul-out periods were defined as the TDR being continuously out of the water for >2.4 h, a conservative threshold chosen to remove known tag-out-of-the-water intertidal stalking behavior. The haul-out periods during which instruments were deployed or recovered were excluded from analysis because total lengths were unknown. Utilizing time-date stamps, and instrument ‘dry’ periods we calculated the number and length of foraging trips, the number and length of haul-out periods, number of dives per foraging trip, and mean maximum depth per foraging trip.

Subsequent data analysis was conducted using R (R-Core-Team 2015). Haul-out probabilities were calculated empirically by dividing the total of all possible haul-out opportunities into the actual haul-out periods by hour of day. A haul-out opportunity was any hour during which a free-ranging seal was carrying an instrument. Three seals were excluded because they did not have a complete haul-out period during their deployment. To determine if environmental covariates were related to leopard seal haul-out probability, two sets of models were run: 1) all-subsets linear regression models with haul-out probability by hour as the dependent variable and time (in hours) from local apparent noon (*dLAN*), and tide level (in meters) for a given hour as independent variables, and 2) logistic regression models with haul-out by day (yes or no) as the dependent variable, and air temperature (daily mean in ^{0}C), and wind chill temperature (daily mean in ^{0}C) for that day as independent variables. All model assumptions for ordinary least squares regressions were met (Pena and Slate 2014).

Dive observations were filtered to remove tag-derived errors, first by removing dives with ascent or descent rates >6 ms^{-1} (Burns *et al.* 2004), and then to remove other unlikely values (ascent rate = 0, descent rate = 0, wiggles >50/min). Four additional variables were calculated as per Schreer and Testa (1996): bottom time/dive duration (bttmA), bottom time/maximum depth (bttmB), average ascent rate/average descent rate (upq), and average descent rate/average ascent rate (dnq). In order to test for changes in dive behavior on different temporal scales, each observation was classified by hour-of-day, week (number of weeks since the first week of January), month and year (Grolemund and Wickham 2011, James and Hornik 2013). Finally, as a proxy for foraging effort, “wiggle-rate” was calculated by dividing the wiggle count during the ‘bottom’ portion of the dive by bottom time (min). Wiggle count was filtered to select only wiggles ≥1 m to remove the effects of flipper mounted tags from 2008 to 2011. A wiggle-rate value of 2.0 wiggles/min, or one complete vertical diversion away and back from the original trajectory, was considered foraging behavior.

Three data sets were created for further analysis: 1) “full” includes all postfilter dives from all years 2) “cluster” made up of all postfilter dives excluding the 2013 records (seals with tags numbered 394Y, 406Y and 422Y) which were not directly comparable with WC records for k-means cluster analysis because of differences in sample rate and/or formatting, and 3) “parametric” created by randomly subsampling the full data set (~45%) to remove first-order correlations between sequential dive records (maximum depth, duration, and local hour of day). All dive-behavior summaries utilize the full data set, and cluster analyses use the cluster data set. The parametric data set was used for all parametric tests. The level of significance used is $P < 0.05$. All values are listed as mean ($\bar{X}$) ± standard deviation (SD) unless otherwise indicated. SDs reported as summaries across individual seals (*e.g.*, overall mean dive duration) were calculated from all dives.

Maps were constructed (Wickham 2009) using Antarctic coastline data from the Scientific Committee on Antarctic Research (SCAR) Antarctic Digital Database.

K-means Cluster Analysis

The predominant techniques for classifying marine vertebrate diving profiles utilize cluster analysis (Schreer and Testa 1996; Schreer *et al.* 1998, 2001; Davis *et al.* 2003), machine learning algorithms such as Random Forests (RF) (Thums *et al.* 2008, Eguchi *personal communication* [2]), or modeling approaches (*e.g.,* Frost *et al.* 2001, Dowd and Joy 2010). RF algorithms are appealing for classifying large, multi-dimensional diving data sets because they are effective on weak and/or correlated predictors (Lennert-Cody and Berk 2007), and are invariant to monotonic transformations of predictors (Hastie *et al.* 2009). RF, though, must be trained on pregrouped data, and models are typically verified using supplemental data on known foraging behavior. Both RF and modeling approaches require *a priori* knowledge of the system. K-means cluster techniques, on the other hand, do not require *a priori* knowledge. K-means cluster techniques have been used extensively to study diving behavior, which facilitates interstudy comparisons (Schreer *et al.* 2001). And, they have consistently performed better than principal components analysis, discriminant function analysis (Schreer and Testa 1995), shape fitting algorithms (Schreer and Testa 1996), fuzzy c-means clustering, and artificial neural networks (Schreer *et al.* 1998). Given the paucity of *a priori* information about leopard seal diving behavior and the proven performance of k-means clustering, we applied this technique to all dive observations and categorized dives into distinct groups (Schreer and Testa 1995).

Variables were selected for cluster analysis using principal components analysis and retaining those with loadings above the natural break in the data (>0.4) from the four most significant principal components (Everitt and Hothorn 2010). All variables were centered and scaled to unit variance to limit magnitude effects.

The optimal number of clusters was determined by selecting the minimum value of within group sum of squares [WGSS] (Everitt and Hothorn 2010), that corresponds to

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a local maximum of the Calinski Index [$CI = (BGSS/k-1)/(WGSS/n-k)$] where *BGSS* is between groups sum of squares, *n* is sample size and *k* is the cluster number for each cluster grouping (Figure S2-1) (Caliński and Harabasz 1974, Oksanen *et al.* 2013). Results were further evaluated by identifying the minimum classification error rates derived from both an RF (Liaw and Wiener 2002) and a discriminant function analysis (Venables and Ripley 2002) of cluster results. The four cluster parameter was chosen for final analysis (R package kmeans, centers = 4, nstart tuned to 100).

For simplicity, cluster numbers (1-4) were assigned directly as ‘Dive Type’, and each was summarized with descriptive statistics. General dive characteristics and shape were described by manual review of a randomly selected 10% subset of all observations (n = 4,031). For dive-behavior summaries we define “foraging” as both “movement in search of prey” and “prey capture attempts” (Townsend *et al.* 2008). “Exploration” refers to pelagic dives without indications of foraging. Additionally, each observation, per dive type, was ranked by time (in hours) from local apparent noon (*dLAN*), and a Spearman rank correlation was used to test for a diel pattern in dive depth.

Cluster Analysis Performance

K-means cluster analyses do not allow for internal cross-validation (Hastie *et al.* 2009). Therefore, as a proxy for measuring cluster performance, classification error rates and estimates of predictor variable importance were determined using a RF algorithm trained by the cluster-classified observations. Previous studies have used linear discriminant function analyses for this purpose (Schreer and Testa 1996, McGarigal *et al.* 2000, Jay *et al.* 2001), however, RF are more appropriate. For example, predictor interactions are automatically captured in RF and results are easy to visualize (Verikas *et al.* 2011). Furthermore, predictions are internally cross-validated in a robust and straight forward way (Breiman 2001). The RF was implemented with ntree = 500 and mtry = 4. All response and predictor variables were coerced as factors as per Liaw and Wiener (2002).

Random forests can be used to estimate classification error by holding out a random subset of the bootstrap data for each tree. This cross-validation sample is used to check the predictions of that tree, results are aggregated across the forest and an error rate returned for each classification category (Breiman 2001). An estimate of the importance of each predictor can also be calculated by individually excluding each predictor from the analysis in turn and recording the marginal decrease in prediction accuracy (Breiman 2003).

Animal-borne Video

Four of the leopard seals that collected TDR data used in the cluster analysis, also carried animal-borne video cameras. The deployment of these instruments (Marshall *et al.* 2007) and analysis of the data recorded by them has been described in detail (Krause *et al.* 2015). Cluster and wiggle-rate derived predictions of leopard seal behavior were compared to previously-scored, temporally-overlapping CRITTERCAM footage.

For video scoring, “foraging” behavior was defined as searching with intent to locate prey, including a low to medium rate of speed, directional changes indicating searching, or following benthic relief. Prey capture attempts and feeding were combined with “foraging” to facilitate comparison with cluster analysis results. There were two categories of “foraging”: “benthic”, clearly focused on the sea floor; and “pelagic”, in open water with no benthos visible during the dive. “Traveling” indicated movement from one place to another without prey searching en route, including, a high rate of swimming speed without sign of searching behavior. Behaviors that included a dive but were primarily focused at the surface (*e.g.,* surface feeding, intertidal searching, waiting, resting) were combined into an “other” category.

Dive Activity

The total numbers of dives per hour of day were plotted on a 24-hour rose plot using the full data set (*n*=40,308 dives) for each individual (*n*=21 seals) and all individuals pooled by year (*n*=7 years). Mean vectors (representing the average time and frequency of dive activity) were calculated for each plot (Agostinelli and Lund 2011). Differences in the temporal distribution of dive activity in the parametric data set were tested using either an unbalanced one-way ANOVA and a Tukey’s Honest Significant Difference (HSD) test, where treatment groups were day (0800 - 1959), night (0000 - 0359) and crepuscular (± 1 h from sunset and sunrise, 0400 - 0759 and 2000 - 2359), or a Watson’s two sample test of homogeneity. The Watson’s tests were applied to examine differences in dive activities between defined groups of seals. First, dive activities were pooled for years with ≥2 seals and >5,000 dives (2010, 2011, 2014) and compared, and then individual seals within a given year were evaluated (*n*=3 seals in 2010, *n*=2 seals in 2011 and *n*=9 seals in 2014).

Results

The average deployment period for all TDRs was 13.65 ± 11.45 d (Table 2-1). The full data set contained 40,308 postfilter dives recorded on 229 foraging trips. Dive durations averaged 2.20 ± 1.23 min. Despite consistently brief diving (Figure S2-2), two animals dove in excess of 20 min, including the longest recorded dive by a free-ranging leopard seal at 22 min 58 s (previously ~ 15 min (Nordøy and Blix 2009)). However, all dives >15 min in length (*n*=7) exhibited extended periods at a single shallow depth (<5 m) which may represent sleeping behavior (*e.g.,* Figure S2-3). The mean of the maximum dive depth of each seal was 16.60 ± 10.99 m, and the maximum dive depth was 229 m. Leopard seal dives were shallow with 90.1% ≤30 m depth, and 97.6% ≤60 m depth (Figure S2-4). The mean foraging trip duration was 17.0 ± 11.8 h.

An empirical probability distribution of haul-out time featured a distinct peak centered at 1400 local time (70.56%). This pattern was consistent across years, individuals, and months (Figure 2-2a). The only significant environmental driver of haul-out probability was *dLAN*, and the most informative model was a polynomial regression [$haul\text{-}out\ probability = 71.01 - 1.5dLAN^2 + 0.10dLAN^3$] ($R^2 = 0.985$, $P < .000001$, Figure 2-2b, (Fox and Weisberg 2011)). Haul-out periods lasted an average of 14.4 ± 9.6 h.

Leopard seals spent 45.0 ± 12.1 (range: 24.7-72.2) % of their deployment time hauled out, 34.3 ± 6.4 (range: 21.4 - 42.7) % of the time at the surface of the water, and 20.7 ± 9.6 (range: 6.4 - 40.7) % of the time diving.

The cluster data set had 38,338 dives from 18 individual seals, and the parametric data set contained 18,143 dives from all 21 seals.

K-means Cluster Analysis

The eight variables selected for dive classification analysis were: maximum depth, duration, bottom time, bottom time/dive duration (bttmA), bottom time/maximum depth (bttmB), average ascent rate/average descent rate (upq), wiggle count, and average descent rate. The proportion of dives classified into each dive type was consistent across all individuals in the study (Figure 2-3). Category names and descriptions of the four dive types are in Table 2-2. Type 1 dives were the deepest dives of the study, and were consistently symmetrical and round or square-bottomed in shape with limited foraging effort at depth; the depth range was 80 – 229 m (*e.g.*, Figure S2-5a). Type 2 dives were symmetrically round or "v" shaped dives; the depth range was 39 – 79 m (*e.g*., Figure S2-5b). Type 3 dives were predominantly nonsymmetrical dives displaying a wide variety of shape; the depth range was 16-38 m (*e.g.*, Figure S2-5c). Type 4 dives were by far the most common across all animals in the study. They were characterized as shallow and symmetrical with extended time at a single bottom depth (*e.g.*, Figure S2-6). They frequently occurred in long bouts (>5) separated by a short bout of type 3 dives; the depth range was 6-17 m. With the exception of types 3 and 4, each dive type has a nonoverlapping depth range. Patterns in dive shape by dive type were consistent; however, variance in dive shape was present across all animals. Rank correlation tests per dive type of mean maximum depth *vs*. *dLAN* for leopard seals showed a diel pattern of deeper dives near noon for types 3 and 4 (Table 2-2).

Dives with a wiggle-rate value >2.0 wiggles/min were considered “foraging”, while those ≤2.0 wiggles/min were classified as “nonforaging”. Predicted behaviors were assigned to all dives per dive type (Figure 2-4a).

Cluster Analysis Performance

The cluster-trained RF classified all dives correctly 99.94% of the time, suggesting that the k-means cluster analysis created robust classifications. The most important predictor variable was mean maximum depth followed by wiggle count and dive duration (Figure S2-7).

Animal-borne Video

All dives classified to dive type by cluster and wiggle-rate analyses were compared with corresponding video footage when available (n=309 dives). There was only type 1 dive, which was a pelagic foraging dive. Type 2-4 dives were predominantly scored as pelagic foraging (range: 63.7% – 92.3 %) with a smaller proportion of dives classified as traveling (range: 7.7% – 15.3 %).

Dive Activity

The mean dive rate was 11.65 ± 3.09 dives/h with individuals ranging widely from 3.1 to 18.7 dives/h. Dive activity for all animals was higher during crepuscular and night periods (Figure 2-5a) than during the day (Tukey’s HSD, day-crepuscular and day-night: $P < 0.0001$). The angular distribution of dive activities pooled between seasons showed no significant difference from each other or the overall pattern (Figure 2-5 b-d).

However, the dive activities of individuals compared within the same year were concentrated at significantly different times of day (*e.g.*, Figure 2-6).

Discussion

The diving and haul-out behavior patterns observed at Cape Shirreff are consistent with those from earlier studies while differing notably in magnitude and detail. Leopard seal behavior falls into three main categories: at-surface, haul-out, and diving. The at-surface behavior of leopard seals at Cape Shirreff was recently summarized (Krause *et al.* 2015 and references therein).

Haul-out behavior

The pattern of haul-out probability across all animals, months and years was higher during the day than at night and highest near midday (1500 – January; 1300 – February) in agreement with previous reports (Rogers and Bryden 1997, Kuhn *et al.* 2006, Nordøy and Blix 2009). However, in contrast to a finding that wind chill index was negatively related to haul-out probability (Rogers and Bryden 1997), time (in hours) from local apparent noon (*dLAN*) was the only significant covariate, accounting for 98.5% of the variance in the data. The effect of temperature on leopard seal haul-out probability may be limited to the colder, southern extent of the leopard seal range where the previous study was undertaken.

A comparison between our results and the Nordøy and Blix (2009) satellite-linked histogram data shows substantial differences during February. Both studies report on adult female leopard seals, albeit in different locations and years. While the Nordøy and

Blix (2009) haul-out probabilities dropped to zero at night, they rarely dropped below 20% at Cape Shirreff. Additionally, the Nordøy and Blix (2009) probability midday peaks were lower by a factor of two (40% *vs.* 80%). Haul-out probabilities are integral tools in the process of correcting regional phocid censuses (Southwell *et al.* 2012). There are many biological and environmental factors that may explain the observed differences; however, these disparities emphasize the need to study haul-out behavior on the local as well as regional scale.

Diving behavior

When analyzing the diving behavior of vertebrates, a diel pattern of decreasing dive depth at night implies the pursuit of a vertically migrating prey, such as krill or myctophid fishes (Kooyman 1989). While diel depth patterns were detected for dive types 3 and 4, the actual change in depth across 24 h was small: <3 m for dive type 3, and <1 m for dive type 4. These patterns reflect pursuit of prey at relatively static depths, not vertically migrating prey. Such small but consistent changes in dive depth may result from the slightly deeper foraging by a visual predator with greater light availability near midday.

Compared to other phocids, the diving behavior of leopard seals at Cape Shirreff was both shallow and brief, in accordance with previous reports (Kuhn *et al.* 2006, Nordøy and Blix 2009). Despite this general similarity, leopard seal dives at Cape Shirreff were notably shallower than previous observations across a number of indicators. The mean maximum depth was >20 m shallower than previous studies, the overall maximum depth was >70 m shallower, and the percentage of dives shallower than 50 m was >32% higher. The extremely coastal distribution of leopard seals at Cape Shirreff (Krause *et al.* 2015) suggests that such shallow dives were consistent with the available depth (*i.e*., benthic diving), which is <50 m over the observed foraging area (Warren and Demer 2010). Accordingly, these observations may not represent the diving behavior of leopard seals foraging in pack ice where bottom depths are typically much deeper.

K-means Cluster Analysis

Two-dimensional dive profiles, like those summarized in Table 2-2, contain only limited behavioral information (Simpkins *et al.* 2001, Davis *et al.* 2003). To reduce the risk of over-simplifying diving behavior, we reviewed the TDR data in concert with available corresponding data. For example, changes in vertical movement (wiggles) and time at depth have been used to represent concentrated foraging effort at depth in a variety of pinniped systems (Bonner 1990, Hindell *et al.* 1991, Bengtson and Stewart 1992, Le Boeuf *et al.* 1992, Fedak *et al.* 2001, Hanuise *et al.* 2010). Wiggle rates increased with decreasing depth, suggesting that foraging effort for these leopard seals was focused in the shallow portion of their depth range.

Infrequent deep dives

Despite the predominantly shallow dive repertoire of leopard seals in this study, occasional deep dives (>80 m) were recorded. All were classified as type 1 and most were “round” in shape. These occasional deep dives were generally isolated or occurred in short bouts. Generally, these dive profiles did not exhibit foraging activity at depth (wiggle-rate ≤2), or steep ascent or descent rates. Type 1 dives are noteworthy because they are consistent with both previous leopard seal diving studies (Kuhn *et al.* 2006, Nordøy and Blix 2009) and seem to correspond to “Type IV” dives reported by Bengston and Stewart (1992) for crabeater seals (*Lobodon carcinophaga*). The occurrence of these dives even within our coastal and shallow-diving study population may provide additional context for understanding this behavior.

Several theories have been put forth to explain occasional deep dives including prey chase, killer whale (*Orcinus orca*) avoidance (Nordøy and Blix 2009), escape from ice noise, navigational orientation, and obtaining access to improved acoustic conditions (Bengtson and Stewart 1992). Many of these situations do not apply at Cape Shirreff. It is unlikely that the type 1 dives we recorded involve prey chase, or killer whale avoidance given that average descent rates did not exceed the overall study mean (0.64 m/s and 0.73 m/s respectively). Furthermore, killer whales have not been observed hunting in proximity of Cape Shirreff since the camp was established in 1997 (U.S. AMLR *unpublished data*). Leopard seals would have no need to escape ice-created noise at Cape Shirreff given its rare summer occurrence, nor need to orient for navigation given their restricted seasonal distribution. It does, however, seem plausible that type 1 dives allow the seals to enter more favorable acoustic conditions that may facilitate intraspecific communication, as suggested by Bengston and Stewart (1992) for crabeater seals.

Pinnipeds have evolved keen listening skills which support social interactions and foraging behaviors (Schusterman 2000). The bottom sections of all recorded type 1 dives were deeper than the typical surface mixed layer and thermocline at Cape Shirreff (Warren *et al.* 2009). Broadcast vocalizations are utilized by leopard seal males and females to facilitate mating (Rogers *et al.* 1996, Rogers *et al.* 2013), and their breeding season may overlap with this study. In East Antarctica mating likely takes place between November and January (Southwell *et al*. 2003), but may take place from January through March in other areas (Shirihai 2002). The deep and offshore characteristics of these type 1 dives may allow females to listen for singing males whose loud, low frequency (Stirling and Siniff 1979, Rogers 2007, Rogers 2014) mating vocalizations can spread over hundreds of km^2 (Rogers *et al*. 2013).

