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Segregation in a sexually dimorphic mammal: a mixed-effects modelling analysis of diving behaviour in southern elephant seals

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ABSTRACT: Sexual segregation in habitat use occurs in a number of animal species, including southern elephant seals, where differences in migration localities and dive behaviour between sexes have been recorded. Due to the extreme sexual size dimorphism exhibited by southern elephant seals, it is unclear whether observed differences in dive behaviour are due to increased physiological capacity of males, compared to females, or differences in activity budgets and foraging behaviour. Here we use a mixed-effects modelling approach to investigate the effects of sex, size, age and individual variation on a number of dive parameters measured on southern elephant seals from Marion Island. Although individual variation accounted for substantial portions of total model variance for many response variables, differences in maximum and targeted dive depths were always influenced by sex, and only partly by body length. Conversely, dive durations were always influenced by body length, while sex was not identified as a significant influence. These results support hypotheses that physiological capability associated with body size is a limiting factor on dive durations. However, differences in vertical depth use appear to be the result of differences in forage selection between sexes, rather than a by-product of the size dimorphism displayed by this species. This provides further support for resource partitioning and possible avoidance of inter-sexual competition in southern elephant seals.

KEY WORDS: Sexual segregation · Sexual dimorphism · Dive behaviour · Southern elephant seals · Linear mixed-effects models · *Mirounga leonina*

INTRODUCTION

Sexual segregation has been defined as the separation of members of a species, such that sexes live apart, either singly or as single-sex groups (Wearmouth & Sims 2008). It is a phenomenon present in reptiles (Ford & Hampton 2009), fish (Mucientes et al. 2009), birds (González-Solís et al. 2008, Morales et al. 2008, Palacin et al. 2009) and mammals. In mammals, sexual segregation has been studied mostly in terrestrial species, particularly ungulates and other group-living mammals, where it appears to be very common (MacFarlane & Coulson 2007, Ciuti & Apollonio 2008, Hay et al. 2008, Li & Jiang 2008, Shannon et al. 2008). It is less well documented in marine mammals, though it appears to play an important role for various cetacean species, notably for species that live in social groups (Whitehead & Weilgart 2000, Martin & da Silva 2004). Recent advances in satellite-tracking devices for marine species have led to new understandings of the pelagic phases of pinniped life cycles across the globe. As a result, sexual segregation in migration patterns and depths utilised has increasingly been reported for a number of seal species (Slip et al. 1994, Page et al. 2005, Wolf et al. 2005, Breed et al. 2006, Staniland & Robinson 2008).

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Mechanisms presented to explain such difference in behaviour between sexes include (1) predator avoidance, (2) forage selection, (3) differences in activity budgets, (4) thermal niche-fecundity in ectotherms, and (5) social factors (Ruckstuhl 2007, Staniland & Robinson 2008, Wearmouth & Sims 2008). Notably, many of these hypotheses are associated with sexual size dimorphism and predict positive correlations of sexual segregation with sexual size dimorphism.

Southern elephant seals are extremely sexually dimorphic, with males sometimes being up to 10 times larger than females (Le Boeuf & Laws 1994). Adult animals haul out at breeding colony sites twice during a year — once during the breeding period (austral spring) and once for the annual moult (austral mid to late summer). Segregation in forage locations between the sexes in southern elephant seals have been reported for animals from various localities (Slip et al. 1994, Campagna et al. 1995, McConnell & Fedak 1996, Campagna et al. 1999, Bornemann et al. 2000, Tosh et al. 2009). Similarly, a number of studies demonstrate segregation in dive behaviour, with females foraging mostly pelagically while males tend to either forage benthically or show greater variation in forage strategy, often employing both pelagic and benthic strategies (Hindell et al. 1991, McConnell et al. 1992, Campagna et al. 1995, Jonker 1997, Malherbe 1998, Campagna et al. 1999, Field et al. 2005b).

Such differences in forage locations and dive behaviour are thought to be associated with sex-specific foraging strategies in this species, with males reportedly adopting more risky foraging strategies in order to maximise early growth (Lewis et al. 2006, Field et al. 2007a). Such segregation has largely been attributed to inter-sexual competition avoidance in this species (Field et al. 2005b, Lewis et al. 2006). While such investigations reported clear differences in foraging strategies between males and females, no attempts were made to quantify the effects of body size differences between sexes. This is important since the extreme sexual dimorphism of this species is likely to influence dive parameters and cloud the potential influence of sex versus body size on the dive behaviour of elephant seals.

Here we investigate sexual differences in dive behaviour of southern elephant seals from Marion Island. Our aims were specifically to determine if differences in dive parameters between sexes were a result of inherent sex-related traits or merely a by-product of size differences between sexes. Because of the unbalanced nature of available data, we utilised a mixed-effects modelling approach to elucidate the effects of sex, standard length and age on the depth utilisation of elephant seals.

