The ontogeny of at-sea behaviour in male southern elephant seals (*Mirounga leonina*) at Marion Island

Kiara G Lasch[a] (u18087371@tuks.co.za) https://orcid.org/0000-0001-7933-0384

Cheryl A Tosh[b] (cheryl.tosh@up.ac.za) https://orcid.org/0000-0003-0243-5422

Marthan N Bester[a] (mnbester@zoology.up.ac.za) https://orcid.org/0000-0002-2265-764X

P. J. Nico de Bruyn[a] (pjndebruyn@zoology.up.ac.za) https://orcid.org/0000-0002-9114-9569

[a] Mammal Research Institute, Department of Zoology and Entomology, Private Bag X20, Hatfield, 0028, University of Pretoria, South Africa
[b] Research Office, Faculty of Health Sciences, University of Pretoria, Pretoria 0002, South Africa

Corresponding author:
Kiara G Lasch (u18087371@tuks.co.za) (+31 (6) 38 33 06 80)

Abstract

Megafauna, such as southern elephant seals (SESs) (*Mirounga leonina,* Linn.), forage in diverse, seemingly limitless habitats. In pelagic settings, their behaviour is more likely to be limited by physiological ability and prey distribution, than physical barriers. For elephant seals, their rapid growth in body size corresponds to changing physiological abilities. These changes are most pronounced for male elephant seals. While most studies have compared male and female SESs in terms of changing body size and physiological ability, few studies have compared the influence of changing body size on behaviour of male SESs from the same population using long term satellite tracking data. We describe age-related differences in movement and diving behaviour for male SESs from Marion Island. We analysed satellite tracking data collected from 23 male SESs seals fitted with Sea Mammal Research Unit Satellite Relay Data Loggers at Marion Island between 2005 and 2011. Each dive was assigned a behavioural mode, either 'searching' or 'transit', using state-space modelling. We used mixed-effects models to quantify the influence of age and behavioural mode on dive duration, surface duration, dive depth and number of daily dives. Younger seals travelled significantly further from Marion Island and spent most of their dives in transit mode, whereas older seals stayed closer to the island but were in searching mode for most of their tracks. When searching, older seals dived more frequently, displayed longer dive and surface durations, and reached greater depths than younger seals. These differences in diving behaviour seem to reflect changing physiological ability. For male SESs, changes in physiological ability necessitate behavioural plasticity, which may be the key to survival and future breeding success. Robust males are more likely to breed and must therefore, maintain their body size by adapting to local oceanic conditions.

Keywords: Male southern elephant seals, behaviour, diving, Marion Island

1. Introduction

Marine mammals inhabiting non-tropical regions experience a wide range of habitats (Hindell *et al.* 2020; Noren, 2020). These habitats are in constant flux caused by changing climates and/or by dynamic physical oceanographic processes (Austin *et al*. 2006; van den Berg *et al*. 2021). Environmental changes influence food distribution and resource availability, ultimately cascading through various trophic levels (Orgeret *et al.* 2019; van den Berg *et al*. 2021). Top predators respond to changing environments by modifying their foraging and diving behaviour to obtain enough food for survival (Austin *et al.* 2006). The foraging behaviour of many marine mammals is linked to body size, which largely depends on sex or age (Jeglinski, 2012; McIntyre *et al.* 2010b).

In seals, behavioural differences are attributed to ontogeny, which is defined as the development from one life stage to the next (Carter *et al.* 2017; Orgeret *et al.* 2019). As seals mature, they experience ontogenetic changes which include physiological and morphological changes in body size, body composition, energy requirements, oxygen storage, and cardiac function (Falke *et al*. 1985; Field *et al*. 2001; Irvine *et al.* 2000; Tarnawski *et al.* 2014). These modifications influence diving ability, movement patterns, foraging capacity, and dietary preferences (Chaigne *et al*. 2013; Davis, 2019; Orgeret *et al.* 2019). Ontogenetic changes may be more pronounced in sexually dimorphic species, such as elephant seals, especially for males. Ontogenetic changes may explain differences in diving behaviour displayed by juvenile, sub-adult, and adult elephant seals (Le Boeuf *et al.* 2000; McMahon *et al*. 2003). Previous studies have found that the maturation of elephant seals, and consequently the development of physiological aptitudes, enables older seals to travel greater distances, reach greater depths, hold their breath for longer durations, and forage in a wider variety of habitats (Field *et al.* 2005; McConnell *et al.* 1992; Orgeret *et al.* 2019).