Foraging dives

In contrast to other phocids in the Antarctic Peninsula region which target vertically migrating prey (Bengtson and Stewart 1992, Asaga *et al.* 1994, Kuhn *et al.* 2006), leopard seals at Cape Shirreff focused on prey at relatively static depths; this suggests a benthic foraging strategy (Costa and Gales 2003). Correspondingly, type 3 dives showed a wide variety of dive shapes. Bathymetry has been shown to affect dive shape in some pinnipeds (Goebel *et al.* 2000, Sala *et al.* 2011), and it is assumed to define dive shape in known benthic foragers (Jay *et al.* 2001). The lack of biologically significant diel change in dive depth, variable dive shape, and the correspondence of dive depth to bottom depth suggest that both foraging (42.9%) and nonforaging (56.1%) type 3 dives are consistently focused on the benthos. The nonforaging type 3 dives may be traveling dives. Type 2 dives seem to be a transitional grouping between types 1 and 3 with some characteristics of both.

Type 4, or rectangular dives, were by far the most common dive type, which agrees with the previously noted trend of an increasing percentage of rectangular dives with body size (Schreer *et al.* 2001). The nonforaging type 4 dives (37.3%) were shallow and flat in shape. These characteristics typically describe traveling dives (Bengtson and Stewart 1992, Burns *et al.* 1997). Cape Shirreff is surrounded on all sides by reefs that extend up to 3 miles offshore; such traveling dives may allow the seals to conserve energy by swimming below (6-10 m) the turbulent surf zone. Some adult female leopard seals also come into estrus at this time of year, and advertise that status by vocalizing (Rogers *et al*. 1996). These wiggle-free type 4 dives frequently occur in long bouts; therefore, it is possible that they represent stationary female singing behavior (Rogers 2007). The remaining 62.7% of foraging type 4 dives, over 45% of all dives in the study, require further investigation.

Based on previous reports for leopard seals in the Antarctic Peninsula region, the most likely foraging behaviors associated with shallow square dives are krill foraging (Laws 1984, Siniff and Stone 1985, Casaux *et al.* 2009) and ambush hunting of penguins (Kooyman 1965, Hiruki *et al.* 1999). Hunting behavior focused on Antarctic fur seal pups, although common at this time of year (Hiruki *et al.* 1999, Vera *et al.* 2005), does not typically involve diving below 6 m (Krause *et al.* 2015). An alternative hypothesis for these dives, based on video evidence, is benthic foraging for demersal prey (Krause *et al.* 2015). Acoustic scatters of small pelagic organisms recorded near-shore at Cape Shirreff exhibited pronounced daily vertical migrations[3]. Given a lack of corresponding diel depth change for type 4 dives, krill foraging is unlikely. An ambush behavior focused on penguins should increase during periods of peak penguin activity (Mader 1998, Ainley *et al.* 2005). Pygoscelid penguins tend to depart and return to the colony during mornings and afternoons, but rarely at night (Trivelpiece *et al.* 1986, Jansen *et al.* 1998). The

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frequency of type 4 dives peaked at 0214 with no peaks during daylight hours, suggesting that penguin hunting is not closely linked to rectangular diving. The hypothesis that dive types 3 and 4 (93.3% of dives in the study) represent benthic foraging, though, is consistent with previous reports based on animal-borne video (Krause *et al.* 2015). Finally, there was a high level of consistency across individuals in the proportion of their dives by dive type (Figure 2-3), which does not support individual specialization of foraging behavior. However, signals of specialization in dive type may be masked by the extensive influence of local bathymetry.

Although preliminary, video-based behavioral observations indicated that predictions of dive behavior based on TDR data alone should be viewed with caution (Figure 2-4 a and b). Unfortunately, type 1 and type 2 dives had extremely small sample sizes (*n* = 1 and 13 respectively). Video-based behavior results for dive types 3 and 4 supported the predicted focus on benthic foraging (72.4% and 63.7% respectively). However, as with Antarctic fur seals (Viviant *et al.* 2014), the wiggle-rate analysis lacked resolution to identify prey capture attempts and consistently underestimated foraging behavior. Correspondingly, wiggle-rate overestimated likely traveling dives when compared with video data (*e.g.*, 37.3% *vs.* 11.4% respectively for type 4 dives). However, agreement between TDR and video data increased as the corresponding video sample sizes increased (*e.g.,* 63.7% *vs.* 62.7% benthic foraging for type 4 dives). As video sample sizes grow, it may be possible to calibrate the wiggle-rate parameter to refine and improve the predictive power of time-depth records.

Temporal diving activity comparisons

The daily foraging patterns of large carnivores have important implications for their foraging success, and for illustrating the influence of sympatric competitors (Mills and Biggs 1993, Kotler *et al.* 1993, Linnell and Strand 2000). In fact, for some carnivores time of day is more important to hunting success than hunting tactic (Van Orsdol 1984). The mean dive rate for leopard seals at Cape Shirreff was significantly higher during crepuscular and night periods than during the day. Therefore, as with many predatory carnivores (Stirling 1974, Bertram 1979, Bengtson and Stewart 1992), foraging effort for leopard seals follows a daily cycle that may reflect the availability of target prey.

High predator density and limited access to resources seem to be generating intraspecific competition between leopard seals at Cape Shirreff (Krause *et al.* 2015). Competition for limited resources results from an overlap in target prey, space use, and time (Trivelpiece *et al.* 1987, Townsend *et al.* 2008, Miller *et al.* 2010, Santora *et al.* 2010, Villegas-Amtmann *et al.* 2013). Such conflicts are particularly intense among carnivores due to the high likelihood of niche overlap (Schoener 1983) and the potential for injury from dominant carnivores (Linnell and Strand 2000). Populations tend to alleviate competitive pressure by expanding their niche width through individual specialization for alternative prey, expanded habitat use, and temporal access to resources (Palomares and Caro 1999, Svanbäck and Bolnick 2005, Svanbäck and Bolnick 2007). Prey and space use specialization by leopard seals have been observed near mesopredator breeding colonies (Rogers and Bryden 1995, Hiruki *et al.* 1999, Krause *et al.* 2015), but temporal shifts have not been examined.

If niche overlap in competitive carnivore systems does not allow for sufficient separation in prey selection or space, competitors may adjust their daily activity patterns (Johnson *et al.* 1996). Temporal niche partitioning is well established in plant, insect (Albrecht and Gotelli 2001, Townsend *et al.* 2008) and small mammal populations (Rudzinski *et al.* 1982, Kotler *et al.* 1993) that can be easily monitored or tested in controlled environments. However, it has been more difficult to describe in free ranging carnivore systems (Palomares and Caro 1999). While some field studies found no apparent time-based shift (Major and Sherburne 1987, Litvaitis and Harrison 1989, Hass 2009, Schmidt *et al.* 2009, Wikenros *et al.* 2010, Mattisson *et al.* 2011), compelling evidence for temporal niche partitioning has been reported (Mills and Biggs 1993, Kozlowski *et al.* 2008), especially in systems where the competing carnivores were similar in body size or relatedness (Rudzinski *et al.* 1982, Scognamillo *et al.* 2003, Harmsen *et al.* 2009).

We examined the likelihood that individual leopard seals are temporally adjusting their foraging effort in order to avoid intraspecific competition and gain access to a spatially-limited hunting area at Cape Shirreff. As with previous studies (Kooyman 1981, Rogers and Bryden 1995, Hiruki *et al.* 1999), during 2013-14 we observed only a small subset (range: 1 – 5) of the known adult female leopard seals in the area (range: 12 – 25) actively hunting at any given time (U.S. AMLR *unpublished data*). Tracking all individuals over time was not possible, but the proportions of active to resting seals were similar during the day throughout January and February. It follows that when an individual leaves the hunting ground to haul-out and rest, it is replaced by a seal from the larger population. During a previous study at Cape Shirreff, individual leopard seals were observed to consistently forage at particular times of day (Vera *et al.* 2005). Additionally, TDR-derived patterns of dive activity for individual leopard seals were striking.

The dive activity patterns of multiple individuals pooled within a given year were extremely consistent (Figure 2-5) suggesting that prey availability, search profitability, or some other aspect of foraging was predictably better during those times of day. While sample sizes remain small, no individual's dive activity aligned with the pooled activity pattern or another seal's (*e.g.*, Figure 2-6); therefore it seems that foraging activity was shared over time. Although records of the temporal foraging activity of leopard seals remain limited and intraspecific mechanisms are not well understood, these observations suggest that there are key foraging times during the summer at Cape Shirreff, and that individuals may temporally shift their activity to gain access to hunting areas.

Summary

The widely-used, k-means cluster dive classification technique produced robust classifications of leopard seal diving behavior. Animal-borne video evidence suggests that wiggle analysis alone may underestimate foraging behavior, though increased video sample sizes are needed. Leopard seals at Cape Shirreff appear to have a shallow dive repertoire, and they haul-out in a pattern that is predictable and positively correlated with available daylight.

Although leopard seals have largely been reported as pelagic and surface foragers, there was a high proportion of benthic foraging at Cape Shirreff. Similar behavior may be common near other mesopredator colonies in shallow, coastal areas, and, such areas may be expanding as sea ice loss restricts leopard seals towards the coast in the western Antarctic Peninsula (Meade *et al.* 2015). The prevalence of benthic foraging at Cape Shirreff emphasizes the potential for top-down ecosystem impacts beyond direct predation. The two most probable explanations for the high proportion of benthic foraging are hunting demersal notothen fishes, which may create resource competition with sympatric seabirds (Krause *et al.* 2015), and facultative scavenging. Scavenging by leopard seals represents a potentially vital energy pathway (DeVault *et al.* 2003, Wilson and Wolkovich 2011), and there is some evidence that it occurs in both coastal and pack ice regions (Krause *et al.* 2015). Therefore, this population of leopard seals exhibits a bimodal foraging strategy that is split between hunting mesopredators at dawn and dusk using at-surface tactics (Vera *et al.* 2005, Krause *et al.* 2015), and benthic searching during crepuscular periods and at night.

Broad scale mammalian diving studies suggest that dive patterns in marine vertebrates converge for those occupying similar ecological niches (Kooyman 1989, Schreer *et al.* 2001). Therefore, we expect leopard seals that hunt mesopredators to diverge from other seals given their unique position as apex predator. In large part, this appears to be the case. Although leopard seal dive depths and activity patterns overlap with those reported for crabeater (Bengtson and Stewart 1992, Burns *et al.* 2004) and Antarctic fur seals (Boyd *et al.* 1994), the variety of dive shapes is more complex. Furthermore, leopard seals did not exhibit the extensive diel changes in dive depth reported for other pinnipeds in the Antarctic Peninsula. And, while sample sizes remain small, we've seen evidence of individual specialization in foraging effort by time of day from land-based observations and dive records.

Despite greatly expanding our knowledge of leopard seal diving behavior, all such profile-based analyses are speculative to some degree. Given the potential impact that leopard seals could have on coastal ecosystems around the Antarctic, we suggest expanding current studies to integrate diet data, and increased animal-borne video and acoustic data sets to verify and quantify the ecosystem effects of these seals.

Chapter 2, in full, is a reprint of the material as it appears in Marine Mammal Science 2016. Krause, Douglas J.; Goebel, Michael E.; Marshall, Gregory J.; Abernathy, Kyler. The dissertation author was the primary investigator and author of this material.

Acknowledgements

This paper was greatly improved by suggestions and comments by T. Eguchi, L. Ballance, P. Dayton, G. Watters and three anonymous reviewers. We are grateful to K. Pietrzak, M. Mudge, J. Wright, N. Cook, M. Zimmerman, M. Goh, T. Joyce, R. Burner, B. McDonald, N. Pussini, R. Buchheit, D. Vejar and J. Hinke for their assistance in the field. We thank N. Lyon, N. Miao, K. Searles and L. Rodriguez for manually classifying dive and video data. Crucial financial, infrastructure and logistical support was provided by the U.S. AMLR Program. Funding for instruments and travel was provided by the National Geographic Society (NGS)/Waitt Grant # W256-12 and the Mary Maude and Vestal B. Hughes Pay-It-Forward Grant. Transportation to our study site was kindly provided by Lindblad/NGS Expeditions, and logistical support by NGS Remote Imaging. Leopard seal observations and captures were conducted in accordance with Marine Mammal Protection Act Permit Nos. 16472-01 and 774-1847-04 granted by the Office of

Protected Resources, National Marine Fisheries Service, the Antarctic Conservation Act Permit Nos. 2012-005 and 2008-008, and the NMFS-SWFSC Institutional Animal Care and Use Committee Permit No. SWPI2011-02.

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Tables

Table 2-1: Individual seal identification and summary deployment statistics for time-depth records recovered from leopard seals between 2008 and 2014 (*n*=21). Values are mean ($\bar{X}$) ± standard deviation (SD).

Seal id - Year	Deployment Length (d)	No. of Dives	No. of Foraging Trips	Mean Haul-Out Duration (d)	Foraging Trip Mean Duration (d)	Mean Max. Depth of Dive (m)	Max. Dive Depth (m)	Mean Dive Duration (min)	Max. Dive Duration (min)	Mean Dive Rate (dives/h)
396G – 2008	10.57	1167	9	0.61 ± 0.41	0.63 ± 0.37	14.00 ± 7.70	61	2.19 ± 1.22	20.07	9.40
422Y – 2009	30.83	3380	19	0.86 ± 0.80	0.81 ± 1.14	33.60 ± 28.83	215	3.06 ± 1.75	9.97	9.50
04OR – 2010	18.34	5094	14	0.51 ± 0.15	0.84 ± 0.68	13.20 ± 10.53	163	2.10 ± 0.92	6.93	18.70
09OR – 2010	29.31	5074	28	0.45 ± 0.36	0.61 ± 0.56	17.20 ± 11.84	229	2.11 ± 1.35	9.77	13.50
390G – 2010	37.68	3205	27	0.70 ± 0.63	0.72 ± 0.49	15.00 ± 7.81	58	2.50 ± 1.38	22.97	7.20
13OR – 2011	31.66	4502	29	0.55 ± 0.26	0.56 ± 0.24	13.90 ± 7.79	74	1.56 ± 0.83	5.33	12.10
390G – 2011	29.37	2043	31	0.51 ± 0.29	0.44 ± 0.42	15.40 ± 8.10	61	2.41 ± 1.44	9.10	3.10
04OR – 2012	19.38	3754	11	0.48 ± 0.36	1.33 ± 0.67	13.80 ± 9.88	88	2.45 ± 1.05	6.40	11.80
62OR – 2012	13.15	1396	14	0.55 ± 0.35	0.43 ± 0.24	16.10 ± 9.94	61	1.16 ± 0.94	6.07	10.00
394Y – 2013	4.69	1232	2	0.59 ± NA	1.94 ± NA	13.12 ± 6.46	47	2.48 ± 2.43	10.02	13.22
406Y – 2013	1.94	616	1	NA	1.94 ± NA	12.18 ± 8.23	82	1.08 ± 1.16	7.15	13.24
422Y – 2013	0.86	138	1	NA	0.86 ± NA	14.13 ± 9.31	52	1.54 ± 1.41	5.47	7.33
09OR – 2014	8.53	1834	6	0.45 ± 0.20	1.05 ± 0.78	15.90 ± 6.70	57	2.06 ± 1.07	6.98	12.20
16OR – 2014	4.32	1064	1	NA	4.32 ± NA	17.70 ± 12.21	84	3.07 ± 1.41	7.85	10.27
18OR – 2014	7.53	1393	6	0.48 ± 0.22	0.86 ± 0.97	19.20 ± 11.00	59	2.43 ± 1.43	14.57	11.30
37OR – 2014	4.28	472	3	0.86 ± NA	0.85 ± 0.66	15.00 ± 8.76	49	2.25 ± 1.12	6.15	9.90
63OR – 2014	8.55	1010	9	0.55 ± 0.25	0.46 ± 0.19	15.90 ± 9.43	57	1.86 ± 1.02	5.97	10.70
84OR – 2014	8.46	751	8	0.65 ± 0.37	0.49 ± 0.19	17.80 ± 11.95	60	1.74 ± 1.18	7.77	8.20
397G – 2014	5.49	290	3	1.98 ± NA	0.51 ± 0.06	14.60 ± 10.50	59	1.75 ± 1.09	5.87	8.00
401Y – 2014	3.92	650	2	1.64 ± NA	1.14 ± NA	16.10 ± 8.61	59	2.75 ± 1.26	6.77	11.90
406Y – 2014	7.71	1269	5	0.67 ± 0.49	1.01 ± 0.53	14.10 ± 7.62	56	2.12 ± 1.26	7.05	10.90
	13.65±11.45	40308	229	0.60 ± 0.40	0.71 ± 0.49	16.60 ± 10.99	229	2.20 ± 1.23	22.97	11.65±3.09

Table 2-2: Summary statistics and descriptions of the 4 dive types output from k-means cluster analysis (*n*=38,338). “Shape” indicates the most common dive profile shapes. “Animals” lists the identities of individuals that exhibited a given dive type. “Diel Depth Pattern” indicates whether the mean maximum depth of that dive type was significantly correlated with time (h) from local apparent noon (Spearman rank correlation, significance $P<0.05$, n=18,139). Bottom time, and wiggle-rate values are listed as mean ($\bar{X}$) ± standard deviation (SD).

Dive Type	*n*	Description	Shape	Depth Range (m)	Animals	Diel Depth Pattern	Bottom Time (min)	Wiggle-rate (wiggles/min)
1	472	Round		80-229	422Y, 4OR, 9OR, 16OR, 406Y	NO r=-0.140 p=0.5125	2.93 ± 1.42	1.14 ± 1.00
2	2,093	U		39-79	All	NO r= 0.1887 p= 0.3755	2.20 ± 1.35	2.35 ± 3.61
3	8,256	Skew		16-38	All	YES r= -0.6139 p= 0.0018	1.71 ± 1.16	3.06 ± 5.88
4	27,517	Rectangular		6-17	All	YES r= -0.6643 p= 0.0005	0.93 ± 0.91	7.69 ± 23.80

Figures

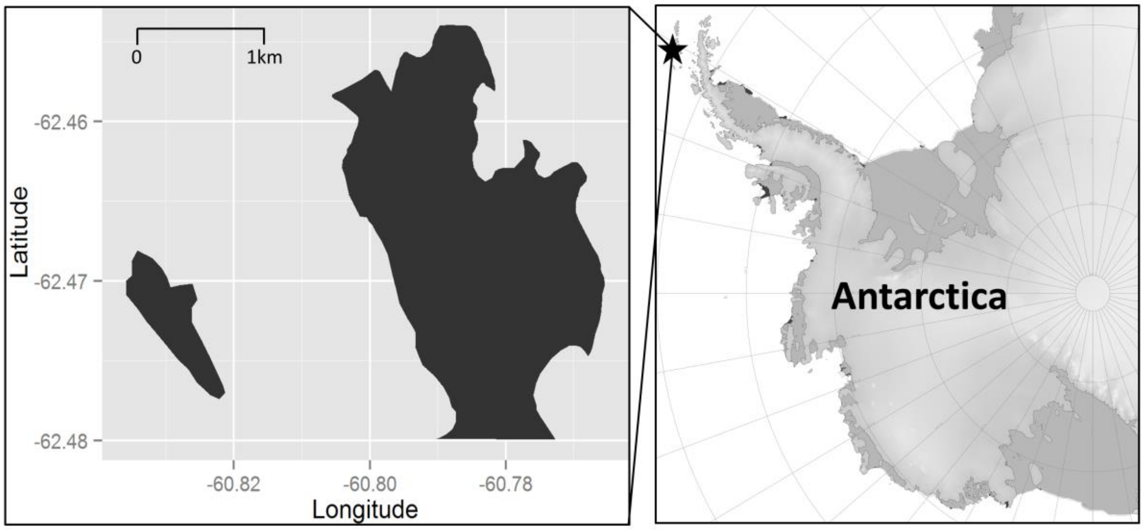

Figure 2-1: Cape Shirreff, Livingston Island, Antarctica. The black star in the right pane indicates the location of Cape Shirreff in the western Antarctic Peninsula region.