MATERIALS AND METHODS

Satellite-tag deployments. A total of 57 satellite-relay data loggers (Sea Mammal Research Unit, University of St. Andrews, Scotland) were deployed on southern elephant seals of known age and sex hauled out at Marion Island (46° 54′ S, 37° 45′ E). Deployments were made on known individuals, born and flipper-tagged on the island as part of a long-term mark-recapture investigation (Bester 1988, de Bruyn et al. 2008). Two types of satellite-relay data logger (SRDL) were used in this investigation: 33 SRDL Series 9000 and 24 SRDL-CTD devices. Devices were glued onto the cranial pelage of immobilised animals (for further details see Tosh et al. [2009]). All SRDLs were programmed to measure pressure every 4 s during each dive of the animal. Only dives deeper than 6 m were recorded. Detailed dive data were compressed onboard the instruments, prior to transmission, using a broken-stick algorithm to provide 4 dive points reflecting the greatest inflections, as well as the maximum depth reached within the dive (Fedak et al. 2001, Boehme et al. 2009). This information was relayed via service Argos (Argos 1996), along with environmental data (SRDL Series 9000 devices recorded temperature profiles, while SRDL-CTD devices recorded temperature and conductivity profiles), and position estimates calculated from Doppler shift measurements in successive uplinks. All dive and environmental meta-data are available in open access via the PANGAEA information system (www.pangaea.de).

For the purposes of this investigation we included data obtained only from animals for which deployments were made prior to post-moult migrations (as opposed to post-breeding migrations). Also, only tracks obtained from animals with measured standard length data (with the seal in ventral recumbency) and known ages at the time of deployment were included. Few mass measurements were available for the study animals, precluding the inclusion of mass as an indication of body size. We further removed data obtained from the largest males and smallest females of known lengths (males: n = 2; females: n = 3) in order to ensure substantial overlap in standard lengths between sexes and remove a possible confounding effect between sex and standard length (see Results). This resulted in data being retained from 20 (12 females and 8 males; Table 1) tracks for this study.

Filtered tracks (see Tosh et al. 2009) were plotted in Arcview 3.3 (ESRI 1998). Space use and the extent of movements were calculated using Animal Movement Analyst (Hoodge & Eichenlaub 1997). Kernel density estimators based on all locations further than 200 km from Marion Island were calculated in order to determine space use probabilities (95% and 50%) for females and males separately. Minimum convex poly-

Table 1. Dive characteristics of selected southern elephant seal tracks used in this investigation. Only dives with a positive residual value resulting from the regression of bottom time as a function of maximum dive depth and dive duration (indicating increased forage effort) were included. Stdl = standard length (cm); DD = dive duration (min); MD = maximum depth (m); ED = exploited dive depth (m). Values arepresented as means (±SD) of individual seal averaged values

Animal	Track	Sex	Year	Age (yr)	Stdl	DD_{DAY}	DD_{NIGHT}	MD_{DAY}	MD_{NIGHT}	ED_{DAY}	ED_{NIGHT}
BB081	BB081	m	2008	5.3	252	36 ± 12	29 ± 10	732 ± 149	465 ± 219	687 ± 142	439 ± 197
BB128	BB128	m	2008	5.3	293	38 ± 13	26 ± 10	743 ± 148	426 ± 166	723 ± 155	375 ± 147
BB253	BB253	m	2005	2.6	214	24 ± 5	19 ± 4	563 ± 90	457 ± 164	530 ± 90	406 ± 153
BB263	BB263	m	2006	3.7	231	30 ± 5	22 ± 6	684 ± 130	501 ± 175	632 ± 128	445 ± 176
GG335	GG335_2	f	2008	8.3	235	34 ± 12	30 ± 9	556 ± 150	422 ± 120	518 ± 146	388 ± 118
OO021	OO021_2	f	2008	6.3	225	34 ± 8	25 ± 6	546 ± 102	394 ± 92	520 ± 100	355 ± 91
OO052	OO052_1	m	2006	4.6	280	43 ± 13	32 ± 11	722 ± 181	572 ± 261	682 ± 183	526 ± 258
OO086	OO086	m	2005	3.5	260	33 ± 10	23 ± 8	682 ± 194	498 ± 164	615 ± 182	428 ± 155
OO418	OO418	f	2008	6.4	230	28 ± 8	21 ± 6	550 ± 154	367 ± 164	504 ± 145	327 ± 160
PO043	PO043_1	f	2007	8.3	254	18 ± 15	24 ± 23	310 ± 142	332 ± 142	265 ± 142	291 ± 146
RR009	RR009	m	2008	3.2	210	16 ± 14	20 ± 19	310 ± 140	405 ± 203	270 ± 132	360 ± 207
WW058	WW058	f	2008	7.3	244	31 ± 8	24 ± 7	555 ± 178	372 ± 187	510 ± 169	330 ± 178
WW061	WW061	f	2008	7.3	233	33 ± 6	25 ± 5	592 ± 109	407 ± 128	550 ± 106	361 ± 123
YY150	YY150	m	2008	4.2	265	36 ± 14	28 ± 9	638 ± 200	423 ± 179	599 ± 200	373 ± 166
YY189	YY189_1	f	2006	2.5	222	35 ± 6	23 ± 5	625 ± 98	427 ±108	579 ± 97	383 ± 106
	YY189_2a	f	2007	3.3	224	28 ± 9	20 ± 5	563 ± 102	432 ± 98	524 ± 100	390 ± 100
	YY189_3a	f	2008	4.3	242	30 ± 10	24 ± 7	522 ± 116	372 ± 97	491 ± 119	334 ± 96
YY193	YY193_2	f	2008	4.3	224	31 ± 10	24 ± 9	502 ± 115	286 ± 128	467 ± 114	254 ± 125
YY264	YY264_2	f	2008	4.4	236	32 ± 10	23 ± 7	497 ± 133	297 ± 125	467 ± 132	260 ± 123
YY348	YY348_2	f	2008	4.4	227	35 ± 10	22 ± 6	571 ± 173	370 ± 185	537 ± 166	329 ± 176

gons (MCPs) were drawn to determine the maximum extent of movements for both sexes.

