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The diving behaviour of adult southern elephant seal, *Mirounga leonina*, cows from Marion Island

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The diving patterns of eight adult southern elephant seal, Mirounga leonina, cows (seven post-breeding and one post-moulting) from subantarctic Marion Island were recorded during the pelagic phase of their annual cycle, using geolocating time-depth recorders attached to the seals. A total of 28 948 dives have been categorised into seven distinct types representing transit, exploratory and foraging dives. No benthic foraging dives were recorded and all but one cow showed a marked diel variation in dive depth, dives being deeper during the day (by 30 to 300 m) than during the night. Mean (\pm SE) dive depth ranged from 406 ± 157 m to 585 ± 226 m and mean dive duration from 19.08 ± 5.77 min to 33.41 ± 14.62 min, the deepest and longest dives being 1 444 m and 113 min respectively. Dive depth and duration were positively correlated and unimodal in their frequency distribution, and two cows had secondary modes at 800 to 900 m and 40 to 44 min respectively. Post-dive surface intervals ranged from 2.03 ± 1.64 min to 4.99 ± 53.34 min between individuals and were unrelated to dive depths and durations of previous dives, as were extended surface intervals (>10 min) which were more frequent at night than during the day. Extended surface intervals were also more common during long journeys at sea and were probably associated with successful foraging. The frequency of occurrence and the bottom times of foraging dives varied with the season, the highest frequency of occurrence and longest bottom times being recorded during the post-moulting (winter) period. It is postulated that the seasonal and individual variation in the diving behaviour of the southern elephant seal cows are related to their geographic locations and the abundance and behaviour of their prey.

Die duikgedrag van agt volwasse (sewe ná teling en een ná verharing) suidelike olifantrobkoeie, Mirounga leonina, van subantarktiese Marion-eiland is gedurende die pelagiese fase van hul jaarlikse siklus opgeneem deur die gebruik van geolokasie-tyddieptemeters wat aan die robbe vasgeheg is. 'n Totaal van 28 948 duike is in sewe duiktipes onderverdeel, wat deurtog-, verkennings- en voedingsduike verteenwoordig. Geen bodemvoedingsduike is aangeteken nie en al die koeie,

met die uitsondering van een, het 'n beduidende verskeidenheid in duikdiepte oor 24-uur tydperke vertoon, met die duike dieper gedurende die dag (tussen 30 tot 300 m) en vlakker gedurende die nag. Die gemiddelde (\pm SF) duikdiepte strek van 406 ± 157 m tot 585 ± 226 m en duur gemiddeld 19.08 ± 5.77 min tot 33.41 ± 14.62 min. Die diepste en langste duike was onderskeidelik 1 444 m en 113 min. Daar was 'n positiewe verband tussen duikdiepte en duurte en die frekwensieverdelings was enkel-modus, terwyl twee koeie sekondêre modusse by onderskeidelik 800 tot 900 m en 40 tot 44 min gehad het. Na-duikse verposings aan die oppervlakte het van 2.03 ± 1.64 tot 4.99 ± 53.34 min tussen individue gewissel en het nie verband gehou met duikdieptes en duurtes van voorafgaande duike nie, soos ook in die geval van lang verposings (>10 min) aan die oppervlakte wat meer in die nag as in die dag voorgekom het. Verlengde verposings aan die oppervlakte het ook meer gedurende lang seereise voorgekom en kan met suksesvolle voeding verband hou. Die frekwensie van voorkoms en die bodemtye van voedingsduike het met die seisoene verander. Die hoogste frekwensie van voorkoms en langste bodemtye is gedurende die na-verharingstydperk (winter) aangeteken. Daar word bespiegel dat die seisoenale en individuele veranderlikheid in die duikgedrag van die suidelike olifantrobkoeie verband hou met hul geografiese verspreiding en die volopheid en gedrag van hul prooi.

Introduction

Southern elephant seals breed and moult on Marion Island during the austral spring and summer (Condy 1978). Breeding elephant seals are ashore from August to November and after a few months at sea (the post-breeding period), they return for the moult haulout that peaks in January and February for cows and bulls respectively. In individuals the period of moult lasts approximately 30 days. From May to August elephant seals are presumably feeding at sea (the post-moulting period) because few occur on the island (Condy 1979).

The population of southern elephant seals at Marion

Island is declining at a rate of 4.8% per annum (Bester & Wilkinson 1994). Moreover, elephant seal cows from Marion Island mate at an early age, reproduce at the maximum rate, but are not living long enough to maintain the population (Bester & Wilkinson 1994). Furthermore, most of our knowledge of the behaviour of the southern elephant seal has been focused onshore (Laws 1956; Carrick *et al* 1962; Condy 1978, 1979; Hindell & Burton 1988), but 70% to 80% of the individual's time is spent at sea (Condy 1979; Hindell *et al* 1991a). Given current knowledge of the terrestrial component of the life cycle at Marion Island, factors affecting these animals during the pelagic phase of the annual cycle may explain the population decline (Bester & Wilkinson 1994).

Studies on local and long-range movements of southern elephant seals from Marion Island have relied exclusively on resightings of tagged animals (Panagis 1981; Bester 1989; Wilkinson & Bester 1990). Recent developments of instrumentation have allowed studies on the behaviour of northern (Le Boeuf *et al* 1986, 1988; Naito *et al* 1989; DeLong & Stewart 1991) and southern elephant seals (Boyd & Arnborn 1991; Hindell *et al* 1991a & b, 1992; McConnell *et al* 1992), including those at Marion Island (Bester & Pansegrouw 1992). Since the distribution of prey in space and time may have an influence on especially the feeding behaviour of southern elephant seals, information obtained through the use of recorders in monitoring behavioural activities can improve knowledge of their diving patterns and abilities. This can ultimately only be meaningfully interpreted together with data on prey distribution and abundance (Croxall *et al* 1985), but it is conceivable that knowledge of the diving and ranging behaviour of southern elephant seals, and by inference, their diet, might contribute towards understanding why the elephant seal population is declining at Marion Island.

The present paper classifies and characterises dives performed by southern elephant seal cows from Marion Island as the basis of a study of the temporal and spatial variation of the behaviour of individuals at sea, and its relationship with potential prey distributions.

Methods

Recording of data

Diving and ranging behaviour of post-breeding ($n=7$) and post-moulting ($n=1$) southern elephant seal cows were studied using microprocessor-controlled geolocation time-depth recorders (GLTDRs, Wildlife Computers) deployed at Marion Island (46°54'S, 37°45'E) during 1990-93. Individuals were immobilised through intramuscular injections of a mixture of ketamine hydrochloride and xylazine hydrochloride (Bester 1988a). The recorders were deployed on tagged, adult cows ($n=16$) between four to eight years of age, which

had shown fidelity to Marion Island during previous breeding and/or moulting haulouts. Eleven cows returned to the island with their recorders in place. Nine recorders were recovered, one of which malfunctioned, and circumstances prevented two recorders from being retrieved.

The attachment of recorders was by quick-setting epoxy resin adhesive (Araldite AW 2101/HW 2951, Ciba-Geigy) following Bester & Pansegrouw (1992). The recorders were programmed to measure depth using a two-stage pressure transducer (0 to 500 m, sampled every 30 s and accurate to within 2 m; 500 to 1500 m, sampled every 60 s and accurate to within 6 m) and sea-surface light intensity, and the readings were stored in an electronic memory. Functional GLTDR models Mk3+ (256 kbytes of memory) and Mk3e (512 kbytes of memory) were retrieved from six and two cows respectively. Duty-cycling (one day on, one day off) was employed in the case of the post-moulting cow to allow coverage of most of the journey from and to the island before the memory (256 kbytes) was filled.

Dive analysis

The Dive Analysis (ver. 2.0) software programme of Wildlife Computers was used to measure the following parameters for each individual dive:

- dive depth (m): the maximum depth reached during a dive;
- dive duration (min): elapsed time between submergence and resurfacing;
- bottom time (min): the amount of time spent at the bottom of a dive between descent and ascent;
- rate of descent (m/s): the depth at the start of bottom time of a dive/time elapsed to reach that depth from the surface;
- rate of ascent (m/s): the depth at the end of bottom time of a dive/time elapsed to reach the surface;
- post-dive surface interval (min): the amount of time spent at the surface following a dive.

These data were converted into graphical representations of each dive. Each dive made by a seal was categorised based on the dive configuration as determined by depth, duration, descent/ascent rates, amount of time spent at the bottom of the dive, and the presence of wiggles (up and down movements) during the dive, following Le Boeuf *et al* (1988).

The duration and depth of dives, and the duration of the surface intervals preceding dives, were measured by the Dive Analysis programme. Lack of recognition of surface intervals, which would lead to the concatenation of dives and a decline in the total number of dives recorded, was unlikely at the selected sampling frequencies (30 s intervals - *vide* Boyd 1993). Bottom time was user-selected, and the mean rates of descent and ascent were calculated automatically from the beginning and the end of each dive to the beginning

Table 1

Summary statistics from the diving records of eight southern elephant seal cows from Marion Island.