Juvenile elephant seals are known to be more physiologically limited than other elephant seal sex and age classes, and thus tend to be most susceptible to fluctuating resource availability (McMahon *et al*. 2003), which is evident in low survival rates of this early-life stage (Lloyd *et al*. 2020b; Oosthuizen *et al*. 2018). To survive, juvenile elephant seals need to improve their foraging skills and adjust their behaviour without exceeding physiological limits (Orgeret *et al*. 2019; Ponganis, 2015). The sub-adult phase of elephant seal development is an informative age for observing age-and-sex related behavioural changes, since male sub-adults start to differentiate from female elephant seals in terms of body size and foraging ability (Field *et al.* 2007; Stewart, 1997; Taylor *et al.* 2005). During their fourth to sixth year of life, male sub-adult elephant seals undergo a secondary growth spurt (Tarnawski *et al.* 2014). This growth spurt increases their energy requirements which influences foraging behaviour to ensure they obtain sufficient nutrients and energy (Tarnawski *et al.* 2014; Taylor *et al.* 2005). Sub-adult elephant seals experience metabolic changes in relation to their energetic requirements, and they start to metabolize more fat reserves than younger seals, retaining more lean tissue for continued growth (Field *et al.* 2007). Adult male elephant seals attain maximum body size at about seven years old and then either become active breeders, which is energetically costly, or fringe males (Lloyd *et al.* 2020a). Within populations, different aged male elephant seals may respond to their environment differently, which has important demographic implications (Oosthuizen *et al*. 2019).

In the Southern Ocean specifically, extensive demographic data has been collected for the southern elephant seal (SES)(*Mirounga leonina*, Linn.) population at Marion Island (Pistorius *et al.* 2011; Oosthuizen *et al.* 2021). SESs are the most polygynous and sexually dimorphic mammals among extant species (Authier *et al.* 2012; Tarnawski *et al*. 2014). Adult male SESs weigh up to ten times more than female SESs, which is beneficial during fights for dominance to ensure breeding opportunities (Le Boeuf and Laws, 1994; McIntyre *et al*. 2010b). At Marion Island, female SESs exhibit more consistent behaviour, whereas male SESs display much variability in their diving behaviour (Jonker and Bester, 1994; McIntyre *et al.* 2010b). This varied behaviour has been ascribed to sex-specific differences in physiological capacity due to male SESs being much larger than female seals (McIntyre *et al*. 2010b). The ontogeny of male and female SESs has also been described at Macquarie Island (Field *et al.* 2005), Heard Island (Slip, 1997), and the Iles Kerguelen (Orgeret *et al.* 2019). To date, no studies have described age-associated differences in diving behaviour of male SESs at Marion Island. Marion Island is surrounded by deep waters and is remote from other land masses and ice edges (McIntyre *et al.* 2010). These features may therefore promote a largely pelagic lifestyle for SESs at Marion Island, creating different diving behaviour to elephant seals inhabiting other islands (McIntyre *et al*. 2010). Recent evidence suggests that male SES survival plays an important role in the population dynamics of the SES population at Marion Island (Lloyd *et al*. 2020b). To better understand how age-related, and therefore body size, differences influence diving behaviour and affect demography and SES populations, we analysed a unique dataset of satellite tracked male SESs from Marion Island. We assessed age-related differences in dive-duration, frequency, and depth during either searching or transit phases of at-sea migrations of male SESs.

2. Materials and Methods

2.1. Satellite tagging

Between 2005 and 2011, 23 Sea Mammal Research Unit (SMRU) Satellite-Relay Data Loggers (SRDL) (Sea Mammal Research Institute, University of St. Andrews, Scotland) were deployed on male juvenile, sub-adult, and adult SESs at Marion Island (46° 54’ S, 37° 45’ E). Devices were deployed on seals of known age and birth site indicated by their double flipper-tags. These double flipper-tags form part of the ongoing, long-term mark-recapture experiment on Marion Island, whereby every weaned seal born on Marion Island has been marked since 1983 (Pistorius *et al*. 2011). The SRDLs were deployed on five juvenile (Class 1, 2.5 - 3.5 years old), eight sub-adult (Class 2, 4 - 6 years old) and 10 adult male seals (Class 3, older than 6 years old) (Table 1). Yearlings (younger than 2 years) were excluded from this study because they are not as philopatric to the island as older SESs. Deployment details are shown in Table 1, from the youngest to the oldest seal included in this study.

The immobilisation of seals and deployment of SRDLs followed the methods described by Tosh *et al.* (2012). The SRDL devices collected both diving and location data. The diving data included the dive duration (s), surface duration (s), maximum dive depth (m), and the number of dives per day. The location data included the latitude and longitude coordinates of the seal at a specific point in time.