Dive analyses. We removed all incomplete (containing missing values) or unrealistic (containing sequential time values that are not chronological) dive sequences prior to analysis. Due to the compressed format in which dive data are received, estimating times spent by animals within various depth layers is problematic. We therefore used a simple interpolating algorithm, assuming constant swim speeds and directions between transmitted dive points, to calculate estimated times spent within various depth layers (100 m increments from the surface to 1000 m, thereafter 1000–1250 m, 1250–1500 m, 1500–2000 m, and >2000 m) for each transmitted dive profile (see McIntyre et al. 2010 for further details). We then identified the mid-depth value of each depth layer in which an animal spent the most time during any particular dive (e.g. if the seal spent the largest amount of time in the 0 to 100 m depth layer, then 50 m). This was referred to here as the exploited depth.

To account for variation in dive behaviour associated with differing activity (e.g. foraging, travelling or resting) we identified individual dives with longer-than-average bottom times for each track (Bailleul et al. 2008). Accordingly, we calculated bottom time as the time spent by an animal at depths exceeding 80% of the maximum depth point for that dive (Lesage et al. 1999, Schreer et al. 2001, Burns et al. 2008). We then used linear regressions to calculate average bottom times for dives with given dive durations and maximum dive depths (Bailleul et al. 2008). The residual values obtained from these regressions then identified individual dives as being characterised by longer- and shorter-than-average bottom times. Dives with positive residuals (indicating longer-than-average bottom times) were assumed to suggest increased foraging effort and were retained for further analysis.

Diel variation in dive behaviour has been documented for a number of seal species, including southern elephant seals (Jonker & Bester 1994, Campagna et al. 1995, Bennet et al. 2001, Bajzak et al. 2009). We therefore classified each dive according to day-stage (day, night, sunrise, sunset), accounting for spatial position and season. Local times for each dive were calculated according to the associated longitude values of each dive and the appropriate standard time zone (based on UTC). Seasonal local times of sunrise and sunset for 2009 (by latitude) were obtained from the National Oceanic and Atmospheric Administration (NOAA) (www.srrb.noaa.gov/highlights/sunrise/sunrise.html). Local-time hour values of dives, season and local times of sunrise/sunset were then used to classify the day-stages of individual dives.

To account for the potential influences of sea ice on individual dive behaviour, we further removed all dive data collected at latitudes higher than 60° S. Data used in the models were therefore restricted to dives with positive bottom dive residuals, completed at latitudes lower than 60° S.

