Borras-Chavez Renato (Orcid ID: 0000-0002-6415-2121)
Hückstädt Luis A (Orcid ID: 0000-0002-2453-7350)
Costa Daniel P (Orcid ID: 0000-0002-0233-5782)

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ARTICLE

Time and behavioral adjustments to lactation: Insights from a marine predator

Renato Borras-Chavez[1] | Michael E. Goebel[2,3] | Stella Villegas-Amtmann[2] | Luis A. Hückstädt[2,4] | Carla Rivera-Rebella[1] | Daniel P. Costa[2] | José M. Fariña[1] | Francisco Bozinovic[1]

[1] Center of Applied Ecology and Sustainability (CAPES), Pontificia Universidad Católica de Chile, Santiago, Chile

[2] Institute of Marine Sciences, University of California Santa Cruz (UCSC), California

[3]Antarctic Ecosystem Research Division, SWFSC, NMFS, NOAA, La Jolla, California

[4]Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall, UK

Correspondence

Renato Borras-Chavez, Pontificia Universidad Católica de Chile, Depto. de Ecología, CAPES, 340 Libertador Bernardo O'Higgins Avenue, Santiago, 8331150, Chile.

Email: rborras@gmail.com

Abstract

The energetic costs of lactation have been studied in many marine mammals, but little is known about the behavioral adjustments needed to cope with this event. By simultaneously measuring foraging behavior of lactating and nonlactating Antarctic fur seal females, we estimate the behavioral changes necessary to cope with the constraints of lactation and include the first comparative record of dive behavior between lactating and nonlactating female otariids. Nonlactating females exhibited highly variable foraging trip duration but spent long times onshore between trips. In contrast, lactating females exhibited consistently shorter trips and spent half the time hauling-out compared to nonlactating females likely to maximize offspring provisioning. Lactating females show a reduced mean times per dive but greater percentage of time per trip spent diving compared to nonlactating animals. The reduction in time onshore and trip duration, together with modifications in dive performance suggests additional effort of lactating females to compensate for the constraints of rearing a pup, which has not been observed previously due to the lack of simultaneous comparison of lactating and nonlactating individuals. When possible, future studies of maternal investment should also include nonlactating individuals, since lactation may have a strong synergistic effect with other aspects shaping foraging behavior.

KEYWORDS

Antarctic fur seal, *Arctocephalus gazella*, breeding, diving behavior, foraging ecology, lactation, otariids

1 | INTRODUCTION

Lactation is the most expensive reproductive event in both terrestrial (Clutton-Brock et al., 1989; Gittleman & Thompson, 1988; Naya et al., 2008; Poppitt et al., 1993) and marine mammals (Arnould, 1997; Boyd, 1998; Costa et al., 1986; Fedak & Anderson 1982; Oftedal et al., 1987; Williams et al., 2007). In pinnipeds such as elephant seals (*Mirounga angustirostris*) and gray seals (*Halichoerus grypus)*, lactation accounts for ~60%–75% of the mother's energetic expenditure (Boyd, 1998; Costa et al., 1986; Fedak & Anderson, 1982). In fur seals, it can account for 31% of the energy expenditure (Arnould, 1997), which, in some species, forces to increase food intake almost four times the baseline energy requirements (Williams et al., 2007). The high energetic demand implicit in lactation seems to be mostly compensated by an increase in energy intake rather than changes in metabolic rate (Costa & Gentry, 1986; Costa & Trillmich, 1988; Harder et al., 1996; Oftedal et al., 1987; Zhu et al., 2015). This additional intake requirement will necessarily modify foraging activities (Arnould et al., 1996).

Comparative studies focused on lactating and nonlactating individuals are necessary to understand the consequent changes in behavior associated to the constraints of lactation. However, only a few studies, mainly in terrestrial mammals, have been able to do so (Scantlebury et al., 2002; Schmid et al., 2003). Usually, lactating females will use cost-effective strategies that focus on obtaining more or better food. Lactating females will regulate the foraging effort by increasing the time spent eating (Watts, 1988; Zhu et al., 2015) or increasing the energy storage for later use when food is available (McCabe et al., 2013). Other species will focus on higher quality food items, fat reserves, or behavioral changes (Costa & Williams, 1999; Gittleman & Thompson, 1988; Shero et al., 2018). Income breeders, such as otariids, obtain the energy necessary for milk production during lactation and must, therefore, inevitably modify their behavior (Arnould et al., 1996; Bonner, 1984; Costa & Gentry, 1986; Oftedal et al., 1987). These behavioral modifications are poorly understood in otariids since we lack comparative studies between nonlactating and lactating female´s diving behavior during the breeding season (Ponganis, 2015).

Otariids are central place foragers (Orians & Pearson, 1979), and during lactation females make multiple trips to sea to supply—upon return to the breeding beach—the energy needed by their offspring. When females are foraging, pups fast usually between 1 to 6 days, with some species going far beyond these numbers (Gentry & Kooyman, 1986). While at sea, mothers will perform bouts of multiple dives interspersed with brief interdive surface time intervals (Rosen et al., 2017). While foraging, adjustments in behavior to balance energy acquisition and pup provisioning can occur while traveling, provisioning, and/or diving. In addition, behavioral plasticity in otariid diving and foraging behavior has been observed in response to other variables. In the Antarctic fur seal (*Arctocephalus gazella* Peters, 1875), the use of different foraging areas (Costa et al., 1989; Goebel et al., 2000; Staniland et al., 2007), female age status, and mass (Lea et al., 2009, Mcdonald et al., 2009) and/or population size (Staniland et al., 2011) will shape behavioral variables such as trip duration, niche use and/or diving behavior. Moreover, under complex scenarios, such as increasing oceanographic variability (Boyd, 1999; Lea et al., 2006) or different prey distribution and/or abundance (Boyd, 1999; Boyd et al., 1994; Ichii et al., 2007; Lea et al., 2006; Staniland et al., 2010), lactating females will modify their foraging trip duration or the time spent ashore (Boyd, 1999; Costa, 2008; Costa et al., 1989). In other words, trip duration would be limited by the availability and abundance of the prey (Boyd, 1999; Lea et al., 2002) and haul-out time (time ashore) by the rate of energy that is transferred to the offspring (Boyd, 1999; Gentry, 1998). However, if females are operating at their maximum capacity, under no circumstances they would modify their diving effort (Boyd, 1999; Costa, 2008; Costa et al., 1989, 2000).

In years when prey availability is limited, Antarctic fur seals will adjust their time budget. Boyd (1999) hypothesized that Antarctic fur seal females reduce the time spent ashore and increase trip duration to maximize food delivery to their offspring (sustaining a threshold energy intake even during pup fasting). In contrast, in years when prey is abundant, animals would perform shorter trips to sea. Here, we argue that the short trips observed in lactating females under abundant prey scenarios, could also be associated with the constraints of lactation and/or attendance (Arnould, 1997; Arnould et al., 2001) and not solely shaped by prey availability. The use of only lactating females in previous studies does not allow for a clear estimation of the additional effort that lactation has on breeding females, especially considering that modifications in diving effort have been observed in other pinniped species under similar demanding reproductive events such as pregnancy (Shero et al., 2018; energetic differences between gestation and lactation not withstanding).

In this study, we simultaneously compared nonlactating Antarctic fur seal females' foraging, diving, and haul-out behavior with lactating fur seal females' behavior to test the hypothesis that nonlactating individuals perform longer trips to sea and have longer times hauling out than lactating females due to the absence of restrictions associated to lactation. In addition, given the same foraging environment, lactating animals would show additional effort by increasing their diving activities as a result of the additional energetic costs of lactation.

2 | METHODS

2.1 | Study site

The study was part of a long-term, multispecies ecosystem monitoring program at Cape Shirreff, Livingston Island, Antarctica (62°28′S, 60°46′W) led by the US Antarctic Marine Living Resources Program (AMLR) of the National Oceanic and Atmospheric Administration (NOAA). We considered only known-aged, adult reproductive Antarctic fur seal females in this study, minimizing behavioral differences related to age and size. Regardless of whether they gave birth, females will make regular foraging trips to sea during the breeding season (from early December to the end of March). We conducted the study during the breeding seasons of 2015–2016 and 2016–2017 (hereafter called season 2015 and season 2016, respectively). Nonlactating females did not carry instruments for the entire breeding season since the risk of losing instruments is too high when they are not nursing due to fewer constraint on their behavior on land and the unpredictability of animals departing from the area. Therefore, we limited the analyses only to foraging trips that allowed simultaneous comparison within the timeframe of each season that nonlactating animals carried instruments (2015: from January 28 to March 3 and 2016: December 13 to February 4), excluding first and second postparturition foraging trips of lactating females.

We captured lactating (designated “L”; *n* = 15) and nonlactating (“NL”; *n* = 7) females with hoop nets, sedated them with a 5 mg intravenous midazolam injection (0.1–0.15 mg/kg), and anesthetized them with isoflurane gas and oxygen using a portable field vaporizer (Gales & Mattlin, 1998; McDonald et al., 2009). Once the seals were anesthetized, we attached VHF radio transmitters (55 mm × 22 mm × 10 mm and 23 g; Advanced Telemetry Systems, Isanti, MN), and time-depth recorders (TDR, MK9; Wildlife Computers, Redmond, WA) to their fur with 5 min Devcon marine epoxy (dorsal to the midline and posterior to the maximum axial girth). While the seals were anesthetized, we obtained the mass, length (from nose to the tip of the tail), and axial girth of all females. A body condition index (BCI) on each animal was calculated by dividing the body mass (kg) by the body length (cm) (BCI: mass/length; validated in Arnould, 1995).

Although we controlled for similar sizes when selecting the individuals, nonparametric preliminary comparison of BCI between L and NL females showed that there was statistical differences between groups (Kruskal-Wallis: $\chi^2[1] = 5$, $df = 1$, $p = .03$). Therefore, BCI was incorporated in the initial models proposed for each behavioral variable (see section 2.5 | Statistical analysis). We used the same capture protocol to recover instruments and followed all applicable institutional and national guidelines for the care and use of animals (see Acknowledgments).