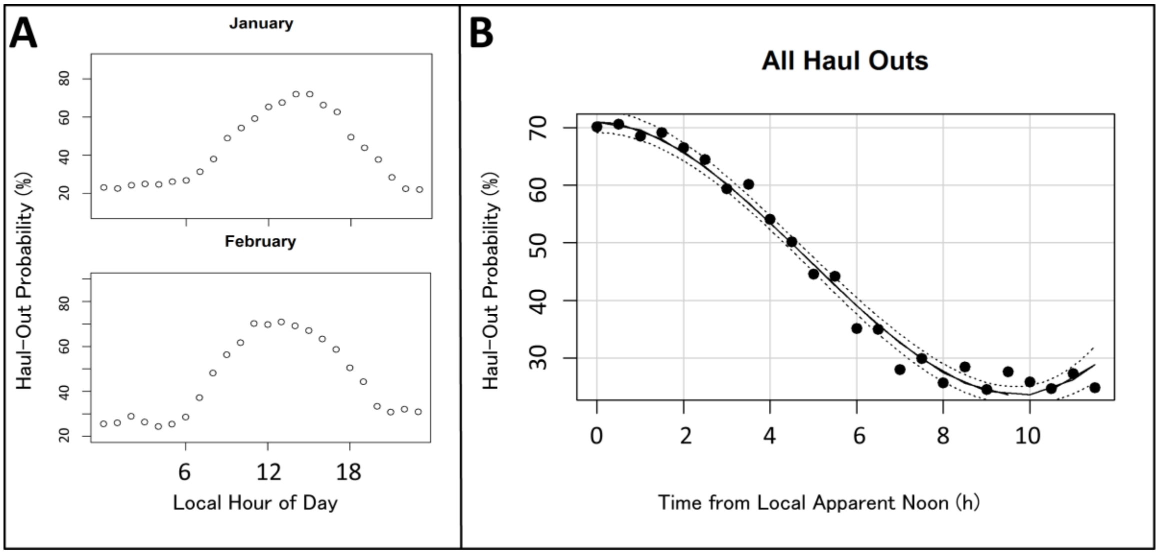

Figure 2-2: (A) Empirical haul-out probability distributions for leopard seals at Cape Shirreff based on 209 haul outs from 18 animals in January and February from 2008 to 2014. (B) A polynomial linear regression (solid line) with *y* = haul out probability and *dLAN* = time (h) from local apparent noon; 95% confidence intervals (dashed lines).

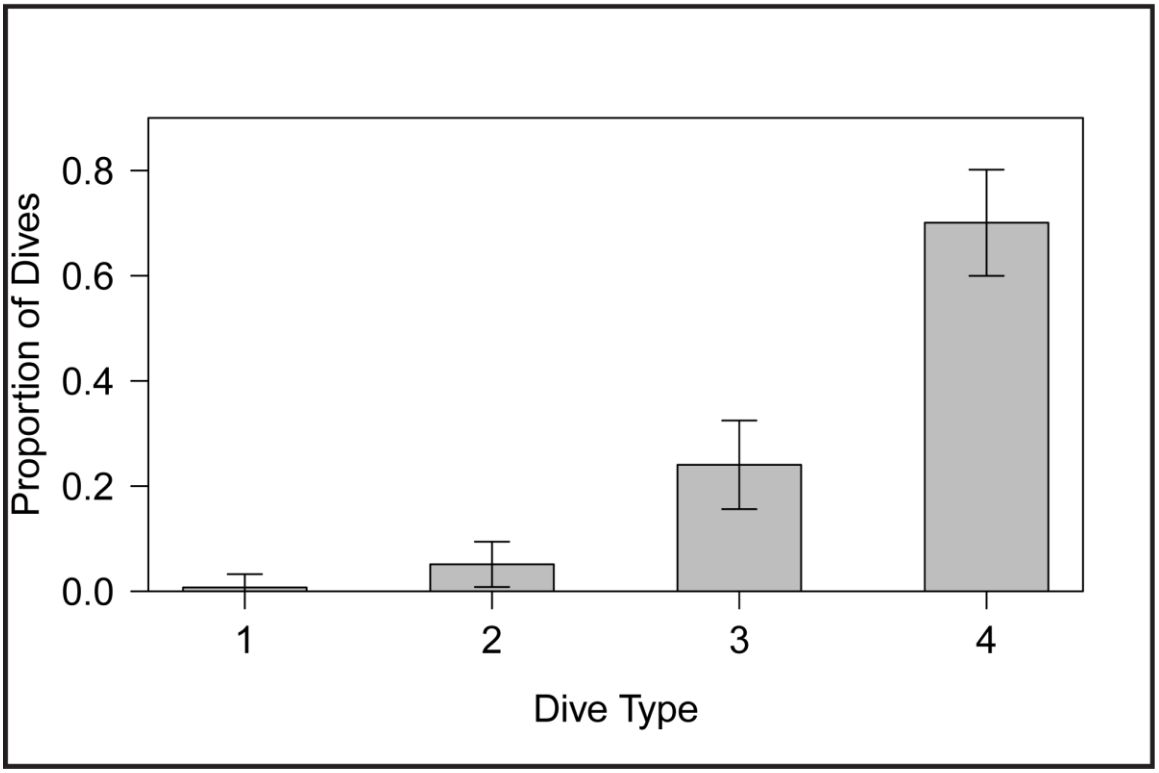

Figure 2-3: The mean proportion (with SD whiskers) of dives that were classified into each dive type (1-4) for all dives in the cluster data set (*n*=38,338).

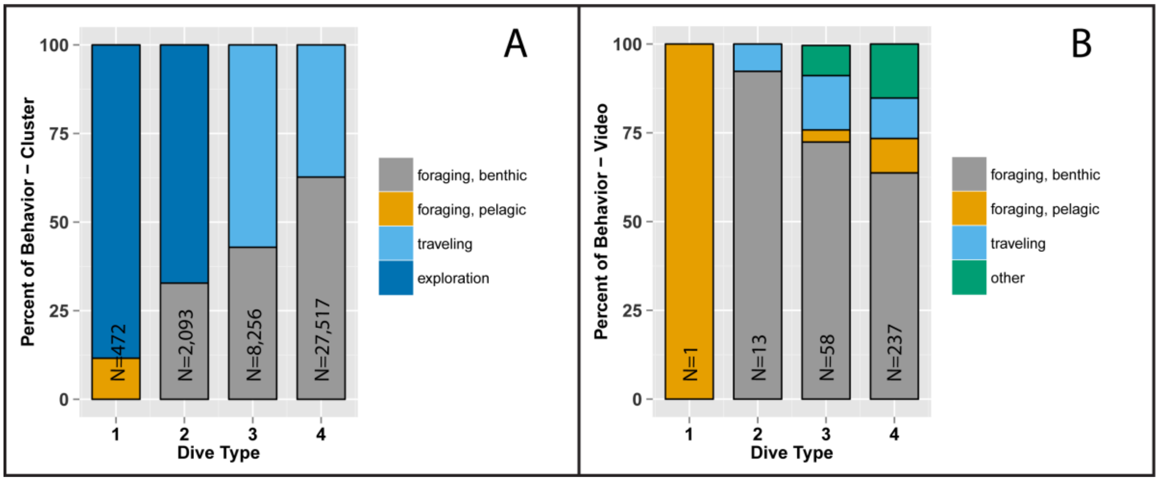

Figure 2-4: Comparison by dive types between A) behavior predicted from the k-means cluster analysis of time-depth dive records (*n*=38,338) and B) behavior manually scored from animal-borne video dive data (*n*=309).

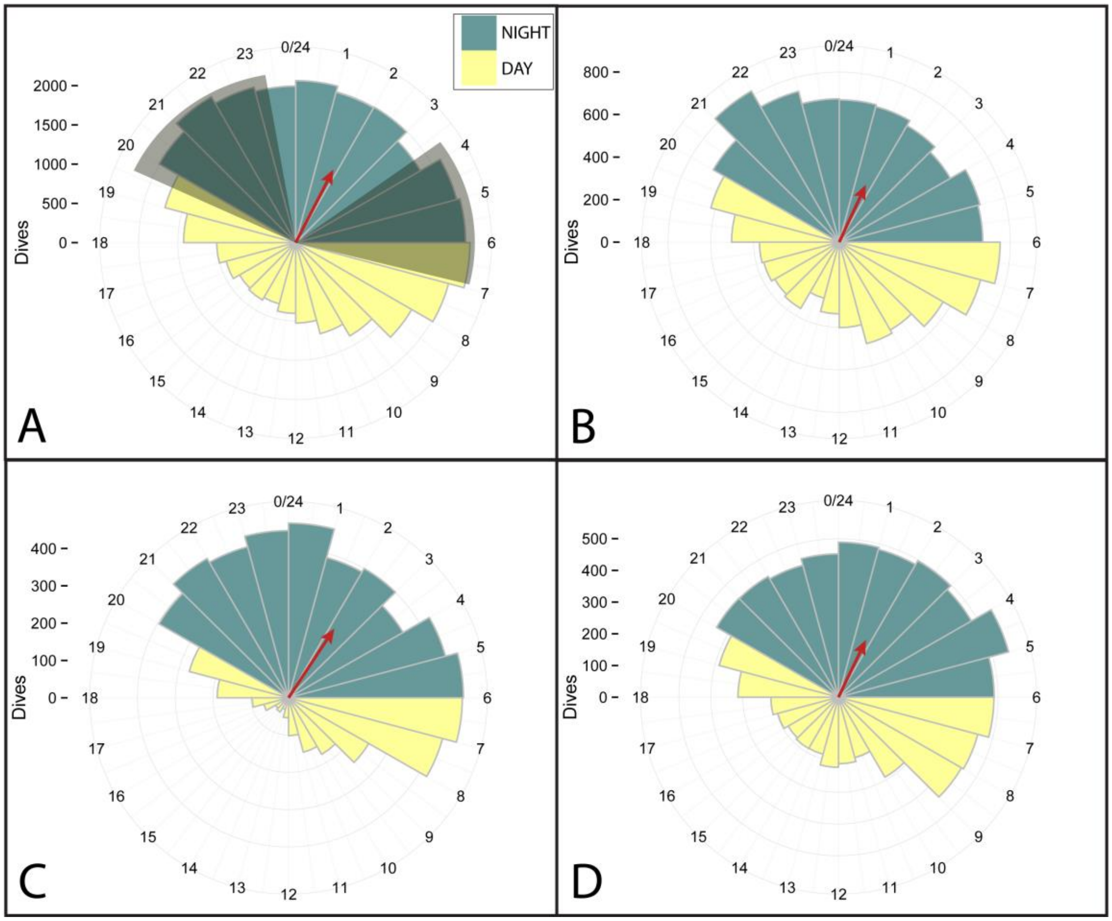

Figure 2-5: 24-hour rose plots of dive activity by hour of day. The red arrows represents the mean vector (direction = time of day, length = mean number of dives) of dive activity (dives/h) for: A) all dives (*n*=40,308). Gray shaded areas represent the crepuscular periods (± 1 h from sunset and sunrise across the study period) across the study; B) all dives pooled from the 2010 season (*n*=13,373); C) all dives pooled from the 2011 season (*n*=6,545); D) all dives pooled from the 2014 season (*n*=8,723). The null hypothesis that patterns of diel dive activity were equivalent between seasons could not be rejected (Watson's two-sample tests, *P* > 0.05).

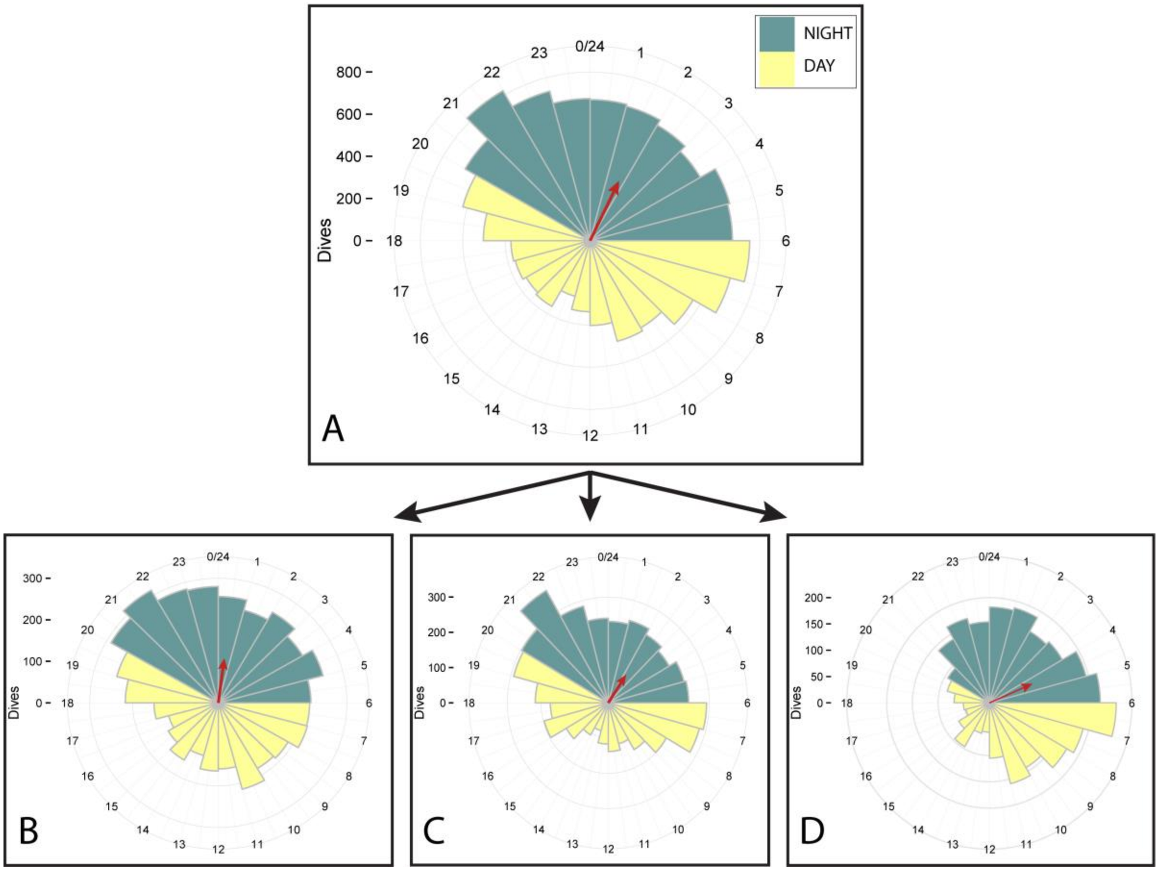

Figure 2-6: 24-hour rose plots of leopard seal dive activity by hour of day from the parametric data set. Red arrows represent the mean vector of dive activity. A) all dives pooled from the 2010 season (*n*=6,017) from three seals (4OR, 9OR and 390G); B) Activity for leopard seal 4OR (*n*=2,292 dives) was significantly different from the 2010 mean and the other two seals; (Watson’s two sample tests, *P*<0.05). C) Activity for leopard seal 9OR (*n*=2,283 dives) was significantly different from the 2010 mean and the other two seals; (Watson’s two sample tests, *P*<0.001); D) Activity for leopard seal 390G (*n*=1,442 dives) was significantly different from the 2010 mean and the other two seals; (Watson’s two sample tests, *P*<0.001).

CHAPTER 3:

The diet of leopard seals (*Hydrurga leptonyx*) at Cape Shirreff, Antarctic Peninsula examined with scat and stable isotope analysis

Douglas J. Krause and Carolyn M. Kurle

Abstract

Leopard seals are a widespread and important component of Antarctic coastal ecosystems. Previous studies have identified a wide range of prey items; however, due to anecdotal or otherwise limited information leopard seal diets remain largely unresolved by seal sex, inter individual variability, age class, region or season. As a result, leopard seals are widely reported as generalist predators. Over two summer field seasons we collected visual, scat and stable isotope tissue (blood and plasma) data from nineteen adult female leopard seals foraging near mesopredator breeding colonies at Cape Shirreff. We summarized *a priori* diet information and applied a two isotope (δ^{13}C and δ^{15}N), four source (fish, fur seal, krill, penguin) Bayesian mixing model to examine temporal variability in both prey sources and leopard seal tissues, and define their trophic position within the local food web. Leopard seals known to be foraging on Antarctic fur seal pups, showed a trophic signature co-incident rather than above their prey suggesting that krill are a major prey source despite *a priori* evidence to the contrary. Although variability in leopard seal isospace values was low, 3 of 9 seals from 2014 showed a significant δ^{15}N shift indicating the possibility of individual-based foraging specialization. Additionally, δ^{15}N values were consistently enriched for plasma versus red blood cells implying a seasonal diet change. While the four prey groups appear to explain the entire leopard seal diet, their linear distribution in isospace prevented informative posterior probabilities of prey proportions.

Introduction

Leopard seals (*Hydrurga leptonyx*) are a widespread and important component of Antarctic coastal ecosystems (Rogers 2009). They are apex predators capable of consuming resources across a range of trophic levels from mesopredators (e.g., penguins and seals) to fish and krill (Laws 1984). Additionally, they are likely affecting coastal communities indirectly through predator-induced stress effects (Creel and Christianson 2008, Krause et al. 2015). As circumpolar predators, trends in their diet, body condition, and population level could serve as indices of ecosystem health for Antarctic conservation and management (Reid and Croxall 2001, Derocher et al. 2004, Boyd et al. 2006). Establishing their role within an ecosystem context, though, is dependent upon understanding their habitat use and foraging ecology. Focal studies of leopard seals have been difficult to conduct, however, leading to a poor understanding of their demographics and diet.

Reports on leopard seal diets utilizing anecdotal data (e.g. reviewed by Hall-Aspland and Rogers 2004), and stomach contents (Laws 1984, Siniff and Stone 1985), scats (Hall-Aspland and Rogers 2004, Casaux et al. 2009), and fatty acid analysis (Guerrero et al. 2016) indicate that leopard seals prey on planktivorous krill and fish, as well as squid, seabirds, and seals. Krill stands out as a potentially key diet component, but is not consistently observed (e.g., Walker et al. 1998, US AMLR[1] unpublished Data), and these studies generally employ techniques that return biased results. For example, stomach content and scat data differentially represent recently consumed prey (Goebel

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[1] The United States Antarctic Marine Living Resources (U.S. AMLR) Program is administered by NOAA Fisheries through the Antarctic Ecosystem Research Division (AERD), SWFSC La Jolla, CA, USA.

2002, Staniland 2002, Bowen and Iverson 2012) and are further biased due to marked variations in prey digestion rates (Hobson et al. 1996). Additionally, prey handling techniques may bias scat results. For instance, leopard seals commonly detach fish heads before consumption (Krause et al. 2015) thereby removing the otoliths upon which many scat protocols rely to count and identify fish intake. Therefore, while leopard seal prey items have been identified, previous studies were unable to resolve diet in terms of variation between seal sexes, or among seal individuals, age classes, regions, or seasons. As a result, leopard seals are widely reported as generalist predators by default.

Recently, multiyear behavioral studies utilizing focal observation, bio-loggers, and animal-borne cameras have shown evidence of specialization by individual leopard seals in prey selection, area use (Rogers and Bryden 1995, Hiruki et al. 1999, Krause et al. 2015), and temporal foraging activity (Krause et al. 2016). It has been shown that individual foraging specialization is both taxonomically widespread and ecologically important (Bolnick et al. 2003). For instance, carnivore populations facing intraspecific or intraguild competition may alleviate competitive pressure by expanding their niche width through individual specialization for alternative prey, expanded habitat use, and/or temporal access to resources (Palomares and Caro 1999, Svanbäck and Bolnick 2005, 2007). Therefore, examining the prevalence of individual or temporal variations in leopard seal diets will accomplish two things. It will help establish the importance of individual prey specialization to leopard seals and increase our understanding of their overall function within the Antarctic ecosystem.