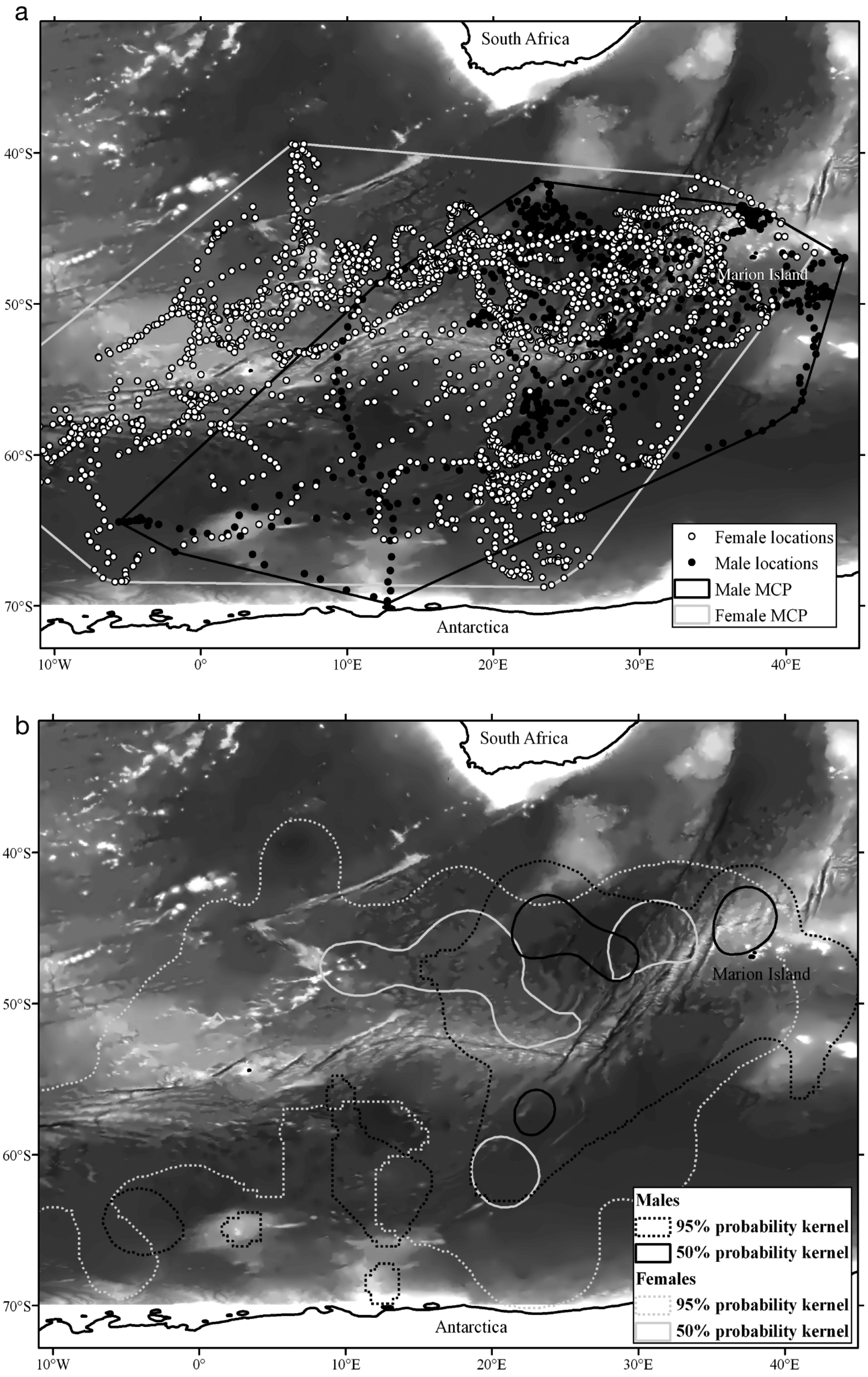

Fig. 1. (a) Daily averaged dive locations of the 20 animals (8 males; 12 females) tracked in this study. Minimum convex polygons (MCPs) of their track data are indicated. Background shading indicates the underlying bathymetry (dark shading = deeper water; light shading = shallower water) (b) Kernel density estimates of the 20 (8 males; 12 females) southern elephant seal tracks included in this investigation

Statistical analyses and model selection. All parameters presented were summarised to daily mean values per track. This was done to smooth out potential biases associated with unsuccessful transmissions of dive profiles (Vincent et al. 2002, Boehme et al. 2009), and potential biases in the likelihood of successful transmissions associated with geographic positions and the orbit of Argos satellites (Argos 1996). Daily mean values further allowed for modelling of temporal autocorrelation, using functions that were computationally too intensive to use on raw data (see below).

Maximum dive depths (MD_{DAY}/MD_{NIGHT}), dive durations (DD_{DAY}/DD_{NIGHT}) and exploited depths (ED_{DAY}/ED_{NIGHT}) were compared with linear mixed-effects models (LMEs). Three covariates were considered in the models: sex, start age (age of animals at the time of deployment) and standard length. These were included in the models as fixed effects, and individual tracks as a random effect. Restricted maximum likelihood (REML) estimation was employed in all model fits, following Bolker et al. (2009).

Autocorrelation plots revealed significant temporal autocorrelation evident in all models. We therefore modelled temporal autocorrelation dependencies, by including autoregressive functions (Pinheiro & Bates 2004, Crawley 2007). Final model covariates were chosen using backwards selection, starting with the 3 covariates models. We used second order Akaike's information criterion (AIC) statistics for small sample sizes (Burnham & Anderson 2002) to govern initial model selection, along with various plot types to assess model fits (Pinheiro & Bates 2004). Hypothesis tests (*F* tests) were carried out on the final models to distinguish significance of the various fixed effects (Bolker et al. 2009). Variance components analyses were also carried out on the final mixed-effects models to estimate the variation explained by random effects (individual) (Börger et al. 2006, Crawley 2007, Bunnefeld et al. 2009).

Models were run using R version 2.7.1 (R Development Core Team 2008). The significance level for all tests was set at $p \leq 0.05$.

RESULTS

Male and female animals in our study travelled in similar directions from Marion Island, predominantly to the west and southwest (Fig. 1a). MCPs indicated substantial overlap in total areas utilised between sexes. Fifty percent kernel density estimates indicated less overlap between the sexes, though these areas were in similar regions (Fig. 1b). Males appeared to concentrate their movements closer to Marion Island than did females. Bottom depth estimates (Smith & Sandwell 1997) of the individual dive locations indicated substantial overlap in bottom depths between sexes, though males tended to dive in areas with slightly shallower water depths than females (males: 3523 ± 1622 m; females: 4399 ± 851 m) (Fig. 2).

The 20 tracks resulted in 99 302 dives that were successfully transmitted. The filtering process removed 5090 dives, resulting in 94 212 dives remaining for analyses. Of these, 72 794 dives had calculated bottom times greater than 0 and were used to calculate bottom time residuals. After removal of dives located at latitudes higher than 60° S, daily averaging resulted in 2810 'dive days' and 2924 'dive nights'.

Start age was not significantly correlated with standard length (Pearson: $r = 0.24$, $df = 18$, $p = 0.31$), and standard length was not significantly correlated with sex (Pearson: $r = 0.41$, $df = 18$, $p = 0.07$) in our study animals. While backwards selection was employed, models were always run with all possible combinations of fixed variables. Models including each of the fixed variables provided the best fit to the data set for each of the dive parameters in our study (Table 2).