Satellite tag deployment procedures on SESs were performed under the Marion Island Marine Mammal Programme ethics approval (EC077-15; NAS003/2021), approved by the Ethics Committee of the Faculty of Natural and Agricultural Sciences at the University of Pretoria, South Africa.

2.2. Data processing

All data were initially filtered to remove data points with missing latitude or longitude coordinates or indiscriminate variables. Using the ‘*foieGras’* package (Jonsen and Patterson, 2020) in R (R Development Core Team, 2008), we applied a continuous-time state-space model (SSM) and a move persistence model (MPM) to each track. The SSM filtered the Argos locations of each track and generated one location per day to provide the best estimate of each seal’s path. The MPM estimated changes in movement patterns of seals during their tracks. The SSM and MPM outputs were joined, resulting in an SSM-predicted location and an MPM-estimated behavioural index, giving us filtered tracks and unique gamma (γ) values for each seal. The SSM returned a γ value for each location. The γ value is an index metric which represents the likelihood of the seal being in a specific behavioural mode. We imported the filtered tracks and γ values into ArcGIS 10.8.1 (ESRI Inc) and classified each seal’s γ values into two γ ranges. ArcGIS discriminated the two γ ranges according to each seals movement profile. These γ ranges differentiated two behavioural modes, as either ‘searching’ or ‘transit’ mode (Supplementary Table S1).

Searching mode was characterised by movements within a small area, with high turning angles and a lower change in displacement, suggestive of foraging. The alternative behaviour, transit mode, was characterised by movement between areas with low turning angles and a higher change in displacement. Since the SSM modelled tracks represented one location per day, each day was assigned a behavioural mode. We then calculated the percentages of dives spent in each behavioural mode for each track. The minimal threshold that SMRU SRDL’s qualified as a dive was when the seal was below a depth of six meters for over 10 seconds. Dives were no longer recorded when the seal hauled out for over 10 minutes, or when the seal was at, or remained at, the surface for longer than 10 minutes. For diving frequency, we counted the number of dives performed in a 24 hour period. For dive duration, we averaged the duration of dives performed over a 24 hour period. Similarly, we averaged the depths of dives performed over a 24 hour period. We recorded the maximum distance travelled from the island for each seal. The value of each seal’s maximum distance was then averaged across each age class and a mean maximum distance was recorded. Travel distance was not corrected by deployment duration since we were interested in the average maximum distance travelled from the island between the age classes of seals.

2.3. Data analysis

To assess whether age or behavioural mode influenced diving behaviour, we ran a series of linear mixed effect models (lme) and generalized linear mixed effect models (glmer) using the ‘*lme4*’ package in R (Bates *et al*. 2015). The response variables included diving parameters, namely, dive frequency, dive depth, dive duration and surface duration. The predictor variables included age and behavioural mode with individual and date as random effects. Estimated marginal means for each co-efficient were compared in a pairwise fashion using the TUKEY adjustment in emmeans (Lenth, 2019). Models with interaction terms were compared using the ANOVA function in emmeans (Lenth, 2019).

We used the dredge function from the ‘*MuMIn*’ package (Barton, 2009) to select the most parsimonious model according to the lowest second-order Akaike Information Criterion (AICc) value (Burnham and Anderson, 2002). The full model, which included the interaction between age class and behavioural mode, was the best model for each response variable (Table 3).

3. Results

We recorded diving and location data for 23 male SESs between 2.5 and 13 years old, from 2005 to 2011. A total of 63 535 dives were recorded across all three age classes. We recorded 12 658 ± 1517.36 dives for juveniles, 28 933 ± 2326.93 for sub-adults, and 21 944 ± 1479.40 for adults. The summary results of the diving parameters for each SES are recorded in the supplementary material (Supplementary Table S2).

Table 1: Data for male southern elephant seals from Marion Island fitted with SMRU SRDLs between 2005 and 2011. Average number of dives per day shown as Mean ± SD. Age classes

are: J = Juveniles, SA = Sub-adults, and A = Adults. Mode is abbreviated as: SM = Searching mode and TM = Transit mode. Seals that were deployed on more than once at different stages of their lives are indicated by a ‘*’.