2.2 | Instrument configuration and data processing

TDRs recorded temperature (°C), time (seconds), and depth (meters) every second when instruments were submerged in saltwater. After instrument recovery, raw data were filtered in MatLab 9.0 (MathWorks, Inc., Natik, MA) using the IKNOS toolbox (software developed by Y. Tremblay, unpublished data). This algorithm allows for a zero-offset correction at the surface and identifies dives based on a user-defined minimum depth (4 m) and dive duration (6 s). This accounts for instrument error at the surface when detecting minimum depth (Tremblay, unpublished data; Tremblay et al., 2009). We considered only trips of L females occurring within the same timeframe that NL females were carrying instruments.

2.3 | General assessment of diet and foraging time of the day

To have a general qualitative idea of prey items consumed by this colony, we analyzed 10 scats per week throughout the breeding season, reaching a total of 100 scats (methods for scat collection and prey identification can be found in Klemmedson et al., 2020). We calculated the percentage frequency of occurrence of the three main prey types consumed (fish, krill, and squid) dividing the total number of scats in which each prey was present by the total number of scats collected per breeding season (100 scats; Figures S1 and S2). We estimate differences between L and NL females in the time of the day that foraging took place since previous studies have described variations in the vertical daily migration patterns of prey (fish and krill; Collins et al., 2008; Croxall et al., 1985). To do so, we assigned foraging dives to “Day” or “Night” based on the sun angle at the time of foraging (night at this location: from a 90° to 110° sun angle), and interpolated the location of the dive, using the function sun_position in MatLab (Reda & Andreas, 2003).

2.4 | Foraging effort

There are multiple ways of measuring effort while foraging. Animals increase their foraging activities by working harder, changing the way they dive (e.g., performing deeper or longer dives, increasing dive frequency), reducing the resting time, or multiple combinations of these aspects. We determined differences in foraging effort between L and NL females by comparing four groups of behavioral variables: (1) trip duration, (2) dive frequency (dives/hour), (3) mean of dive performance variables (see below), and (4) bout behavior (while diving, Antarctic fur seals perform “dive bouts”—groups of dives interspaced with surface time intervals). We also evaluate if differences in effort between L and NL females are observed in adjustments of time spent nonactive (on land or at sea, thereby passive time). For this, we investigated changes in (5) haul-out (days/hours spent ashore between foraging trips) and time (minutes) between bouts at the surface (postdive surface intervals; PDI).

(1) We calculated trip duration (days) using VHF data. Two automated VHF receiving stations were used to monitor presence/absence from the colony at 30 min intervals. Automated monitoring of the two stations were compared and matched for accuracy. In addition, VHF data were confirmed with daily visual observations (technicians walked through all breeding beaches twice a day (morning and afternoon) to confirm that females detected by the automated VHF stations were onshore). Further validation of VHF data was made by comparing records of animals

onshore with TDR data after recovery of instruments.

(2) We calculated dive frequency for each foraging trip based on the time-depth data collected by the TDRs. We analyzed all dives within each trip and estimated dive frequency as the mean number of dives per hour of the nontransit portion of each trip. The mean dive frequency per trip obtained was the statistical unit used to compare frequency of dives between L and NL female trips.

(3) To determine if dive performance (dive variables) was different between L and NL females, we calculated the differences between groups comparing the mean of eight dive variables, i.e., maximum dive depth (m), bottom time (s), descent time (s), descent rate (m/s), ascent time (s), ascent rate (m/s), dive duration (s), and the mean percentage of accumulated diving time per trip. Following Bestley et al. (2015), we also determined if dive duration was longer or shorter than expected for a given depth, which may indicate relatively higher/lower effort of one group respect to the other. This was obtained from a linear relationship between the residuals of dive duration (seconds) and maximum depth (meters; see section 2.5 | Statistical analysis).

(4) Metrics of behavior calculated at the scale of a complete foraging cycle (mean dive frequency (dives/hour) and the mean of

all diving variable per trip) may mask differences observed within individual dive bouts. For this, we calculated mean dive frequency, mean dive duration, and mean dive depth per dive bout. Also, we calculate mean bout duration per group (L and NL females). We performed the dive bout analyses following Boyd and Croxall (1992) definition of a dive bout (a group of dives defined by preceding and succeeding surface intervals lasting a specific number of minutes). To identify a dive bout, we set the following parameters: (a) a minimum number of five dives and (b) a minimum postdive surface interval (PDI; surface time between dives) of 10 min (i.e., a PDI of <10 min was considered the following dive as part of the same dive bout). We choose these parameters after a visual exploration of the data as suggested in Boyd et al. (1994).

(5) Passive time was represented by: (a) haul-out time between foraging trips, which was calculated based on the time interval between foraging trips (days) given by the TDR data and confirmed daily by visual observation of the females at the breeding beaches. (b) We calculated time spent at the surface between dives (postdive surface intervals; PDI) as the mean PDI time (minutes) per trip per female considering only those intervals equal or over a minimum PDI time of 10 min.

2.5 | Statistical analysis

To compare the diurnal or nocturnal proportional time invested foraging between groups (L and NL females), we built a linear mixed-effects model (LMM) after assigning all dives to one of these categories: “Day” or “Night.” We compared dive frequency as a function of two fixed factors: (1) groups (L/NL) interacting with BCI as a covariate and (2) the foraging time (Day/Night). We added to the model the female’s identity as the random factor to account for individual variability and repeated measures.

To test for differences between groups (L and NL) for each behavioral variable in all five groups (trip duration, dive frequency, diving variables, bout behavior, and passive time), we fitted LMM or Generalized Linear Mixed model (GLMM) using the R packages “NLME” (Pinheiro et al., 2014) and “lme4” (Bates et al., 2015), respectively. We proposed an initial model for each behavioral variable (i.e., response variables) based on biological information (predictors). On each initial model, we incorporated “Group” (L or NL), “BCI,” and “Season” as fixed factors to account for variance explained by the lactating status, female mass, and the breeding season (2015–2016), respectively. We also incorporate as fixed factors two interactions of interest: Group interacting with BCI and Group interacting with Season (see initial model “M1” in Table S1).

For the initial model of the diving variables: Ascent rate (m/s), Descent rate (m/s), Ascent time (s), Descent time (s), Bottom time (s), Maximum depth (m) and Dive duration (s), we also considered if dives were influenced by the diurnal/nocturnal migratory patterns of either krill or fish prey targeted (Collins et al., 2008; Croxall et al., 1985). Therefore, we added whether each dive was performed during the day or night (D/N) as a fixed factor. Finally, we used female´s identity as the random factor to account for individual behavioral variability in all models (see all models tested in Table S1). For both groups (L and NL females), we selected and matched known-aged females; thus, age was excluded from the model’s structure. We selected the best model for each variable according to Zuur et al. (2009), using backward stepwise model selection from the initial model proposed for each variable and an adjusted formula of the Akaike information criterion accounting for small sample sizes (AICc, *MuMin* R package; Barton, 2017, for model selection; see Table S1). On each variable, when ΔAICc between all models tested was <2, we selected the model with the smallest number of fixed factors. Homoscedasticity and normality were tested by visual inspection (q-q plots and histograms, Zuur et al., 2007). Because trip duration data appeared to show much greater variance in one group (NL) with respect to the other (L), we tested for equality of variances (homoscedasticity) in trip duration between L and NL females using a Fligner-Killen test. The behavioral variables that did not meet the basic assumptions of normality were transformed to a logarithmic scale (Ln) or square root and tested again. Data of the variable maximum depth, descent time, ascent time, and mean dive depth per bout were gamma distributed, and therefore a GLMM with gamma-distributed error was fitted.

In addition, we calculated dive residuals by fitting an LMM between dive duration (seconds) and maximum depth (meters, fixed factor) using the identity of each female as the random intercept since the duration-depth relationship may vary across females. Then, to determine if there were differences between groups, we tested the Pearson residuals obtained from the previously described LMM as a response variable against group as fixed effect with BCI as covariant and female ID as the random factor again using LMMs.

To check if there was a significant contribution of each behavioral variable to each model, we obtained *p*-values of all fixed factors and interactions using a Type III Wald chi-square test with the *car* R package (Fox & Weisberg, 2019; Table S2). The significance threshold in all tests was set with a 95%

confidence interval (CI). Marginal means and CIs are shown in each variable’s original scale, and all data log or square root transformed for the model were back-transformed.

We performed all statistical tests in R (R Core Team, 2017). The LMMs were fitted via restricted maximum-likelihood estimation and GLMM by maximum likelihood.

3 | RESULTS

We obtained diving records from 15 lactating females (76 trips and 87,734 dives total; six individuals in 2015 and nine in 2016), and five out of the seven nonlactating females instrumented (27 trips and 24,825 dives total; two out of three individuals in 2015 and three out of four individuals instrumented in 2016). Table 1 presents the morphometric data used to calculate the body condition index (BCI) after the initial capture in all females. Preliminary assessments of diet suggest that in 2015 and 2016, prey targeted was very similar between seasons with three prey species accounting for more than 95% of the diet: one crustacean: krill (*Euphausia superba*) and two myctophid fishes: (*Electrona antarctica* and *Gymnoscopelus nicholsi*) (Figures S1 and S2). The complete model selection outcome for each behavioral variable can be found in Table S1 and the Type III Wald chi-square test results of all behavioral variables are summarized in Table S2. Here, in Table 2, we show only the selected model for each behavioral variable tested when comparing lactating (L) versus nonlactating individuals (NL).

All females exhibited similar percentages of time diving during daylight or night regardless of whether they were lactating (average percentage of dives occurring at night in L female's trip: 53%) or not (average percentage of dives occurring at night in NL female's trips: 54%). Both groups exhibited a slightly higher frequency of dives per hour during the night than during daylight, but we failed to find a significant difference between groups; L or NL ($\chi^2[1]= 0.9694$, $p = .3$; Figure 1).