Stable isotope analyses (SIA) avoid some of the biases of traditional methods and are commonly used to study the trophic ecology of free ranging pinnipeds (e.g., Kelly

2000, Kurle and Gudmundson 2007, Cherel et al. 2008, Polito and Goebel 2010, Hückstädt et al. 2012) . Stable carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopes are most commonly used in diet studies because they reflect the corresponding isotope values of the consumer's prey field plus tissue-specific trophic discrimination factors that occur due to the processes of diet assimilation and excretion (Minagawa and Wada 1984, Ben-David and Flaherty 2012). Additionally, if isotope values for the consumer and prey items are known, stable isotope mixing models can quantitatively estimate the relative proportions of prey within consumer diets (e.g., Peterson and Fry 1987, Phillips and Gregg 2003, Hopkins et al. in review). For example, a relatively early isotope mixing model (Hall-Aspland et al. 2005a) illustrated seasonal variation and individual dietary separation for three leopard seals in East Antarctica (Hall-Aspland et al. 2005b). However, these earlier models were unable to incorporate uncertainties in isotopic measurements which can have dramatic effects on their dietary estimates (Phillips et al. 2014). Newer, Bayesian stable isotope mixing models explicitly characterize uncertainties around the isotopic measurements of consumer tissues, the trophic discrimination factors (Moore and Semmens 2008, Parnell et al. 2010, Newsome et al. 2012, Phillips 2012), and prey sources (Ward et al. 2010, Hopkins and Ferguson 2012, Parnell et al. 2013, Stock and Semmens 2013) to ensure that dietary proportions are reported with associated uncertainty.

A further advantage of SIA over conventional diet observations is that consumer tissues assimilate digested diet components over a period of time. The corresponding time frame depends on the protein turnover rate of the sampled tissue. Therefore, temporal changes in diet can be detected by aligning the time scale of consumer tissue turnover rates with potential diet shifts (Hobson et al. 1996, Dalerum and Angerbjörn 2005, Kurle 2009, Kurle et al. 2011). Several studies have established turn-over rates for various pinniped tissue types (e.g., Kurle and Worthy 2002, Hall-Aspland et al. 2005b, Phillips and Eldridge 2006, Heady and Moore 2013), allowing for estimations of diet shifts over time. For example, isotope values from blood plasma and red blood cells provide dietary information on the order of approximately one week to one month, respectively, previous to the time of tissue collection (Hobson and Clark 1993, Kurle 2002, 2009).

There are limitations to using SIA for quantifying consumer diets, particularly when there is overlap in the stable isotope values from prey resources (Phillips et al. 2005). Historically, the greatest dietary resolution has been derived from studies which combined SIA and more traditional field data collection (e.g., observations, gut contents, and fecal samples) (Harrigan et al. 1989, Burns et al. 1998, Fry 2006, Layman et al. 2007, Moore and Semmens 2008, Polito et al. 2011, Stock and Semmens 2013) as these methods can add *a priori* or *a posteriori* information to models to help ensure all prey sources are identified, which is a basic assumption of stable isotope mixing models (Phillips et al. 2014). In addition, the incorporation of additional stable isotopes (e.g. δ^{34}S) beyond the more traditionally applied δ^{13}C and δ^{15}N values can also contribute to greater resolution with Bayesian mixing models when isotope values from potential prey overlap (Hopkins et al. In review).

Understanding the extent of individual foraging specialization and the components, relative proportions, and trophic levels of the leopard seal diet are central to quantifying its ecological impact on coastal ecosystems. Therefore, the objectives of our study were to: 1) identify potential leopard seal prey sources via analysis of beach-collected seal scats and visual observations of seal foraging behavior, 2) estimate trophic position and proportions of different potential prey in leopard seal diets using the δ^{13}C and δ^{15}N values from prey sources and leopard seal tissues within a Bayesian stable isotope mixing model, and 3) assess temporal and individual variation in seal diets via SIA of seal red blood cells (RBCs) and plasma from different years.

Methods

Study Site

We conducted field studies within the U.S. AMLR research area at Cape Shirreff on the north shore of Livingston Island, Antarctic Peninsula (62.47^{o} S, 60.77^{o} W). Before 1996 leopard seals were rarely seen foraging at Cape Shirreff (Aguayo and Torres 1967, Weddell 1970, Aguayo 1978, Bengtson et al. 1988, D. Torres *pers. Comm.* in Boveng et al. 1998), but since that time their numbers have risen steadily (Goebel et al. 2014). The local increase in leopard seal abundance may be part of a geographical redistribution driven by the substantial reduction of pack-ice habitat in the western Antarctic Peninsula (Massom and Stammerjohn 2010, Forcada et al. 2012). Reduced sea ice tends to concentrate leopard seals (Bester et al. 1995, Meade et al. 2015); therefore, the loss of sea ice near Cape Shirreff may have further increased leopard seal density by limiting available haul-outs to coastal beaches.

Adult female leopard seals have been hauling out annually between December and June with peak numbers in January and February near mesopredator breeding colonies at Cape Shirreff in densities (>20 seals/nautical mile^2, Krause *et al.* 2015) two orders of magnitude higher than those reported by regional surveys (Erickson and Hofman 1974, Forcada et al. 2012). Predation by leopard seals on breeding populations of penguins and Antarctic fur seal pups (*Arctocephalus gazella*) is common between December and March (Vera et al. 2005, Krause et al. 2015), but the contribution of these mesopredators to leopard seal diets has been difficult to quantify.

Isotope Sampling: Consumer

During the course of the 2013 and 2014 field seasons healthy adult female leopard seals were selected and chemically immobilized (Pussini and Goebel 2015, Krause et al. 2016). Once sedated, a hypodermic needle (5.25 inch, 16 gauge) was set in the intervertebral extradural vein of the lumbar region (Hubbard 1968, Sweeney 1974). Blood samples were drawn via the hypodermic needle using a modified Cline blood draw technique (Cline et al. 1969) into evacuated vials without additives. Additional tissues were collected including vibrissae, skin, nail, and fur, and bio-logging instruments were deployed (Table 3-1, Krause et al. 2015, Krause et al. 2016). Each animal was measured for standard length and girth (Scheffer 1967), and weighed using a sling, tripod, hand winch, and a tensionometer (MSI-7300 Dyna-Link 2, capacity 1,000 ± 0.5 kg). Scats deposited during the capture event were collected in two-gallon plastic bags. Upon capture completion, sedative-reversal pharmaceuticals were administered (Pussini and Goebel 2015).

Each animal's recovery was visually monitored until it reached a mobile state. After handling, all animals in this study were re-sighted in a healthy state at least once within two weeks of capture. No reduced motor function or infection was observed.

Nineteen adult female leopard seals were sampled for plasma and RBC during the 2013 (n=9) and 2014 (n=10) field seasons (Table 3-2); and, of those animals sixteen were re-captured (Table 3-1) after ~ 1 week (6.34 ± 2.76 days) to recover instruments, re-sampled for blood (RBC/plasma), and re-weighed. All blood samples were centrifuged to separate plasma and RBCs, and stored at -20^{o} C. During those field seasons we were also able to collect 42 scats, and 25 visual prey-consumption observations of study animals (Table 3-1).

Scat samples collected during capture events were frozen and later examined in a wet lab. Defrosted scats were rinsed with fresh water through a series of stainless steel sieves (range: 2.8 mm – 710μm). Hard prey parts (fish bone, otolith, fur seal bone, etc.) were noted and identified to species when possible, and krill carapaces were measured for length and width as per Goebel et al. (2007). Study beaches were patrolled daily and fresh scats (warm, no evidence of scavenging by shorebirds) collected from study animals. These were sorted over plastic bags on study beaches, components identified to species when possible, and the wet volume of each prey component visually estimated. Any visual observations of foraging leopard seals were noted including identification of prey to species when possible. The proportion of each component prey item was estimated by multiplying frequency of occurrence (Walker et al. 1998) by a live mass estimate per prey species.

Isotope Sampling: Prey Sources

Based on a literature search from regional sites, scat analysis, and visual observations, the potential prey field of leopard seals at Cape Shirreff was determined to contain demersal fish (notothen spp), Antarctic fur seal pups, gentoo (*Pygoscelis papua*) and chinstrap (*Pygoscelis antarcticus*) penguins, and Antarctic krill (*Euphausia superba*). Samples of each prey type were collected from Cape Shirreff during each of the 2013 and 2014 field seasons (Table 3-3). Because baseline stable isotope signals of potential prey sources can vary greatly even over small spatial and temporal scales (Kurle et al. 2011, Zamzow et al. 2011, Phillips et al. 2014), we collected prey samples from Cape Shirreff concurrent with field sampling of leopard seal tissues.

Antarctic fur seal pup and penguin muscle tissue samples (~2 cm x 2 cm) were extracted with a scalpel from recently deceased animals that did not appear to be emaciated or obviously diseased. Krill were collected whole from the shoreline opportunistically following large storms. Muscle tissue from fish heads and bodies was collected opportunistically from fish discarded by predatory shorebirds. Penguin muscle tissue was cleaned with deionized water, and dried at 60^{o}C for $\geq$ 24 hours. All other prey samples were packed in plastic bags and frozen to -20^{o}C until prepared for stable isotope analysis.

Stable Isotope Sample Preparation

All samples were thawed and rinsed thoroughly with deionized water, freeze-dried for $\geq$ 24 hours, and homogenized by hand with a metal spatula. Marine animal tissues with C:N ratios ≥ 3.5 should be lipid extracted or analytically corrected to account for decreased δ^{13}C values in lipids (Post et al. 2007). As such krill and plasma

(Table 3-3) tissues were lipid extracted according to Folch et al. (1957) as modified by Sweeting et al. (2006) and Post et al. (2007). Each sample was placed in an 18 ml glass tube, 10 ml of petroleum ether was added, and the samples were sonicated at 40 Khz for 10 min in a water bath warmed to 60^{o} C. We centrifuged the samples at 12,000 g for 5 min, poured or pipetted off the petroleum ether, rinsed the sample with micro-pure water, then sonicated the sample again with micro-pure water for 10 min. Sample vials were centrifuged again for 10 min and excess water removed. Finally, the tissue was transferred to cryovials and dried at 43^{o}C for 24-48 hours.

Stable Isotope Analysis

Dried tissue samples (0.5 – 1.0 mg) were packaged into 5mm x 9mm tin caps for dual δ^{13}C and δ^{15}N analysis. Samples were combusted in a PDZ Europa ANCA-GSL elemental analyzer which interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Raw δ stable isotope values were normalized using laboratory standards calibrated against NIST Standard Reference Materials. Sample precision was 0.2 ‰ and 0.3 ‰ for δ^{13}C and δ^{15}N, respectively. The abundance of stable isotopes is expressed in notation according to the following equation:

$$\delta \mathrm{X} = \frac{\mathrm{Rsample} - \mathrm{Rstandard}}{\mathrm{Rstandard}} * 1000 \qquad (1)$$

Where X is ^{13}C or ^{15}N and R is the corresponding ratio of ^{13}C/^{12}C or ^{15}N/^{14}N. The Rstandard value is set by PeeDee Belemnite for δ^{13}C or atmospheric N_2 for δ^{15}N.

Data Analysis

Statistical analyses were conducted using R (R-Core-Team 2016). Uncertainty in SIA analyses is strongly related to how distinct the sources are in two-dimensional (2D) space (Phillips and Gregg 2001). We treated all δ^{13}C and δ^{15}N, or "isospace" data as spatial (Cressie 1993) and tested for differences between groups of isotopic data using either a K nearest-neighbors randomization test (KNN) (Ben-David et al. 1997, Rosing et al. 1998) for 2D data, or Welch's two-sample t tests for one-dimensional data. All values are listed as mean ($\bar{X}$) ± standard deviation (SD) and all tests relied on a level of significance of $P \leq 0.05$ unless otherwise indicated.

A Priori Data Summary

We combined all scat and foraging observation diet data in order to summarize our evidence for chosen prey sources for SIA analysis, and to provide information on the importance of each prey source (Table 3-4). The data were broken into three categories: 1) Scats analyzed in a lab 2) Scats analyzed in the field 3) visual observations of foraging events. For each individual leopard seal, and each observation, the estimated volumetric proportions per category were averaged, then weighted: 0.4 x lab scat, 0.3 x field scat, 0.3 x visual observations. The weights were chosen to balance the time period over diet information that was integrated (scats ~ 12-18 hours (Mårtensson et al. 1998)) and visual observations (~ 1-4 hours), and confidence in the findings. For example, we are more confident in lab versus field scats because field scats were not soaked, therefore small prey items may have been missed.

Grouping Isotopic Data

Reducing the number of sources to the fewest ecologically-relevant groups is likely to improve the explanatory power of mixing models (Phillips et al. 2005). Therefore, we grouped each prey (a.k.a. “source”) into taxonomic categories and included only species which we could verify (using ancillary diet data, see Table 3-4) were part of leopard seal diets. The “krill” and “fur seal” groups contained only a single species and all samples were included. Two species of notothen demersal fishes, *Notothenia coriiceps* and *Trematomus newnesi*, were combined as “fish.” And, for the final group we found no significant isospace separation between gentoo and chinstrap penguins (KNN, P=0.89), so they were combined into “penguin.”

We were able to collect representative prey source samples from the “krill”, “fur seal” and “penguin” categories during both seasons. We were only able to collect “fish” tissue during the 2014 season. However, the δ^{15}N values corresponded closely with published values from a locally conducted study (Zamzow et al. 2011), therefore the 2014 data were used for both years (Table 3-3).

A basic assumption of SIA mixing models is that each of the source groupings are distinct in isospace (Ben-David et al. 1997, Phillips et al. 2005). Therefore, we tested the source data from each of the two field seasons and found that all groupings were distinct, except for fur seal and fish in both years (Table 3-5). Because fish and fur seals are ecologically distinct and because the probability scores, while not significant, were low we elected to keep them as separate groups in the model.

All leopard seal isotopic data was grouped by tissue type, capture order (1st or 2nd capture), and year. During subsequent analyses each group was matched with the corresponding source data (by year) and tissue-specific discrimination factor. For inter-annual or inter-tissue comparisons only capture 1 data were used to maintain independence.

Tissue Discrimination Factors

The rate at which stable isotopes fractionate as prey tissues are assimilated into a consumer vary by species and tissue type (Vanderklift and Ponsard 2003, Kurle et al. 2014) and are affected by a host of environmental and physiological variables (Wolf et al. 2009, Phillips et al. 2014 and references therein).

We selected species and tissue specific isotope fractionation or discrimination factors (TDF) for plasma and red blood cells (RBC) from the literature. In order to maximize the accuracy of the mixing model (Bond and Diamond 2011) we chose a captive feeding study and selected seals with the closest phylogenies to leopard seals (Beltran et al. 2016). Further, we selected multiple species (ringed seal (*Pusa hispida*), spotted seal (*Phoca largha*) and Hawaiian monk seal (*Monachus schauinslandi*)) to more accurately reflect the uncertainty of this measurement (Moore and Semmens 2008, Parnell et al. 2010). The TDF for all prey sources in both seasons were 1.20 ± 0.14 ‰ ^{13}C, 3.85 ± 0.49 ‰ ^{15}N for plasma and 1.53 ± 0.10 ‰ ^{13}C, 2.75 ± 0.44 ‰ ^{15}N for RBC (Beltran et al. 2016).

Isotopic Mixing Model

We used the MixSIAR Bayesian mixing model (Stock and Semmens 2013) to explore our ability to quantify leopard seal diet composition. We built a four-source (fish, fur seal, krill, penguin), two isotope (δ^{13}C and δ^{15}N) model. Consumer, source, and TDF data were input for each year and tissue including standard deviations. Due to our low sample sizes (<20), source data were modeled using a “fully Bayesian” implementation (Ward et al. 2010). Prior distributions for source data were Dirichlet , or “generalist,” distributions which are uninformative on the simplex, making all combinations of source data equally likely (Stock and Semmens 2013). The model ran 3 Markov Chain Monte Carlo (MCMC) chains with 1 million iterations, a burn-in of 500,000, thinned by 500. Results were reported as mean, 1 SD, and 95% credible interval (CI) for each posterior density distribution per prey source. Model performance and convergence was tested using Gelman-Rubin and Geweke diagnostics as well as posterior density, trace, running means, and autocorrelation plots.

Results

A Priori Data

The resultant proportions of leopard seal diet components from scat and visual observation data for 2013 and 2014 are summarized in Table 3-4. In both years Antarctic fur seal was by far the largest prey source identified by volume (2013 – 71.9%; 2014 – 61.7%) followed by penguin (2013 – 13.7%; 2014 – 19.6%), fish (2013 – 10.0%; 2014 – 18.6%), and krill (2013 – 5.4%; 2014 – 0.0%).

Stable Isotope Data

The δ^{13}C and δ^{15}N values for each of the four categories of leopard seal tissue (plasma and RBC from each of 2013 and 2014) grouped closely together in isospace (Figures 3-1 and 3-2, and Table 3-2). K nearest-neighbor randomization tests showed no statistically significant spatial separation between the 1st and 2nd captures within those groups ($P \geq 0.53$; Table 3-2), and there were no significant differences between leopard seal tissue δ^{13}C values. However, there were several notable trends within the δ^{15}N values. The mean plasma δ^{15}N values for 2013 are enriched compared with 2014 (Table 3-3). That difference is not significant (P=0.11, t = 1.71, df = 15.83), but was driven by three of nine individual leopard seals from 2014 which had significantly lower δ^{15}N values (Welch's two-sample t test: P =0.046, t = -3.42, df = 2.82). There was a consistent enrichment in the δ^{15}N values for all four tissue categories between captures 1 and 2, although it was not significant (P=0.23, t=-1.2, df=31.41). Finally, the δ^{15}N values from RBCs were higher than those for plasma for both seasons (P<0.000001, t=7.42, df=34.94; Figure 3-3) in agreement with results from captive feeding studies of northern fur seals (*Callorhinus ursinus*) (Kurle 2002).

The δ^{13}C and δ^{15}N values for the four prey source groups are summarized in Table 3-2. There were no significant differences between 2013 and 2014 for either δ^{13}C or δ^{15}N values. However, there was separation between source groups, and all were significantly separated in isospace except for fur seals and fish (Table 3-5). Isospace plots showing source ($\bar{X}$ ± SD) and individual leopard seal δ^{13}C and δ^{15}N values by capture (Figures 3-1 and 3-2) illustrate that all consumer values fall within the range of the isotope values from the prey sources (Phillips et al. 2014). In addition, a plot of 2013 plasma data (Figure 3-4), without discrimination factors added to the source data, indicates that leopard seals are at the same trophic position as fur seals and fish.

Isotopic Mixing Model

The Gelman diagnostic for our model was < 1.05 for all variables, and the Geweke score showed only a single variable (out of 7) outside of range. Additionally, posterior density plots by chain showed high correspondence, traceplots showed broad mixing through parameter space, running means converged over time, and autocorrelation plots showed a decrease with increasing iterations. The preponderance of evidence suggests that the MCMC chains for this model converged. Posterior distribution plots (Figure 3-5), and 95% CIs with associated variance (Table 3-6) showed roughly equal proportions of each of the four prey sources with relatively large credible intervals.

Discussion

The *a priori* observations of all four groups of leopard seal prey sources (fish, fur seal, krill and penguin) were consistent between years, and appear to be supported by stable isotope data. For example, the distribution of all categories of consumer tissues (plasma and RBC for both years) falls entirely within the δ^{13}C and δ^{15}N isospace created by the four source groups (e.g., Figure 3-1). Additionally, the variance of δ^{13}C and δ^{15}N for leopard seal tissues was relatively low indicating a high level of inter-annual dietary consistency during the study period in contrast to previous reports of crabeater seals

(*Lobodon carcinophaga*) (Huckstadt et al. 2012) and leopard seals in East Antarctica (Hall-Aspland et al. 2005b).