Seal tag	Age (years)	Age class	Deployment date (month/day/year)	Track duration (days)	Avg. number of dives per day in SM	Avg. number dives per day in TM
BB253	2.5	J	4/21/2005	28	0	34.54 ± 8.20
RR009	3	J	12/21/2007	61	21.56 ± 7.06	21.44 ± 9.06
BB263	3.5	J	6/23/2006	265	0	30.58 ± 9.57
OO086	3.5	J	4/19/2005	142	0	8.11 ± 5.73
YY361	3.5	J	5/3/2007	187	0	20.80 ± 7.26
YY150	4	SA	12/21/2007	300	23.78 ± 8.12	39.42 ± 13.87
BB116	4.5	SA	4/21/2007	105	19.69 ± 7.52	19.93 ± 7.31
OO052*	4.5	SA	4/18/2006	180	20.02 ± 6.68	17.78 ± 7.53
BB081	5	SA	1/12/2008	197	14.40 ± 7.22	28.21 ± 7.315
BB128	5	SA	1/5/2008	212	16.15 ± 8.028	20.05 ± 9.18
OO052	5.5	SA	4/23/2007	200	15.44 ± 5.92	15.57 ± 7.15
OO052	6	SA	1/10/2008	212	15.94 ± 7.10	15.64 ± 9.72
PEB799	6	SA	3/25/2007	140	6.84 ± 3.33	0
GG178	7	A	4/22/2007	118	19.20 ± 6.86	20.44 ± 9.76
WW005*	7	A	11/12/2007	61	0	33.72± 7.57
PO225*	8	A	3/27/2007	171	10.06 ± 4.29	9.56 ± 4.25
WW005	8	A	11/2/2008	79	24.53 ± 8.49	26.37 ± 9.98
WW005	9	A	3/15/2010	13	25.38 ± 11.23	0
PO225	10	A	11/9/2008	77	19 ± 7.85	17.71 ± 6.52
WR029*	11	A	11/15/2008	87	21.43 ± 7.67	22.29 ± 10.04
PO225	12	A	3/16/2011	163	36.87 ± 10.42	38.38 ± 15.38
WR029	12	A	11/11/2009	47	35.19 ± 13.02	41.6 ± 6.70
WB057	13	A	4/2/2008	118	20.65 ± 7.81	19.15 ± 9.38

3.1. Distance travelled

Seals mostly travelled to the west, southwest and the northwest of Marion Island, with a few SESs travelling south (Figure 1). Juvenile SESs travelled furthest from the island (one-way ANOVA: $F = 5.09$, df = 2, residual df = 20, $P = 0.016$). A post-hoc comparison indicated that juvenile seals travelled, on average, further (2189.79 ± 918.59 km; Figure 1) from the island than sub-adult seals (697.94 ± 962.04 km; Figure 1) but travelled similar distances to adult SESs (1283.27 ± 633.40 km; Figure 1). In the sub-adult age class, one 4-year-old seal (YY150) travelled similar distances to juvenile SESs (Figure 1). A 3-year-old juvenile SES (RR009) travelled 3339.37 km from the island, which was the furthest distance recorded.

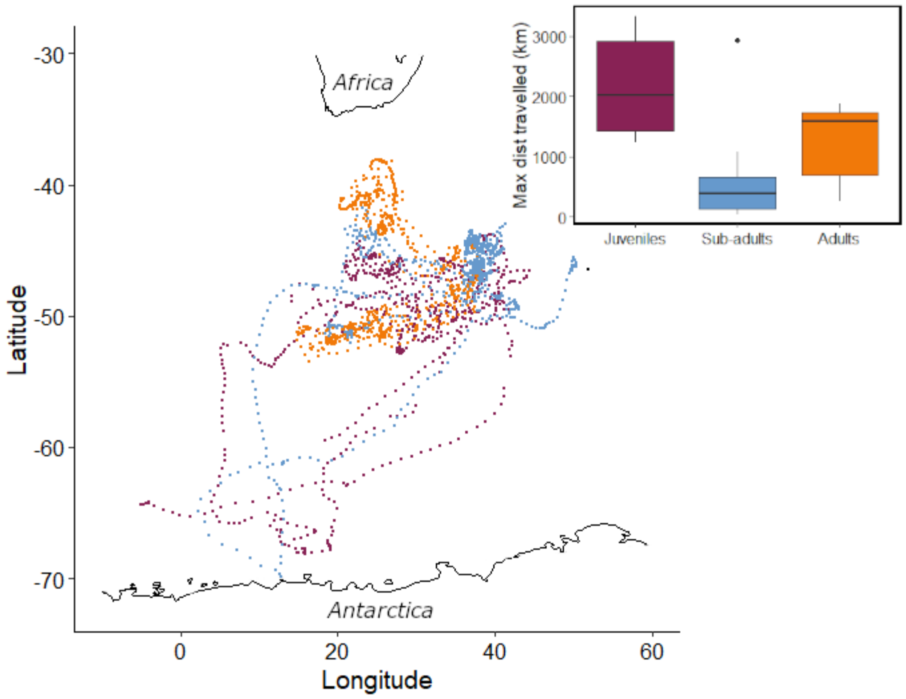

Figure 1: State-space modelled locations for 23 male southern elephant seals (*Mirounga leonina*) tracked from Marion Island between 2005 and 2011. The average maximum distance travelled (km) by juvenile (n=5), sub-adult (n=8) and adult (n=10) male elephant seals is indicated in the top right corner.