Cows	Age	Recording duration (days)	Total number of dives	Mean dive depth (m)	Maximum dive depth (m)	Mean dive duration (min)	Maximum dive duration (min)	Mean descent rate (m/s)
R101	4	58 (*77)	3770	445 (147)	1000	20.10 (5.20)	59	1.98 (0.36)
R357	5	53	2688	406 (157)	1204	23.53 (7.40)	76	1.47 (0.32)
P537	5	64 (*66)	3621	457 (194)	1284	24.31 (8.60)	66	1.79 (0.42)
Y333	6	51	2539	562 (169)	1444	27.28 (8.48)	76	1.68 (0.23)
R202	6	86	5096	476 (171)	1066	19.08 (5.77)	51	2.02 (0.44)
O138	7	58 (*67)	3419	585 (226)	1096	23.62 (5.76)	49	2.25 (0.39)
O390	7	53 (*67)	3334	531 (155)	1114	24.22 (5.56)	49	1.80 (0.40)
O144	8	112 (*239)	4481	487 (194)	1190	33.41 (14.62)	113	1.53 (1.75)
Cows	Maximum descent rate (m/s)	Mean ascent rate (m/s)	Maximum ascent rate (m/s)	Mean surface interval (min)	Maximum surface interval (min)	Mean bottom time (min)	Maximum bottom time (min)	
R101	2.8	-1.75 (0.26)	-3.2	2.03 (1.64)	205	8.55 (5.12)	24	
R357	2.8	-1.44 (0.32)	-2.1	4.99 (53.34)	55	9.96 (5.36)	45	
P537	3.2	-1.74 (0.45)	-3.2	4.46 (3.61)	29	24.27 (8.64)	66	
Y333	2.8	-1.33 (0.22)	-2.3	3.48 (0.51)	4	9.82 (18.65)	34	
R202	3.3	-1.64 (0.26)	-2.6	2.18 (7.52)	110	19.08 (5.77)	51	
O138	3.2	-1.81 (0.22)	-2.6	2.53 (22.18)	62	9.61 (5.43)	28	
O390	3.8	-1.53 (0.23)	-1.9	2.55 (22.18)	100	9.60 (4.74)	27	
O144	3.2	-1.23 (0.31)	-3.3	3.41 (3.52)	113	19.78 (12.83)	98	

() - standard deviation
(*) - total days at sea

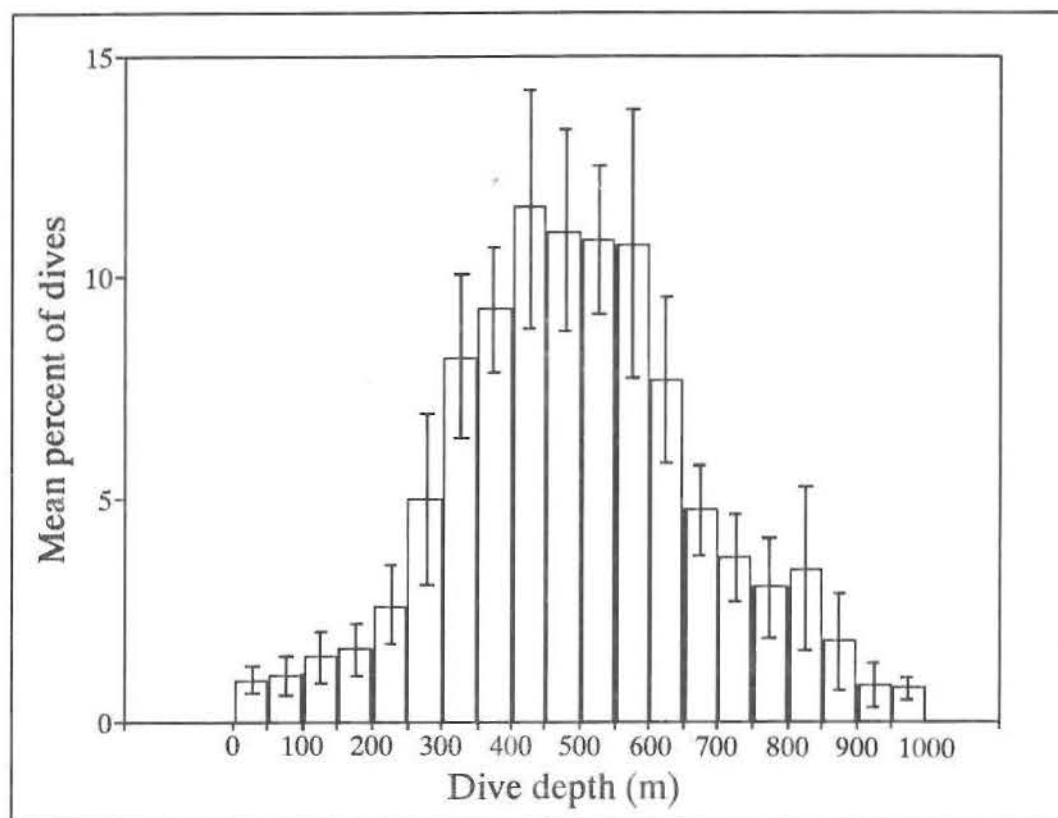


Fig 1a: Frequency distribution of dive depth (50 m increments) for eight southern elephant seal cows (error bars are standard errors of the mean)

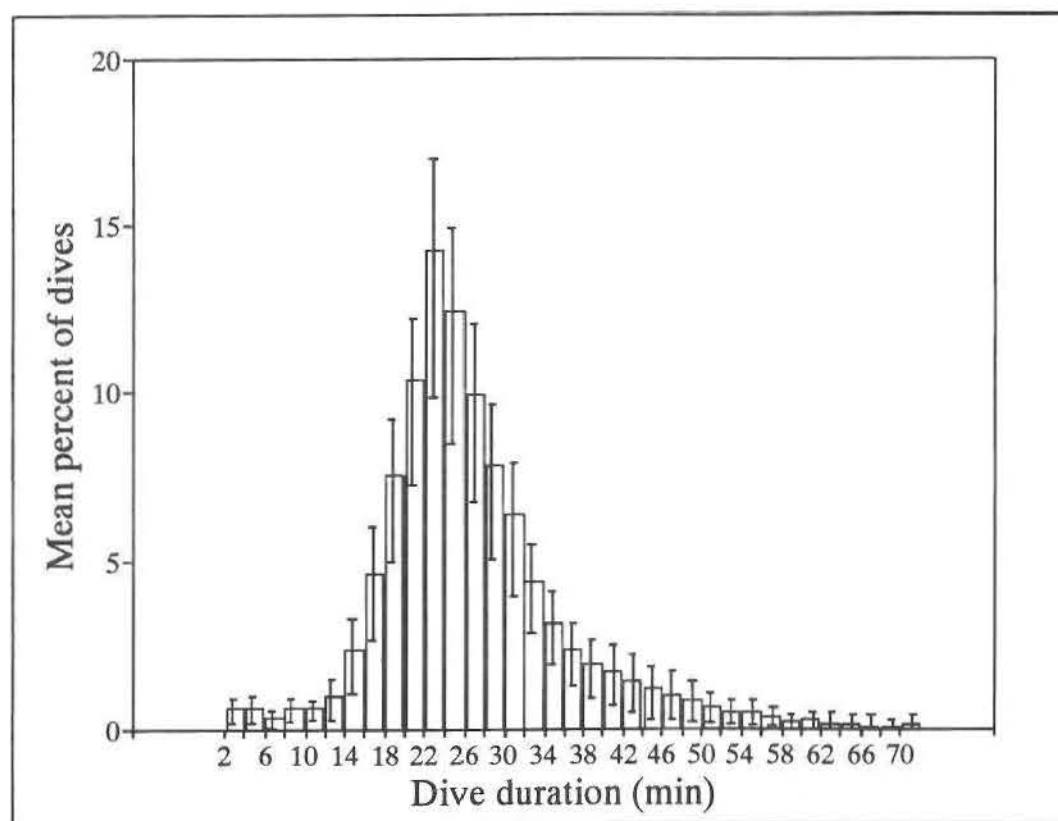


Fig 1b: Frequency distribution of dive durations (2 min increments) for eight southern elephant seal cows (error bars are standard errors of the mean)

and end of the user-selected bottom time respectively. No further alterations were needed on dive parameters. The dive parameters were stored in a statistical file following categorisation. The extended surface intervals (ESIs) were defined as surface intervals longer than ten minutes (Le Boeuf *et al* 1988). Time spent hauled out was defined as the period when the recorder was dry. Diel changes in individual dive patterns were calculated during the first 40 days of the diving record for all seals. This was done to allow direct comparison amongst all individuals since the memory of the GLTDRs was filled for seals R101, P537, O138, O390 and O144 while still at sea (Table 1). The Geolocation Analysis software package (ver. 1.0) was used to calculate the locations of the seals on a daily basis from light level data and therefore the times of dusk and dawn (Bester & Pansegrouw 1992; Hill 1994).

Statistical procedures

All statistical analyses were performed using the SAS statistical package (SAS Institute Inc 1982) and Statgraphics (ver. 2.0). Two-sample analysis (t-tests) was used to test the significance of differences in dive parameter means between different dive types (Le Boeuf *et al* 1988). A one-way analysis of variance (ANOVA) with a Tukey multiple-range test (Sokal & Rohlf 1981) was used to examine differences between dive parameters of individuals (Bengtson & Stewart 1992). The

analysis of covariance (ANCOVA) was used to test for differences in the slopes of regression lines correlating dive depth and dive duration for each cow (Hindell *et al* 1992), and the Komolgorov-Smirnov two-sample test (Conover 1980) compared the depth, duration and surface interval distributions of cows (*vide* DeLong & Stewart 1991). The 0.05 level of probability was considered significant in the statistical procedures. Sample means (\bar{x}) are expressed with their standard deviations (SD) as summary statistics for all dives of each seal, whereas standard errors (SE) were used when combining data for all individuals. Unless stated otherwise all dives in the diving record of each seal were used in the analyses following Le Boeuf *et al* (1988). Chi-square (χ^2) analysis was used to test for differences in ratios of frequency of occurrence of dive types using the original data.

Results

All seals began diving as soon as they entered the water and dived virtually continuously throughout the recording period, which lasted between 51 and 86 days for the post-breeding cows ($\bar{x} = 66.7 \pm 12.33$; $n = 7$) and 239 days for the post-moulting cow (Table 1).