Trophic Position and Diet

Given the consistently high proportion of fur seal in our *a priori* diet observations (Table 3-4) and previous reports to that effect from Cape Shirreff (Vera et al. 2005, Krause et al. 2015), the δ^{15}N values were surprising. In both years leopard seal plasma and RBC occupy the same trophic level as demersal fish and fur seal pups (e.g., Figure 3-4). Visually it is clear that the fur seal and demersal fish portions of the diet must be balanced with substantial contributions of krill or penguin (e.g., Figure 3-2). And, that balance is unlikely to be provided only by penguin tissue. Calculations multiplying the number of actively foraging leopard seals at Cape Shirreff (~60 US AMLR unpublished data) by realistic penguin take rates (Penney and Lowry 1967) would deplete the stock of penguins at Cape Shirreff (Mudge et al. 2014) in ~ 10-20 days. Additionally, colonies at Cape Shirreff are likely too small to sustain any dedicated predation (Ainley et al. 2005). Therefore, despite its virtual absence from scat and visual data, krill is likely a key prey item for these leopard seals. This finding supports the designation of leopard seals as a krill dependent predator (Siniff and Stone 1985), and emphasizes the potential biases of diet reports based solely upon scat data (Goebel 2002, Staniland 2002, Bowen and Iverson 2012).

Specialization and Prey Switching

In general, all four categories of leopard seal δ^{13}C and δ^{15}N values seem closely grouped in isospace (Figures 3-1 and 3-2) implying low levels of individual diet specialization, or prey shifting over week and month time scales. However, 33% of individual seals from 2014 had plasma δ^{15}N values that were significantly lower than other sympatric seals indicating they have an alternate diet. Additionally, there was a significant shift up in δ^{15}N between RBC and plasma in both years (Figure 3-3) implying that leopard seals change their diet and forage higher on the food web upon arrival to Cape Shirreff. Some of the apparent difference in δ^{15}N between RBC and plasma may result from differences in their amino acid composition (Kurle 2002). However, the trend of δ^{15}N enrichment is consistent across all observations, and between each first and second capture, which strongly implies a diet change between pre- and post-arrival to Cape Shirreff.

Isotopic Mixing Model

Posterior distributions from the mixing model did not provide useful dietary resolution. All source groups received roughly equal proportional probabilities (Figure 3-5). Although our source groupings were relatively distinct (Table 3-2), they were distributed linearly in isospace resulting in limited separation, a.k.a. the “muddled middle” (Fry 2006).

However, the existing experimental sampling design is promising for several reasons. Based on isospace plots and *a priori* data, it is likely that our prey field is correct. The metabolic turn-over rates of our tissues line up temporally with our questions about diet shifts (Hobson and Clark 1993, Kurle 2002, Kurle and Worthy 2002). Our catalog of *a priori* diet information is large. Further, we have supporting data indicating that the movements of our study animals are minimal (Krause et al. 2015), limiting error from small scale differences in source isotopes (Kurle et al. 2011). Our number of source groups is falls within suggested limits (Phillips et al. 2014). We have captive feeding derived tissue-specific fractionation factors with associated uncertainties (Wolf et al. 2009, Beltran et al. 2016). And our data and implementation allow us to incorporate uncertainties in a fully Bayesian framework (Ward et al. 2010, Stock and Semmens 2013). Due to all of these factors, we feel confident that re-analyzing our samples to add an additional stable isotope, δ^{34}S, will enable a fully resolved model.

Conclusions

Resolving the preferred prey items, and dietary proportions of leopard seals will be crucial to understanding food-web dynamics in the rapidly warming Antarctic Peninsula region. This is particularly true for large adult females, which are important predators of fur seals and penguins (Rogers and Bryden 1995, Hiruki et al. 1999, Vera et al. 2005, Krause et al. 2015). By integrating a combination of scat, visual observation and stable isotope data we've addressed some key questions, and built a promising framework for future studies.

The diet of female leopard seals at Cape Shirreff is likely comprised of demersal notothen fishes, Antarctic fur seal pups, krill and penguins. Additionally, leopard seals known to be foraging on fur seal pups, show a trophic signature co-incident rather than above their prey. Further, the distribution of prey sources in isospace strongly suggests that krill are a major prey source despite *a priori* evidence to the contrary (this study, Krause et al. 2016). There is some evidence in the 2014 plasma data of individual diet specialization, although more insight will be provided by a three-source resolved mixing model. Finally, there is an extremely consistent increase in δ^{15}N values as leopard seals arrive to Cape Shirreff in the summer, which is likely driven by the incorporation of fur seal pups and demersal fish into their diet.

Future studies should consider increasing source samples sizes to further reduce uncertainty in model parameters and include a third isotope, such as δ^{34}S, to provide additional information to the mixing model. In addition to adding another dimension to isospace, there would be only one more prey source than isotope tracers (n+1), therefore, the mixing solution would be deterministic (Fry 2006). Applying a working mixing model to individual study animals, and their associated *a priori* diet as well as movement data may resolve the importance of individual specialization to this population.

Acknowledgements

This paper was greatly improved by suggestions and comments by M. Goebel, and analytical advice and support from B. Stock, J. Hopkins and M. Ben-David. We are grateful to K. Pietrzak, M. Mudge, J. Wright, N. Cook, M. Zimmerman, M. Goh, T. Joyce, D. Vejar, G. Marshall, K. Abernathy, and J. Hinke for their assistance in the field, and to R. Steinitz for support in the lab. We thank M. Polito and S. Emslie for help with sample collection and transportation. Crucial financial, infrastructure and logistical support was provided by the U.S. AMLR Program. Transportation to our study site was kindly provided by Lindblad/NGS Expeditions, and logistical support by NGS Remote

Imaging. Leopard seal interactions and captures were conducted in accordance with Marine Mammal Protection Act Permit No. 16472-04 granted by the Office of Protected Resources, National Marine Fisheries Service, the Antarctic Conservation Act Permit Nos. 2012-005 and 2013-003, USDA Permit No. 42994, and the NMFS-SWFSC Institutional Animal Care and Use Committee Permit No. SWPI2011-02.

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Tables

Table 3-1: Individual identifications and summary foraging statistics for leopard seals sampled for blood and scat in 2013 and 2014 at Cape Shirreff (*n*=19). Scat numbers (n) represent scats collected during capture events or opportunistically. "Visual Observation" numbers (n) are successful foraging events witnessed.

Seal id - Year	Deployment Length (d)	No. of Foraging Trips	Recaptured Post Deployment?	Capture Scat (n)	Opportunistic Scat (n)	Visual Observation (n)
12OR – 2013	6.98	3	Yes	--	3	--
36OR – 2013	3.5	2	Yes	1	--	6
37OR – 2013	--	--	No	--	2	--
62OR – 2013	12.10	4	Yes	--	--	--
70OR – 2013	--	--	No	1	--	--
71OR – 2013	6.12	3	Yes	--	--	1
394Y – 2013	4.69	2	Yes	1	1	--
406Y – 2013	9.12	4	Yes	1	--	3
422Y – 2013	0.86	1	Yes	1	--	3
09OR – 2014	8.53	6	Yes	--	4	2
16OR – 2014	4.32	1	Yes	1	--	--
18OR – 2014	7.53	6	Yes	2	3	--
37OR – 2014	4.28	3	Yes	--	--	--
58OR – 2014	--	--	No	1	--	--
63OR – 2014	8.55	9	Yes	--	2	--
84OR – 2014	8.46	8	Yes	1	--	--
397G – 2014	5.49	3	Yes	1	3	4
401Y – 2014	3.92	2	Yes	2	6	6
406Y – 2014	7.71	5	Yes	1	4	--
Mean (±SD)/Total	6.34 ± 2.76	62	Yes = 16	14	28	25

Table 3-2: The mean (±SD; ‰) δ^{13}C and δ^{15}N values and C:N ratios for leopard seal tissues grouped by year and capture. KNN lists results of K nearest-neighbors randomization tests between years for a given tissue.

Tissue	Year	Capture	n	δ^{13}C (‰)	δ^{15}N (‰)	KNN	C:N
Plasma	2013	1	9	-23.91 ± $0.43^{\#}$	13.02 ± 0.56	P=0.99	3.86 ± 0.04
		2	6	-23.82 ± $0.32^{\#}$	13.39 ± 0.31		
	2014	1	10	-24.28 ± $0.39^{\#}$	12.46 ± 0.84	P=0.53	3.92 ± 0.34
		2	9	-24.33 ± $0.60^{\#}$	12.89 ± 0.44		
Red blood cells	2013	1	9	-23.33 ± 0.22	11.05 ± 0.63	P=0.99	3.43 ± 0.16
		2	6	-23.43 ± 0.30	11.39 ± 0.43		
	2014	1	10	-23.87 ± 0.36	11.03 ± 0.67	P=0.99	3.43 ± 0.06
		2	9	-23.81 ± 0.32	11.18 ± 0.44		

Table 3-3: The mean (±SD; ‰) δ^{13}C and δ^{15}N values and C:N ratios for all prey grouped by year. KNN lists results of K nearest-neighbors randomization tests between years for a given tissue.

Prey	Year	n	δ^{13}C (‰)	δ^{15}N (‰)	KNN	C:N
Fish	2014	5	-23.42 ± 1.24	11.57 ± 0.84	--	3.43 ± 0.07
Fur seal	2013	3	-22.79 ± 0.82	12.76 ± 0.28	P=0.298	3.37 ± 0.03
	2014	5	-21.69 ± 0.46	12.66 ± 0.70		3.38 ± 0.04
Krill	2013	5	-28.12 ± 0.30	4.95 ± 0.28	P=0.471	3.77 ± 0.05
	2014	5	-28.72 ± 0.69	4.21 ± 0.46		3.86 ± 0.11
Penguin[1]	2013	8	-26.61 ± 0.45	7.42 ± 0.89	P=0.726	3.49 ± 0.09
	2014	15	-26.12 ± 0.57	7.89 ± 0.86		3.43 ± 0.14

[1] The δ^{13}C and δ^{15}N values for gentoo and chinstrap penguins were not different (t-test; P=0.26) and were therefore combined

Table 3-4: Estimated volumetric proportions of prey items in leopard seal diets for 2013 and 2014 based on scat and visual observation data; n is the number of observations per category.

		Laboratory Sorted Scat					Field Sorted Scat					Visual Observation			
Year	Tag ID	n	Fur seal	Penguin	Fish	Krill	n	Fur seal	Penguin	Fish	Krill	n	Fur seal	Penguin	Fish
2013	12 OR						3	1							
	36 OR	1	0.8	0.2								6	1		
	37 OR						2	1							
	70 OR	1	0.99	0.01				0.5	0.5						
	71OR							0.5	0.5			1	1		
	394 Y	1	0.8			0.2	1	1							
	406Y	1	0.9			0.1		1				3	0.6		0.4
	422Y	1	0.99	0.01				1				3	1		
2014	09OR						4	0.5	0.5			2			
	16OR	1	1												
	18OR	2	1				3	1							
	58OR	1	0.9	0.1											
	63OR						2		1						
	84OR	1	1												
	397G	1	1				3	1				4	1		
	401Y	2	0.8	0.2			6	0.5	0.5			6	0.1		0.9
	406Y	4	1				4	1							

Table 3-5: Results of K nearest-neighbors randomization tests of proximity in isospace for all prey source groups from 2013 and 2014. The $H_o$was that there is no spatial separation between groups which was rejected for values below P=0.05.

		Fish	Fur seal	Krill	Penguin
2013	Fish	--	0.262	0.014	<0.000
	Fur seal	0.262	--	0.011	0.009
	Krill	0.014	0.011	--	0.002
	Penguin	<0.000	0.009	0.002	--

		Fish	Fur seal	Krill	Penguin
2014	Fish	--	0.143	0.004	<0.000
	Fur seal	0.143	--	0.010	<0.000
	Krill	0.004	0.010	--	<0.000
	Penguin	<0.000	<0.000	<0.000	--

Table 3-6: The estimated mean proportions, with standard deviations (SD) and 95% credible intervals (CI), of potential prey sources in diets of leopard seals as determined by a Baysian stable isotope mixing model (MixSIAR).

	Mean	SD	95% CI
Fish	0.221	0.142	0.484
Fur seal	0.279	0.128	0.478
Krill	0.241	0.114	0.413
Penguin	0.259	0.162	0.546

Figures

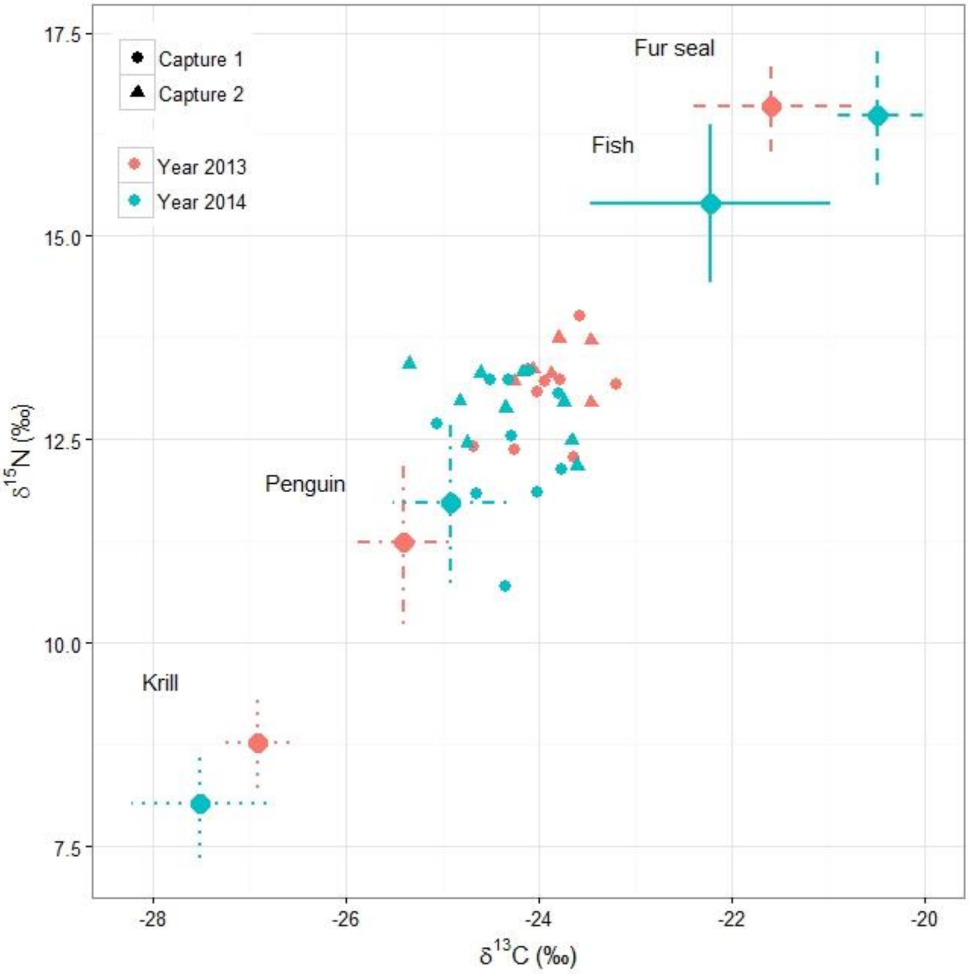

Figure 3-1: $\delta^{13}C$ and $\delta^{15}N$ isospace plot of leopard seal plasma values (n=34) plotted by capture with concurrent prey source values from 2013 and 2014. The prey sources have been corrected by incorporating both the tissue trophic discrimination factor and the associated uncertainty (standard deviation bars).

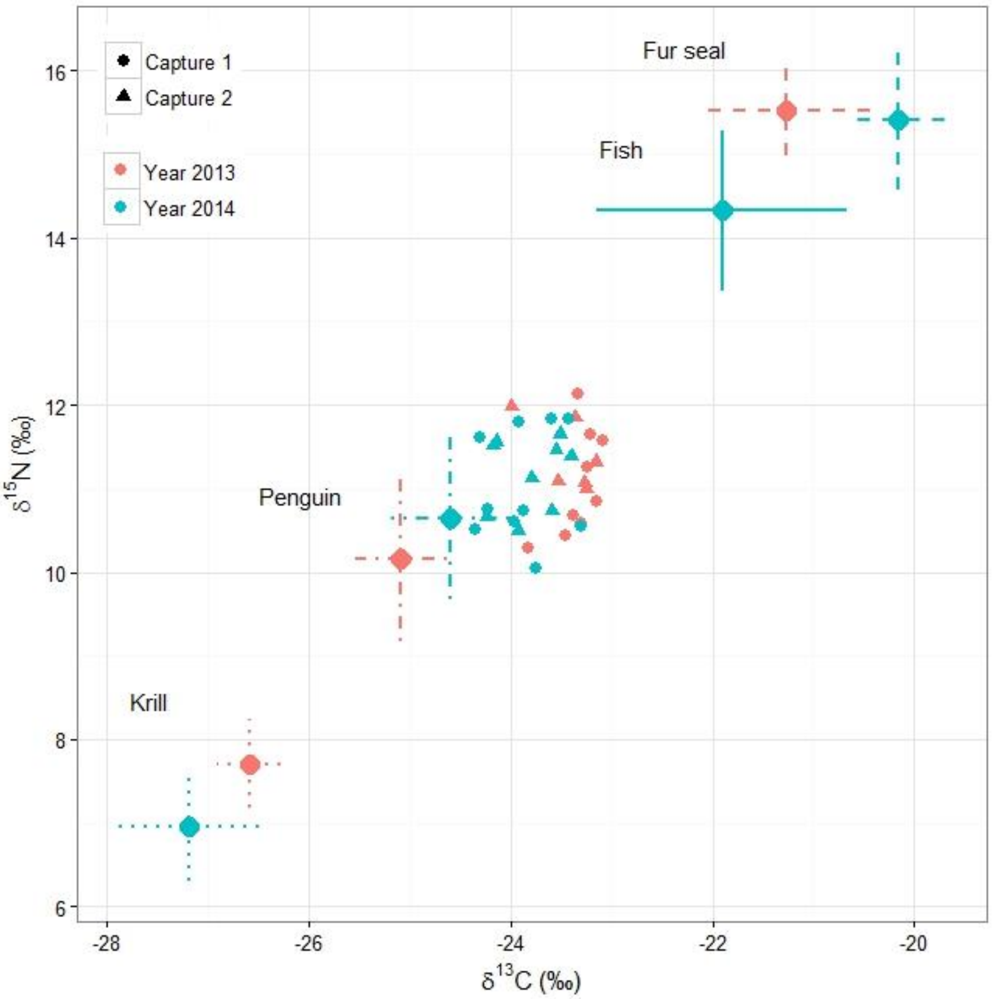

Figure 3-2: δ^{13}C and δ^{15}N isospace plot of leopard seal red blood cell values (n=34) plotted by capture with concurrent prey source values from 2013 and 2014. The prey sources have been corrected by incorporating both the tissue trophic discrimination factor and the associated uncertainty (standard deviation bars).