3.1 | Trip duration and haul-out time

Statistical differences in mean trip duration between groups were found (Group: $\chi^2[1] = 13.5$, $p < .01$; Figure 2a, Table 3); driven by long trips performed by NL females in 2016 (Group*Season: $\chi^2[1] = 6.1$, $p = .01$) and differences in mass between L and NL females driven by high BCI values in L females (Group*BCI: $\chi^2[1] = 13.7$, $p < .01$; Table S2). In contrast, in 2015 L and NL females spent on average ~3.5 days at sea. When testing for equal variance between groups, statistical differences were also found ($\chi^2[1] = 13.064$, $p < .0003$; Figure 2b). NL females made the shortest (<1 day) and the longest trips to sea of all studied females (e.g., female ID 326: 11.43 days), with most NL females showing both long and short trips (female ID 4970 performed trips as short as 7 hr to longer than 5 days), explaining the greater variance observed in NL females (Figure 2b). In contrast, L females' foraging trips were very similar in duration between individuals throughout the study period regardless of the breeding season that the trips were performed (~3 days; Table 3, Figure 2b), with the longest trip being 7.02 days. Haul-out time varied significantly between groups ($\chi^2[1] = 4.5$, $p = .04$; Figure 3, Table 3). Mean haul-out duration of NL females doubled the time spent on land by L females (Table 3) with the interaction between BCI and Group also explaining partially the variance (Group*BCI: $\chi^2[1] = 7.2$, $p = .01$; Table S2). The relationship between trip duration and time spent hauling-out after each trip shows that, regardless of trip duration, L females spent less time ashore compared to NL females during the entire period monitored (Figure 3).

3.2 | Diving behavior

We found no statistical differences in the dive frequency (dives per hour, $\chi^2[1] = 2.4$, $p = .12$; Table 3) or the frequency of dives per bout between L and NL females ($\chi^2[1] = 1.3$, $p = .26$; Table 3; see also Table S2). However, there were statistically significant differences in mean dive duration, where L females made shorter dives than NL females ($\chi^2[1] = 5.8$, $p = .02$; Table

3). L females spent less time in the bottom phase of each dive ($\chi^2[1] = 7.9$, $p = .005$) compared to NL females (Table 3). Although there was a statistical difference between the descent time of L females and that of NL females ($\chi^2[1] = 5$, $p = .03$) we did not find statistical differences between groups in any other variable of the vertical phase of each dive (i.e., descent rate: $\chi^2[1] = 0.8$, $p = .4$; ascent rate: $\chi^2[1] = 0.8$, $p = .4$; ascent time: $\chi^2[1] = 0.02$, $p = .9$; or maximum depth: $\chi^2[1] = 0.3$, $p = .6$; Table 3). We also found statistical differences in the interaction between Group and BCI in most of the dive variables (all except for ascent rate, descent rate and the bout variables; Table S2). Likewise, we found statistically significant differences in dive behavior when Group interacted with Season, which was observed for the variables: maximum depth, descent and ascent time, and mean dive duration per bout (Table S2). The mean percentage of diving time per trip of L females was ~10% higher in 2015 than NL females ($\chi^2[1] = 7.1$, $p = .008$) but similar between groups in 2016 (Figure 4, Table 3).

The residuals obtained from the relationship between dive duration and maximum depth showed no statistical differences between groups ($\chi^2[1] = 0.0017$, $p = .97$). Based on the fitted model, the positive (higher effort) and negative (lower effort) residuals showed a similar pattern in all females of both groups regardless of the differences found in dive duration (Figure S3).

3.3 | Bout analysis and postdive surface intervals

We found no statistical difference in bout duration between groups ($\chi^2[1] = 0.7$, $p = .6$; Table 3) or in any dive variables within bouts (number of dives per bout: $\chi^2[1] = 1.4$, $p = .2$; mean dive duration: $\chi^2[1] = 1.25$, $p = .3$; and mean dive depth: $\chi^2[1] = 0.34$, $p = .6$; Table 3). Statistical differences in mean dive duration and mean dive depth were only present for Group and Season interactive effects (Group*Season, mean dive duration: $\chi^2[1] = 4.67$, $p = .03$; mean dive depth: $\chi^2[1] = 7.9$, $p = .005$; Table S2). When comparing PDI time between groups (L and NL), no statistical differences were found ($\chi^2[1] = 0.1$, $p = .7$; Table 3).

4 | DISCUSSION

Lactation is the most energetically expensive reproductive event in mammalian life history (Clutton-Brock et al., 1989; Gittleman & Thompson, 1988; Veloso & Bozinovic, 2000). As a result, females increase their energy intake 2- to 6-fold, in some cases, modifying their foraging behavior substantially (Perez & Mooney, 1986; Sadleir, 1984; Thometz et al., 2016; Williams et al., 2007). Studies must compare lactating and nonlactating individuals under similar conditions to understand these changes in behavior, but the unconstrained, unpredictable behavior of nonlactating marine animals makes simultaneous comparisons difficult. To the best of our knowledge, we obtained, for the first time, diving records of free-ranging nonlactating female otariids simultaneously with lactating females during the breeding season, allowing us to understand how animals adjust their behavior due to lactation. Our results show that, under similar environmental conditions, lactating females showed more regular and structured attendance cycles than nonlactating individuals. This is reflected primary in less variation in dive time, as well as lack of variation in reduced haul-out time irrespective of trip duration when females are lactating. In addition, fine scale differences within diving behavior were also observed. Lactating females minimize the cost of transportation within dives by performing shorter dives with respect to nonlactating individuals. The necessary adjustments to reduce the duration of each dive may not affect energy intake and allow lactating females to increase the proportion of time spent diving per trip.

4.1 | Rearing a pup; behavioral adjustments

Lactating females (L females) show a consistent pattern of shorter trips to sea and a reduced mean time hauling out compared to nonlactating females (NL females). Shorter trips performed by L females would provide the advantage of increasing the opportunity for providing milk to offspring. At the same time, L females have limits to how long they can fast and remain on shore feeding their pups, so their haul-out periods are constrained by the need to sustain milk delivery. The time spent ashore is known to be driven by milk delivery per visit (i.e., provisioning hypothesis) independent of trip duration (Boyd, 1999; Gentry, 1998). Thus, L females show very consistent time ashore maximizing nursing time while also being driven to replenish on board milk reserves (Boyd, 1999; Boyd et al., 1997; Gentry, 1998; this study). Boyd (1999) showed that L females would reduce trip duration when prey is abundant. However, our concurrent observation of longer foraging trips to sea in NL females and short foraging trips in L females when prey abundance is not limited, suggests that short foraging trips in highly heterogeneous environments can also be a consequence of pup rearing constraints and not necessarily the result only of abundant prey as previously suggested.

4.2 | Diving behavior

Antarctic fur seal females can modify diving behavior based on the characteristics of the prey targeted. These modifications are associated with diurnal/nocturnal variations in the vertical migration patterns of the prey (fish and krill; Collins et al., 2008; Croxall et al., 1985) and the prey’s temporal variation in abundance across the breeding season at this location (Polito & Goebel, 2010; Santora, 2013) as well as other similar locations (Boyd et al., 1991). Our models tested for differences in behavior that could be driven by the time of the day that dives are performed (diurnal/nocturnal) as well as the breeding season (2015–2016; Table S2). By doing so, we accounted for differences associated with the prey targeted and could isolate the variance in each model explained exclusively by the lactating status of the females (L or NL; Table S2; but see section 4.3 | Prey availability and abundance) which can account for 31% of the total energetic expenditure in this species (Arnould, 1997).

Females can also modify the phase of a dive (vertical and/or bottom phase) to increase the total foraging time and maximize the energy return (e.g., Boyd et al., 1995; Crocker et al., 2001) or minimize the costs of transportation per dive. In our study, L females mostly reduce dive duration relative to NL females by decreasing the time spent in the bottom phase (Table 3). For shallow divers of this species, the bottom time of a dive is not always a good predictor of foraging success (Viviant et al., 2016), and reducing the bottom time of a dive may not substantially affect energy acquisition. In addition, we found that L females showed shorter mean descent time than NL females, whereas a similar descent rate was found. To reach the same depth, L females can perform steeper dives than NL females and, with this, reduce the metabolic cost of a dive without changing descent speed (Sato et al., 2010). Several penguin species reduce the descent time of dives by doing steeper dive angles which reduces the cost of transportation (Sato et al., 2010). This behavioral strategy has also been observed in Antarctic fur seals performing steeper dives to compensate for slow speed dives (Boyd et al., 1997). We propose that, when diving, L females minimize the cost by reducing diving time rather than maximizing energy return per dive. By performing shallow dives, this strategy may not impact foraging success substantially. However, to prove this hypothesis, comparative metabolic measurements coupled with diving records are necessary between NL and L females.

Behaviorally, modifying diving bouts (e.g., frequency and duration) can also lead to increase energy intake (Fahlman et al., 2008; Gerlinsky et al., 2013; Hastie et al., 2007; Ramasco et al., 2014). For example, female Weddell seals (*Leptonychotes weddellii*) would increase the frequency and duration of dive bouts to increase foraging time and cope with the energetic cost of gestation (Shero et al., 2018). Although L females in our study did show some of the longest bouts registered in this study (Figure S4), differences in dive behavior between L and NL females explained by the bout variables (mean dive duration per bout, mean dive depth per bout, mean dive frequency per bout, or mean bout duration) were not observed. This has also been shown in previous studies where bout characteristics did not influence foraging strategies of L females at this location (McDonald et al., 2009).

Differences between L and NL females in Body Condition Index (BCI) interacting with Group (BCI*Group) was statistically significant for several diving variables (Table S2), and modifications in dive performance may have been driven by the effect of buoyancy and/or drag. In many phocid species, differences in buoyancy influence diving behavior by modifying descent and ascent rate (Beck et al., 2000; Webb et al., 1998) or by adjustments in gliding and stroking patterns to maintain vertical speed (Aoki et al., 2011). However, in otariid, drag seems to have a higher impact in dive performance than buoyancy which is observed in species with similar percentage of adipose tissue than Antarctic fur seals (Suzuki et al., 2014). Although we controlled for size/age when females were selected, the drag effect of only minor differences in mass (250 g) can reduce the time that females spent diving significantly (Boyd et al., 1997). McDonald et al. (2009) also found a reduction in dive effort in larger females compared to smaller ones in this species which is consistent with our findings where L females “heavier” show shorter dives compared to NL females “lighter.” Although in our study, the BCI differences observed represent only the initial state of the breeding season (we measured mass and length when instruments were deployed) modifications in diving behavior may have been driven by larger L females. However, BCI results should be interpretated with caution.