3.2. Behavioural mode

The percentage of dives in each behavioural mode varied considerably, ranging from 0% to 100% in both searching mode (SM) and transit mode (TM). Post-hoc comparisons indicated that the percentage of dives in each behavioural mode (SM or TM) differed with age (one-way ANOVA: F = 17.78, df = 2, residual df = 20, $P < 0.001$). We found that only one juvenile seal (RR009) out of the five juveniles in our dataset displayed detectable behaviour in SM (Table1). Therefore, for the remainder of this manuscript, behaviour in searching mode for juvenile seals refers to that of this individual seal. According to the state-space models, juvenile seals' tracks comprised largely of locations in TM, and they performed most of their dives in TM ($P < 0.001$; Figure 2a). In contrast, sub-adult and adult seals performed most of their dives in SM ($P < 0.001$; Figure 2b).

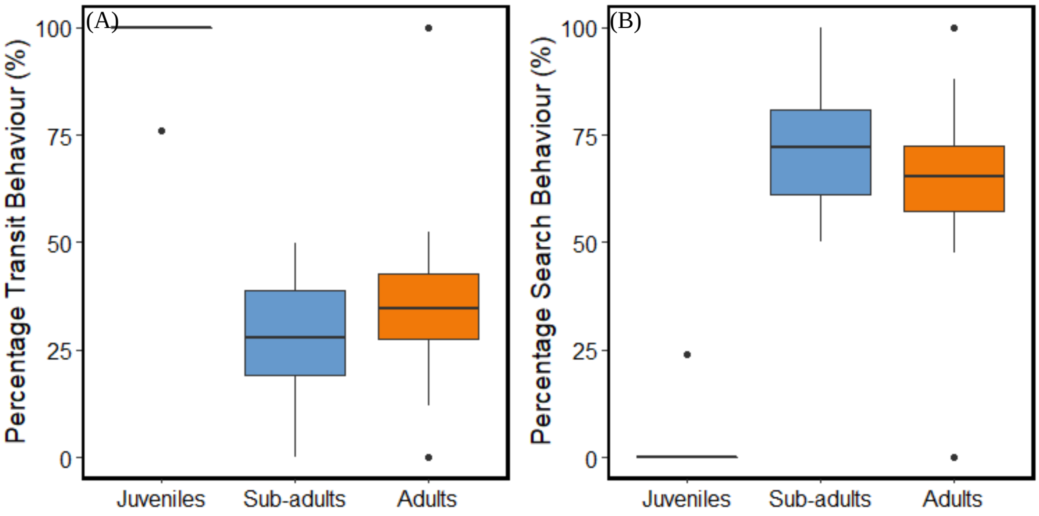

Figure 2: The percentage of dives (%) that male juvenile (n=5), sub-adult (n=8), and adult (n=10) southern elephant seals spent in (A) transit mode (TM) versus (B) searching mode (SM). Horizontal bars represent median values.

3.3. Diving behaviour

The interaction between age and behavioural mode yielded significantly different model estimates when predicting diving duration, maximum dive depth, and the number of daily dives (Figure 3). Juveniles dived for longer durations during TM compared to the individual seal in SM (emmeans: estimate = -0.239, SE = 0.030, z-ratio = -7.901, $P < 0.001$; Table 2), whereas sub-adults dived for longer durations during SM compared to TM (emmeans: estimate = -0.072, SE = 0.007, z-ratio = -9.781, $P < 0.001$; Table 2). Adults dived for relatively constant durations during SM and TM (emmeans: estimate = -0.0001, SE = 0.013, z-ratio = -0.014, $P = 1$, Table 2).

Juveniles reached the greatest maximum depth during TM compared to the individual seal in SM (emmeans: estimate = -0.212, SE = 0.035, z-ratio = -6.082, $P < 0.001$; Table 2). However, the greatest depths were reached during SM rather than TM for sub-adults (emmeans: estimate = -0.079, SE = 0.008, z-ratio = -9.559, $P < 0.001$) and adults (emmeans: estimate = -0.129, SE = 0.014, z-ratio = -9.285, $P < 0.001$; Table 2). The deepest dive recorded was 2168.8m, which was performed by a 13-year old adult seal (WB057) in SM.

