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

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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/hour) 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.

Key words: leopard seal, apex predator, diving, TDR, animal-borne video, cluster analysis, random forest, temporal niche partitioning, chemical immobilization.

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

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been estimated at 300,000 (Erickson 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) were 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 ($n \leq 2$), 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/square nautical mile, 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,[2] 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.* 2015). Estimating the extent of facultative scavenging (Wilson and Wolkovich

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[2] 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.

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 activity budgets and 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 summarized robust groupings of diving behavior (dive types), and 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°S, 60.77°W) on Livingston Island (Fig. 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 1). Five seals (with tags numbered 422Y, 04OR, 09OR, 390G, and

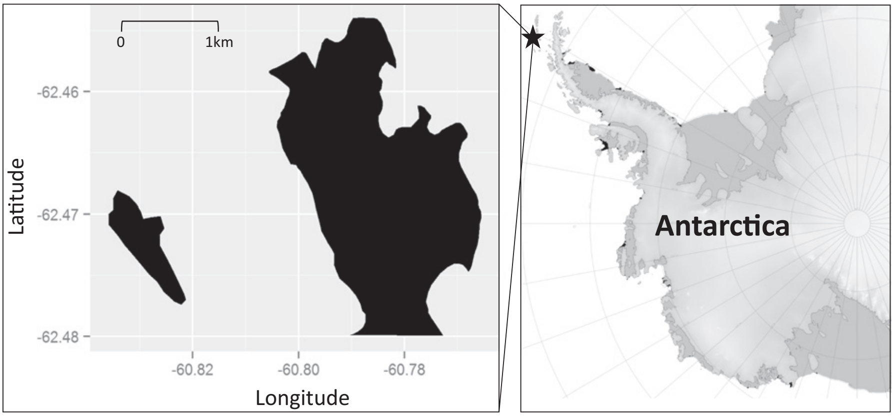

Figure 1. Cape Shirreff, Livingston Island, Antarctica. The black star in the right pane indicates the location of Cape Shirreff in the western Antarctic Peninsula region.

Table 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 ± standard deviation.

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	1,167	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	3,380	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	5,094	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	5,074	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	3,205	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	4,502	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	2,043	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	3,754	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	1,396	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	1,232	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	NA	12.18 ± 8.23	82	1.08 ± 1.16	7.15	13.24
422Y – 2013	0.86	138	1	NA	NA	14.13 ± 9.31	52	1.54 ± 1.41	5.47	7.33
09OR – 2014	8.53	1,834	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	1,064	1	NA	NA	17.70 ± 12.21	84	3.07 ± 1.41	7.85	10.27
18OR – 2014	7.53	1,393	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	1,010	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	1,269	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	40,308	229	0.60 ± 0.40	0.71 ± 0.49	16.60 ± 10.99	229	2.20 ± 1.23	22.97	11.65±3.09

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 × 17 × 17 mm, 30 g, Wildlife Computers [WC], Redmond, WA; sample rate: 30 samples/minute) 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 1), recoveries were difficult and instruments were often lost when the tags pulled free from the flipper (seven recoveries from 14 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 14 TDRs (Mk9, WC, sample rate: 60/min, $n = 11$; or National Geographic CRITTERCAM VI, Washington, DC, sample rate: 60/min, $n = 1$; or DST-Milli-TD/100, Star Oddi, Gardabaer, Iceland, sample rate: 12/min, $n = 2$) and 14 VHF transmitters (Advanced Telemetry Systems, Isanti, MN) were attached to the forward-dorsal midline pelage using Devcon 5 min 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 5 cc pistol dart using an air-compressed compensated dart gun (Dan-inject, Denmark) chosen to minimize disturbance (Higgins *et al.* 2002). The 2 × 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). Post-capture, 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 resighted at least once within 2 wk 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 (WC Instrument Helper) 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 °C), and wind chill temperature (daily mean in °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 m/s (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 (minutes). 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, T. Eguchi[3]), or modeling approaches (*e.g.,* Frost *et al.* 2001, Dowd and Joy 2010). RF algorithms are appealing for classifying large, multidimensional 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*

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[3] Personal communication from Tomo Eguchi, NOAA Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037, May 2013.