Maximum dive depths

Males dived to deeper mean maximum dive depths than females, and both sexes dived to deeper mean depths during daytime, when compared to night-time dives ($\text{Males}_{DAY} = 663.6 \pm 186$ m; $\text{Males}_{NIGHT} = 466.8 \pm 196.58$ m; $\text{Females}_{DAY} = 548.5 \pm 138$ m; $\text{Females}_{NIGHT} = 382.3 \pm 140.8$ m). Males displayed more variation in maximum dive depths than females (ANOVA_{DAY}: $F_{1,17230} = 2100.2$, $p < 0.001$; ANOVA_{NIGHT}: $F_{1,18514} = 1071$, $p < 0.001$; Fig. 3). Maximum dive depths were

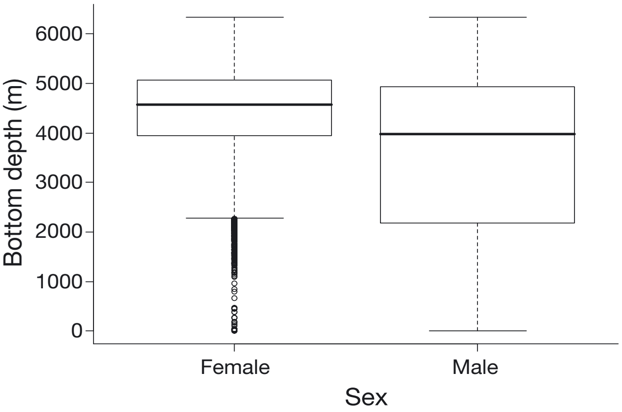

Fig. 2. Box-and-whisker plot indicating estimated water depths (Smith & Sandwell 1997) of dive locations recorded for the selected southern elephant seal tracks in this investigation. Bold line = median, box = 25th and 75th percentiles, points = outliers, whiskers = 1.5 times the interquartile range, or the maximum values (when there are no outliers)

Table 2. Summary of models with best fits. Models without an asterisk (*) are final models prior to the inclusion of an autocorrelation function. Models with an asterisk (*) indicate final models that included an autoregressive autocorrelation function. DD = dive duration, MD = maximum dive depth, ED = exploited dive depth, stdl = standard length, AIC_c = second order AIC statistic, and RE = random effect

Parameter	Model	AICc	Significant effects	RE (%)
DD_{DAY}	Sex + start age + stdl	43 569.4	Stdl	29.4
	Sex + start age + stdl*	41 460.4	Stdl	16.5
DD_{NIGHT}	Sex + start age + stdl	43 522.4	Start age + stdl	19.2
	Sex + start age + stdl*	41 835.7	Start age + stdl	12.9
MD_{DAY}	Sex + start age + stdl	35 113.9	Stdl	43.7
	Sex + start age + stdl*	34 040.3	Sex + stdl	38
MD_{NIGHT}	Sex + start age + stdl	37 125.6	Sex	16.3
	Sex + start age + stdl*	36 158.8	Sex	11.1
ED_{DAY}	Sex + start age + stdl	34 911.1	Stdl	44.4
	Sex + start age + stdl*	33 880.9	Sex + stdl	39
ED_{NIGHT}	Sex + start age + stdl	36 754.8	Sex	17.9
	Sex + start age + stdl*	35 849.1	Sex	12.8

rarely constrained by estimated water depths, and few evident benthic dives were observed in either sex (Fig. 4). Sex and standard length significantly affected maximum dive depths during the day, while sex was the only fixed effect influencing maximum dive depths at night in the final models (Tables 2 & 3). Individual track (random effect) explained 38 % of the variance in the final model for MD_{DAY} and 11.1 % of the variance in the final model for MD_{NIGHT}.

Dive durations

Dive durations (DD) were longer in males than females, and both sexes dived for longer mean periods of time during the day than during night-time dives ($Males_{DAY}$ = 35.5 ± 2.8 min; $Males_{NIGHT}$ = 26.2 ±

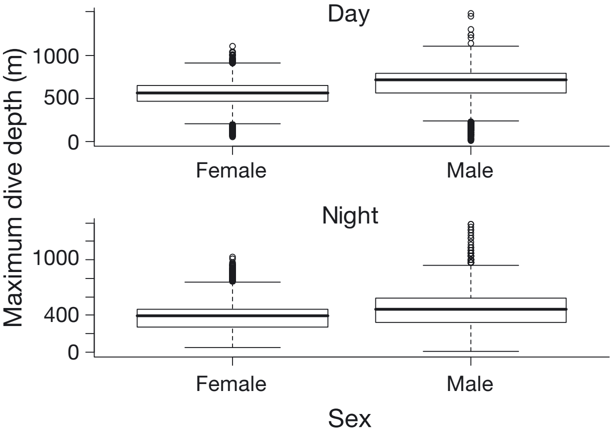

Fig. 3. Box-and-whisker plots of maximum dive depths attained by animals in the selected tracks. For definition of box plots see Fig. 2