The individual juvenile seal exhibited more dives on the days it was in SM (emmeans: estimate = -3.391, SE = 0.226, z-ratio = -14.992, $P < 0.001$; Table 2). In contrast, dives were more frequent during TM for sub-adults (emmeans: estimate = 3.548, SE = 0.083, z-ratio = 42.573, $P < 0.001$) and adults (emmeans: estimate = -0.535, SE = 0.1359, z-ratio = -3.939, $P < 0.001$; Table 2).

Table 2: Diving parameters for juvenile (n=5), sub-adult (n=8), and adult (n=10) male southern elephant seals in each of the behavioural modes, shown as Mean ± SD. SM= Searching mode. TM= Transit mode.

Age class	Behavioural mode	Diving duration (s)	Dive depth (m)	Number of daily dives
Juveniles	SM	1221.45 ± 1182.22	337.87 ± 222.73	21.6 ± 7.06
	TM	1539.17 ± 791.40	492.72 ± 225.12	18.5 ± 11.9
Sub-adults	SM	2144.5 ± 610.55	576.54 ± 266.57	16.5 ± 8.41
	TM	1723.82 ± 799.11	497.82 ± 254.54	24.2 ± 13.8
Adults	SM	1799.26 ± 610.55	574.87 ± 374.95	22.2 ± 12.1
	TM	1653.02 ± 585.94	475.73 ± 243.53	26.1 ± 13.7

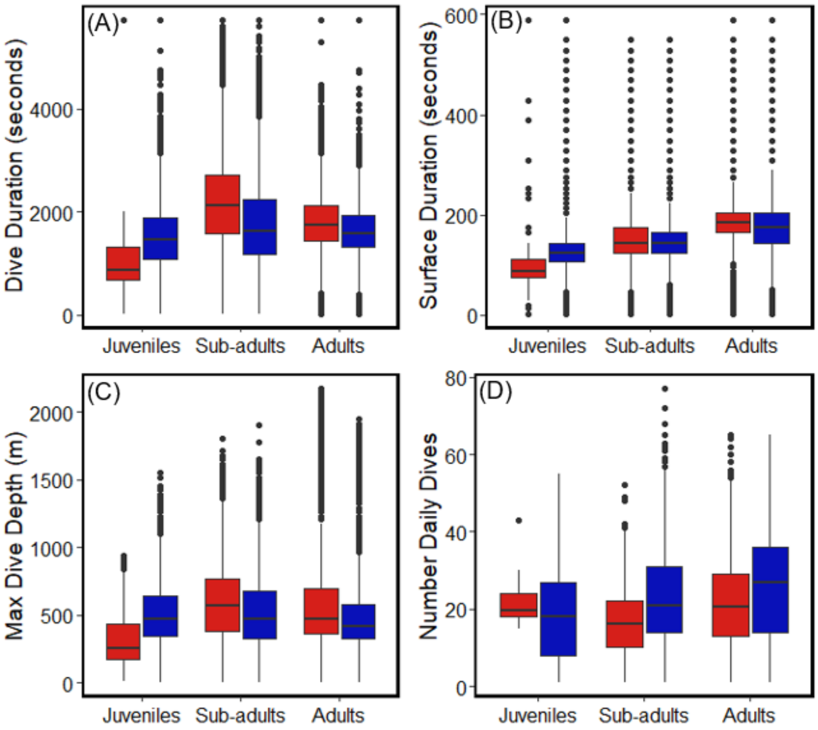

Figure 3: Box and whisker plots for (A) dive duration (s), (B) surface duration (s), (C) maximum diving depth (m) and (D) number of daily dives of male southern elephant seals as a function of age class (juveniles, sub-adults, and adults) and behavioural mode (SM: red bars, TM: blue bars). The data for the juvenile SM group is represented by one individual that recorded search behaviour. Horizontal bars represent the median values.

Surface duration models did not have any significantly different estimated marginal means for interactions (ANOVA: df = 2, *P* = 0.132). Age-class yielded a significantly different marginal mean in the surface duration model (ANOVA: df = 2, *P* < 0.001). Post-hoc tests revealed that all three age classes yielded different estimates in terms of surface duration (*P* < 0.001; Figure 3). Juveniles spent the least time at the surface (126.96 ± 49.29 seconds), sub-adults spent longer times at surface (146.55 ± 63.46s) and adults spent the longest time at surface (187.07 ± 61.10s). Surface duration was also influenced independently by behavioural mode, where seals spent longer times at surface in SM (166.89 ± 67.53s) compared to when in TM (145.79 ± 59.03s) (*P* < 0.001).

Table 3: Model outputs during model selection. The top three best fit models according to the lowest second-order Akaike Information Criterion (AICc) values are indicated for each response variable.