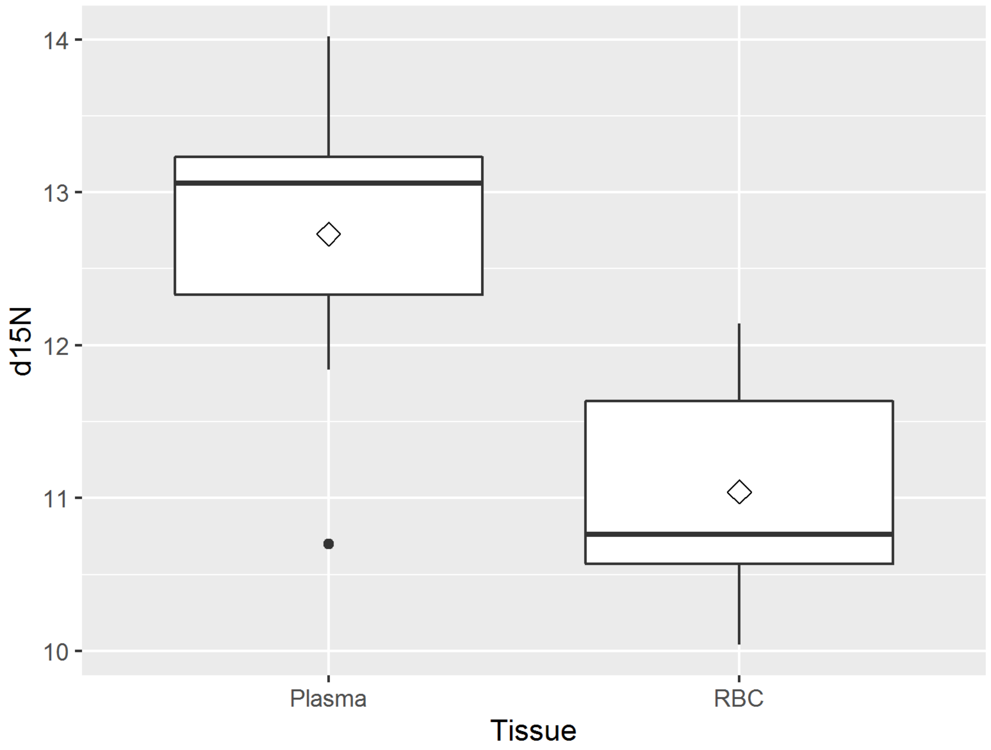

Figure 3-3: Box and whisker plot showing leopard seal plasma (n=15) and blood (n=15) $\delta^{15}N$ values from 2013. The open diamond indicates the mean value.

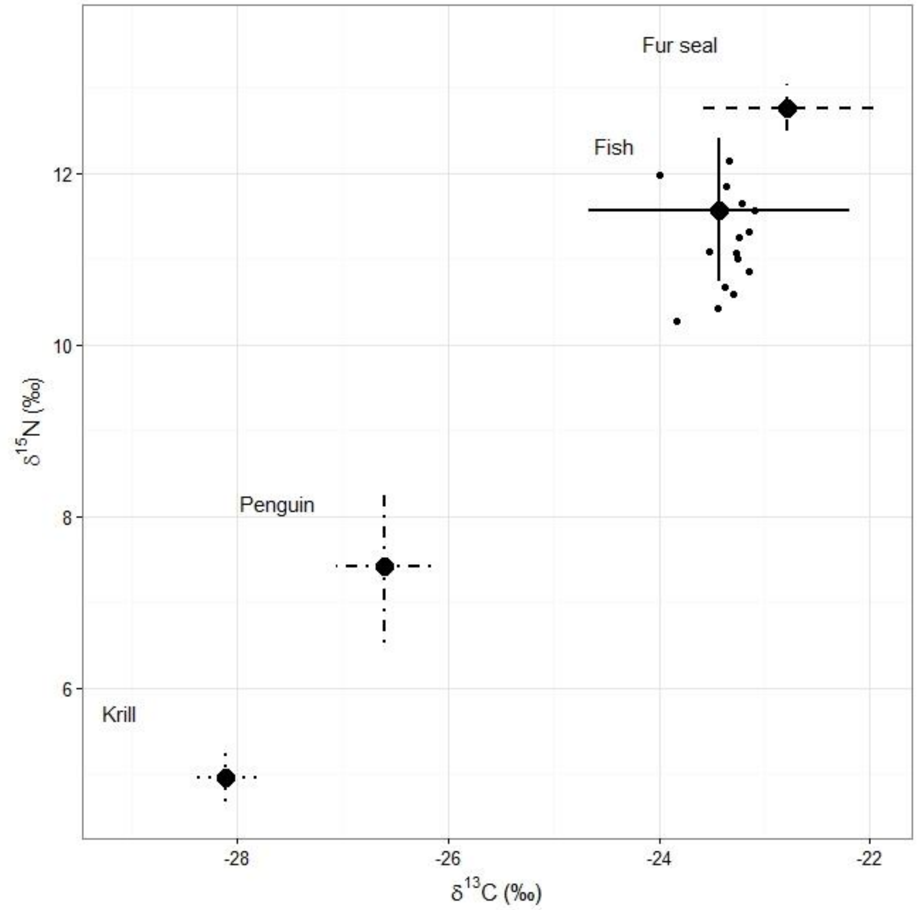

Figure 3-4: $\delta^{13}C$ and $\delta^{15}N$ isospace plot of leopard seal plasma values (n=16) from 2013 plotted with concurrent prey source values which are un-corrected for tissue trophic discrimination.

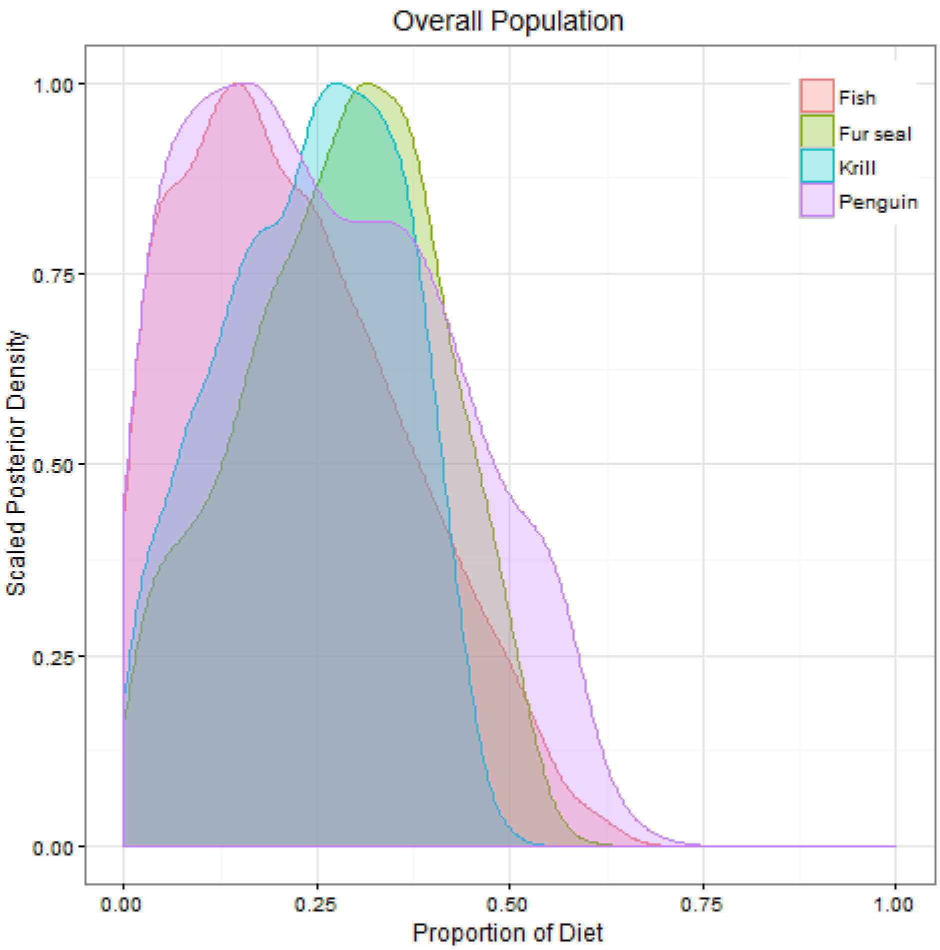

Figure 3-5: A scaled posterior density plot showing mixing model derived probability distributions for the four prey sources.

CHAPTER 4:

An accurate and adaptable photogrammetric approach for measuring the size, mass, and body condition of a large pinniped using an unmanned aerial system

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Abstract

Measurements of body size and mass are fundamental to pinniped population management and research. Manual measurements tend to be accurate but are invasive and logistically challenging to obtain. Ground-based photogrammetric techniques are less invasive, but inherent limitations make them impractical for many field applications. The recent proliferation of unmanned aerial systems (UAS) in wildlife monitoring has provided a promising new platform for the photogrammetry of free-ranging pinnipeds. Leopard seals (*Hydrurga leptonyx*) are an apex predator in coastal Antarctica whose body condition could be a valuable indicator of ecosystem health. We aerially surveyed leopard seals of known body size and mass to test the precision and accuracy of photogrammetry from a small UAS. Flights were conducted in January and February of 2013 and 2014 and 50 photogrammetric samples were obtained from 15 unsedated, unrestrained seals. UAS-derived measurements of standard length were accurate to within 2.01 ± 1.06 %, and paired comparisons with ground measurements were statistically indistinguishable. A linear model predicted leopard seal mass within 15.55 kg (3.5% error for a 440 kg seal). Photogrammetric measurements from a single, vertical image obtained using UAS provide a noninvasive approach for estimating the mass and body condition of pinnipeds that may be widely applicable.

Introduction

Obtaining measurements of body size and mass is a fundamental part of pinniped research and population management. Simple metrics such as body length and mass provide valuable information about the age (Laws 1957, Wilson 1974, Jeglinski et al.

2010, Lydersen et al. 2012), physiology (Gentry and Kooyman 1986, Kooyman 1989), foraging ecology (Webb et al. 1998, Horning and Trillmich 1999, Irvine et al. 2000, Weise et al. 2010), life history, and evolution (Bryden 1969, Calder 1984, Schmidt-Nielsen 1984, Costa 1991) of marine mammals. The mass and body condition of marine predators can be an indicator of prey availability and habitat quality for managed populations (Hanks 1981, Costa et al. 1989, Read 1990, Trillmich and Dellinger 1991, Merrick et al. 1995, Monson et al. 2000, Springer et al. 2008), or serve as indices of ecosystem health (Boyd and Murray 2001, Derocher et al. 2004, Reid et al. 2005). Accordingly, there is a long history of attempts to measure or estimate the size of free-ranging pinnipeds.

For studies with limited sample requirements, accessible pinnipeds may be captured and measured directly. Such hands-on measurements are typically accurate and are referred to as “manual” measurements. If it is impractical to weigh an animal due to its size or position, reliable mass estimates can be derived using multiple girth and blubber thickness measurements (McDonald et al. 2008, Shero et al. 2014). Alternatively, mass can be estimated using only length and girth (Usher and Church 1969, Hofman 1975, Castellini and Kooyman 1990, Castellini and Calkins 1993, Van den Hoff et al. 2005), which reduces capture times. However, the accuracy of such models vary when compared to direct weights, and even the most reliable models were inaccurate for large (>400 kg) phocids (Hofman 1975, Castellini and Calkins 1993, Van den Hoff et al. 2005). Moreover, manual techniques for collecting morphological data necessarily involve physical contact with the study animal, which is stressful and carries substantial risk for both animals and researchers. Capturing and weighing large pinnipeds requires heavy equipment that can be difficult to transport, and capture events are time- and resource-intensive which limits sampling. Finally, large pinnipeds are typically immobilized chemically which requires accurate mass estimates to properly administer powerful sedatives. Overdosing can result in animal mortality (Mitchell and Burton 1991, Higgins et al. 2002) and under-dosing puts the researcher at risk of injury. Therefore, manual measurement approaches create an operational paradox, where girth is needed to set safe pharmaceutical dosages for capture, but a captured animal is required to obtain girth.

Wildlife photogrammetry has offered opportunities to measure, *inter alia*, body size and nutritive condition from a distance (e.g., Perryman and Lynn 2002, Miller et al. 2012), thereby reducing animal disturbance, effort, and risk. A straight line distance on an object can be calculated exactly from a photograph as long as the lens focal distance and the distance from lens to object are known (Baker 1960, Wolf 1983, Gilpatrick 1996, Fearnbach et al. 2011). In fact, reliable straight line measurements of animals in ideal positions have been obtained (e.g., Bell et al. 1997, Waite et al. 2007, Meise et al. 2014). However, substantial challenges to this approach remain. First, useful photographs must capture enough information in a two-dimensional (2D) image to estimate mass, which is essentially a volumetric value. Second, practical photogrammetric methods must be scalable beyond a few individuals. Finally, experiments must be designed that address the inherent challenges of sampling wild pinnipeds. For many practical reasons, previous photogrammetric studies have circumvented these limitations by gathering data from anesthetized or trained animals. Consequently, while reported error ranges are often reasonable (Table 4-1), the associated methods are often too sensitive to animal movement or body alignment relative to the camera.

Three dimensional (3D) volumetric models of pinnipeds have been created to estimate mass using multiple photographs from multiple angles (Waite et al. 2007, de Bruyn et al. 2009). While promising for limited (e.g., underwater) applications (Waite et al. 2007), they require either complex synchronized multi-camera set-ups, or are overly sensitive to animal movement (de Bruyn et al. 2009). Another approach involves taking 1 or 2 photos (e.g., lateral, anterior, posterior) of a seal at ground level from a known distance and regressing the photo-derived surface areas to approximate volume (Haley et al. 1991, Bell et al. 1997, McFadden et al. 2006). Though reasonably accurate, this approach was only recommended (Haley et al. 1991) for sedated animals or specific groups of pinnipeds, like northern elephant seal (*Mirounga angustirostris*) bulls or Hawaiian monk seals (*Monachus schauinslandi,* McFadden et al. 2006) that haul-out alone and tolerate close approach by humans. Pinniped approach distances can be increased, though, by supplementing manual scale references with an accurate estimate of camera to seal distance (Wolf 1983). For example, Meise et al. (2014) utilized a laser distance meter with their single camera system. However, their measurements (Table 4-1) were sensitive to body position, and changes of substrate. Despite being less invasive than hands-on approaches, all of these techniques have caveats that make them impractical for many field applications. Lateral photo techniques do not work well for crowded haul-outs where neighbors obscure target animals. It would be difficult to scale these techniques up to cover a large population, and all of them involve working in proximity to target animals.

Multi-camera stereoscopic photography systems mounted in manned aircraft cover a large area, and can provide field measurements without ground references (Cubbage and Calambokidis 1987, Miller et al. 2012, Merkel et al. 2013). However, the suitability of such systems for morphometric studies could not be assessed because ground truth errors were not reported. Additionally, surveys using manned aircraft are expensive (Hodgson et al. 2013), logistically challenging or impossible in remote areas (Linchant et al. 2015), and are dangerous for wildlife biologists (Sasse 2003). Manned aircraft surveys also require highly-trained pilots, and are slow to launch during the typically-small weather windows in high latitude areas (Hodgson et al. 2013, Goebel et al. 2015).

The recent proliferation of unmanned aerial systems (UAS) has provided promising new tools for wildlife monitoring and research (Watts et al. 2010, Whitehead et al. 2014, Linchant et al. 2015). When compared with manned aircraft, UAS are logistically simple, low cost, and safe (Watts et al. 2012). Rapid improvements in UAS technologies have increased stability, flight duration, and the ground resolution of photography (Koh and Wich 2012, Durban et al. 2015). And, because UAS can be launched quickly and fly safely below cloud cover (Jones et al. 2006), they can be operated regularly even in the most extreme weather regions (Goebel et al. 2015). Battery powered vertical takeoff and landing (VTOL) UAS, in particular, are well suited for the collection of photogrammetric data on pinniped populations. Without need for a landing strip, they can operate in rugged environments. Furthermore, they are quiet, which limits disturbance to wildlife, and they are self-leveling, which improves photograph quality and simplifies image post-processing (Durban et al. 2015, Goebel et al. 2015).

Overhead images of wild animals provide information not available from lateral photos, but they are cumbersome to obtain from the ground (Ireland et al. 2006). Vertical photograph angles do not require adjustments to correct perspective angle error (Wolf 1983, Merkel et al. 2013, Meise et al. 2014), which reduces both measurement error and processing time. Finally, overhead photos from UAS are easily collated with accurate altitude data (Durban et al. 2015), thereby eliminating the need for scale references on the ground. Recently, a small VTOL with a single downward facing camera has shown promise for accurately measuring cetaceans (Durban et al. 2015) and pinnipeds (Goebel et al. 2015).

The population of leopard seals (*Hydrurga leptonyx*) at Cape Shirreff, Livingston Island, Antarctica presents a unique opportunity to test the performance of this VTOL UAS photogrammetry approach. Both because they are a large pinniped (Wilson 1902), which has been a historically challenging size class for mass estimation models. And, paradoxically, their streamlined body shape (Van den Hoff et al. 2005) contains elements of both phocid (e.g., spindle-shaped body) and otariid (e.g., long neck, developed fore-flippers) dimensions. Therefore, a successful photogrammetric technique for leopard seals would likely be applicable to other pinnipeds.

Leopard seals are apex predators (Rogers 2009) with the potential to affect Antarctic coastal ecosystems through direct and indirect predation of mesopredator (e.g., penguin, Antarctic fur seal (*Arctocephalus gazella*) populations (Siniff and Stone 1985, Boveng et al. 1998, Ainley et al. 2005, Krause et al. 2015, Krause et al. 2016), or consumption of the keystone Antarctic krill (*Euphausia superba*) (Laws 1984, Casaux et al. 2009). As such, leopard seal body condition is a valuable indicator of ecosystem health. Tracking their mass over time could improve predation models (Forcada et al. 2009). Additionally, accurate estimates of mass could improve population management through safer animal selection (Fulton 1998) and chemical immobilization (Van den Hoff et al. 2005). Leopard seals have been difficult to sample because they are typically solitary (Wilson 1905, Southwell et al. 2008), associated with marginal pack ice habitat (Gilbert and Erickson 1977, Rogers and Bryden 1997, Bester et al. 2002, Rogers et al. 2005), and have a low tolerance for approach (Nordøy and Blix 2009). However, some leopard seals congregate seasonally in higher densities near mesopredator colonies (Hofman et al. 1977, Kooyman et al. 1990, Rogers and Bryden 1995, Walker et al. 1998, Hiruki et al. 1999, Krause et al. 2016). UAS may provide a non-disturbance observation platform for studying pinniped haul-out sites like these.

Here, we assess a non-invasive method for determining leopard seal size, condition, and mass, based on vertical images taken from VTOL UAS calibrated against individuals of known body size. Aerial photogrammetric and manual measurements were compared in order to: 1) test the accuracy of pinniped body measurements obtained using aerial photogrammetry, and 2) compare the precision of both manual and photogrammetric measurements. 3) We subsequently examined the sensitivity of photogrammetric measurement accuracy to changes in the haul-out substrate, body position of target animals, and the altitude of the UAS. 4) We built and evaluated several modeling approaches to estimate the mass of this large pinniped from a single 2D photograph. 5) Finally, we discuss the utility of a body condition index for leopard seals and other phocids.

Methods

Study Site

Field studies were conducted at Cape Shirreff (62.47° S, 60.77° W) on the north shore of Livingston Island, Antarctic Peninsula. This previously described (Krause et al. 2015) field site was selected because it provided access to a seasonally resident population of leopard seals that regularly haul-out along the coast (Krause et al. 2016). Photographic missions over leopard seals, conducted in conjunction with ongoing monitoring studies[1], were completed in January and February of 2013 and 2014.

UAS Platform

The APH-22 (Aerial Imaging Solutions, Old Lyme, CT) is a battery powered VTOL UAS system which was described in previous studies (Durban et al. 2015, Goebel et al. 2015). It consists of a 2.4GHz radio transmitter, and weatherproof hexacopter and ground station with a live video display (Figure 4-1). It was chosen for its portability, durability, high-resolution photography, and its stability in flight across a variety of weather conditions (Goebel et al. 2015) despite its low weight (1.2 kg, payload capacity: 1 kg). Our field configuration featured a downward facing Olympus E-PM2 digital camera (16.1 Megapixel, Micro Four-Thirds format, 0.23 kg) with an Olympus M.Zuiko 45 mm f/1.8 lens, and a single battery (QuadroPower 6200 mAh Li-PO, 0.13 kg) as payload. The camera was set to record Large Super Fine JPEG and RAW images, ISO 1250, aspect ratio: 4:3, Shutter Priority Mode (shutter speed 1/2000). The 45 mm lens

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[1] The United States Antarctic Marine Living Resources (U.S. AMLR) Program is administered by NOAA Fisheries through the Antarctic Ecosystem Research Division (AERD), SWFSC La Jolla, CA, USA.

was designed for the E-PM2 Micro Four-Thirds sensor, allowing undistorted coverage across the entire photograph. Calibration flights utilizing a contrast (8:1) resolution target (RST-704, Series C) produced undistorted photographs with a ground-resolved distance of 1.0 cm at 30 m altitude (Perryman unpublished data).