The deepest recorded dive was 1 444 m, whereas mean dive depths of all seals ranged between 406 m and

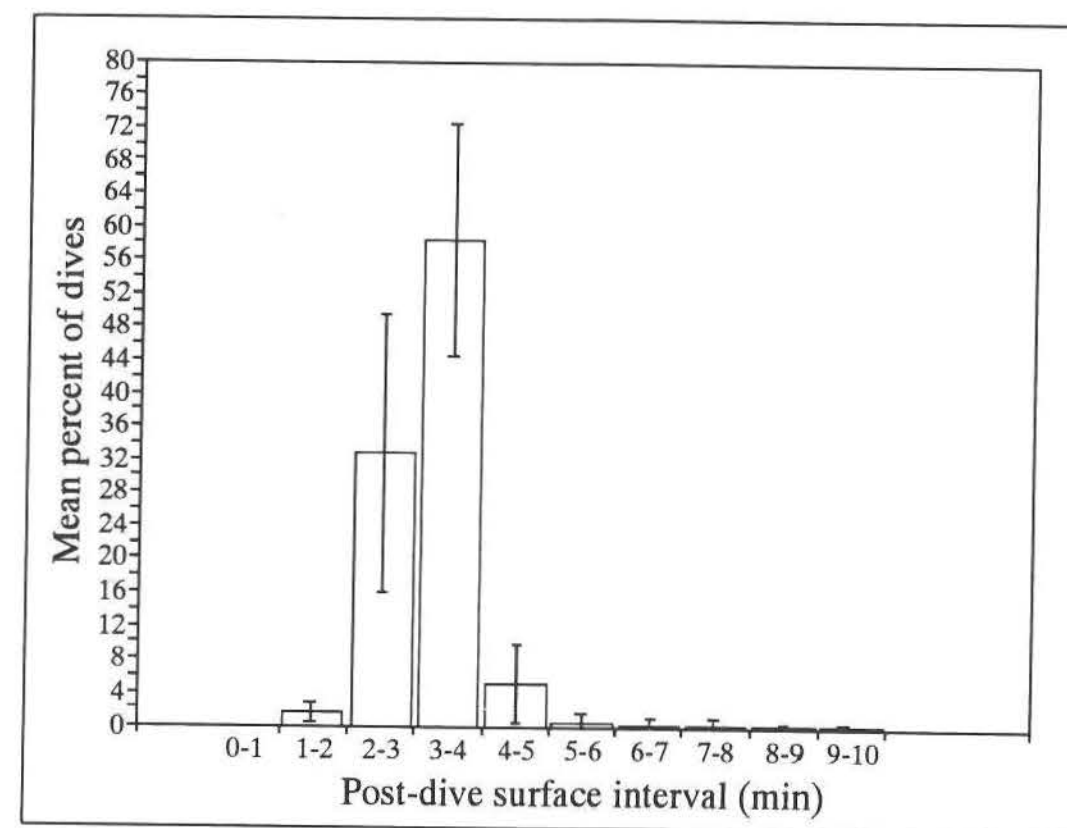


Fig 1c: Frequency distribution of post-dive surface intervals for eight southern elephant seal cows (error bars are standard errors of the mean)

585 m (Table 1). Dives deeper than 800 m and shallower than 200 m contributed < 10% of all dives recorded (Figure 1a). A maximum dive duration of 113 min was recorded with the mean dive durations of all seals ranging between 19 min and 33 min (Table 1). Dives shorter than 16 min and longer than 32 min occurred in < 20% of dives recorded (Fig 1b). Approximately 58% of post-dive surface intervals ranged between 3 to 4 min, whereas 32% of post-dive surface intervals lasted for 2 to 3 min (Fig 1c). Surface intervals shorter than 2 min and longer than 4 min constituted < 13% of recorded surface intervals.

A total of 28 948 dives were recorded for all eight cows. On departure from the island all seals started diving to shallow depths, which progressively became deeper, then returning to shallow dives as the elephant seal cows finally approached the island again.

Classification and characterisation of dives

Seven dive types were identified (Figure 2):

Type 1 dives

These dives are 'spiked', shallow (mean depth of 34 ± 24 m), of short duration (1 ± 1.6 min) and accounted for 0.46% of all dives recorded (Table 2). The descent and ascent rates are relatively slow and identical (Table 2). The mean bottom time of dive type 1 was 0.16 min (Table 2) constituting 14% of the total mean dive duration, whereas the mean descent and ascent duration each constituted the remaining 86%. Type 1 dives only occurred in the first and the last week (for those cows with complete diving records) of the period at sea.

Type 2 dives

Table 2

Summary statistics of the seven dive types that appeared in the diving records of eight southern elephant seal cows.

Dive types	Mean depth (m)	Mean duration (min)	Mean descent rate (m/s)	Mean ascent rate (m/s)	Mean bottom time (min)	Mean descent & ascent durations, combined (min)	Frequency of occurrence (%)
1	34 (8.48)	1.01 (0.57)	1.36 (0.14)	-1.32 (0.11)	0.16 (0.47)	0.85	0.46
2	95 (5.65)	5.95 (0.47)	1.15 (0.07)	-1.17 (0.12)	2.58 (0.44)	3.37	0.33
3	458 (16.61)	24.30 (0.86)	0.94 (0.04)	-1.26 (0.01)	2.24 (0.20)	22.06	8.43
4	455 (12.72)	21.00 (1.35)	2.17 (0.62)	-0.97 (0.03)	2.93 (0.24)	18.07	5.18
5	592 (14.14)	21.62 (0.78)	1.39 (0.01)	-1.26 (0.01)	4.46 (0.13)	17.16	12.26
6	567 (8.83)	26.46 (1.12)	1.23 (0.02)	-1.15 (0.02)	2.70 (0.44)	23.76	6.62
7	494 (10.96)	25.11 (1.00)	1.62 (0.13)	-1.40 (0.01)	13.50 (0.96)	11.61	66.49

() - standard error

These dives were relatively shallow and similar in depth to type 1 dives ($t = 2.32$, $df = 119$, $P > 0.05$). The mean dive duration was 4.9 min longer than that of type 1 dives. In type 2 dives the descent and ascent rates were identical, but slower than type 1 dives by 0.18 m/s. There was a significant increase in mean bottom times by 2.4 min over type 1 dives ($t = 6.47$, $df = 327$, $P < 0.001$), with a concomitant increase in the percentage time spent at the bottom of a dive from 15.8% in type 1 dives to over 43.3% in type 2 dives. Type 2 dives represented 0.33% of all recorded dives, and occurred predominantly during the first and last week of the journey but were also found infrequently amongst other dive types during other stages of the period at sea.

Type 3 dives

These dives were on average deeper (516 ± 97 m) by 393 m ($t = 11.05$, $df = 20$, $P < 0.001$) and 20 min longer (25.1 ± 3.61 min) than types 1 and 2 dives. The ascent rates were also significantly faster ($t = 64.5$, $df = 460$, $P < 0.001$) by 0.32 m/s, and of longer duration (4.12 min) than the descents (Table 2). The mean bottom time of 2.2 min constituted 9.2% of the mean dive duration of 24.3 min and the descent and ascent contributed the remaining 90.8%. The occurrence of dive type 3 increased to over 8% compared to type 1 and 2 dives which represented less than 0.5% of all dives (Table 2).

Type 4 dives

At a mean depth of 455 ± 36.9 m these dives were similar to type 3 dives ($t = 1.72$, $df = 3281$, $P > 0.05$), but of shorter duration by 3 min (mean dive duration 21.0 ± 3.83 min) (Table 2). The time spent at the bottom of the dive increased from 9.2% (type 3 dives) to 13.9% of the

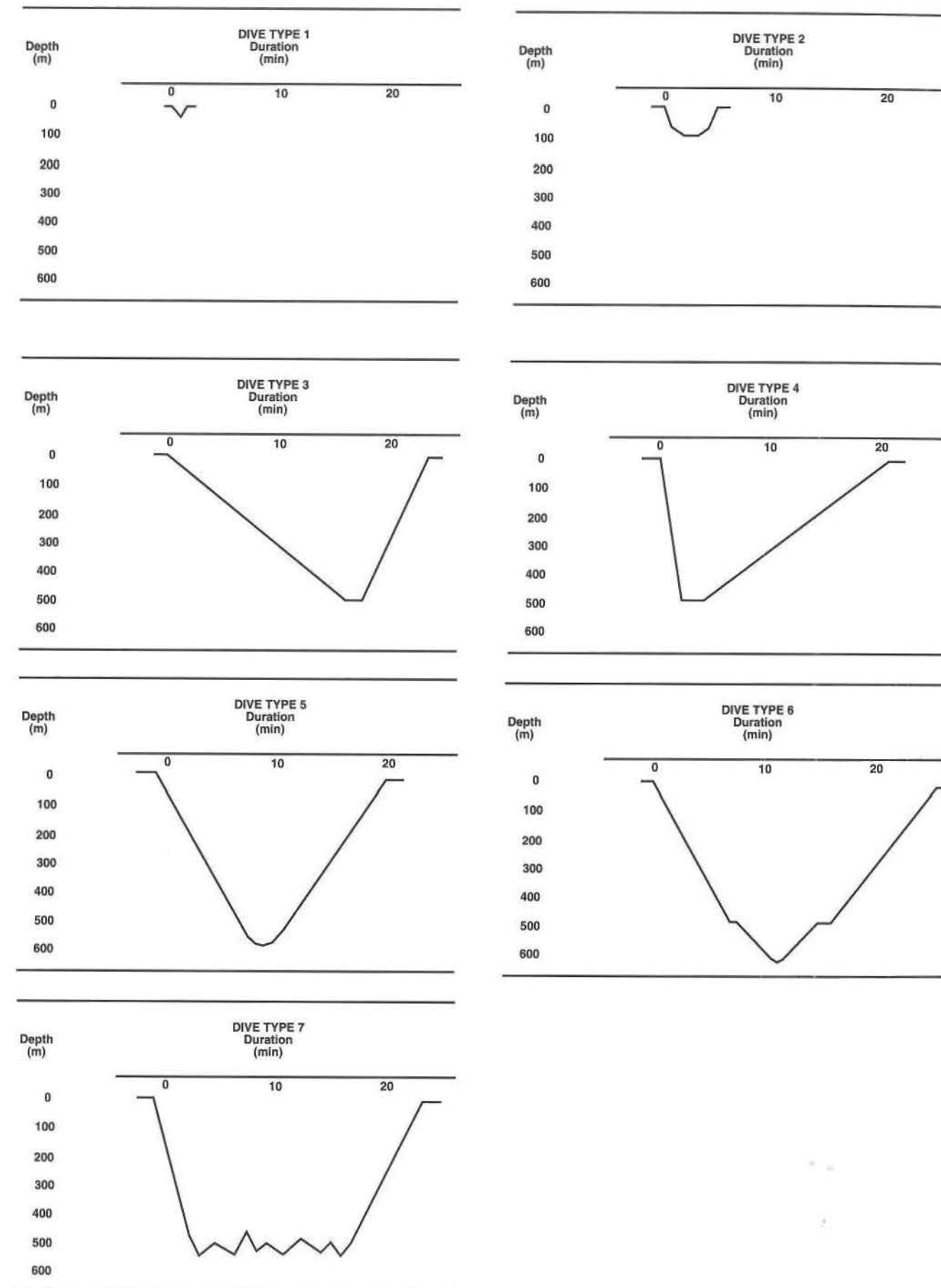


Fig 2: Schematic representation of the seven dive types that appear in the diving record of eight southern elephant seal cows, adjusted for depth and duration

total mean dive duration. Descent rates were significantly faster ($t = 72.4$, $df = 520$, $P < 0.001$) by 1.20 m/s compared to type 3 dives. Type 4 dives contributed 5.18% of all dives in the record.