Response variable	Predictor variables					
	Age Class	Behav Mode	Age Class* Behav Mode	AICc	Delta	Weight
Dive Duration (s)	+	+	+	1011575.83	0	1
		+		1011633.28	57.45	3.34E-13
	+	+		1011634.59	58.76	1.74E-13
Surface Duration (s)	+	+	+	706952.55	0	0.65
	+	+		706953.81	1.26	0.35
		+		706968.45	15.89	0.00023
Maximum Depth (m)	+	+	+	876797.53	0	0.99
		+		876812.65	15.13	0.000519
	+	+		876815.30	17.78	0.00014
Number of daily dives	+	+	+	408513.83	0	1
		+		409254.87	741.05	1.2E-161
	+	+		409256.05	742.22	6.7E-162

4. Discussion

Male southern elephant seals (SESs) of different ages from Marion Island demonstrated varied diving behaviour depending on their behavioural mode. In our study, juvenile male SESs behaved markedly differently compared to older male SESs. The juvenile seals in this study travelled consistently further from Marion Island and were in transit mode (TM) for most of their tracks. Juvenile seals dived to shallower depths and performed fewer dives per day. In contrast, sub-adult and adult SESs remained relatively close to the island but spent a larger percentage of their dives in searching mode (SM). In SM, older seals dived for longer and deeper, and spent more time at surface. Older seals also dived more frequently, especially when in TM.

The at-sea behaviour of SESs is influenced by a complex interplay of environmental conditions, physiological factors, and phenology. The annual cycles of SESs govern much of how they behave, and which conditions they encounter during the 90% of their lives they spend at sea (Hindell *et al.* 1991; McConnell *et al.* 1992). Different aged SESs are known to behave differently due to physiological limitations (Bennett *et al.* 2001; Le Boeuf and Laws, 1994). We propose that similar physiological limitations govern the differences observed in diving behaviour when male SESs travelled from Marion Island. As seals age and grow up to 10 times in size, they are able to exploit food patches for longer periods of time, as suggested by remaining closer to the island, and diving to deeper depths for longer durations when in SM.

SESs are wide-ranging and opportunistic generalist feeders that exploit a range of oceanographic regions (Field *et al*. 2001; Hindell *et al*. 2003). It is likely that SESs feed largely opportunistically, travelling in a certain direction until they encounter prey. In our study, we modelled the movements of SESs and identified the probability of a seal at a location being in SM or TM based on metrics such as turning angle, speed and restricted area (Jonsen and Patterson, 2020). We assume that seals will slow down and remain in a restricted area when they encounter food patches and thus be in SM. SESs from Macquarie Island (Field *et al.* 2005) seem to behave similarly to those from Marion Island.

De Grissac *et al.*'s (2017) study on marine air-breathing predators suggested that juvenile seals have a less developed ability to locate high-quality foraging patches than older age classes. In our study, juvenile SESs spent most of their track in TM, and travelled the furthest from the island suggesting lower energy requirements or a less developed ability to locate food due to their smaller size and naivety. In contrast, we show that sub-adult SESs remained relatively close to the island and spent most of their track in SM. Sub-adult SESs experience a secondary growth spurt resulting in a larger body size, higher energy requirements, and enhanced physiological capabilities (Tarnawski *et al.* 2014). Hindell *et al.* (2021) found that male subadult SES from Iles Kerguelen also focused their feeding within close proximity to the island, which they concluded was attributed to inherited behaviour. Adult SESs spent most of their tracks in SM, but recorded more SM bouts and travelled further from Marion Island than sub-adult seals (Richard *et al*. 2016). Aside from differences in horizontal behaviour, we also observed differences in diving behaviour associated with age and behavioural mode.

Diving behaviour, associated with vertical movement, is measured using parameters such as maximum dive depth, dive duration, surface duration, and number of daily dives. In our study, different aged male SESs displayed varied diving behaviour using these four diving parameters. We observed that juvenile SESs executed shorter dives and reached shallower depths which was expected given their physiological limitations. Similar findings have been reported for juvenile SESs from Heard Island and the Iles Kerguelen (Orgeret *et al*. 2019; Slip, 1997). Younger, fatter seals are more buoyant and tend to sink less rapidly, reaching shallower depths than older, leaner seals (Biuw *et al.* 2003, Orgeret *et al*. 2019). Younger, smaller seals also have limited oxygen reserves and therefore restricted aerobic capacities (Bennett *et al*. 2001; Irvine *et al.* 2000; Orgeret *et al.* 2019). Consequently, they struggle to remain submerged for long enough to reach greater depths (Bennett *et al*. 2001; Irvine *et al.* 2000; Orgeret *et al.* 2019).