Leopard Seal Capture Protocol

Healthy adult female leopard seals were selected and chemically immobilized (Pussini and Goebel 2015, Krause et al. 2016). While sedated, the following manual morphometrics were taken to the nearest 0.5 cm from seals in ventral recumbancy (prone position): standard length (SL), curviliniear length (CL), and axillary girth (AG) (Scheffer 1967); an additional umbilicus girth (UG) was taken at the mid-point posterior to the rib cage and anterior to the hip girdle. SL was taken using a measuring tape affixed to a rigid length pole; a weighted plumb line was used to increase accuracy. In 2014, SL was measured by three independent observers (readings were not shared) to estimate observer variance. Girths and curvilinear lengths were measured with a calibrated line. Each animal was weighed to obtain mass (M) using a sling, tripod, hand winch, and a tensionometer (MSI-7300 Dyna-Link 2, capacity 1,000 ± 0.5 kg).

After manual measurements were taken, sedative-reversal pharmaceuticals were administered (Pussini and Goebel 2015). Each animal’s recovery was visually monitored until it reached a mobile state. After handling, all animals in this study were re-sighted at least once within two weeks of capture in a healthy state. No reduced motor function or infection was observed.

UAS Flight Protocol

Aerial survey flights were conducted over leopard seals immediately following capture events (N=14), or within 24 hours (N=3) to reduce measurement error between measured mass and estimated mass. Due to the sedative-reversal agents, rapid recovery times (2.68 ± 2.08 min, a subset of data reported in Krause et al. 2016) ensured that coverage was obtained from non-sedated, free-ranging leopard seals in multiple, natural body positions.

The APH-22 system, including the hexacopter, camera, transmitter, and ground station were set up and calibrated before capture events >50 m from the target animal to reduce disturbance. Two reference markers, either 6 or 10 m apart, were placed near target animals to provide a control known-distance scale reference. The flight team included one pilot and one ground station operator who tracked mission information, including target position, system voltages, altitude, and relevant distances. After take-off, the hexacopter was flown to target elevation before approaching the animal to decrease potential disturbance. Aerial photographs were automatically taken every 2 seconds above target seals from altitudes of 23, 30 and 45 m. Photo images and flight log data were stored internally on SD flash cards, and downloaded post-flight.

Data Analysis

Representative photographs containing the entire leopard seal and a ground scale reference were selected from each target altitude (23, 30, 45 m). For each photo, the substrate under the seal (snow or sand) and two bimodal categories of seal body position (POS1: straight or curved; POS2: dorsal or lateral) were recorded (e.g., Figure 4-2). All references to the seal's identity were removed, and photographs were measured by three independent observers to assess measurement variation. The multi-observer mean of each photogrammetric measurement was used for subsequent analysis.

Images were measured in pixels (*Pixels*) using ImageJ, a Java-based open access software package (Abramoff et al. 2004). Customized Java script (Figure S4-1) allows for semi-automated photo processing. The user defines SL markers (nose to tail) and the script creates 10 equidistant width landmarks over the image. The photogrammetric measurements (Table 4-2, Figure 4-3) were standard length (PSL), overall length (POL), widths (edge to edge of the animal measured orthogonal to PSL) at landmarks 1 through 10 (W1-W10), axillary width (PAW), and umbilicus width (PUW).

Subsequent data analysis was conducted using R (R-Core-Team 2015). The focal length (*fl*) of our lens was 45 mm, and the pixel width (*pw*) was calculated from the camera sensor size and the sensor resolution (Fearnbach et al. 2011). Photograph pixel measurements were converted to ground distance by converting pixel measurements to photo distance:

$$\textit{Photo Distance} = \textit{Pixels} * pw$$

Then, ground distance was calculated using the altitude of the UAS as the distance from sensor to object (Wolf 1983):

$$\textit{Ground Distance} = (\textit{Altitude}/fl) * \textit{Photo Distance}$$

Three data sets were created for further analysis: 1) the “accuracy” data set, which contained all photogrammetric measurements for every observation (N=50), 2) the “manual” data set of all ground-based measurements from each seal that was both captured and aerially surveyed (N=17), and 3) the “mass estimation” data set, which contained one randomly-selected set of photogrammetric measurements for each aerially surveyed seal (N=17). Standard parametric assumptions of ordinary least squares regressions (independence, normality, linearity and homoscedasticity) were tested for each data set (Fox and Weisberg 2011, Pena and Slate 2014). Two outlier observations were eliminated from the manual and mass estimation data sets (final sample size, N=15), and all three sets met all assumptions.

Precision Tests

The values for all 15 photogrammetric measurements (Table 4-2) were compared among and between observers in order to assess the measurement variance. Comparisons were made using balanced one-way ANOVA tests among observers, and Tukey’s Honest Significant Difference (HSD) test between observers.

To compare the precision of ground versus UAS-derived measurements, the mean and the standard error of the mean (*se*) were calculated for multiple-observer repeated manual measures of SL (N=9), and the paired PSL values (N=9). The group means were compared with a two-group, independent, paired t-test (Venables and Ripley 2002).

Accuracy Tests

For comparisons of accuracy, manual morphometrics were assumed to be “true”. For SL measures from 2014, the mean value was used. Measurement error was calculated for photometrically-derived standard length using the percent difference between mean PSL and mean SL as follows:

$$\%\ \text{Error} = \left| [1-(SL/PSL)]*100 \right|$$

Subsequently, potential changes in photogrammetric measurement accuracy (% Error) due to differences in substrate, seal body position, and UAS altitude were tested using unbalanced one-way ANOVA and HSD tests.

Mass Estimation

Leopard seal body mass was estimated using ordinary least squares linear regression, multiple linear regression, and power regression models. For each set of regression models, M was the dependent variable, and all photogrammetrically derived measurements were predictor variables. All subset combinations were run for each family of regression analysis (Venables and Ripley 2002, Lumley and Miller 2009), and the most informative models were selected by maximizing R^2, and minimizing mean squared error (MSE, an effective measure of the predictive accuracy of regression models, Kabacoff 2011). All multiple linear regression models were evaluated for multicollinearity using a variance inflation factor test (Fox and Weisberg 2011).

Previously published mass estimation models, based on manual measurement data from leopard seals, were also run to evaluate their performance (Hofman 1975, Van den Hoff et al. 2005). The level of significance used for all tests was $P < 0.05$. All values are listed as mean ($\bar{X}$) ± standard deviation (*sd*) unless otherwise indicated.

Results

APH-22 VTOL missions were flown through a variety of weather conditions, temperatures, and wind speeds without a single technical failure. Twenty-two UAS surveys were flown on 15 days, providing complete coverage of 15 individual leopard seals including 50 sample images at a variety of altitudes, substrates, and body positions (Figure 4-2).

Flights were conducted in a variety of weather conditions including snow (N=1) and fog (N=2), but the most flight days were partly-cloudy across a spectrum of light conditions. The mean wind speed was 7.22 ± 4.85 (range: 1-18) knots, and the mean flight duration was 7.37 ± 3.14 min (well below the system capability of >25 min, Durban et al. 2015). We did not observe any behavioral responses from leopard seals when the hexacopter altitude was ≥ 23 m.

Precision Tests

No significant differences were detected for any photogrammetrically-measured value among or between observers (Figure 4-4, N=50, ANOVA $F_{2,147}$=2.009, P=0.138; Tukey’s HSD: Obs2 – Obs1 P=0.1307, Obs3 – Obs1 P=0.852, Obs3 – Obs2 P=0.343).

Mean values of SL (301.30 ± 1.73 cm (*se*), N=9) and PSL (302.75 ± 1.48 cm (*se*), N=9) obtained from multiple observers of the same seal from the same day were not significantly different ($t_9 = 1.0767$, P= 0.3096, $\bar{X}$ of the differences=1.427 cm).

Accuracy Tests

The mean % Error of PSL for all photographs in the study (N=50) was 2.01 ± 1.06 %. PSL was highly correlated with corresponding manual measurements (Figure 4-5). No differences in PSL % Error were identified among photographs grouped by UAS altitude, substrate, or body position (Table 4-3).

Mass Estimation

The most informative regression equations, and their corresponding R^2 values and mean squared errors (MSE) are listed in Table 4-4 for each family of models. Results based on previous manual measurement approaches are listed for comparison (Table 4-4). The multiple-linear regression model was rejected due to multicollinearity. We determined the linear regression model is the most practical for estimating pinniped mass from UAS photogrammetry in field settings (Figure 4-6), based on low MSE (± 15.55 kg, or 3.5% error for a 440 kg seal).

Discussion

Two-dimensional photographs provided highly-accurate mass estimates for adult leopard seals based on body measurements from vertical overhead images. Historically, comparative studies found manual measurement models were more accurate than photogrammetric models (Haley et al. 1991, Bell et al. 1997, Meise et al. 2014). To our knowledge, this is the first report in which a photogrammetric model was more accurate. Such accuracy derived from a combination of limited measurement error for each model predictor and the added width information from overhead photographs.

Precision and Accuracy

The extremely low variance between independent observers (Figure 4-4) indicates a precise photogrammetric approach with limited measurement error. Another key metric of precision is photogrammetric variance compared with the historical “gold standard”, manual morphometric variance. In fact, Hofman (1975) directed future research programs to conduct repeat length measures on captured pinnipeds to increase accuracy and estimate precision. With exceptions (e.g., Haley et al. 1991, Meise et al. 2014), however, most studies have not reported variance for manual measurements. The nearly identical standard error for PSL vs. SL, and the fact that differences could not be detected between the means, emphasize the precision of this technique.

The straight line measurement accuracy in this study (~2%) was as, or more accurate than previous pinniped photogrammetry reports. Additionally, the use of sedation-reversal pharmaceuticals facilitated rapid recovery from immobilization (~2.5 min). Hence, manual measurements were conducted on sedated leopard seals, yet proximate UAS flights captured images of mobile animals in multiple body positions. Subsequent comparisons of the measurement error between various flight altitudes, changing substrate, and the entire suite of natural leopard seal body positions did not detect significant differences between any groups.

Less Error More Information

Improving manual morphometric or photogrammetric approaches is an exercise in maximizing information per observation and reducing measurement error. There is error in all measurements, and those errors can be compounded when introduced into complex models. Therefore, ideal approaches should reduce error in data acquisition and data processing, and employ simple models.

An approach utilizing a single vertical image from a VTOL UAS provides a suite of features that reduce error in data acquisition, including: a vertical photo angle that obviates complex lateral angle distortion corrections (Wolf 1983), a lens matched to the camera sensor, which reduces image distortion (Durban et al. 2015), and the inherent slow speed and low-altitude of the UAS supports high-resolution photography. While altitude was calculated from ground scale markers in this study, such markers are not necessary for two reasons: First, the high accuracy of the Freescale MPX4115A air pressure altimeter produced a ground measurement error of < 1% (Durban et al. 2015), and second, the next generation of APH-22 are optionally equipped with laser altimeters to increase altitude accuracy by measuring absolute lens to target distance. Also, many approaches require multiple photos of the same animal, or multiple photo lens calibrations, but each additional required image increases user effort and the potential for error. Therefore, a single photograph, single camera approach inherently limits measurement error.

Estimates of pinniped mass are also subject to errors derived from non-proportional changes in body measurements. Phocids, in particular, experience large changes in percent body fat as they fast during the breeding season (e.g., Costa et al. 1986, Gales and Burton 1987), and subsequently forage (e.g., Crocker et al. 2006). And, whereas mass changes with percent body fat, many rigid body structures do not (Gales 1989). For example, adult pinniped length does not change with mass (Anderson and Fedak 1986) or any other factor (Laws 1957), and changes in height, width, or girth are likely masked by rigid skeletal structures (e.g., skull, thorax, and hip girdle). Therefore, measurements from non-skeletally-restricted body regions are more likely to inform changes in body condition (Miller et al. 2012).

The leopard seals at Cape Shirreff during January and February are actively foraging adult females (Krause et al. 2015), presumably recovering body fat following their breeding season.

Analyses of overhead photos measured at multiple, regularly-spaced widths (Figure 4-3), revealed that umbilicus width (PUW) was by far the most informative. And, PUW was selected in the most informative models for all model families (Table 4-4). Further testing is required to determine if PUW is equally informative for other age classes of leopard seals or other pinniped species. But, it is likely that width measurements from non-restricted body regions will strongly correlate with mass because those dimensions will change more directly with fluctuations in percent fat.

Early modeling approaches used a geometric approach and basic linear regression (Hofman 1975), but required girth. Later approaches applied log-transformations of variables because power relationships are common in allometric relationships (Peters 1983), and data sets are frequently not normally distributed (Bell et al. 1997, Van den Hoff et al. 2005). These power regressions, however, require back-transformations for accurate predictions, which may mask measurement error (Afifi et al. 2012). Linear regressions are easy to understand and apply. They also avoid the problem of multicollinearity, which is common in morphometric studies. When needed, non-normal data sets can be shifted into generalized linear model (Kabacoff 2011) or random forest regression (Breiman 2001) frameworks.

Body Condition

Tracking the responses of pinnipeds to environmental changes will continue to be vital to understanding and managing marine ecosystems. Leopard seals are a particularly important apex predator in Antarctic coastal systems. While focal studies of demographics, diet, and foraging behavior are needed, simple indices of predator nutritive state are valuable as ecosystem indicators. An index should track body condition, and be collected over an appropriate scale. While mass estimates are biologically valuable, they do not provide information on the nutritive state of an animal. The fineness ratio (length/maximum diameter) has been used to study the swimming efficiency of fish and pinnipeds (Webb 1975, Williams and Kooyman 1985), and a modified version (SL/height) was suggested as a condition index for leopard seals (Van den Hoff et al. 2005). Although useful for small-scale monitoring, height must be obtained from the ground, which is not viable for large scales. Aerial approaches, however, are easily scaled to larger areas.

We suggest that monitoring programs expand the use of UAS platforms, and utilize non-skeletally-restricted width measurements to develop body condition indices for pinnipeds. Because PUW correlates more strongly with mass change for the leopard seals than maximum diameter (R^2=.78 and R^2=.38 respectively), an appropriate condition index (CI) would be:

$$CI = PSL/PUW$$

Another major advantage of an index is that relative measurements such as these can be obtained from any aerial platform with no need for scale.

Conclusions

Aerial photographs derived from a VTOL UAS and processed by amateur volunteer observers using open source software provided precise and accurate estimates of body size and mass for free-ranging adult leopard seals. Results were robust to changes in substrate and body position, and accurate for animals > 400 kg. This sampling approach is promising for focal or longitudinal monitoring studies of leopard seals, and perhaps other pinnipeds, without the need for costly, invasive animal captures (Anderson and Fedak 1986). We believe similar approaches could be scaled up to provide body condition indices for ecosystem-based resource management. We suggest expanding future studies to integrate larger sample sizes and new pinniped species to verify and quantify the efficacy of UAS photogrammetry.

Chapter 4, in part, is currently being prepared for submission for publication of the material. Krause, Douglas J.; Hinke, Jefferson T.; Perryman, Wayne L.; Goebel, Michael E.; LeRoi, Donald J. The dissertation author was the primary investigator and author of this material.

Acknowledgements

The financial, infrastructure and logistical support of the US-AMLR Program has made this work possible, and George Watters, its Director, is thanked enthusiastically. This manuscript was improved by suggestions from J. Walsh, P. Dayton, and L. Ballance. We are grateful to K. Pietrzak, M. Mudge, J. Wright, N. Cook, M. Goh, D. Vejar, M. Zimmerman, K. Abernathy, T. Joyce for their dedicated assistance in the field. Thank you to A. Kownacki, K. Searles, and L. Rodriguez for taking photogrammetric measurements, and E. Keen and H. Fearnbach for Java consultations. Clearance for all UAS missions in this study was arranged with the Argentine air force with the assistance of the US Embassy, Buenos Aires, Argentina. Leopard seal interactions and captures were conducted in accordance with Marine Mammal Protection Act Permit No. 16472-03 granted by the Office of Protected Resources, National Marine Fisheries Service, Antarctic Conservation Act Permit No. 2012-005, and the NMFS-SWFSC Institutional Animal Care and Use Committee Permit No. SWPI2011-02.

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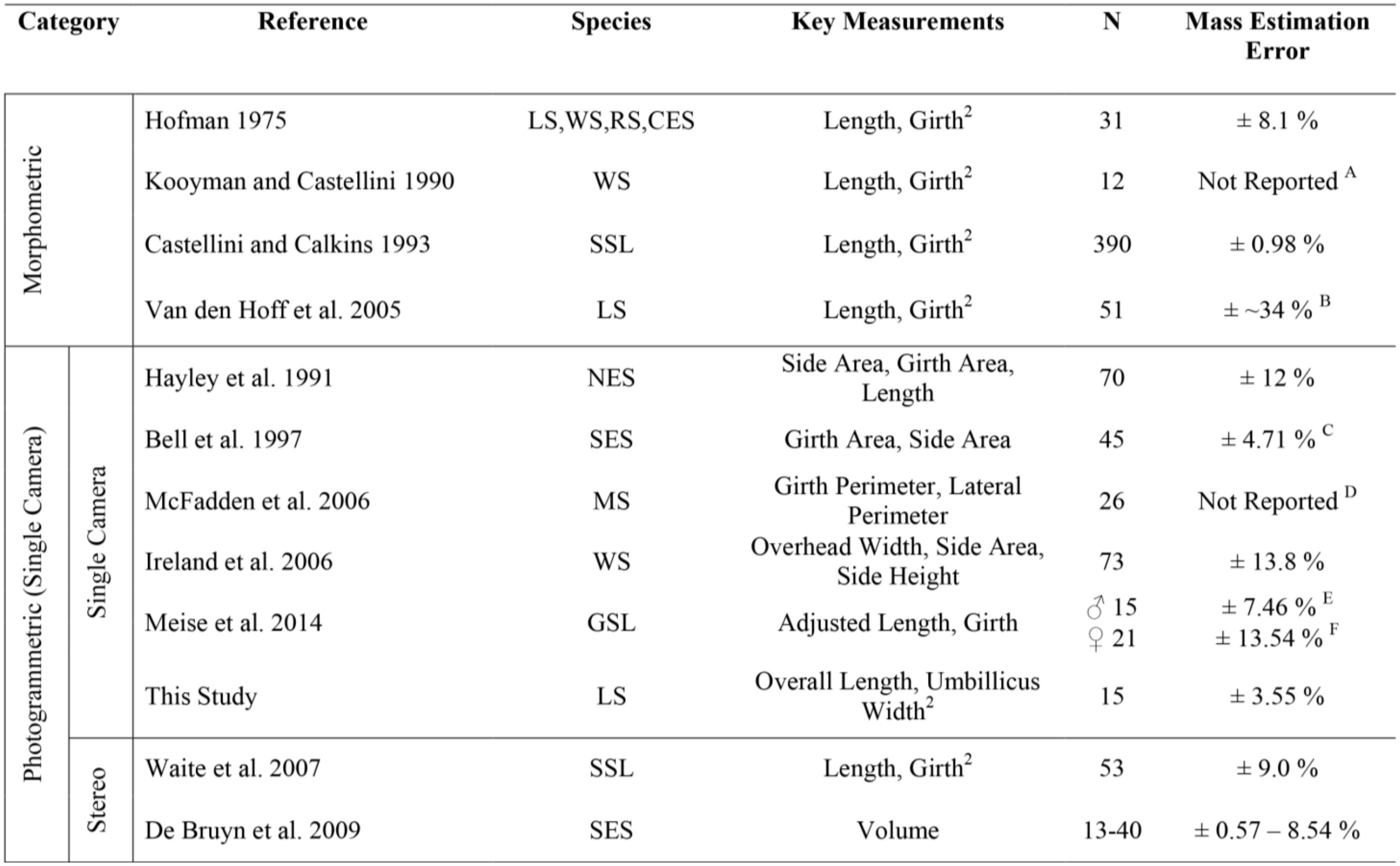
Tables

Figure 4-1: A summary of pinniped mass estimation studies. “Mass Estimation Error” represents either cross validation, or mean squared error of the best model. [A] $R^2 = 0.87$, [B] Based on the reported back-transformed error of 120 kg for an approximately 350 kg seal, [C] error reported as 95% confidence intervals (CI), [D] error was reported as a 95% CI of ±5 kg, but the corresponding mean true mass was not reported, therefore the range of potential error is extremely large, [E] based on reported errors for a 75 kg male, [F] based on reported errors for a 65 kg female.