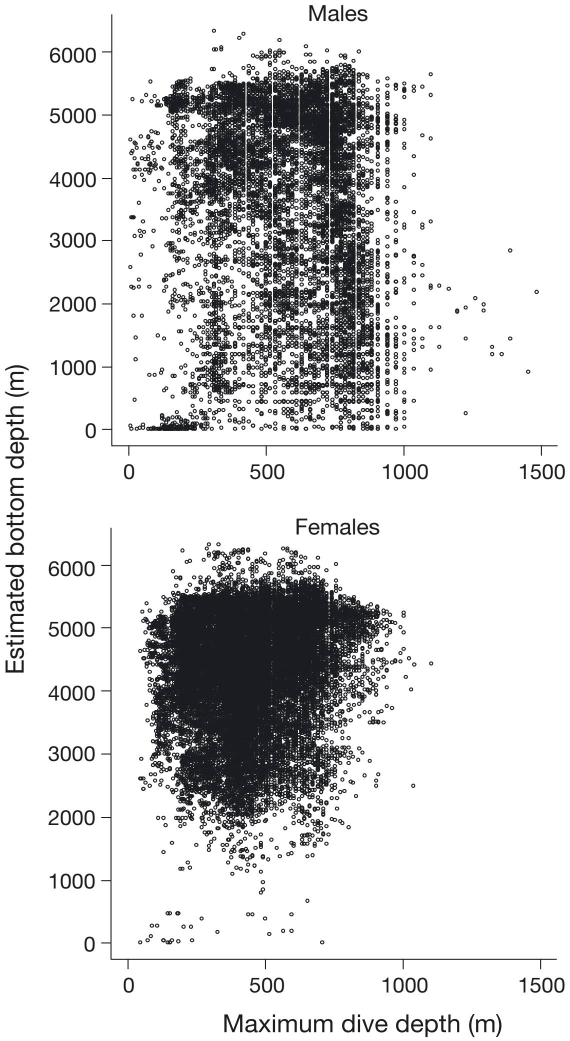

Fig. 4. Scatterplots of maximum dive depths and estimated bottom depths. Estimates of bottom depths were derived from Smith & Sandwell (1997)

Table 3. *F* test results indicating significant fixed effects on final models. **Boldface** indicates statistically significant effects ($p < 0.05$). DD = dive duration, MD = maximum dive depth, ED = exploited dive depth

Response variable	Fixed effect	*F*	df	p
DD$_{\mathrm{DAY}}$	**Intercept**	**924.124**	**1,2790**	**<0.001**
	Sex	1.131	1,16	0.303
	Start age	0.002	1,16	0.969
	Stdl	**10.909**	**1,16**	**0.005**
DD$_{\mathrm{NIGHT}}$	**Intercept**	**1328.123**	**1,2904**	**<0.001**
	Sex	1.761	1,16	0.203
	Start age	**6.58**	**1,16**	**0.021**
	Stdl	**9.933**	**1.16**	**0.006**
MD$_{\mathrm{DAY}}$	**Intercept**	**651.932**	**1,2790**	**<0.001**
	Sex	**4.762**	**1,16**	**0.044**
	Start age	0.018	1,16	0.894
	Stdl	**4.752**	**1,16**	**0.045**
MD$_{\mathrm{NIGHT}}$	**Intercept**	**1162.961**	**1,2904**	**<0.001**
	Sex	**13.609**	**1,16**	**0.002**
	Start age	1.028	1,16	0.326
	Stdl	0.234	1,16	0.635
ED$_{\mathrm{DAY}}$	**Intercept**	**587.416**	**1,2790**	**<0.001**
	Sex	**4.502**	**1,16**	**0.05**
	Start age	0.006	1,16	0.939
	Stdl	**5.374**	**1,16**	**0.034**
ED$_{\mathrm{NIGHT}}$	**Intercept**	**931.25**	**1,2904**	**<0.001**
	Sex	**10.572**	**1,16**	**0.005**
	Start age	1.189	1,16	0.292
	Stdl	0.267	1,16	0.612

9.5 min; Females$_{\mathrm{DAY}}$ = 31.8 ± 9.7 min; Females$_{\mathrm{NIGHT}}$ = 24 ± 7.4 min) (Fig. 5). The best model for DD$_{\mathrm{DAY}}$ indicated that standard length was the only significant fixed effect influencing this parameter (Table 3). A weak, but statistically significant positive correlation existed between DD$_{\mathrm{DAY}}$ and standard length (Pearson: $r = 0.31$, df = 2808, $p < 0.001$). Both standard length and start age were identified as significantly influencing DD$_{\mathrm{NIGHT}}$. Individual track (random effect) explained 16.5% and 12.9% of the variance in the final models for DD$_{\mathrm{DAY}}$ and DD$_{\mathrm{NIGHT}}$ respectively.

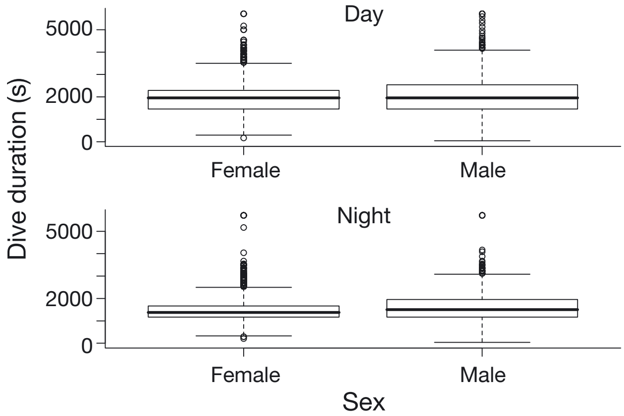

Fig. 5. Box-and-whisker plots of dive durations recorded for the southern elephant seal tracks selected for this investigation. For definition of box plots see Fig. 2

Exploited dive depths

Exploited dive depths were deeper in males than in females, and deeper during daytime dives when compared to night-time dives for both sexes (Males$_{\mathrm{DAY}}$ = 622.2 ± 185.8 m; Males$_{\mathrm{NIGHT}}$ = 416.6 ± 186.4 m; Females$_{\mathrm{DAY}}$ = 511.2 ± 134.1 m; Females$_{\mathrm{NIGHT}}$ = 342.5 ± 136.6 m). Males displayed more variation in exploited dive depths than females (ANOVA$_{\mathrm{DAY}}$: $F_{1,17230} = 2020.8$, $p < 0.001$; ANOVA$_{\mathrm{NIGHT}}$: $F_{1,18514} = 892.77$, $p < 0.001$; Fig. 6). Best models for exploited depth indicated that sex and standard length significantly influenced exploited dive depths during daytime dives (Table 3). Sex was identified as the only fixed effect significantly influencing exploited depths at night. Individual track (random effect) explained 38.9% of the variance in the final model for ED$_{\mathrm{DAY}}$ and 12.8% of the variance in the final model for ED$_{\mathrm{NIGHT}}$.