Type 5 dives

Graphing time over depth produced type 5 dives with distinct slopes of descent and ascent. Mean depths occurred at 592 ± 40 m, with mean durations similar to type 4 dives (Table 2). Dive type 5 was significantly deeper than type 1 and 2 dives ($t > 27.26$, $df > 135$, $P < 0.001$) with no significant difference in depth when compared to dive types 3 to 4 and 6 to 7 ($t < 2.35$, $df < 119$, $P > 0.05$). There was a significant increase in mean descent rates compared to type 3 dives ($t = 12.23$, $df = 38$, $P < 0.001$) with a significant decrease compared to type 4 dives ($t = 3.72$, $df = 38$, $P < 0.001$). Ascent rates were identical to type 3 dives, whereas a significant increase occurred over type 4 dives ($t = 9.93$, $df = 38$, $P < 0.001$). The frequency of occurrence of 12.26% was higher than that recorded for dive types 1 to 4. Maximum dive depth for each cow was attained during a type 5 dive.

Type 6 dives

These dives had profiles similar to type 5 dives, with mean dive depths of 567 ± 25 m and mean dive durations of 26.4 ± 3.17 min, but with significantly ($t = 4.56$, $df = 138$, $P < 0.001$) shorter mean bottom times. At a depth of approximately 400 m the rates of descent and ascent slowed down considerably. The bottom of the dive was spiked owing to a short bottom time and an increase in the rates of descent and ascent before and after reaching the bottom of the dive (Figure 2). The mean descent and ascent rates decreased significantly ($t = 3.83$, $df = 88$, $P < 0.001$) with a significant decrease ($t = 3.47$, $df = 138$, $P < 0.001$) of 10.4% in the percentage bottom time to 2.7 min when compared to type 5 dives. The frequency of occurrence of type 6 dives was 6.62% (Table 2), and this dive type was used throughout the journey, except in the first and last week away from the island.

Type 7 dives

Dive type 7 was characterised by well-demarcated, extended bottom times, the mean bottom time being at least 10 min longer than that recorded for all other dive types, and were significantly ($t = 3.76$, $df = 213$, $P < 0.001$) shallower by 68 m than type 6 dives. Type 7 dives comprised rapid mean descents (1.62 ± 0.38 m/s) and ascents (1.40 ± 0.04 m/s) which together constituted 46% of the total mean duration of 25 min. Mean bottom times of 13.5 ± 2.73 min contributed the remaining 54% of the total mean duration and was significantly different ($t = 18.75$, $df = 236$, $P < 0.001$) from dive type 6, and consequently from all other dive types. These dives occurred the most frequently (66.49%) in the dive record (Table 2), but were rarely used during the first and last week of the journey. Mean bottom time of dive type 7 for cow O144 was significantly longer ($t = 20.06$, $df = 698$, $P < 0.001$) by 10 min than that recorded for the

other cows (Table 1).

Relationships between dive parameters and dive types

There were significant positive correlations ($F = 470$, $P < 0.001$) between dive depths and dive durations amongst individuals when dive types were lumped together. Significant positive correlations existed between dive depths and dive durations for dive types 2 to 7 for 6 of 7 cows ($F = 9$, $P < 0.001$). Dive depths and dive durations for dive type 6 in the remaining cow P537 were not significantly ($F = 2$, $P > 0.05$) correlated. There was a significant positive correlation between dive depths and dive durations in dive type 1 for cow R101 ($F = 49$, $P < 0.001$) but not for cows R357 ($F = 0.1$, $P > 0.05$) and O144 ($F = 2$, $P > 0.05$) for example.

Comparison of diving characteristics amongst individuals

Depth and duration

The relationship between depth and duration of dives differed significantly amongst individuals when comparing the slopes of the regression lines (ANCOVA: $F_{8,2537} = 995.3$, $P < 0.001$). Both diving depth and diving duration were significantly different amongst the majority of individuals ($F = 1130$, $P < 0.001$). Comparing O144 with R202, and P537 with R101 (Table 1), showed significant differences for depth ($F = 4.48$, $P < 0.05$). There was no significant difference when comparing P537 with O390, and R357 with O138 ($F = 0.12$, $P > 0.05$) for duration. Cow O144 however, showed significant longer mean dive durations ($t = 16.82$, $df = 698$, $P < 0.001$) by 12.5 min compared to the remaining cows. The frequency distribution of dive depths did not differ ($T < 0.35$, $n = 20$, $P > 0.05$) amongst individuals (Figure 3), while the frequency distribution for duration differed significantly ($T > 0.62$, $n = 20$, $P < 0.05$) except amongst R357, P537 and Y333 ($P > 0.05$). The frequency histograms for dive depth (Figure 3) and dive duration (Figure 4) were unimodal and matched for each individual, except for cow O144 which was bimodal for duration and unimodal for depth, and for cow O138 which was bimodal for depth and uni-modal for duration.

Post-dive surface intervals

Cows on average spent 20 hours/day submerged, and 3 hours/day at the surface. Most dives in each record were followed by a surface interval of less than 4 min and the mean surface interval ranged from 2.03 to 4.99 min (Table 1). The frequency distributions of surface intervals (including ESIs) were significantly different ($T > 0.8$, $n = 30$, $P < 0.001$) for all eight individuals, but did not differ significantly ($T < 0.7$, $n = 10$, $P > 0.05$) when ESIs were discarded. ESIs averaged one per day for most

cows, with the exception of cows R202, O144 and Y333 (Table 3). Cows R202 and O144 showed up to five consecutive ESIs, separated by single dives, on a single day, with no ESIs recorded for cow Y333. The maximum ESI per record varied from < one to eight hours (Table 3). Similarly, total time per record spent in ESIs ranged from one to 27 hours. The longest sequence of continuous diving without an ESI averaged 1 781 dives, or approximately 30 days of recording. The six-year-old cow, Y333, dived continuously for over 51 days (Table 3). ESIs occurred at all hours, but less frequently (28%) during the day than at night (72%). There was no increase ($t = 0.12$, $df = 36$, $P > 0.05$) in the mean dive durations for dives immediately before and after ESIs for all cows except cow O144 which showed a significant increase ($t = 2.36$, $df = 24$, $P < 0.05$) from 20.8 ± 13.8 to 30.8 ± 15.0 min, both periods being shorter than the mean dive duration (33.4 ± 14.6 minutes). Dives preceding and following ESIs were deep (between 142 and 381 m) for all the cows, and the GLTDRs did not record dry periods during ESIs.

Dive types

The comparison of the ratio of exploratory dives (type 5 and 6 combined, see discussion) with foraging dives (type 7 dives, see discussion), showed that cow Y333 had significantly more exploratory dives ($\chi^2 > 49$, $df = 3$, $P < 0.001$) than the other post-breeding cows, as well as the one post-moulting cow O144 ($\chi^2 = 358.3$, $df = 3$, $P < 0.001$) (Table 4). Comparing cow Y333 (no ESIs and shortest post-breeding period at sea) with cow R202 (most ESIs and longest post-breeding period at sea), both six-year-olds with complete diving records, showed that

the mean bottom time of foraging dives for cow Y333 (Table 5) was significantly longer ($t = 13.16$, $df = 180$, $P < 0.001$) as was the combined duration of the exploratory dives ($t = 10.59$, $df = 190$, $P < 0.001$). The frequency of occurrence of type 7 dives varied between 56% to 84% during periods at sea, and dive types 1 and 2 occurred infrequently (0.1 to 2.3%), followed by dive types 3 to 6 (0.8 to 21.0%) (Table 4).

Diel diving pattern

Depth and duration:

There was a significant difference ($t > 5.75$, $df > 109$, $P < 0.001$) in diving depths for most cows, except cow R357 ($t = 1.86$, $df = 88$, $P > 0.05$), when comparing dives during the four hours around midnight (22h00 to 02h00) with those during midday (10h00 to 14h00) over the first 40 days of the diving record (Figure 5). Deeper dives (500 to 600 m) of longer duration (23 to 40 min) occurred around midday, with shallower dives (300 to 400 m) of shorter duration (15 to 20 min) performed around midnight as exemplified by cow R101 (Figure 6). There were significantly greater ($t = 7.46$, $df = 483$, $P < 0.001$) diel differences (150 to 300 m) in diving depths for cows O138, R101 and O144 compared to cows Y333, O390, R202 and P537 (30 to 90 m) (Figure 5).

Dive types:

The mean hourly frequency of occurrence of the predominant type 7 dive varied between 38% and 97% of all recorded dives throughout the first 40 days of the cows' periods at sea. The frequency of occurrence of dive type 7 remained between 70 to 90% in cow P537 with no clear diel trend (Figure 7a). Cow R101 on the

Table 3

The duration of periods of continuous diving and the frequency of extended surface intervals (ESIs) that appeared in the diving records of eight southern elephant seal cows.