Category		Reference	Species	Key Measurements	N	Mass Estimation Error
Morphometric		Hofman 1975	LS,WS,RS,CES	Length, Girth^2	31	± 8.1 %
		Kooyman and Castellini 1990	WS	Length, Girth^2	12	Not Reported [A]
		Castellini and Calkins 1993	SSL	Length, Girth^2	390	± 0.98 %
		Van den Hoff et al. 2005	LS	Length, Girth^2	51	± ~34 % [B]
Photogrammetric (Single Camera)	Single Camera	Hayley et al. 1991	NES	Side Area, Girth Area, Length	70	± 12 %
		Bell et al. 1997	SES	Girth Area, Side Area	45	± 4.71 % [C]
		McFadden et al. 2006	MS	Girth Perimeter, Lateral Perimeter	26	Not Reported [D]
		Ireland et al. 2006	WS	Overhead Width, Side Area, Side Height	73	± 13.8 %
		Meise et al. 2014	GSL	Adjusted Length, Girth	♂ 15 ♀ 21	± 7.46 % [E] ± 13.54 % [F]
		This Study	LS	Overall Length, Umbillicus Width^2	15	± 3.55 %
	Stereo	Waite et al. 2007	SSL	Length, Girth^2	53	± 9.0 %
		De Bruyn et al. 2009	SES	Volume	13-40	± 0.57 – 8.54 %

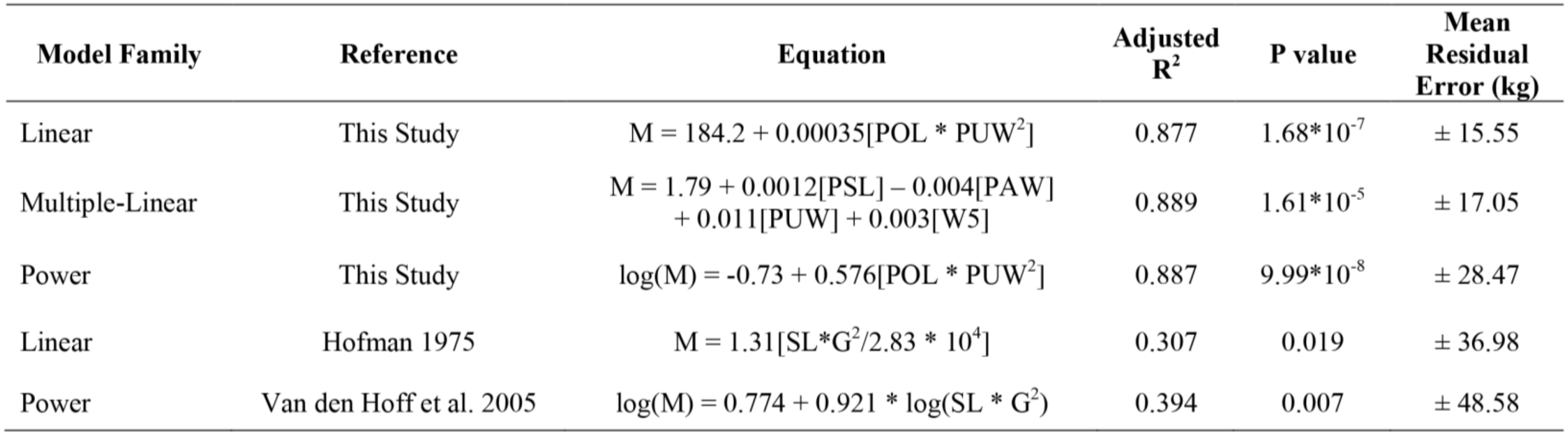
Table 4-2: Photogrammetric (P) and manual (M) measurements used in regression models. The units for all straight line measurements were cm, mass was recorded in kg.

Measurement	Measurement Type	Abbreviation
Standard Length	M	SL
Curvilinear Length	M	CL
Axillary Girth	M	AG
Umbilical Girth	M	UG
Standard Length	P	PSL
Overall Length	P	POL
Curvilinear Length	P	PCL
Axillary Width	P	PAW
Umbilicus Width	P	PUW
Width 1	P	W1
Width 2	P	W2
Width 3	P	W3
Width 4	P	W4
Width 5	P	W5
Width 6	P	W6
Width 7	P	W7
Width 8	P	W8
Width 9	P	W9
Width 10	P	W10

Table 4-3: % Error, ANOVA, and Tukey's HSD test results of PSL compared to SL for each category of photographs. Nulls could not be rejected for, nor were there any significant interactions between, any categories.

Category	**Type**	**N**	**% Error ($\bar{X}$ ± *sd*)**	**ANOVA**	**Tukey's HSD**
UAS Altitude	45 m	23	1.96 ± 0.92 %	F=0.047, P=0.954	45m – 30m (P=0.955)
	30 m	13	2.07 ± 1.49 %		30m – 23m (P=0.978)
	23 m	14	2.03 ± 0.87 %		45m – 23m (P=0.996)
Body Position 1	Dorsal	40	2.06 ± 1.08 %	F=0.067, P=0.879	NA
	Lateral	10	1.81 ± 1.00 %		
Body Position 2	Straight	31	2.15 ± 1.08 %	F=1.468, P=0.222	NA
	Curved	19	1.77 ± 1.01 %		
Substrate	Snow	38	2.14 ± 1.13 %	F=1.06, P=0.385	NA
	Sand	12	1.61 ± 0.70 %		

Figure 4-4: Comparison table of the most informative equation from each family of regression models, and equations from two previous studies. The mean squared error were back-transformed from log space for power models.



Model Family	Reference	Equation	Adjusted R^2	P value	Mean Residual Error (kg)
Linear	This Study	$M = 184.2 + 0.00035[POL * PUW^2]$	0.877	$1.68*10^{-7}$	± 15.55
Multiple-Linear	This Study	$M = 1.79 + 0.0012[PSL] - 0.004[PAW] + 0.011[PUW] + 0.003[W5]$	0.889	$1.61*10^{-5}$	± 17.05
Power	This Study	$\log(M) = -0.73 + 0.576[POL * PUW^2]$	0.887	$9.99*10^{-8}$	± 28.47
Linear	Hofman 1975	$M = 1.31[SL*G^2/2.83 * 10^4]$	0.307	0.019	± 36.98
Power	Van den Hoff et al. 2005	$\log(M) = 0.774 + 0.921 * \log(SL * G^2)$	0.394	0.007	± 48.58

Figures

Figure 4-1: The APH-22 VTOL UAS system. Photo Credit: D. Krause/NOAA.

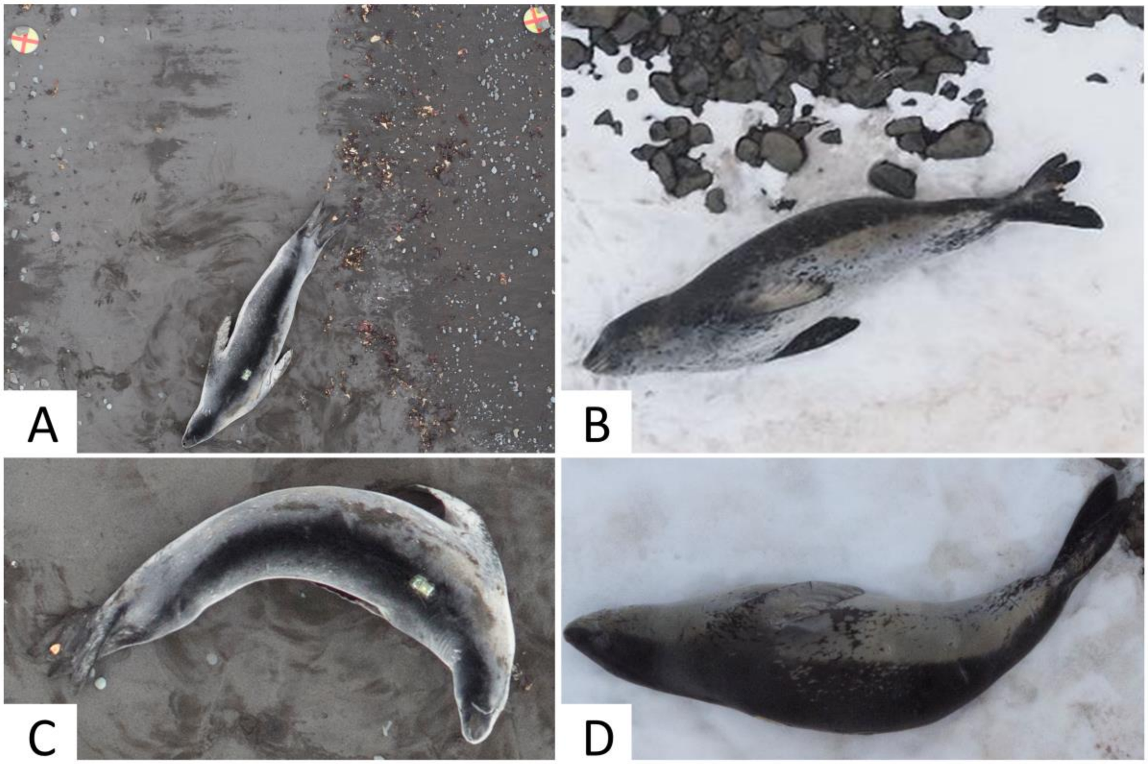


Figure 4-2: Example photos of leopard seal body positions, and substrates. A) A dorsal-straight body position on sand substrate. The ground reference scale is marked by two red x. B) A lateral-straight body position, C) a dorsal-curved body position, and D) a lateral-curved body position.

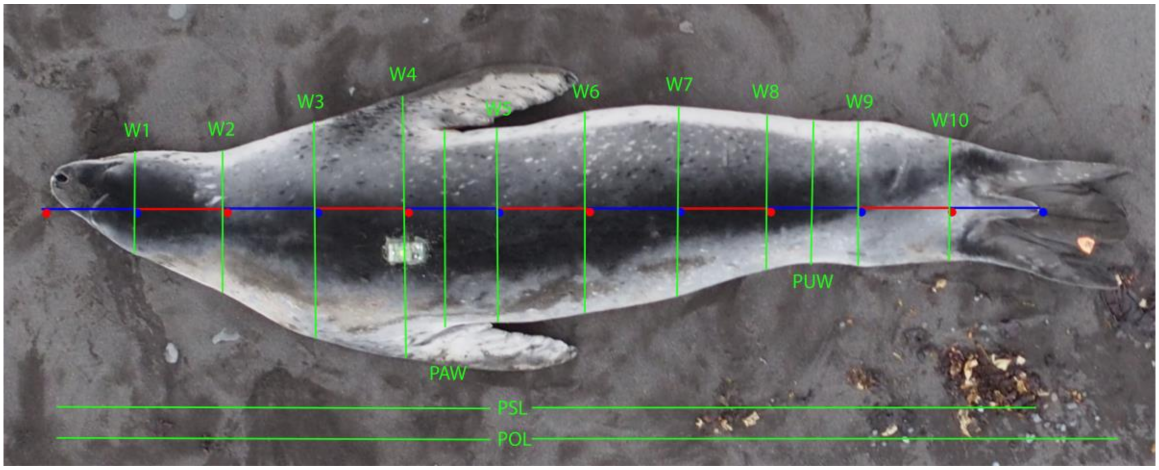


Figure 4-3: An example measured leopard seal with labeled photogrammetric measurements.

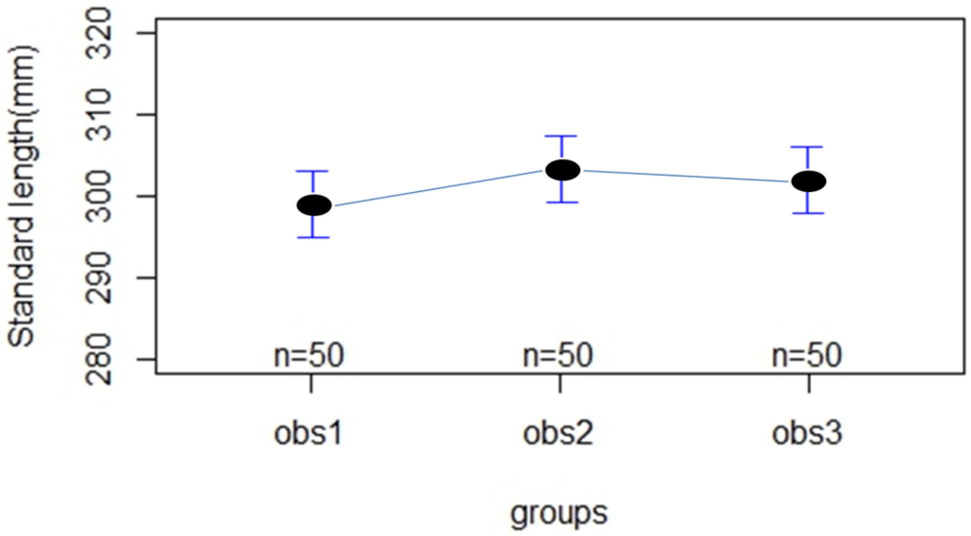


Figure 4-4: The mean values of photogrammetrically derived measurements of leopard seal standard length (N=50). Blue whiskers show standard deviation.

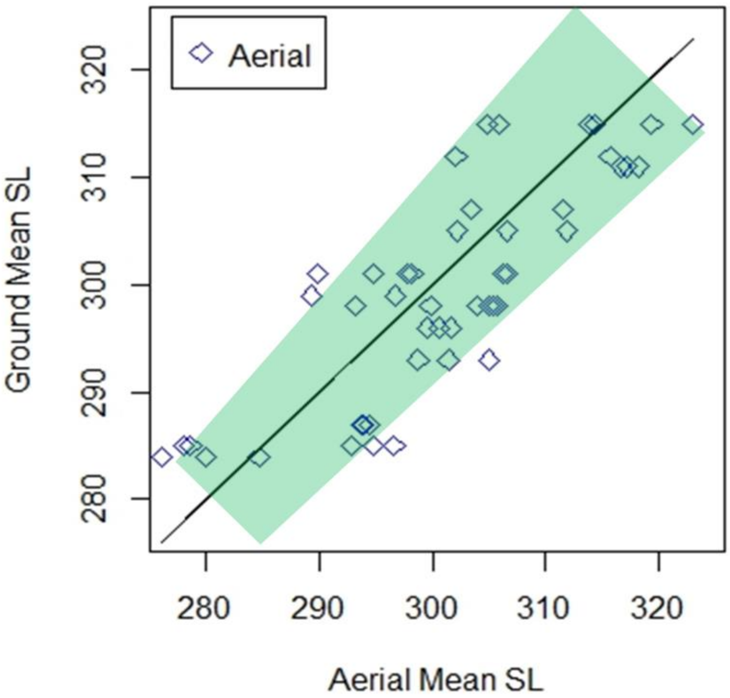


Figure 4-5: Photogrammetrically-derived measurements of leopard seal standard lengths (blue diamonds) correlate strongly with corresponding manual measurements (r=0.85, P<0.00001). All points within the green trapezoid exhibit < 2% error.

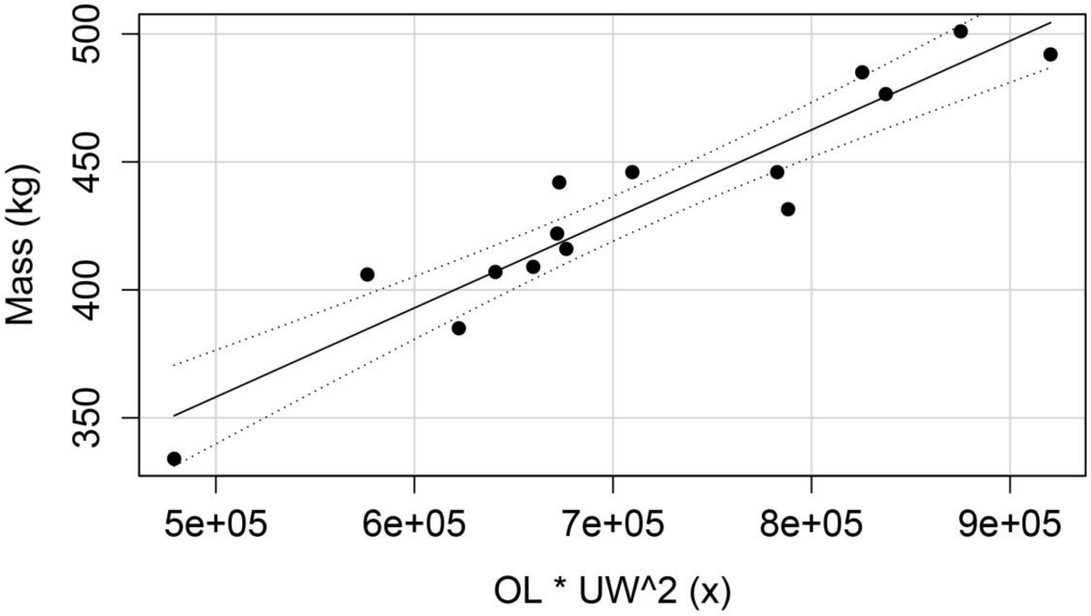


Figure 4-6: Linear regression of overall length (POL) and umbilicus width (PUW) to leopard seal mass with 95% confidence intervals (dashed line). $R^2 = 0.877$, $P=1.68*10^{-7}$.

CONCLUSION

The marine ecosystem in the Antarctic Peninsula region (APR) features incredible biodiversity, high productivity (Ducklow et al. 2007), and a complex history of ecosystem-shifting exploitation (Laws 1977, Ballance et al. 2006). The last several decades have brought two substantial changes that will both intensify the complexity of monitoring the system, and provide optimism for the potential of successful management. The first is a rapidly warming climate, and commiserate cascading changes across physical and biological interactions (Massom and Stammerjohn 2010). The second is the creation of an international management body (Commission for the Conservation of Antarctic Marine Living Resources, CCAMLR) (CCAMLR 1980) which, as opposed to the previous 150 years, is poised to prevent another major over-exploitation event. Effective management, however, requires an understanding of tropho-dynamics at an ecosystem level (Agnew 1997). The research summarized herein contributes substantial scientific progress in understanding how leopard seals trophically interact with the APR ecosystem, and how that is likely to change in the future.

By combining traditional observation techniques and advanced bio-logging instruments, we have been able to describe novel aspects of leopard seal behavior with broad ecological applications including: foraging specialization (Chapters 1-3), intraspecific competition including kleptoparasitism (Chapter 1), and scavenging and food caching (Chapters 1 and 2). We have been able to trophically place large adult female leopard seal within a defined prey field, and demonstrate low niche variability within week and month time scales (Chapter 3). Moreover, we have seen multiple lines of evidence that projected warming and sea-ice loss will likely lead to a broadened leopard seal niche width across prey, space and time, and a regionally intensified impact (Chapter 2). And, finally, we have applied a flexible sampling design with an increasingly-available unmanned aerial platform to count and estimate the mass of leopard seals in a regionally scalable way (Chapter 4).

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