DISCUSSION

This study investigated the effects of sex, size and age on a number of dive parameters measured in southern elephant seals from Marion Island. By examining track and dive data obtained from seals from a range of sizes (standard lengths) in each sex, we were able to elucidate the influence of such effects using a mixed-effects modelling approach.

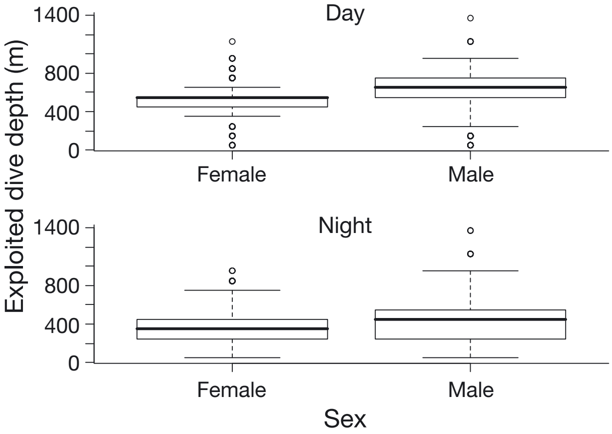

Fig. 6. Box-and-whisker plots of exploited dive depths of southern elephant seal tracks selected for this study. For definition of box plots see Fig. 2

Sex versus size

Males in our sample undertook longer and deeper foraging dives than females — dives characterised by increases in time spent at the bottom of dives. Male southern elephant seals displayed more variation in maximum and exploited dive depths than females (Figs. 3 & 6). Sex was considered a significant effect in final models for maximum dive depth and exploited dive depth during day- and night-time. However, sex did not have a significant effect in final models for dive duration. Standard length was incorporated in the best models for all dive parameters. It was identified as being a statistically significant effect for dive durations during day- and night-times, as well as maximum and exploited dive depths during daytime. While the inclusion of standard length improved all final models, it was not identified as a significant effect for maximum or exploited depths at night.

These results suggest that differences observed in dive durations between sexes are likely to be due largely to increased physiological capability associated with different body sizes. Swim speed and body mass have previously been reported to be positively correlated with dive durations in female southern elephant seals from Macquarie Island (Hindell et al. 2000). Similarly, a positive relationship between body mass and dive durations was reported for underyearling southern elephant seals from the same population (Irvine et al. 2000).

However, body size (standard length) did not appear to drive differences observed between sexes in maximum and exploited dive depths. While sex significantly influenced both these parameters for daytime dives, it was identified as consistently affecting maximum and exploited dive depths during day- and night-time dives. This suggests that male and female southern elephant seals target different depth layers and their associated resources owing to differences in foraging strategy, and that dive depths are not merely a by-product of body size and their associated physiological capacity.

We used standard length as a proxy measurement for body size. While such a measurement was not sufficient to estimate body condition in the study animals, it was considered likely to provide an overall indication of physiological capability over an extended timescale. Body condition in southern elephant seals is known to vary substantially during their foraging migrations and over seasonal timescales (Bennet et al. 2001, Biuw et al. 2007). Such changes in body condition can be expected to directly influence dive performance owing to changes in buoyancy associated with blubber gain and loss. Other seasonal influences on dive performance have been suggested, including reproductive condition of females, seasonal fluctuations in basal metabolic rate, seasonal alterations in oxygen affinity of haemoglobin and myoglobin, increases in muscle oxygen storage capacity, increases in physical fitness, and seasonal changes in prey type (Bennet et al. 2001). Such factors are likely to have resulted in the large variances in dive parameters reported here and require further investigation. Furthermore, differences in metabolic requirements between males and females of similar ages (non-breeding males provisioning for growth and females for breeding) (Field et al. 2005a) were likely to have resulted in different body conditions and dive performance between sexes.

Influence of age

Dietary shifts associated with age have previously been described for juvenile and sub-adult southern elephant seals (Field et al. 2007b, Bailleul et al. 2010). We therefore expected age to exhibit significant influences on maximum and exploited dive depths. Surprisingly, age was only identified as being a statistically significant fixed effect in one of the models selected (DD_{NIGHT}), though it was always included as a contributing effect in the model structures. Since we selected the sample of animals to obtain a sufficient overlap in standard lengths between sexes, the study was limited to individuals of ages between 2 yr 6 mo and 8 yr 4 mo. We therefore did not include any dive data from underyearlings or yearlings — ages at which dietary changes associated with increased dive capacity would perhaps be most evident. Indeed, stable isotope ratios indicate that young males from the Kerguelen Islands show an increase in foraging trophic level from approximately 3 to 4 yr of age (Bailleul et al. 2010). The exclusion of very young and older adult animals (this study) probably also resulted in the lack of correlation between age and standard length in our study sample.