Longest bout of continuous diving			Extended surface intervals				
Cows	Number of dives	Duration (days)	Number ESIs	Mean duration (h)	Maximum duration (h)	Total duration (h)	Maximum ESIs /day
R101*	1445	21	5	1.0 (1.5)	3.4	4.1	1
R357	1124	20	8	0.4 (0.3)	0.8	3.4	1
P537*	1666	29	4	0.3 (0.1)	0.5	1.1	1
Y333	2539	51	0	0.0	0.0	0.0	0
R202	1684	22	26	1.1 (1.7)	8.0	27.4	5
O138*	1512	25	1	1.0 (0.0)	1.0	1.0	1
O390	1781	30	6	0.5 (0.5)	1.6	2.8	1
O144**	407	-	>31	0.6 (0.6)	2.0	18.6	5

() - standard deviation

* - Incomplete diving record for the total days at sea and statistics indicate minimum values

** - Dive record for every second day (half the measuring period)

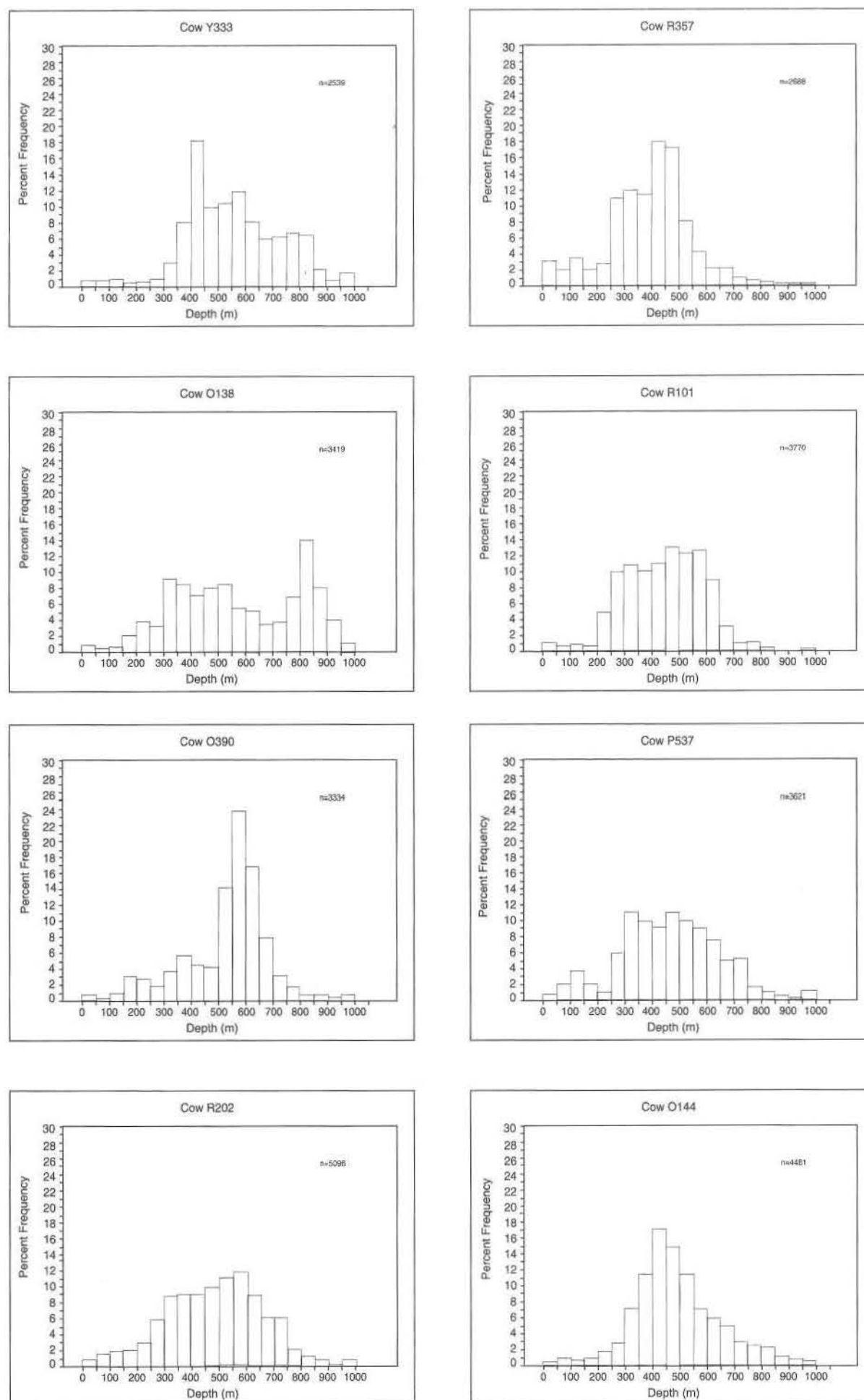


Fig 3: The frequency distributions of dive depth (50 m increments) in eight southern elephant seal cows

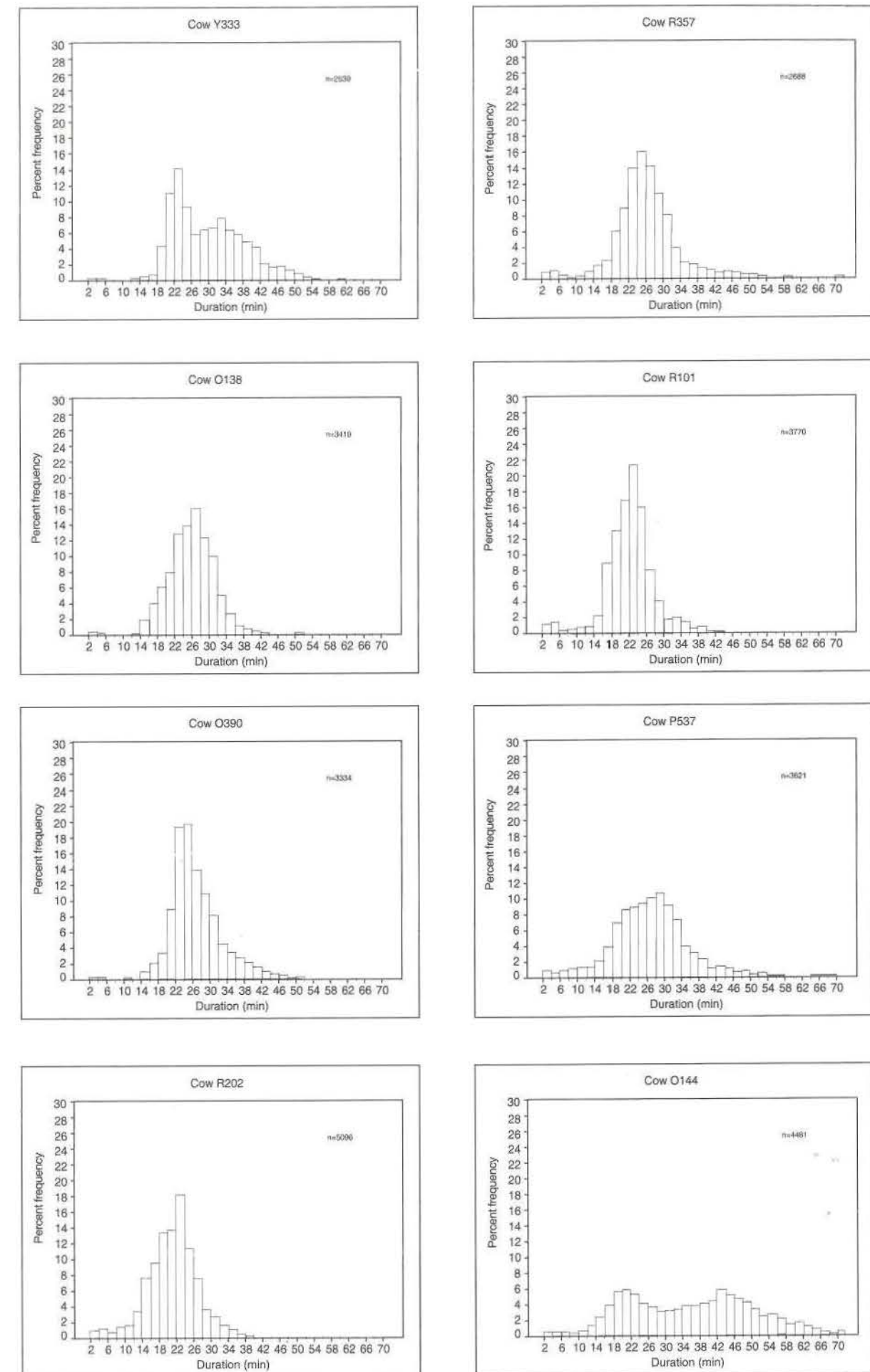


Fig 4: The frequency distributions of dive duration (2 min increments) in eight southern elephant seal cows

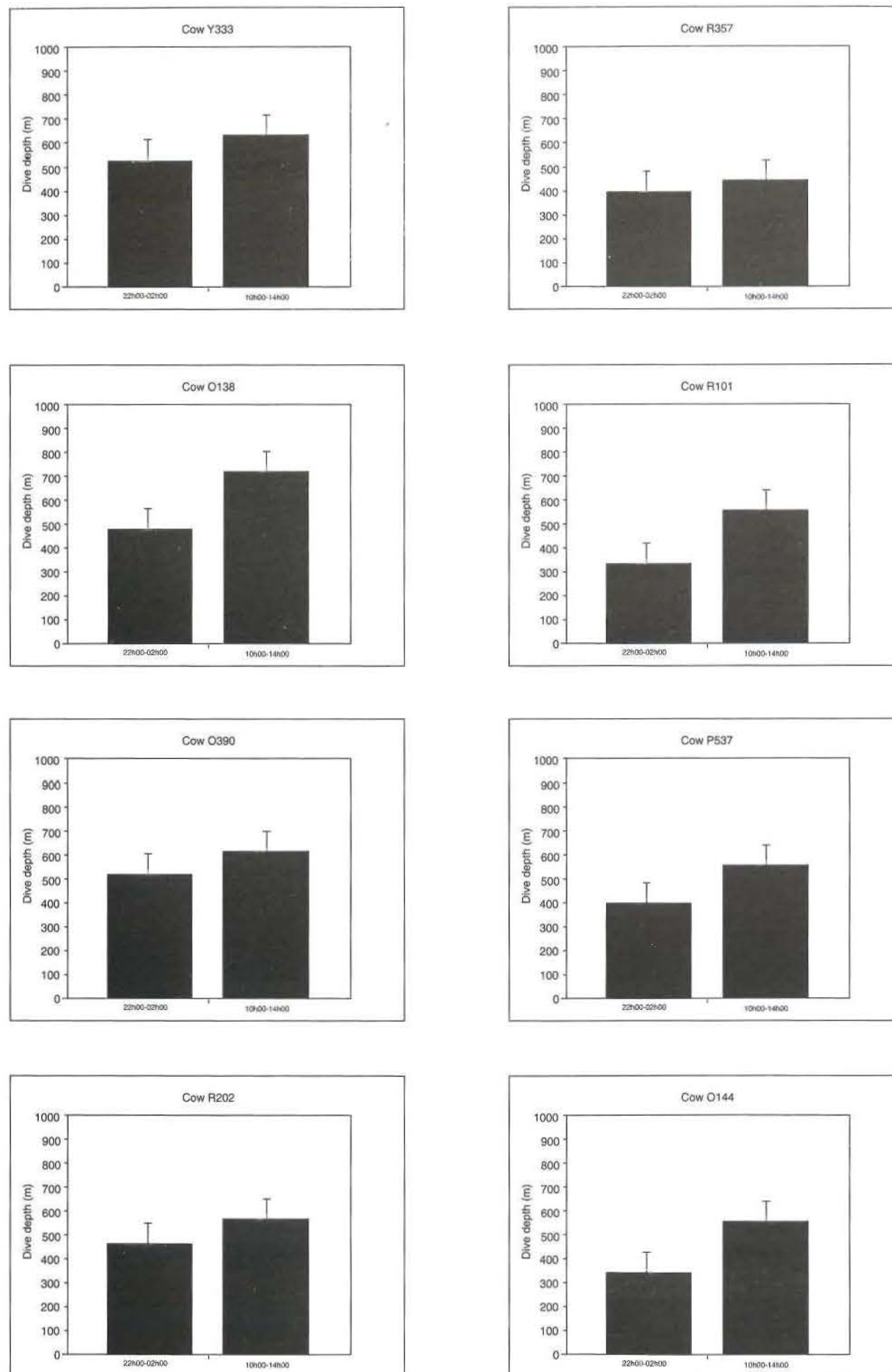


Fig 5: Diel changes in dive depth of foraging dives (dive type 7) in eight southern elephant seal cows (error bars are standard errors of the mean)