4.3 | Prey availability and abundance

At a larger scale (the attendance cycle) interannual difference observed in behavior may be a response to the intraseasonal availability of prey. In our study there were temporal differences in when foraging trip data were obtained. In 2015, trips measured simultaneously between L and NL females occurred later (late January to early March) than in 2016 (mid-December to early February). The mean percentage of time diving per trip for L females in 2015 was approximately twice as high than the time invested by NL females (Table 2, Figure 4). In contrast, in 2016 when collection of diving data began earlier (mid-December), the percentage of time diving was only 5% higher in L females. The marked differences in the percentage of diving time observed in 2015, may be related to differences in the prey targeted since, at this location, there is a well-documented increase in the incidence of fish in the diet after mid-January (Osman et al., 2004; Polito & Goebel, 2010; Figure S1). By not been constrained in their ability to target alternative prey items or explore more productive areas, NL females may consume more fish than L females, reducing the time invested capturing krill by increased consumption of relatively more energy rich prey (Ichii et al., 2007). In contrast, the mean percentage of diving time per trip did not change in L females regardless of the breeding season. This suggest that they are constrained to spend a similar proportional time diving regardless of the prey available. The observed behavior of L females is also similar to previously described patterns in other species, where the increased energetic demands of lactation are compensated by an increase of energy intake rather than changes in metabolic rate (Costa & Gentry, 1986; Costa & Trillmich, 1988; Harder et al., 1996; Oftedal et al., 1987; Zhu et al., 2015).

Alternatively, a reduction in prey abundance in 2016 compared to 2015 (Atkinson et al., 2019) could have caused the increase in the mean percentage of time spent diving observed in NL females. Previous studies have shown that the 2015–2016 El Niño Southern Oscillation (ENSO) event was one of the strongest on record in the last 50 years (Bodart & Bingham, 2019; Turner, 2004). The event is linked with the strongest Southern Annular

Mode (SAM) registered in Antarctica in the last 50 years, triggering the lowest ever recorded Antarctic sea-ice extent during spring 2016 (Stuecker et al., 2017; Turner et al., 2017). The negative impact of the reduction of sea ice extent on the recruitment and abundance of krill is well documented (Atkinson et al., 2004, 2019; Loeb et al., 2009; Siegel & Loeb 1995). Consequently, limited availability of krill during the breeding season of 2016 could have driven NL females to increase the percentage of diving time per trip to almost the same percentage invested by L females (Figure 4). To test this “2016-reduced krill abundance” hypothesis, we need to examine in situ prey abundance measures, of which there are none at this location. However, evidence collected south of Cape Shirreff (Palmer Station Antarctica LTER & Steinberg, 2020; Figure S5) does suggest a reduction in krill density in 2016 compared to 2015. There is also evidence for broad regional concordance in interannual trends in krill abundance and recruitment along the West Antarctic Peninsula (Conroy et al., 2020). Given a reduction in krill abundance in 2016 relative to 2015, the time invested diving for both years by L females (~25%), may represent the maximum percentage of diving time that L females can invest at this location whether the prey is limited (2016) or not (2015). In other words, L females may be incapable of increasing the percentage of diving time per trip even if prey is less available, limiting the behavioral responses that L females can have at this latitude when facing complex scenarios of prey abundance.

In this species, lactating females make longer trips in years when prey availability/abundance is reduced and have little capacity to modify the time spent hauling out (Boyd, 1999; Boyd et al., 1994, 1997; Gentry, 1998; Lea et al., 2002, 2006; Ichii et al., 2007; Staniland et al., 2010). Data close to our study locations suggest that prey abundance was lower in 2016 than in 2015 (Figure S5). However, L females showed similar trip durations between years and similar mean values to those previously reported at this location (this study: ~3 days; McDonald et al., 2009: ~3 days) or other locations where krill is the primary prey (~4 days, Boyd, 1999; see table 4 in Lea et al., 2002 for comparison between locations). Furthermore, we did not find statistical differences in trip duration or haul-out time explained by Season for L females (Table S2), and there were no differences in prey consumed by season (Figures S1 and S2). NL females, however, had on average longer trips in 2016 and had greater within-season variability in trip duration. Thus, seals that do not have the constraints of pup rearing exhibit greater flexibility in behavior. This is especially true for haul-out time as NL females spend on average 2.4× more time onshore than L females. Altogether, it seems that the constant need to balance the competing demands of time onshore and time at-sea foraging, constrained L females to a limited number of behavioral options within the attendance cycle regardless of prey conditions.

The differences in foraging strategies of L versus NL females found in our study only reflect their behavior within a limited timeframe and may not be consistent over time. Furthermore, the differences we found between breeding seasons and the potential intra- and interseasonal variability in prey availability makes it more challenging to disentangle the effects of lactation over environmentally driven effects. The main challenges for comparative studies using NL females (their unpredictable behavior and the fact that they do not return to land for offspring investment), are the reasons why this and other studies have been constrained to narrow temporal scales and smaller sample sizes. A larger sample size of NL females could reduce the probability for type I error and provide knowledge about the intraspecific variation of NL females' foraging behavior (Kernaléguen et al., 2015) over longer temporal scales and/or under different environmental conditions. Furthermore, future studies of NL versus L females coupled with simultaneous field metabolic rate measurements or real time diet estimators, would provide additional power to support our findings and a better understanding on how marine mammals respond to a rapidly changing environment.

4.4 | Conclusions

During the breeding season, NL females' behavior is partially characterized by the absence of breeding constraints. In contrast, lactating females' behavior is characterized by shorter foraging trips to sea and shorter haul-out times, the latter, described in previous studies only when prey availability is not limited (Boyd, 1999; Lea et al., 2006). The combination of shorter foraging trips and shorter time spent ashore is consistent with a strategy that maximizes energy delivery to their offspring. At the same time, at a fine scale, L females may minimize the cost of dives by reducing bottom time and descent time, but increasing the percentage of time spent diving per trip compared to NL females. Less likely, these adjustments in diving behavior can also be the consequence of body composition differences between groups. A diving strategy that combines a reduction of dive duration per dive and an increase in the percentage of time spent diving per trip, would increase the energy intake per trip, a strategy also observed in other marine mammals under energetically expensive reproductive events (Shero et al., 2018; Thometz et al., 2016; Williams et al., 2007). The success of the foraging strategy in allocating greater percentage of diving time and energy during lactation, can shape pup/mother’s fitness (Rogowitz, 1996) and consequently, impact individual and population dynamics (Brose, 2010) especially in females breeding at the edge of the species distribution.

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Availability of data and material*:* The data sets collected and analyzed during the current study are available from the corresponding author on reasonable request.

REFERENCES

Aoki, K., Watanabe, Y. Y., Crocker, D. E., Robinson, P. W., Biuw, M., Costa, D. P., Miyazaki N., Fedak, M. A., & Miller, P. J. (2011). Northern elephant seals adjust gliding and stroking patterns with changes in buoyancy: validation of at-sea metrics of body density. *Journal of Experimental Biology*, *214*(17), 2973–2987. https://doi.org/10.1242/jeb.055137

Arnould, J. P. Y. (1995). Indices of body condition and body composition in female Antarctic fur seals (*Arctocephalus gazella*). *Marine Mammal Science*, *11*(3), 301–313. https://doi.org/10.1111/j.1748-7692.1995.tb00286.x

Arnould, J. P. Y. (1997). Lactation and the cost of pup-rearing in Antarctic fur seals. *Marine Mammal Science, 13*(3): 516–526. https://doi.org/10.1111/j.1748-7692.1997.tb00662.x

Arnould, J. P. Y., Boyd, I., Rawlins, D., & Hindell, M. (2001). Variation in maternal provisioning by lactating Antarctic fur seals (*Arctocephalus gazella*): response to experimental manipulation in pup demand. *Behavioral Ecology and Sociobiology*, *50*(5), 461–466. https://doi.org/10.1007/s002650100386

Arnould, J. P. Y., Boyd, I. L., & Speakman, J. R. (1996). The relationship between foraging behaviour and energy expenditure in Antarctic fur seals. *Journal of Zoology*, *239*(4), 769–782. https://doi.org/10.1111/j.1469-7998.1996.tb05477.x

Atkinson, A., Siegel, V., Pakhomov, E., & Rothery, P. (2004). Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature*, *432*(7013), 100–103. https://doi.org/10.1038/nature02996

Atkinson, A., Hill, S. L., Pakhomov, E. A., Siegel, V., Reiss,

C. S., Loeb, V. J., Steinberg, D. K., Schmidt, K., Tarling, G. A., Gerrish, L., & Sailley, S. F. (2019). Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nature Climate Change*, *9*(2), 142–147. https://doi.org/10.1038/s41558-018-0370-z

Barton, K., (2017). *MuMIn: multi-model inference* (R package version 1[1]) [Computer software]. https://CRAN.R-project.org/package=MuMIn

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Beck, C. A., Bowen, W. D., & Iverson, S. J. (2000). Seasonal changes in buoyancy and diving behaviour of adult grey seals. *Journal of Experimental Biology*, *203*(15), 2323–2330. https://doi.org/10.1242/jeb.203.15.2323

Bestley, S., Jonsen, I. D., Hindell, M. A., Harcourt, R. G., & Gales, N. J. (2015). Taking animal tracking to new depths: synthesizing horizontal–vertical movement relationships for four marine predators. *Ecology*, *96*(2), 417–427. https://doi.org/10.1890/14-0469.1

Bodart, J. A., & Bingham, R. J. (2019). The impact of the extreme 2015–2016 El Niño on the mass balance of the

Antarctic ice sheet. *Geophysical Research Letters*, *46*(23), 13862–13871. https://doi.org/10.1029/2019GL084466

Bonner, W. N. (1984). Lactation strategies in pinnipeds: problems for a marine mammalian group. In M. Peaker, R. G. Vernon, & C. H. Knight (Eds.), *Physiological strategies in lactation*. Academic Press.