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 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 (Fig. S1) (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 number of dives per hour of day were plotted on a 24 h 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 yr). 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 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 (Fig. S2), 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.,* Fig. S3). 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 (Fig. S4). 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 (Fig. 2a). The only significant environmental driver of haul-out probability was *dLAN*, and the most informative model was a polynomial regression [$\textit{haul-out probability} = 71.01 - 1.5dLAN^2 + 0.10dLAN^3$] ($R^2$ = 0.985,

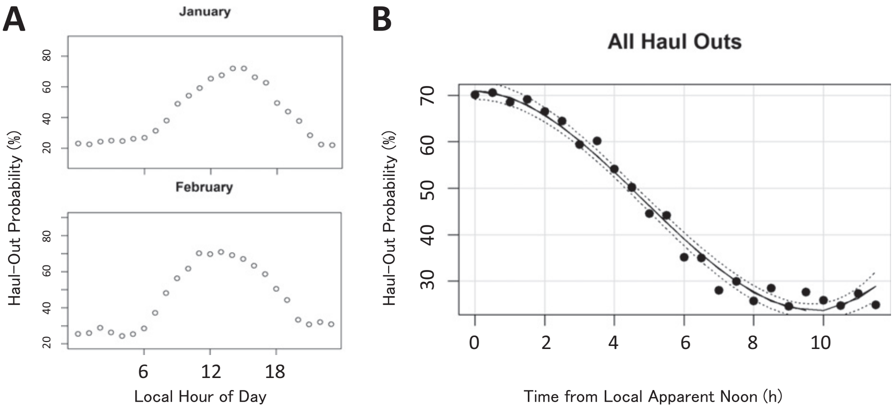

Figure 2. (A) Empirical haul-out probability distributions for leopard seals at Cape Shirreff based on 209 haul outs from 18 animals in January and February from 2008 to 2014. (B) A polynomial linear regression (solid line) which predicts haul-out probability based on time (h) from local apparent noon;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

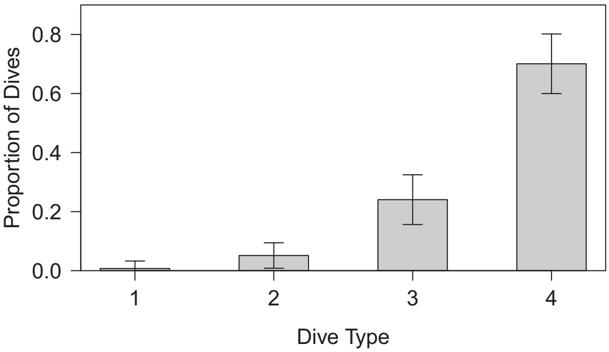

Figure 3. The mean proportion (with SD whiskers) of dives that were classified into each dive type (1–4) for all dives in the cluster data set (n = 38,338).

$P < 0.000001$, Fig. 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

Table 2. Summary statistics and descriptions of the four 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 ± standard deviation.

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

across all individuals in the study (Fig. 3). Category names and descriptions of the four dive types are in Table 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.,* Fig. S5a). Type 2 dives were symmetrically round or "v" shaped dives; the depth range was 39–79 m (*e.g.*, Fig. S5b). Type 3 dives were predominantly nonsymmetrical dives displaying a wide variety of shape; the depth range was 16–38 m (*e.g.,* Fig. S5c). 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.*, Fig. S6). 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).

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 (Fig. 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 (Fig. S7).

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%).