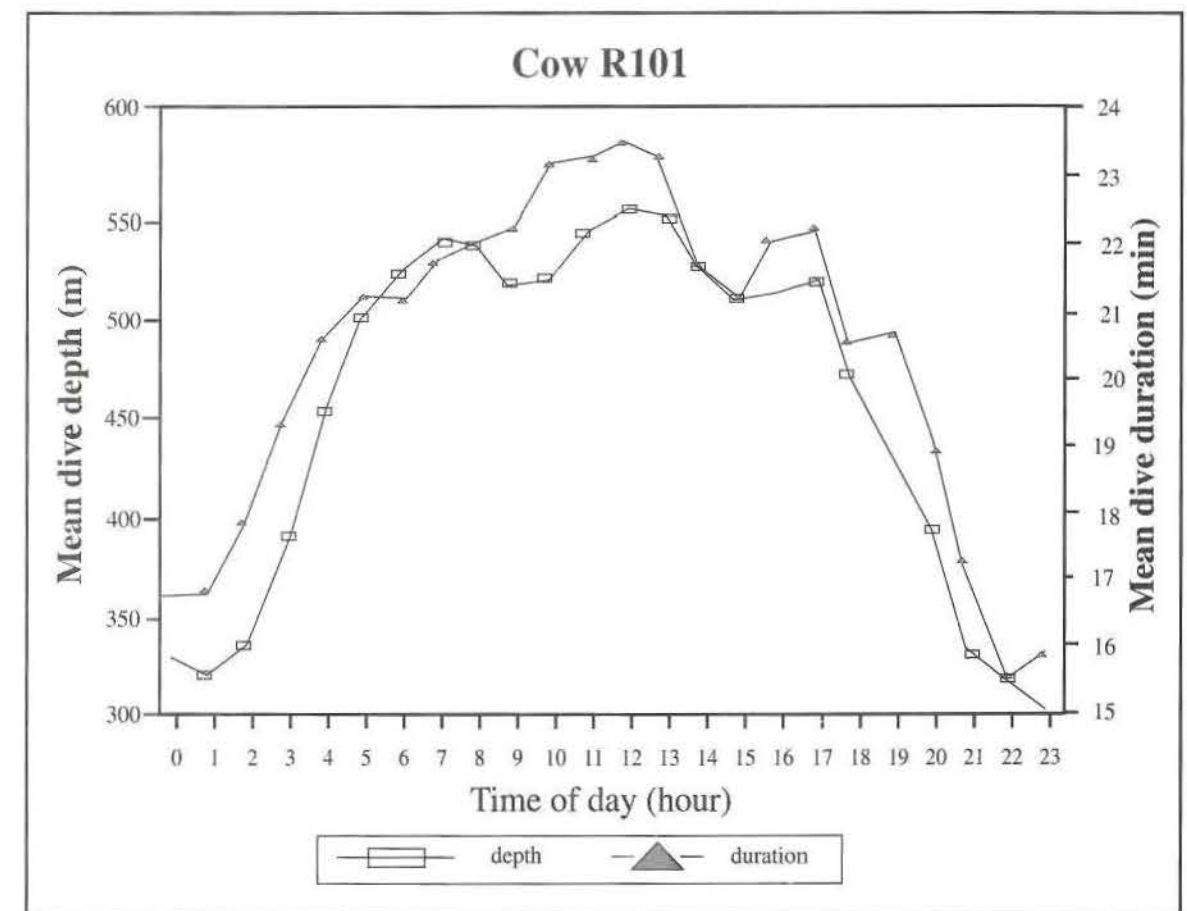


Fig 6: The diel change in dive depth and dive duration shown by cow R101 over the first 40 days of the diving record

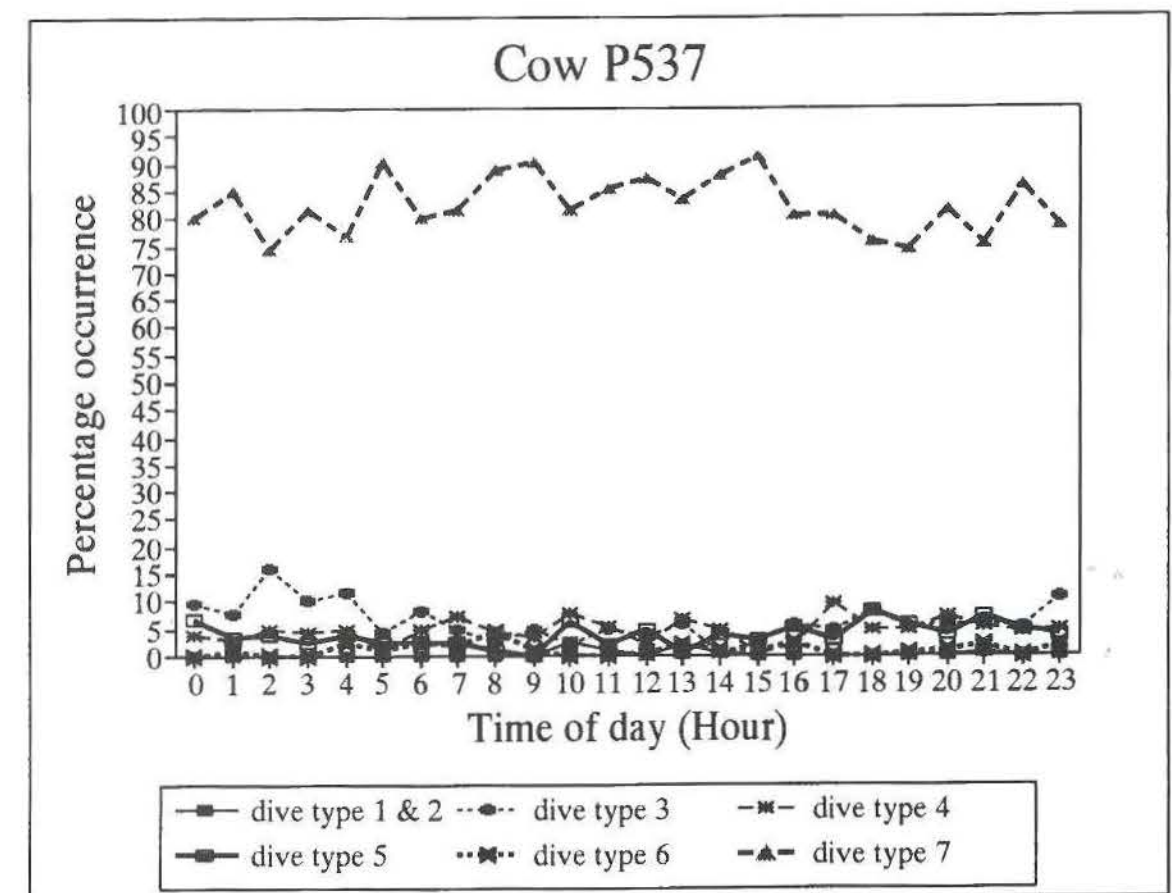


Fig 7a: The diel relationship between dive types that appears in the first 40 days of the diving record of cow P537

Table 4

Percentage frequency of occurrence of the different dive types in the diving records of eight southern elephant seal cows.

Dive type	Cows							
	R101	R357	P537	Y333	R202	O138	O390	O144
1	0.53	0.95	0.20	0.15	0.13	0.24	0.18	0.58
2	0.10	1.11	2.33	0.23	2.09	0.24	0.24	2.28
3	12.47	9.35	6.87	7.62	10.49	8.19	5.12	4.89
4	5.26	5.43	4.81	7.62	8.67	2.54	3.64	2.01
5	12.31	9.67	3.29	20.75	6.25	6.25	12.59	3.58
6	4.89	5.75	0.75	7.38	5.31	10.31	6.04	2.73
7	64.44	67.74	81.75	56.25	67.06	72.23	72.19	83.93

other hand showed a distinct inverse relationship between type 7 and type 3 dives, type 7 dives reaching a low during daylight hours (Figure 7b), when cow Y333, in contrast, reached its peak in the frequency of type 7 dives (Figure 7c). Cow Y333 furthermore exhibited an inverse relationship between type 5 and type 7 dives, the latter reaching a low around 22h00 GMT (\pm 00h30 LAT at Marion Island).