Boyd, I. L. (1998). Time and energy constraints in pinniped lactation. *The American Naturalist*, *152*(5), 717–728. https://doi.org/10.1086/286202

Boyd, I. L. (1999). Foraging and provisioning in Antarctic fur seals: interannual variability in time-energy budgets. *Behavioral Ecology*, *10*(2), 198–208. https://doi.org/10.1093/beheco/10.2.198

Boyd, I. L., Arnould, J. P., Barton, T., & Croxall, J. P. (1994). Foraging behaviour of Antarctic fur seals during periods of contrasting prey abundance. *Journal of Animal Ecology*, 703-713. https://doi.org/10.2307/5235

Boyd, I. L., & Croxall, J. P. (1992). Diving behaviour of lactating Antarctic fur seals. *Canadian Journal of Zoology*, *70*(5), 919–928. https://doi.org/10.1139/z92-131

Boyd, I. L., Lunn, N. J., & Barton, T. (1991). Time budgets and foraging characteristics of lactating Antarctic fur seals. *Journal of Animal Ecology*, *60*, 577–592.

https://doi.org/10.2307/5299

Boyd, I. L., McCafferty, D. J., & Walker, T. R. (1997). Variation in foraging effort by lactating Antarctic fur seals: response to simulated increased foraging costs. *Behavioral Ecology and Sociobiology*, *40*(3), 135–144. https://doi.org/10.1007/s002650050326

Boyd, I. L., Reid, K., & Bevan, R. M. (1995). Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Animal Behaviour*, *50*(3), 769-784. https://doi.org/10.1016/0003-3472(95)80137-5

Brose, U. (2010). Body mass constraints on foraging behaviour determine population and food web dynamics. *Functional Ecology*, *24*(1), 28–34. https://doi.org/10.1111/j.1365-2435.2009.01618.x

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1989). Fitness costs of gestation and lactation in wild mammals. *Nature*, *337*(6204), 260–262. https://doi.org/10.1038/337260a0

Collins, M. A., Xavier, J. C., Johnston, N. M., North, A. W., Enderlein, P., Tarling, G. A., Waluda, C. M., Hawker, J., & Cunningham, N. J. (2008). Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. *Polar Biology*, *31*(7), 837–851. https://doi.org/10.1007/s00300-

008-0423-2

Conroy, J. A., Reiss, C. S., Gleiber, M. R., & Steinberg, D. K. (2020). Linking Antarctic krill larval supply and recruitment along the Antarctic Peninsula. *Integrative and Comparative Biology*, *60*(6), 1386–1400. https://doi.org/10.1093/icb/icaa111

Costa, D. P. (2008). A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *17*(S1): S44-S52. https://doi.org/10.1002/aqc.917

Costa, D. P., Boeuf, B. L., Huntley, A. C., & Ortiz, C. L. (1986). The energetics of lactation in the northern elephant seal, *Mirounga angustirostris*. *Journal of Zoology*, *209*(1), 21–33. https://doi.org/10.1111/j.1469-7998.1986.tb03563.x

Costa, D. P., Croxall, J. P., & Duck, C. D. (1989). Foraging energetics of Antarctic fur seals in relation to changes in prey availability. *Ecology*, *70*(3), 596–606. https://doi.org/10.2307/1940211

Costa, D. P., & Gentry, R. L. (1986). Free-ranging energetics of northern fur seals. In *Fur seals: Maternal strategies on* *land and at sea*. Princeton University Press. https://doi.org/10.1111/j.1469-7998.1986.tb03563.x

Costa, D. P., Goebel, M. E., & Sterling, J. T. (2000). Foraging energetics and diving behavior of the Antarctic fur seal, *Arctocephalus gazella*, at Cape Shirreff, Livingston Island. In W. Davison, C. Howard-Williams & P. Broady (Eds.), *Antarctic ecosystems: models for wider ecological understanding* (pp. 77–84). Cambridge University Press.

Costa, D. P., & Trillmich, F. (1988). Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galápagos fur seals (*Arctocephalus galapagoensis*). *Physiological Zoology*, *61*(2), 160–169. https://doi.org/10.1086/physzool.61.2.30156147

Costa, D. P., & Williams, T. M. (1999). Marine mammal energetics. In J. E. Reynolds (Ed.). (2007). *Biology of marine mammals*. Smithsonian Institution.

Crocker, D. E., Gales, N. J., & Costa, D. P. (2001). Swimming speed and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *Journal of Zoology*, *254*(2), 267–277. https://doi.org/10.1017/S0952836901000784

Croxall, J. P., Everson, I., Kooyman, G. L., Ricketts, C., & Davis, R. W. (1985). Fur seal diving behaviour in relation to vertical distribution of krill. *Journal of Animal Ecology*, *54*, 1–8. https://doi.org/10.2307/4616

Fahlman, A., Svärd, C., Rosen, D. A., Jones, D. R., & Trites, A. W. (2008). Metabolic costs of foraging and the management of O_2 and CO_2 stores in Steller sea lions. *Journal of Experimental Biology*, *211*(22), 3573–3580. https://doi.org/10.1242/jeb.023655

Fedak, M. A., & Anderson, S. S. (1982). The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *Journal of Zoology*, *198*(4), 473–479. https://doi.org/10.1111/jzo.1982.198.4.473

Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (Third ed.). Sage.

Gales, N. J., & Mattlin, R. H. (1998). Fast, safe, field-portable gas anesthesia for otariids. *Marine Mammal Science*, *14*(2), 355–361. https://doi.org/10.1111/j.1748-7692.1998.tb00727.x

Gentry, R. L. (1998). *Behavior and ecology of the northern fur seal*. Princeton University Press.

Gentry, R. L., & Kooyman, G. L. (Eds.). (1986). *Fur seals: Maternal strategies on land and at sea*. Princeton University Press.

Gerlinsky, C. D., Rosen, D. A., & Trites, A. W. (2013). High diving metabolism results in a short aerobic dive limit for Steller sea lions (*Eumetopias jubatus*). *Journal of Comparative Physiology B*, *183*(5), 699–708. https://doi.org/10.1007/s00360-013-0742-7

Gittleman, J. L., & Thompson, S. D. (1988). Energy allocation in mammalian reproduction. *American Zoologist*, *28*(3), 863–875. https://doi.org/10.1093/icb/28.3.863

Goebel, M. E., Costa, D. P., Crocker, D. E., Sterling, J. T., & Demer, D. A. (2000). Foraging ranges and dive patterns in relation to bathymetry and time-of-day of Antarctic fur seals, Cape Shirreff, Livingston Island, Antarctica. In W. Davison, C. Howard-Williams & P. Broady (Eds.), *Antarctic ecosystems: models for wider ecological understanding*. Cambridge University Press.

Harder, J. D., Hsu, M. J., & Garton, D. W. (1996). Metabolic rates and body temperature of the gray short-tailed opossum (*Monodelphis domestica*) during gestation and lactation. *Physiological Zoology*, *69*(2), 317–339. https://doi.org/10.1086/physzool.69.2.30164187

Hastie, G. D., Rosen, D. A., & Trites, A. W. (2007). Reductions in oxygen consumption during dives and estimated submergence limitations of Steller sea lions (*Eumetopias jubatus*). *Marine Mammal Science*, *23*(2), 272–286.

https://doi.org/10.1111/j.1748-7692.2007.00118.x

Ichii, T., Bengtson, J. L., Boveng, P. L., Takao, Y., Jansen, J. K., Hiruki-Raring, L. M., Cameron, M. F., Okamura, H., Hayashi, T., & Naganobu, M. (2007). Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. *Marine Ecology Progress Series*, *344*, 277–297. https://doi.org/10.3354/meps06873

Kernaléguen, L., Arnould, J. P., Guinet, C., & Cherel, Y. (2015). Determinants of individual foraging specialization in large marine vertebrates, the Antarctic and subantarctic fur seals. *Journal of Animal Ecology*, *84*(4), 1081–1091. https://doi.org/10.1111/1365-2656.12347

Klemmedson, A. D., Reiss, C. S., Goebel, M. E., Kaufmann, R. S., Dorval, E., Linkowski, T. B., & Borras-Chavez, R. (2020). Variability in age of a Southern Ocean myctophid (*Gymnoscopelus nicholsi*) derived from scat-recovered otoliths. *Marine Ecology Progress Series*, *633*, 55–69. https://doi.org/10.3354/meps13176

Lea, M. A., Guinet, C., Cherel, Y., Duhamel, G., Dubroca, L., Pruvost, P., & Hindell, M. (2006). Impacts of climatic anomalies on provisioning strategies of a Southern Ocean predator. *Marine Ecology Progress Series*, *310*, 77–94.

https://doi.org/10.3354/meps310077

Lea, M. A., Hindell, M., Guinet, C., & Goldsworthy, S. (2002). Variability in the diving activity of Antarctic fur seals, *Arctocephalus gazella*, at Iles Kerguelen. *Polar Biology*, *25*(4), 269–279. https://doi.org/10.1007/s00300-001-0339-6

Lea, M. A., Johnson, D., Ream, R., Sterling, J., Melin, S., & Gelatt, T. (2009). Extreme weather events influence dispersal of naive northern fur seals. *Biology Letters*, *5*(2), 252–257. https://doi.org/0.1098/rsbl.2008.0643

Loeb, V. J., Hofmann, E. E., Klinck, J. M., Holm-Hansen, O., & White, W. B. (2009). ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. *Antarctic Science*, *21*(2), 135–148. https://doi.org/10.1017/s0954102008001636

McCabe, G. M., Fernández, D., & Ehardt, C. L. (2013). Ecology of reproduction in Sanje mangabeys (*Cercocebus sanjei*): dietary strategies and energetic condition during a high fruit period. *American Journal of Primatology*, *75*(12), 1196–1208. https://doi.org/10.1002/ajp.22182

McDonald, B. I., Goebel, M. E., Crocker, D. E., Tremblay, Y., & Costa, D. P. (2009). Effects of maternal traits and individual behavior on the foraging strategies and provisioning rates of an income breeder, the Antarctic fur seal. *Marine Ecology Progress Series*, *394*, 277–288.

https://doi.org/10.3354/meps08308

Naya, D. E., Ebensperger, L. A., Sabat, P., & Bozinovic, F. (2008). Digestive and metabolic flexibility allows female degus to cope with lactation costs. *Physiological and Biochemical Zoology*, *81*(2), 186–194. https://doi.org/10.1086/527453

Oftedal, O. T., Boness, D. J., & Tedman, R. A. (1987). The behavior, physiology, and anatomy of lactation in the Pinnipedia. In H. H. Genoways (Ed.), *Current mammalogy*. Springer.

Orians, G.H., & Pearson, N.E. (1979). On the theory of central place foraging. In D. J. Horn, E. T. Stairs, & R. T. Mitchell (Eds.), *Analysis of ecological systems*. Ohio State University Press.