Individual variation in dive behaviour

Individual variation explained large proportions of the total variance in many of the final models selected in this study (11.1 to 39%). The influence of individual variation declined in all models after inclusion of the autoregressive correlation functions. Individual track variation explained more of the model variance for all daytime dive behaviour models than for night-time models. Slight increases in variation were evident in most night-time dive behaviour parameters, when compared to daytime dive behaviour (Figs. 3, 5 & 6), though this variation did not appear sufficient to clarify the differences in variance explained by individual tracks between day- and night-time dives.

Individual variation potentially plays a significant role in the behaviour of various animal taxa (Bolnick et al. 2003) and has previously been reported in dive behaviour of southern elephant seals (Field et al. 2001) and other pinnipeds (Staniland et al. 2004, Chilvers & Wilkinson 2009, Kuhn et al. 2009). Individual variation has often been ascribed to the influence of dive localities and the associated bathymetry and prey distribution on an individual's behaviour. Our results did not provide support for any particular explanation for the influence of individual variation in our sample. However, while we acknowledge the likely influence of localised conditions and prey distribution on the dive behaviour of individuals, some differences in individual strategy appear to be evident (T. McIntyre unpubl. data).

The smaller amount of variation explained by the effect of individual for night-time dive parameters suggests that southern elephant seals perhaps use less specialised strategies for night-time foraging purposes. This, in turn, could be the result of prey resources displaying less patchy distributions at night and concentrating their activity in shallower water layers (Collins & Rodhouse 2006, Collins et al. 2008).

Diel variation and diet

Southern elephant seals prey largely on squid and myctophid fishes (Bradshaw et al. 2003, van den Hoff et al. 2003), though substantial inter-population and seasonal differences in diet have been documented (Bradshaw et al. 2003, Cherel et al. 2008). Comparatively little is known about the diet of southern elephant seals hauled out at Marion Island. Diel variation in all dive parameters measured was evident in the sample of tracks investigated. Males and females dive to deeper depths for longer periods of time during daytime dives than during night-time dives (Figs. 3, 5 & 6). Such variation suggests that both male and female southern elephant seals target vertically migrating, pelagic prey species (Hindell et al. 1991, Jonker & Bester 1994, Bost et al. 2002), though males evidently target prey occurring at deeper depths than do females (Fig. 3). Dive depths were rarely constrained by estimated bottom depths, and few benthic dives were recorded in our sample. This is not surprising, given the deep water immediately surrounding Marion Island, and that seals from this population evidently do not often target large areas of shallow bathymetry (e.g. continental shelves). Our results differ from those reported for other populations, notably Peninsula Valdés (Campagna et al. 1999), Kerguelen Islands (Bailleul et al. 2007, Bailleul et al. 2010) and Macquarie Island (Hindell et al. 1991), where males often forage benthically over continental and oceanic shelves. The different foraging strategy reported here for males from Marion Island highlights the evident foraging plasticity between populations of this species.

Resource selection and partitioning

The avoidance of intra-specific competition between sexes, as well as age-classes, has previously been proposed to drive resource partitioning in southern elephant seals (Lewis et al. 2006, Field et al. 2007a, Newland et al. 2009). While elephant seals from other populations segregate spatially between the sexes (Slip et al. 1994, Campagna et al. 1995, Campagna et al. 1999, Bornemann et al. 2000, Tosh et al. 2009, Bailleul et al. 2010), animals from Marion Island appear to largely segregate between the sexes by targeting different water depths in oceanic habitats.

Our results suggest that both sex and body length play important roles in the dive behaviour of southern elephant seals from Marion Island. Segregation between the sexes was evident in the vertical depth layers targeted by animals of either sex — males diving deeper than females and also evidently exploiting increased depths. The dive depths obtained and targeted by animals were evidently not constrained by physiological capacity (associated with body size), but rather selected by the individual animals. This provides support for a hypothesis that segregation in dive depths of southern elephant seals is largely driven by forage selection and an associated avoidance of intra-specific competition.

The comparative lack of influence that sex exhibited on dive durations in this investigation further indicated that the physical size of animals did not govern the depths utilised, but rather the amount of time seals were able to spend at targeted depths. This result supports previous investigations that highlighted a positive correlation between body size and maximum dive durations (Hindell et al. 2000, Irvine et al. 2000).

CONCLUSION

We presented results from mixed-effects models to elucidate the effects of sex, age and size on the dive behaviour of a highly sexually dimorphic mammal, the southern elephant seal. While individual variation accounted for substantial portions of variance in the models, differences in maximum and targeted depths were always influenced by sex and only partly influenced by body length. Conversely, dive durations were always influenced by body length, while sex was not identified as a significant influence. These results support previous investigations in which physiological capability associated with size was hypothesised as being a limiting factor on dive durations (Hindell et al. 2000, Irvine et al. 2000). However, our results suggest that sexual segregation in vertical depth use (i.e. maximum and exploited dive depths) by southern elephant seals is largely a result of forage selection and not a result of size differences between sexes. This provides support for resource partitioning between sexes and the potential avoidance of intra-specific competition in this species (Field et al. 2007a). Furthermore, inter-population differences in sexual segregation (i.e. by using different water depths in pelagic habitats or by utilising different spatial foraging habitats) highlight the plasticity in forage strategies of southern elephant seal populations.

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