Discussion

The near continuous deep (mean = 475 m), prolonged (mean = 23.2 min) dives of the seven post-breeding southern elephant seal cows from Marion Island, with very short mean surface intervals (3.2 min) between dives, were characteristic of post-breeding cows (n = 5) at Macquarie Island (439 m, 21.1 min) and considerably deeper and longer than that recorded for eight post-breeding northern elephant seal cows (400 m, 19.2 min) at Año Nuevo (Le Boeuf *et al* 1988; Hindell *et al* 1991b). Comparison amongst post-moulting cows indicated that the

mean depth and duration of dives by a single southern elephant seal cow from Marion Island (487 m, 33.4 min - this study) and South Georgia (391 m, 17.5 min - Boyd & Arnborn 1991) fall within the range (269 to 552 m, 16.0 - 36.9 min) recorded for cows (n = 14) from Macquarie Island (Hindell *et al* 1991b; Slip *et al* 1994). The duration, but not depth, of dives made by post-moulting cows at Marion and Macquarie Islands was considerably greater than those from the post-breeding period. Hindell *et al* (1991b) found no difference between the two periods in the time spent at the bottom of the dive, and suggested that the seals from the post-moulting period took longer to arrive at the maximum depth of the dive. However, unlike the cows from Macquarie Island (Hindell *et al* 1991b), the post-moulting cow in the present study did not spend a similar proportion of its time on each type of dive between the two periods. It favoured foraging dives (84% of all dives, versus a range of 56.2 to 81.7% for post-breeding cows) which had approximately twice the bottom time compared with the foraging dives executed by post-breeding cows. The post-

Table 5

Mean duration of exploratory (types 5 & 6) dives and bottom time of foraging (type 7) dives that appeared in the diving record of each southern elephant seal cow.

Cows	Dive types		
	5	6	7
	Duration (min)	Duration (min)	Bottom time (min)
R101	19.46 (4.07)	20.42 (5.39)	11.86 (2.58)
R357	22.93 (7.87)	24.98 (6.20)	12.70 (3.74)
P537	25.58 (10.15)	28.90 (7.38)	13.65 (4.34)
Y333	23.21 (5.67)	31.56 (8.90)	13.64 (4.80)
R202	18.03 (5.32)	21.84 (5.28)	9.34 (3.13)
O138	22.50 (5.02)	24.59 (4.97)	12.12 (3.70)
O390	22.06 (4.32)	28.80 (6.39)	11.95 (2.79)
O144	19.45 (9.69)	30.95 (15.23)	22.85 (11.58)

() - standard deviation

Cow R 101

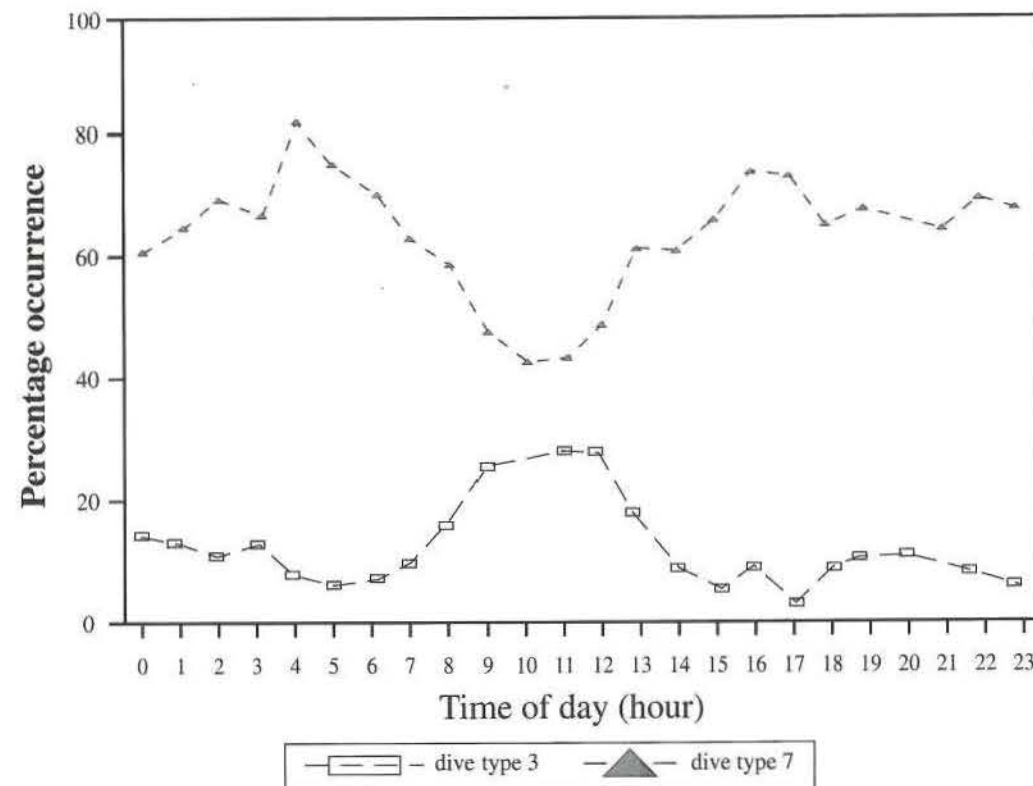


Fig 7b: The diel relationship between dive types 3 and 7 that appears in the first 40 days of the diving record of cow R101

Cow Y 333

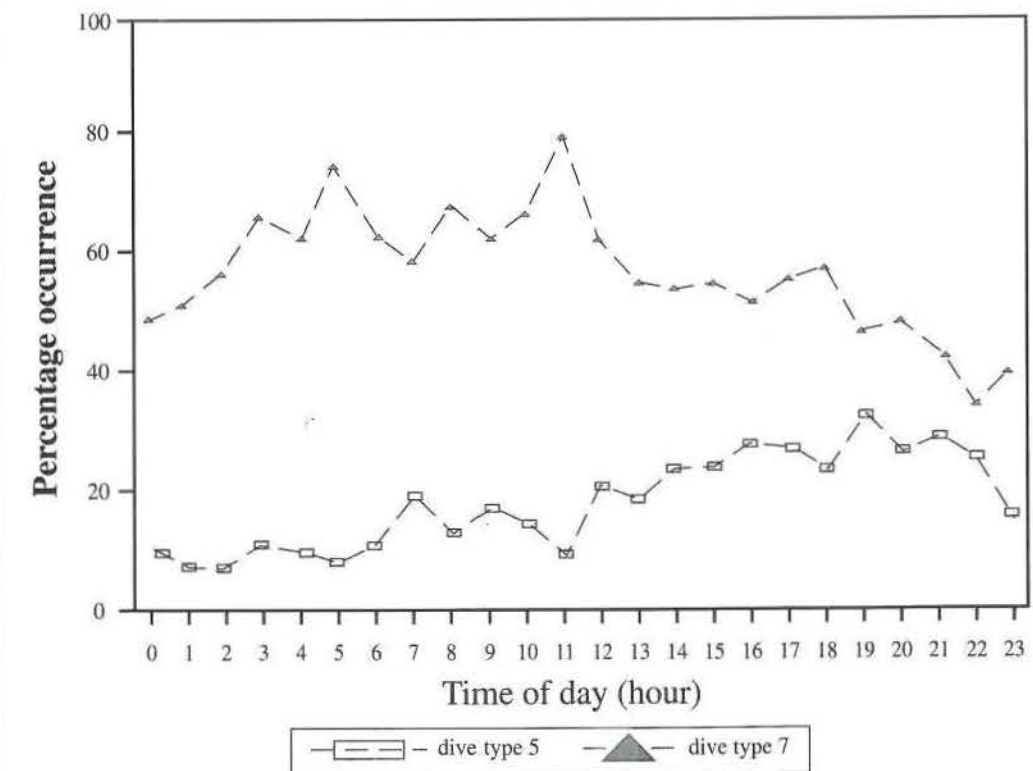


Fig 7c: The diel relationship between dive types 5 and 7 that appears in the first 40 days of the diving record of cow Y333

moulting cow from Marion Island therefore used a different foraging approach, possibly related to seasonal differences in the type of prey available or the abundance and distribution of prey.

Except possibly for the dives close to the island when the cows were presumably still over the shallow Prince Edward Islands shelf area, none of the dives seemed to be limited by the depth of the ocean floor. Foraging therefore appeared to be pelagic and similar to that of cows from Macquarie Island which seldom showed benthic dive patterns (Hindell *et al* 1991b). At least one of three southern elephant seal cows from South Georgia exhibited targeted benthic feeding when over the shallow continental shelf area (McConnel *et al* 1992) and the predominantly pelagic feeding northern elephant seal cows (Le Boeuf *et al* 1988) on occasion also fed benthically (Le Boeuf *et al* 1992). It therefore seems that elephant seal cows do not only feed in the water column, but also feed benthically when circumstances permit.

The maximum dive depth (1 444 m) by a post-breeding cow in this study exceeds that (1 256 m) recorded for southern elephant seal cows (Hindell *et al* 1992), but falls short of the 1 567 m and 1 581 m recorded for a northern elephant seal cow and bull respectively (Stewart & DeLong 1990). The maximum dive duration of 113 min by the post-moulting cow (this study) approximates the previous maximum recorded for a southern elephant seal cow (120 min) but exceeds that of northern (77 min) and southern (88.5 min) elephant seal bulls (DeLong & Stewart 1991; Slip *et al* 1994). Both the afore-mentioned cows undertook these very long dives during the post-moulting period, characterised by longer mean dive durations than during the post-breeding period (Hindell *et al* 1991b; this study) without a concomitant increase in post-dive surface intervals. Since the surface intervals between dives were short, and the dives following these and other exceptionally long dives were not significantly shorter than typical dives (DeLong & Stewart 1991), it seemed that the seals remained well within their aerobic dive limits (DeLong & Stewart 1991). Neither did ESIs follow or precede dives of above-average duration (Hindell *et al* 1992; this study), or depth (Boyd & Arnborn 1991). In addition, the absence of ESIs and post-dive surface intervals longer than 4 min during a 51 day stay at sea (this study), and 40 days without a surface period longer than 6 min when the theoretical aerobic capacity of the animals was regularly exceeded (Hindell *et al* 1991b & 1992), suggests other ways of dealing with by-products of anaerobic metabolism and/or limiting its production (Hindell *et al* 1992).

Of the seven distinct dive types identified in the present study, types 1, 2 and 4 dives have not been described previously for elephant seals. Comparisons are, however, difficult as schematic drawings of dives were presented in different ways and not always backed up

with all the relevant statistics.

The shallow (~ 34 m), rapidly executed type 1 dive of short duration with virtually no bottom time, and the slightly deeper (~ 95 metres) type 2 dive of longer duration with its more distinct bottom times, both occurred predominantly during the initial departure and the final return to the island, and were considered to be travelling dives. The infrequent occurrence of the shallow type 2 dive within a bout of deep foraging dives suggests a non-foraging function for these dive types. The type 2 dive might be analogous to the type F dive of Le Boeuf *et al* (1988), while the type 1 dive was distinct from the type 5 dive of Hindell *et al* (1991b) which they discounted as possible artefacts of the recorders rather than true dives.