Osman, L. P., Hucke-Gaete, R., Moreno, C. A., & Torres, D. (2004). Feeding ecology of Antarctic fur seals at Cape Shirreff, South Shetlands, Antarctica. *Polar Biology*, *27*(2), 92–98. https://doi.org/10.1007/s00300-003-0555-3

Palmer Station Antarctica LTER, & Steinberg, D., (2020). *Zooplankton collected with a 2-m, 700-um net towed from surface to 120 m, aboard Palmer Station Antarctica LTER annual cruises off the western Antarctic Peninsula, 2009–2019* (ver. 7) [Data package]. Environmental Data

Initiative. https://doi.org/10.6073/pasta/434b2f73803b9d3d8088cd094cf46cca

Perez, M. A., & Mooney, E. E. (1986). Increased food and energy-consumption of lactating northern fur seals, *Callorhinus-ursinus*. *Fishery Bulletin*, *84*(2), 371–381.

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. (2014). *nlme: Linear and nonlinear mixed effects models*. (R package version 3) [Computer software]. https://CRAN.R project.org/package=nlme

Polito, M. J., & Goebel, M. E. (2010). Investigating the use of stable isotope analysis of milk to infer seasonal trends in the diets and foraging habitats of female Antarctic fur seals. *Journal of Experimental Marine Biology and Ecology*, *395*(1–2), 1–9. https://doi.org/10.1016/j.jembe.2010.08.015

Ponganis, P. J. (2015). *Diving physiology of marine mammals and birds*. Cambridge University Press.

Poppitt, S. D., Speakman, J. R., & Racey, P. A. (1993). The energetics of reproduction in the common shrew (*Sorex araneus*): a comparison of indirect calorimetry and the doubly labeled water method. *Physiological Zoology*, *66*(6), 964–982. https://doi.org/10.1086/physzool.66.6.30163749

R Core Team (2017) *R: A language and environment for statistical* *computing* [Computer software]. R Foundation for Statistical Computing.

Ramasco, V., Biuw, M., & Nilssen, K. T. (2014). Improving time budget estimates through the behavioural interpretation of dive bouts in harbour seals. *Animal Behaviour*, *94*, 117–134. https://doi.org/10.1016/j.anbehav.2014.05.015

Reda, I., & Andreas, A. (2003). *Solar position algorithm for solar radiation application* (Technical report NREL TP-560-34302). National Renewable Energy Laboratory (NREL).

Rogowitz, G. L. (1996). Trade-offs in energy allocation during lactation. *American Zoologist*, *36*(2), 197–204. https://doi.org/10.1093/icb/36.2.197

Rosen, D. A., Hindle, A. G., Gerlinsky, C. D., Goundie, E., Hastie, G. D., Volpov, B. L., & Trites, A. W. (2017). Physiological constraints and energetic costs of diving behaviour in marine mammals: a review of studies using trained Steller sea lions diving in the open ocean. *Journal of Comparative Physiology B*, *187*(1), 29–50. https://doi.org/ 10.1007/s00360-016-1035-8

Sadleir, R. M. F. S. (1984). Ecological consequences of lactation. *Acta Zoologica Fennica*, *171*, 179–182.

Santora, J. A. (2013). Dynamic intra-seasonal habitat use by Antarctic fur seals suggests migratory hotspots near the

Antarctic Peninsula. *Marine Biology*, *160*(6), 1383–1393. https://doi.org/ 10.1007/s00227-013-2190-z

Sato, K., Shiomi, K., Watanabe, Y., Watanuki, Y., Takahashi, A., & Ponganis, P. J. (2010). Scaling of swim speed and stroke frequency in geometrically similar penguins: they swim optimally to minimize cost of transport. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1682), 707–714. https://doi.org/10.1098/rspb.2009.1515

Scantlebury, M., Russell, A. F., McIlrath, G. M., Speakman, J. R., & Clutton-Brock, T. H. (2002). The energetics of lactation in cooperatively breeding meerkats *Suricata suricatta*. *Proceedings of the Royal Society B: Biological Sciences*, 269(1505), 2147-2153. https://doi.org/10.1098/rspb.2002.2108

Schmid, J., Andersen, N. A., Speakman, J. R., & Nicol, S. C. (2003). Field energetics of free-living, lactating and nonlactating echidnas (*Tachyglossus aculeatus*). *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *136*(4), 903–909. https://doi.org/10.1016/S1095-6433(03)00240-X

Shero, M. R., Goetz, K. T., Costa, D. P., & Burns, J. M. (2018). Temporal changes in Weddell seal dive behavior over winter: Are females increasing foraging effort to support gestation? *Ecology and evolution*, *8*(23), 11857–11874. https://doi.org/10.1002/ece3.4643

Siegel, V., & Loeb, V. (1995). Recruitment of Antarctic krill *Euphausia superba* and possible causes for its variability. *Marine Ecology Progress Series*, *123*, 45–56. https://doi.org/10.3354/meps123045

Staniland, I. J., Boyd, I. L., & Reid, K. (2007). An energy–distance trade-off in a central-place forager, the Antarctic fur seal (*Arctocephalus gazella*). *Marine Biology*, *152*(2), 233–241. https://doi.org/10.1007/s00227-007-0698-9

Staniland, I. J., Gales, N., Warren, N. L., Robinson, S. L., Goldsworthy, S. D., & Casper, R. M. (2010). Geographical variation in the behaviour of a central place forager: Antarctic fur seals foraging in contrasting environments. *Marine Biology*, *157*(11), 2383–2396. https://doi.org/10.1007/s00227-010-1503-8

Staniland, I. J., Morton, A., Robinson, S. L., Malone, D., & Forcada, J. (2011). Foraging behaviour in two Antarctic fur seal colonies with differing population recoveries. *Marine Ecology Progress Series*, *434*, 183–1196. https://doi.org/10.3354/meps09201

Stuecker, M. F., Bitz, C. M., & Armour, K. C. (2017). Conditions leading to the unprecedented low Antarctic sea ice extent during the 2016 austral spring season. *Geophysical Research Letters*, *44*(17), 9008–9019. https://doi.org/10.1002/2017GL074691

Suzuki, I., Sato, K., Fahlman, A., Naito, Y., Miyazaki, N., & Trites, A. W. (2014). Drag, but not buoyancy, affects swim speed in captive Steller sea lions. *Biology Open*, *3*(5), 379–386. https://doi.org/10.1242/bio.20146130

Thometz, N. M., Staedler, M. M., Tomoleoni, J. A., Bodkin, J. L., Bentall, G. B., & Tinker, M. T. (2016). Trade-offs between energy maximization and parental care in a central place forager, the sea otter. *Behavioral Ecology*, *27*(5), 1552–1566. https://doi.org/10.1093/beheco/arw089

Tremblay, Y., Robinson, P. W., & Costa, D. P. (2009). A parsimonious approach to modeling animal movement data. *PLoS One*, *4*(3), Article e4711. https://doi.org/10.1371/journal.pone.0004711

Turner, J. (2004). The El Niño–southern oscillation and Antarctica. *International Journal of Climatology*, *24*(1), 1–31. https://doi.org/10.1002/joc.965

Turner, J., Phillips, T., Marshall, G. J., Hosking, J. S., Pope, J. O., Bracegirdle, T. J., & Deb, P. (2017). Unprecedented springtime retreat of Antarctic sea ice in 2016. *Geophysical Research Letters*, *44*(13), 6868–6875.

https://doi.org/10.1002/2017GL073656

Veloso, C., & Bozinovic, F. (2000). Effect of food quality on the energetics of reproduction in a precocial rodent, *Octodon degus*. *Journal of Mammalogy*, *81*(4), 971–978. https://doi.org/10.1644/1545-1542(2000)081<0971:EOFQOT>2.0.CO;2

Viviant, M., Jeanniard du Dot, T., Monestiez, P., Authier, M., & Guinet, C. (2016). Bottom time does not always predict prey encounter rate in Antarctic fur seals. *Functional Ecology*, *30*(11), 1834–1844. https://doi.org/10.1111/1365-2435.12675

Watts, D. P. (1988). Environmental influences on mountain gorilla time budgets. *American Journal of Primatology*, *15*(3), 195–211. https://doi.org/10.1002/ajp.1350150303

Webb, P. M., Crocker, D. E., Blackwell, S. B., Costa, D. P., & Boeuf, B. J. (1998). Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology*, 201(16), 2349–2358. https://doi.org/10.1242/jeb.201.16.2349

Williams, T. M., Rutishauser, M., Long, B., Fink, T., Gafney, J., Mostman-Liwanag, H., & Casper, D. (2007). Seasonal variability in otariid energetics: implications for the effects of predators on localized prey resources. *Physiological and Biochemical Zoology*, *80*(4), 433–443.

https://doi.org/10.1086/518346

Zhu, W., Mu, Y., Liu, J., & Wang, Z. (2015). Energy requirements during lactation in female *Apodemus chevrieri* (Mammalia: Rodentia: Muridae) in the Hengduan Mountain region. *Italian Journal of Zoology*, *82*(2), 165–171. https://doi.org/10.1080/11250003.2015.1018850

Zuur, A., Ieno, E. N., & Smith, G. M. (2007). *Analyzing ecological data*. Springer.

Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

TABLE 1 Morphometric data of Antarctic fur seals for nonlactating (NL, *n* = 5) and lactating females (L, *n* = 15). Body condition index (BCI) was calculated by dividing the mass (kg) of each individual by its body length (cm).

Female ID	**Group**	**Mass (kg)**	**Body length (cm)**	**Body condition index (BCI)**
342	NL	52.6	131	0.40
A03	NL	43.6	134	0.33
326	NL	53.8	139	0.39
494	NL	45.0	133	0.34
4970	NL	39.2	129	0.31
476	L	57.0	132	0.43
1827	L	50.2	128	0.39
2383	L	52.8	127	0.42
5227	L	46.4	123	0.38
A34	L	51.0	124	0.41
A40	L	59.4	137	0.43
6894	L	46.8	124	0.38
A01	L	57.4	131	0.44
A22	L	59.8	140	0.43
A44	L	49.2	131	0.38
A49	L	54.8	137	0.40
A51	L	48.0	135	0.36
A52	L	55.2	134	0.41
A59	L	47.6	130	0.37
481	L	54.8	131	0.42

TABLE 2 Final linear mixed models (LMM) and generalized mixed models (GLMM) used for each behavioral variable after backward stepwise model selection. Models are presented as follows: Response Variable ~ Fixed Factors + (Random Factor). The model used depends on the distribution of each data set. Data sets that did not meet assumptions of normal distribution were transformed to logarithmic scale or square root. Fixed factors: Group = lactating or nonlactating females, BCI = body condition index, Season = breeding season 2015 or 2016, D/N = time of the day the dive was performed (day or night). PDI: Postdive surface intervals.