Typically, seals that dive the longest reach the greatest depths (Bennett *et al*. 2001; DeLong and Stewart, 1991; Hindell *et al.* 1992). Since older seals are leaner and have greater oxygen storage capacities than juveniles, they can perform longer, deeper dives. Mature seals also undergo changes in cardiac output which increases their resistance to hypoxia (Fahlman *et al*. 2006; Falke *et al*. 1985; McIntyre *et al.* 2010a). Sub-adult seals in SM dived longer and deeper than adult seals. Previous studies have reported similar diving patterns for sub-adult elephant seals (McIntyre *et al.* 2012; Weise *et al.* 2010). Sub-adult seals performed fewer dives whilst in SM suggesting a trade-off between diving for longer to attain greater depths, and their ability to recover after each dive. In contrast, adult SESs displayed relatively consistent dive durations during SM and TM but reached greater depths during SM. Seals that dive to great depths need to return to the surface to breathe, recover and replenish their oxygen supplies (Bennett *et al*. 2001; Orgeret *et al.* 2019). Oxygen supply therefore influences surface duration (Bennett *et al*. 2001). In our study, sub-adult and juvenile SESs spent less time at the surface compared to adults. Smaller bodied seals can replace their oxygen debt more quickly (Butler, 2004; Orgeret *et al*. 2019). Smaller bodied seals may also limit their time at the surface to avoid predators. Predators, such as killer whales, typically spend most of their time hunting near the surface (Jordaan *et al*. 2021; Reisinger *et al.* 2015). Killer whales reside close to Marion Island (Reisinger *et al.* 2015), and sub-adult SESs from Marion Island, especially those that forage close to the island, may need to invest some energy into avoiding predation. In contrast, large male adult SESs exhibited prolonged surface durations, which was most likely to rest and replenish their large oxygen supplies before starting their next dive, which is consistent with previous findings (Hindell *et al.* 1992; Irvine *et al.* 2000. McIntyre *et al*. 2010a; Orgeret *et al*. 2019).

Here we analysed differences in diving behaviour between different aged male SESs from Marion Island. We did not investigate seasonal behavioural differences between seals during post-moult and post-breeding times of the year since our study focused on male SESs that were not necessarily active breeders. Juvenile and sub-adult male SESs also have different phenology compared to adult male SESs, often returning to Marion Island for a winter haul out (Kirkman *et al.* 2003; Kirkman *et al.* 2001). We did not include any environmental covariates in our analysis, since this has been done previously and often concluding that movements vary substantially between individuals (McIntyre *et al.* 2012, McIntyre *et al.* 2010a). As with most tracking studies, data were collected opportunistically, and a limited number of seals were tracked due to various constraints. The modelling process, which accounted for error in the satellite locations, described each location as an average location estimate per day. As a result, we assigned one location per day using the SSM model. While we acknowledge that seals may switch modes within days, this scale accounted for irregularities in the time stamps of the satellite transmissions owed to weather and other external factors. With this being said, sub-daily transmission recordings could lead to better insights into at-sea behaviour, which should be a goal for future research on this topic. We also used modelling to estimate where searching or potential foraging occurred. Seals are likely to forage throughout their tracks, and searching, as predicted by SSMs, could also indicate other behaviour, including responses to storms, encountering predators or at-sea breeding behaviour. Ideally, we need to record actual feeding behaviour. Recent studies have employed technologies that record actual feeding events (Adachi *et al*. 2021; Richard *et al*. 2016). In this way, researchers can monitor how many feeding events occur in a patch, which would circumvent some speculation. This would be ideal for future studies investigating foraging behaviour of SESs from Marion Island.

5. Conclusion

We observed age-related differences in diving behaviour of male SESs from Marion Island. These differences reflect known physiological capabilities of different sized SESs. Irrespective of environmental variables and individual variability, we showed that the largest SESs dived deeper for longer. Sub-adult SESs performed fewer dives per day, often for longer durations, despite diving to similar depths as adult SESs. This supports the idea that sub-adult SESs may have to balance their energy expenditure and as they grow older, they are able to reach deeper depths in shorter times and therefore, perform more dives per day. Since SESs are pelagic feeders, they can adapt their foraging behaviour according to their physiological abilities.

CRediT author statement

Kiara G Lasch: Methodology, Software, Formal analysis, Data curation, Writing - Original Draft, Visualization. **Cheryl A Tosh:** Conceptualization, Validation, Supervision, Writing- Reviewing and Editing. **Marthan N Bester:** Investigation, Resources, Project administration. **P. J. Nico de Bruyn:** Conceptualization, Validation, Supervision, Writing- Reviewing and Editing, Project administration, Funding acquisition.

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