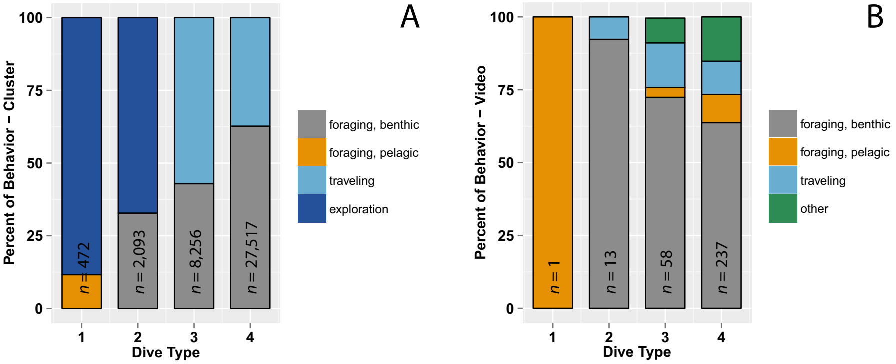

Figure 4. Comparison by dive types between (A) behavior predicted from the k-means cluster analysis of time-depth dive records (n = 38,338) and (B) behavior manually scored from animal-borne video dive data (n = 309).

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 (Fig. 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 (Fig. 5 b–d). However, the dive activities of individuals compared within the same year were concentrated at significantly different times of day (*e.g.*, Fig. 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.

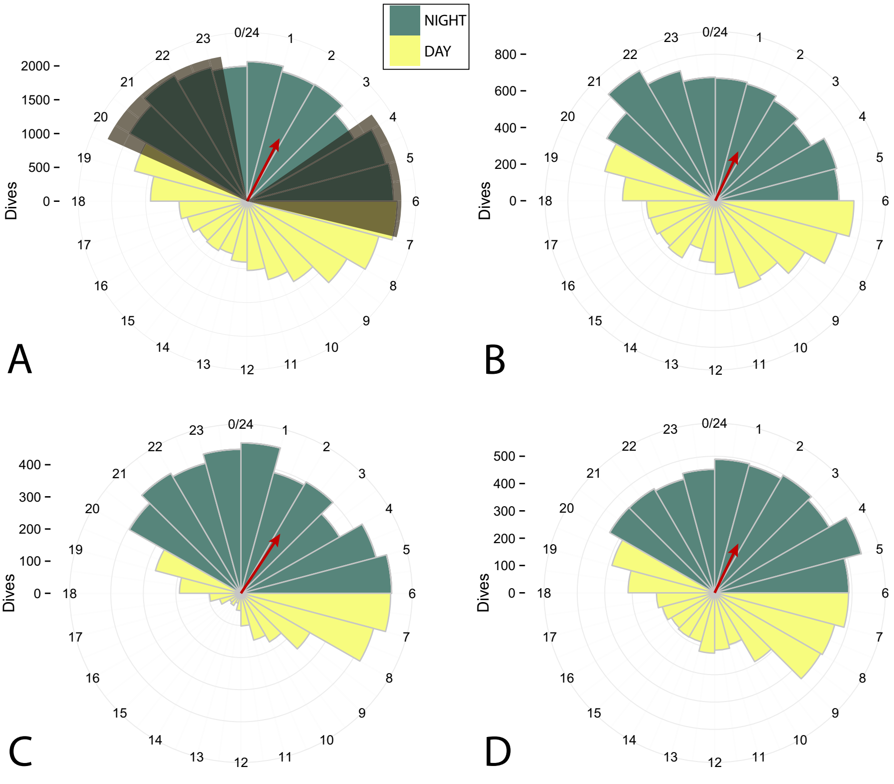

Figure 5. 24 h rose plots of dive activity by hour of day. The red arrows represents the mean vector (direction = time of day, length = mean number of dives) of dive activity (dives/h) for: (A) all dives ($n = 40{,}308$). Gray shaded areas represent the crepuscular periods (±1 h from sunset and sunrise) across the study; (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, $P > 0.05$).