Behavioral variable	Model structure	Data	Model type
Trip duration (days)	Trip Duration~ Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Log transformed	LMM
Haul-out duration (days)	Haul-out Duration~ Group + BCI + Group*BCI + (Female ID)	Log transformed	LMM
Dive frequency (dives/hr)	Dive Frequency~ Group + BCI + Season + (Female ID)	Not transformed	LMM
Ascent rate (m/s)	Ascent Rate~ Group + BCI + Season + D/N + (Female ID)	Square root transformed	LMM
Descent rate (m/s)	Descent Rate~ Group + BCI + Season + D/N + (Female ID)	Not transformed	LMM
Ascent time (s)	Ascent Time~ Group + BCI + Season + D/N + Group*BCI + Group*Season + (Female ID)	Not transformed	GLMM

Descent time (s)	Descent Time~ Group + BCI + Season + D/N + Group*BCI + Group*Season + (Female ID)	Not transformed	GLMM
Bottom time (s)	Bottom Time~ Group + BCI + Season + Group*BCI + D/N + (Female ID)	Not transformed	LMM
Maximum depth (m)	Maximum Depth~ Group + BCI + Season + Group*BCI + Group*Season + D/N + (Female ID)	Not transformed	GLMM
Dive duration (s)	Dive Duration~ Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Not transformed	LMM
Mean percentage of diving time per trip (%)	Diving Time per trip~ Group + BCI + Season + D/N + (Female ID)	Not transformed	LMM
Number of dives per bout	dive freq per bout~ Group + BCI + Season + (Female ID)	Not transformed	LMM
Mean dive duration (min) per bout	Mean Dive duration per bout ~ Group + BCI + Season + Group*BCI + Group*Season + (Female ID)	Not transformed	LMM
Mean dive depth per bout (m)	Mean Dive Depth per bout~ Group + BCI + Season + (Female ID)	Not transformed	GLMM
Bout duration (min)	Mean Bout Duration~ Group + BCI + Season + (Female ID)	Log Transformed	LMM
PDI (min)	PDI ~ Group + BCI + Season + (Female ID)	Log transformed	LMM

TABLE 3 Behavioral variable's model means with 95% confidence intervals (CI) for nonlactating (NL, *n* = 5) and lactating females (L, *n* = 15). Means and CIs were back transformed and returned to the original scale. *P* values in bold represent differences between groups statistically significant (<.05). PDI: postdive surface interval.

Breeding season:	**2015**		**2016**		***p***
Behavioral variables	**L**	**NL**	**L**	**NL**	
Trip duration (days)[b]	3.7 (2.9–4.6)	3.6 (2.4–5.4)	2.9 (2.5–3.4)	5.7 (4.1–7.9)	**0.01**
Haul-out duration (days)[b]	1.4 (1.2–1.8)	3.4 (2.5–4.6)	1.6 (1.4–1.8)	3.7 (2.8–5.0)	**0.04**
Dive frequency (dives/hr)	16.6 (14.7–8.6)	14.1 (11.5–6.7)	17.2 (15.7–18.6)	14.6 (12.4–16.9)	0.12
Ascent rate (m/s)[c]	1.0 (0.9–1.1)	1.1 (1.0–1.2)	0.9 (0.8–0.9)	0.9 (0.8–1.1)	0.37
Descent rate (m/s)	1.2 (1.1–1.3)	1.2 (1.1–1.3)	1.2 (1.1–1.2)	1.2 (1.1–1.3)	0.36
Ascent time (s)[a]	16.8 (15.5–8.3)	14.4 (12.6–6.5)	11.8 (11.1–12.6)	15.2 (13.2–17.4)	0.4
Descent time (s)[a]	16.6 (15.4–7.9)	18.9 (16.9–1.5)	12.5 (11.9–13.1)	13.8 (12.7–15.0)	**0.03**
Bottom time (s)	35.1 (30.4–9.8)	47.8 (40.8–4.8)	40.3 (36.8–43.9)	53.0 (45.9–60.1)	**0.01**
Maximum depth (m)[a]	25.1 (22.2–9.0)	22.4 (18.8–7.7)	18.1 (16.9–19.5)	23.7 (19.6–30.0)	0.6
Dive duration (s)	75.1 (67.7–2.4)	83.2 (71.4–4.9)	68.0 (62.6–73.3)	91.4 (79.2–103.8)	**0.02**
Percentage of time diving per trip (%)	22.8 (18.8–6.8)	9.6 (3.2–16.1)	27.3 (24.4–30.1)	22.4 (16.9–27.8)	**0.01**
Dive frequency per bout	23.4 (19.2–7.6)	19.6 (14.1–5.2)	24.8 (21.7–27.8)	21.0 (15.5–26.6)	0.24
Dive duration per bout (min)	1.3 (1.1–1.4)	1.1 (0.9–1.3)	1.3 (1.2–1.4)	1.8 (1.6–2.0)	0.26
Dive depth per bout (m)[a]	27.1 (24.3–0.5)	21.6 (18.6–5.7)	20.9 (19.7–22.3)	25.3 (21.7–30.5)	0.56

Bout duration (min)[b]	17.7 (15.2–0.5)	17.0 (13.6–1.2)	19.8 (17.7–22.0)	19.0 (15.3–23.6)	0.6
(PDI (min)[b]	1.2 (1.0–1.3)	1.1 (0.9–1.4)	1.1 (1.0–1.2)	1.3 (1.0–1.6)	0.7

[a] Results from generalized linear mixed model fit by maximum likelihood performed with gamma distributed data.

[b] LMM fitted with log transformed data.

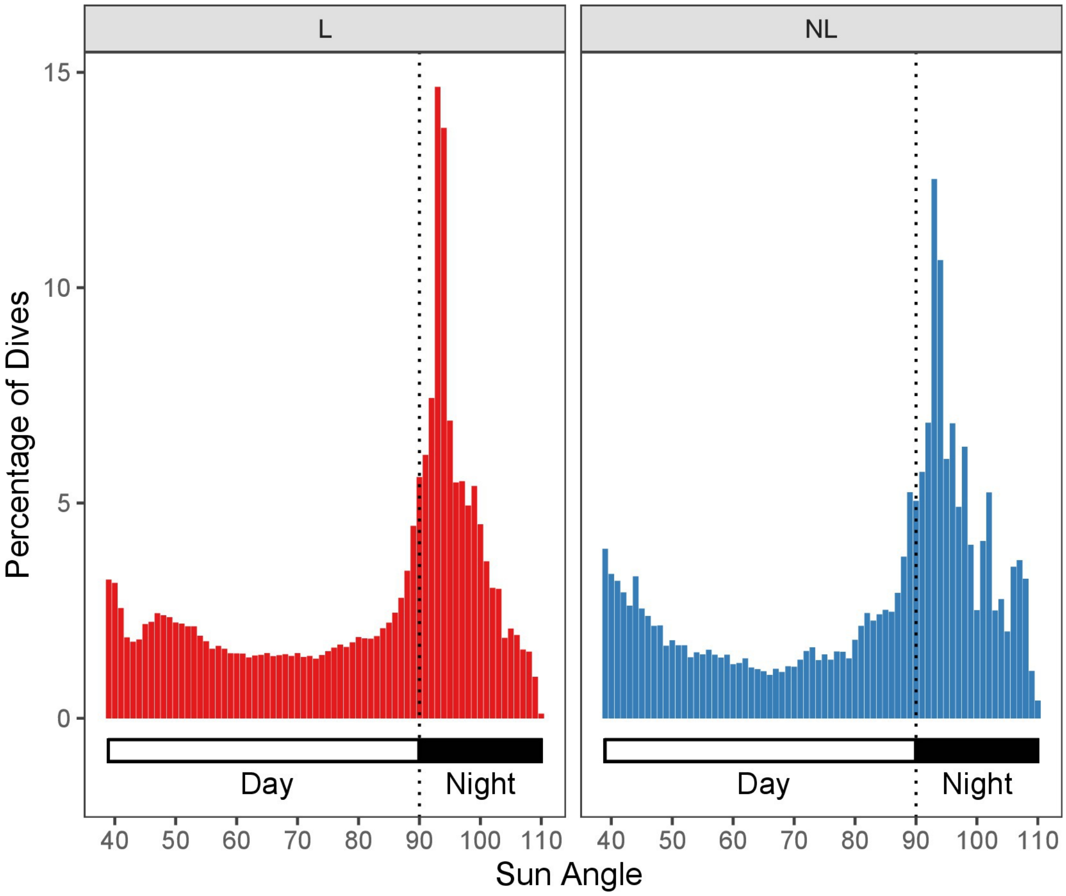
[c] LMM fitted with square root transformed data.

FIGURE 1 Percent frequency of dives occurring during day and night for lactating (L, red) and nonlactating (NL, blue) Antarctic fur seal females. The dotted line indicates the separation between day and night based on the sun angle (*x*-axis) at the location and time where the study was conducted. No statistical differences were found between groups ($p = .3$).

FIGURE 2 Trip Duration. (a) Overall trip duration in days (mean ± SE) of both lactating (L, red) and nonlactating (NL, blue) Antarctic fur seal females. (b) Trip duration (mean ± *SE*) of each trip performed by females during the study period for L (red) and NL (blue) females. NL females had greater variance (gray area) in trip duration than L females ($p < .001$).

FIGURE 3 Haul-out time (days, mean ± *SE*) versus trip duration (days, mean ± *SE*) of lactating (L, red) and nonlactating (NL, blue) Antarctic fur seal females. L females show consistently less overall time spent onshore than NL Females ($p = .04$) regardless of trip duration.

FIGURE 4 Mean percentage of diving time per trip of lactating (L, red) and nonlactating (NL blue) Antarctic fur seal females.



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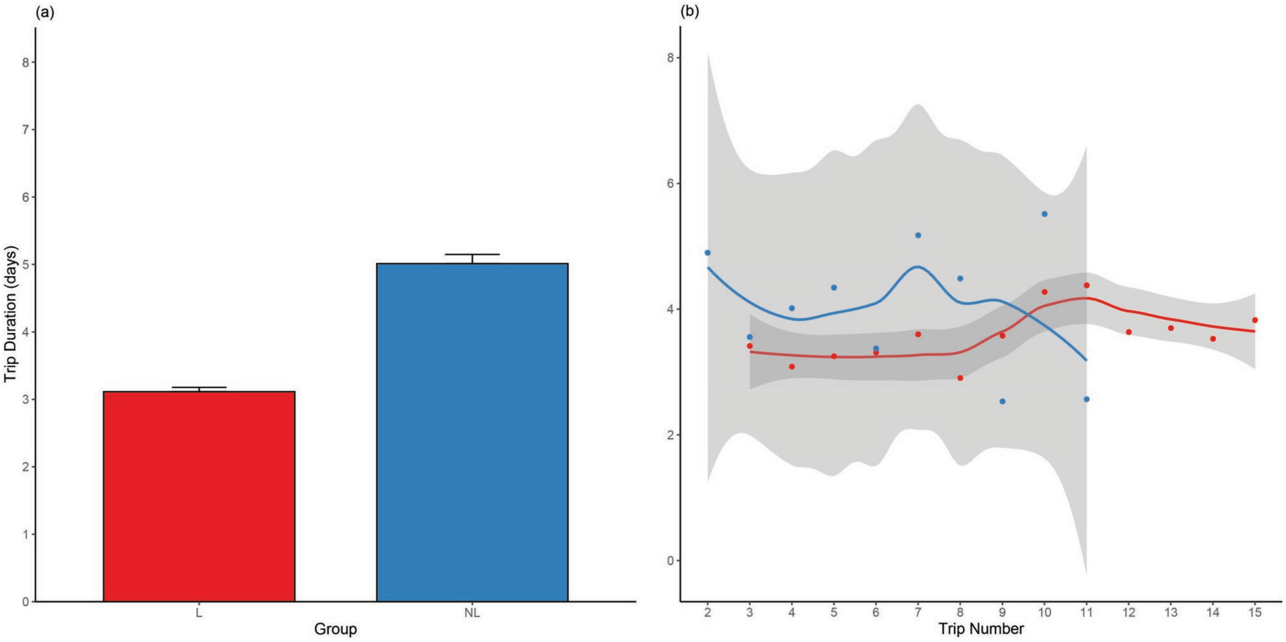

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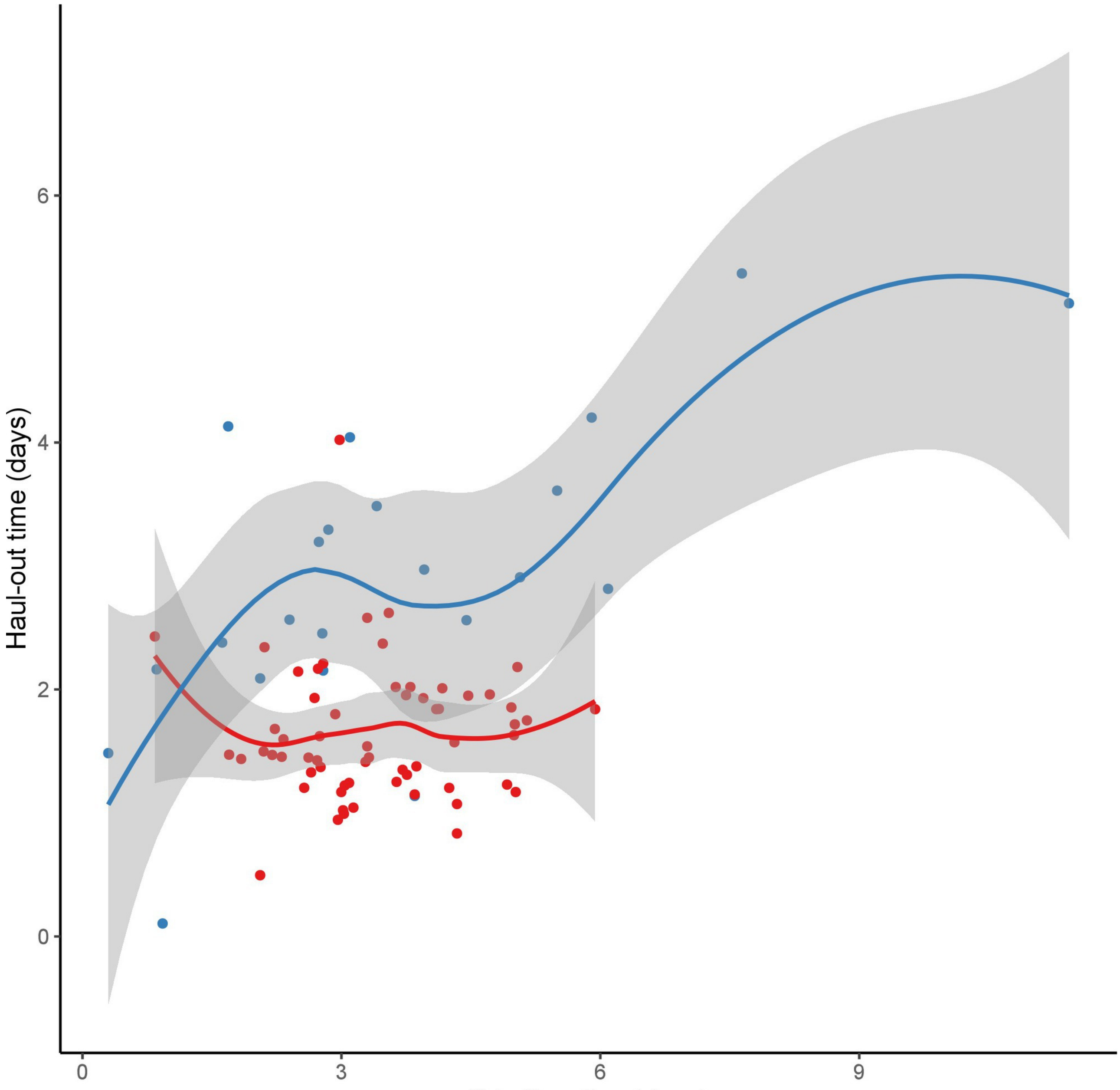

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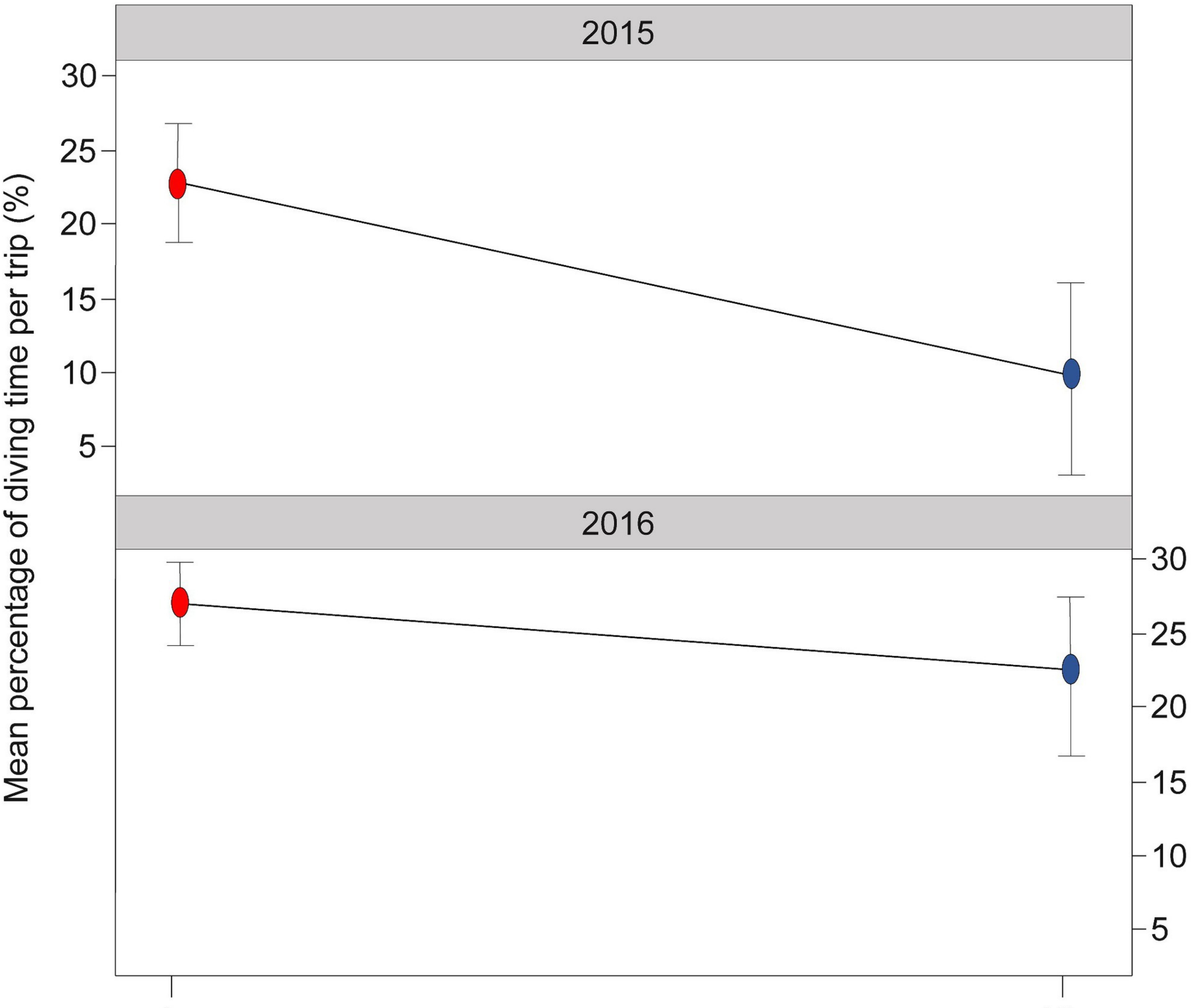

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