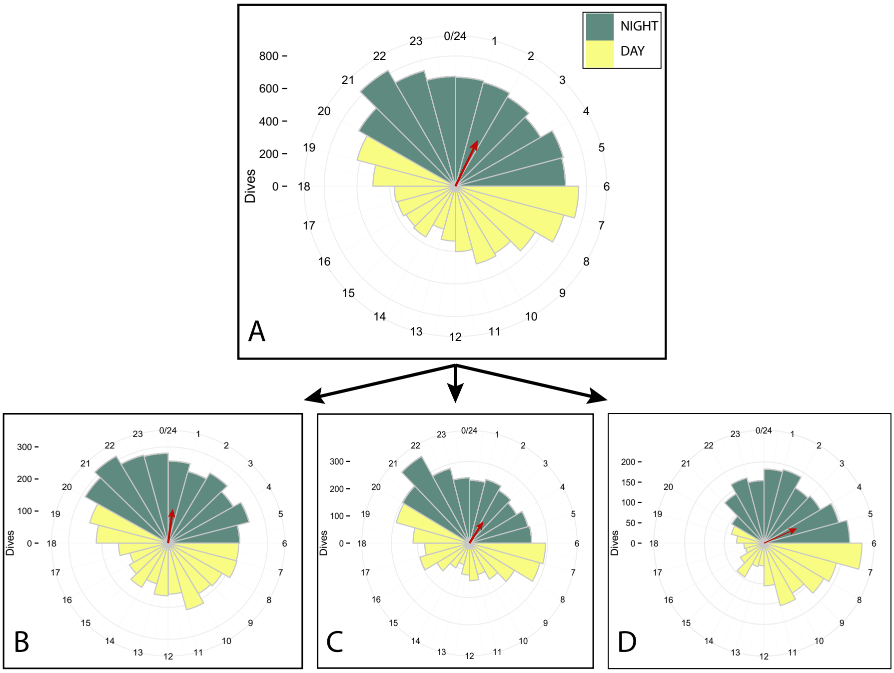

Figure 6. 24 h rose plots of leopard seal dive activity by hour of day from the parametric data set. Red arrows represent the mean vector of dive activity. (A) all dives pooled from the 2010 season (n = 6,017) from three seals (4OR, 9OR, and 390G). (B) Activity for leopard seal 4OR (n = 2,292 dives) 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, $P < 0.001$).

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 in January, 1300 in 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, 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, 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, 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 4.8 km 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.[4] 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 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 (Fig. 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 (Fig. 4a, 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

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[4] Personal communication from David Demer, NOAA Southwest Fisheries Science Center, 8901 La Jolla Shores Drive, La Jolla, CA 92037, March 2015.

(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, 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 2013–2014 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 (Fig. 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.*, Fig. 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 fish, 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 have 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.

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SUPPORTING INFORMATION

The following supporting information is available for this article online at http://onlinelibrary.wiley.com/doi/10.1111/mms.12309/suppinfo.

Figure S1. The optimal number of clusters in a k-means cluster analysis of leopard seal dive observations (n = 38,338). The blue points represent within groups sum of squares differences for each cluster grouping 2–10. The red points indicate corresponding values for the Calinski Index.

Figure S2. A histogram of all leopard seal dives (n = 40,308) by dive duration.

Figure S3. The profile of a 23.97 min leopard seal dive profile recorded near Cape Shirreff, Livingston Island.

Figure S4. A histogram of all leopard seal dives (n = 40,308) by maximum depth per dive.

Figure S5. Example leopard seal dive profiles randomly selected from the cluster data set (n = 38,338) to illustrate (A) "type 1" dives, (B) "type 2" dives, and (C) "type 3" dives.

Figure S6. Example leopard seal dive profiles randomly selected from the cluster data set (n = 38,338) to illustrate (A) "nonforaging type 4" dives and (B) "foraging type 4" dives.

Figure S7. Predictor importance for each variable (n = 8) used in the random forest algorithm; percentage values were based on the marginal decrease in prediction accuracy.