The type 4 dive was different from type 3 dives owing to its very rapid mean descent rate and slow ascent rate despite similar mean depths (~ 456 m), durations, short bottom times and low frequency of occurrence (5 to 8% of all dives). The type 3 dive simulates the type 3 dive of Hindell *et al* (1991b), and the type C dive of Le Boeuf *et al* (1992). The slow descent, negative buoyancy of the animal and positive gravitational forces allowed covering 50% or more of the horizontal distance with a reduced swim effort in northern elephant seal cows (Le Boeuf *et al* 1992). This suggests a resting dive during which energy was conserved (63% of dive duration spent descending and at the bottom of the dive in the present study). The relatively fast ascent (37% of dive duration), with assumed forward movement (as implied by Le Boeuf *et al* 1992) could function as a travelling section of the dive. Conversely, the very fast mean descent of dive type 4 which constituted only 16.6% of the duration of the dive, implied purposeful diving to a considerable depth (in the league of foraging dives), with a bottom time comparable to the type 6 exploratory dive (this study), and followed by the very slow ascent which constituted 69.3% of dive duration. Since the seals were clearly not in a hurry to return to the surface, and the second part of the dive (83.4% of total duration) was likely to involve forward movement (Le Boeuf *et al* 1992), the type 4 dive appeared to have both an exploratory and transit function.

The type 7 dive in the present study with its rapid descent and ascent to/from depth (around 500 m), long duration and extended bottom time at a consistent depth during a series of dives, suggested foraging. Similar to the type D and type 1 dives described elsewhere (Le Boeuf *et al* 1991 & 1992; Boyd & Arnborn 1991; Hindell *et al* 1991b), it maximised feeding time by travelling rapidly to the depth where prey could be found, remained foraging at this depth for an extended period, and then returned quickly to the surface for a short period before diving again (Le Boeuf *et al* 1992). The distinct up and down movements during bottom time thus implied prey pursuit at the bottom of the dive (Bengtson & Stewart

1992) while the overall uniformity of the dive depth over a long series of dives suggested that prey patches remain at the same depth over time and are dense enough for high encounter rates (Le Boeuf *et al* 1988). As the most frequently used dive (66.5% of all dives recorded), particularly during the post-moulting period (83% of all dives), primarily when the seals were away from the island, the type 7 dive was most likely used to forage.

The depths of dive types 5 and 6 exceeded that of other dive types by ~ 100 m and these may have been exploratory dives. The dive profile of the type 5 dive suggested one smooth continuous movement combining the descent, bottom time and ascent. Analogous to the parabolic-shaped type 4 dive of Hindell *et al* (1991b) and possibly the type B dive of Le Boeuf *et al* (1991), type 5 dives occurred throughout the journey in the present study while Le Boeuf *et al* (1992) and Hindell *et al* (1991b) found them predominantly in the first two weeks after the seals' departure from land. Despite the relatively long bottom times, these dives did not appear to be foraging dives. Frequently found singly in among bouts of foraging dives (unpublished data), they seemed to serve an exploratory function as they were deeper on average than the foraging dives with which they were associated. Furthermore, most of the deepest recorded dives were all type 5 dives and it is therefore unlikely that they could function predominantly as transit dives (as suggested by Hindell *et al* 1991b; Le Boeuf *et al* 1992).

The type 6 dive was also an exploratory dive to similar mean depths than the type 5 dive, but was of a considerable longer duration, despite a shorter mean bottom time. This resulted from the temporary decline in the descent rate more than 100 m short of the bottom of the dive and a temporary decline in the ascent rate at a similar depth, which produced the two shoulders in the dive profile. These dives were similar to the type 2 dives described by Boyd & Arnborn (1991) and appear in the graphic representation of dives classified as type 6 dives in Hindell *et al* (1991b). Interspersed among shallower foraging dives similar to the type 5 dives (unpublished data), the shoulder(s) of the type 6 dive appeared to be produced at the same depth as the bottom of the preceding and subsequent foraging dives (this study). This may be interpreted that the type 6 dive is an aborted type 7 foraging dive and that descent to greater depths in this situation suggests exploration as prey were not found at the anticipated depth. Since type 6 dives were also found in other situations not immediately preceded or followed by foraging dives, it may also have a purely exploratory function such as the type 5 dive with which it was also associated, but showing a clear enhanced interest in a shallower depth than the maximum for the particular dive.

The positive correlation between dive depths and dive durations, with few exceptions within dive types (this

study), followed the pattern established for other elephant seals (Le Boeuf *et al* 1988; Boyd & Arnborn 1991; DeLong & Stewart 1991; Hindell *et al* 1991b). Considerable individual variation in diving characteristics existed amongst the cows in the present study as evidenced by (a) the difference in the slopes of the lines regressing depth on duration of dives, (b) the difference in both diving depth and diving duration as well as the frequency distribution of dive durations amongst most of the individuals and (c) the frequency distribution of surface intervals when ESIs were included. Although the distribution of dive depths and dive durations centred on 400 to 600 m and 22 to 24 min, two cows had a secondary depth mode around 800 to 900 m, and yet another had a second mode around 40 to 42 min for duration. Since cows in the present study ranged widely both north and south of the APF (Bester & Pansegrouw 1992) such individual variation in dive parameters was likely to be related to the cows' geographic locations and geographic variations in prey depth and behaviour as speculated by DeLong & Stewart (1991) for northern elephant seal bulls.

The diel diving pattern of deeper dives of longer duration during the day and shallower, shorter dives during the night appeared to be the norm for elephant seals (e.g. Le Boeuf *et al* 1988; Boyd & Arnborn 1991; Hindell *et al* 1991b; this study) and was interpreted as the pursuence of vertically migrating prey, which is more abundant near the surface at night than during the day (e.g. Boyd & Arnborn 1991; DeLong & Stewart 1991). The foraging (type 7) dives of the cows during the four hours around midnight were contrasted with those around midday to eliminate the possible influence of dawn and dusk which would differ according to the season and location of the cows. The absence of a significant difference in diel dive depths for cow R357 in the present study was not due to benthic foraging as speculated for a similarly behaving northern elephant seal bull (Stewart & DeLong 1991), as the cows all appeared to be foraging pelagically (present study). Moreover, the wide range of differences in mean dive depths between night and day (30 to 300 m), and inconsistent relationships between the relative contribution of the different dive types in the diel dive records of individuals, further strengthens the argument of response to seasonal and geographic variation in species composition and behaviour of prey (e.g. Stewart & DeLong 1990).

The post-breeding periods of absence of southern elephant seal cows from Marion Island ($\bar{x} = 66.7 \pm 12.33$; range = 51 to 86 days; $n = 7$) were shorter on average and with a wider range than that determined for conspecific cows from Macquarie Island ($\bar{x} = 73.7 \pm 3$; range 71 to 78; $n = 6$) and northern elephant seal cows from Ano Nuevo Point, California ($\bar{x} = 72.6 \pm 5.0$; range 62 to 78; $n = 8$) (Le Boeuf *et al* 1988; Hindell *et al* 1991b). Cow R202 which spent 8 to 9 days longer at

sea than the other cows during the post-breeding period, was otherwise similar in age (six years), dive characteristics and longest period of continuous diving. However, she had considerably longer extended surface intervals than the post-breeding cows and showed similarities with cow O144 (which had remained at sea for 239 days during the post-moulting period) for number and duration of ESIs. It therefore suggests that the factors determining the presence of ESIs in the dive records of cows may also affect the duration of the post-breeding period.

In determining what these factors might be, it is perhaps significant that the only other six-year-old cow Y333, which spent the shortest post-breeding period (51 days) at sea, had been diving continuously without any ESIs, never spent more than 4 minutes at the sea surface and returned the highest mean as well as maximum dive durations recorded for post-breeding cows. Since cow Y333 also used significantly more exploratory dives (28.1%) and less foraging dives (56.2%) compared to all other post-breeding cows (4.0 to 18.6% and 64.4 to 81.7% respectively), it suggested that she was less successful in encountering prey and consequently had to work harder to sustain herself and gain mass before the moult haulout. This is also supported by the fact that the bottom time of foraging dives of cow Y333 and presumably feeding time, as well as exploratory dives, were of significantly longer duration than that of cow R202, although not necessarily different from all the remaining cows.

Boyd & Arnborn (1991) linked food abundance and the occurrence of ESIs predominantly at night and argued that if food abundance tended to be greater at night, then the single elephant seal cow in their study may periodically have become satiated with food which could explain cessation of diving. Since ESIs also occurred more often during the night (72%) than during the day (28%), it further strengthens the relationship between the occurrence of ESIs and food abundance.

The question, however, remains why cow Y333 did not simply spend a longer period at sea in order to improve her chance of obtaining food in quantity and gain weight, as a significant relationship between days at sea and percentage mass gain for cows during the post-breeding period existed for northern elephant seals (Spearman Rank Correlation Coefficient $r_s = 0.71$, $P < 0.05$, $n = 7$; calculated from Table 1 in Le Boeuf *et al* 1988). One might then also expect that the period spent at sea would depend on the amount of resources used during lactation and time spent on land during the preceding breeding season. Northern elephant seal cows that successfully reared their pups, and therefore by implication used a far greater amount of body fat reserves than those failing to rear their pups, stayed at sea significantly longer than unsuccessful cows (Stewart 1989). In contrast, the length of time spent at sea by southern elephant seal

cows from Marion Island during the post-breeding period was negatively correlated with the duration of the breeding season haulout, but not with maternal age, size or social status, or whether a cow successfully reared her pup (Wilkinson 1992). The relatively short post-breeding period at sea of cow Y333, despite the apparent difficulty in locating prey, could therefore possibly be related to the impending onset of the moult and/or physiological state of the cow.

In contrast to post-breeding cows, which have their available time at sea limited by the haulout for the moult (Bester 1988b) which peaks in mid-January at Marion Island (Condy 1979), the post-moulting cow O144 spent 235 days at sea before hauling out for the breeding season. Concentrating on foraging dives (83.8% of all dives) of approximately double the duration of the foraging dives of post-breeding cows, her behaviour suggested successful foraging as the cow also had a very high rate of ESIs. This concentrated feeding was necessary as pregnant elephant seal cows need to gain condition after the moulting fast and in advance of the breeding season haulout and the rearing of a pup.

By the very nature of the present study, only successful cows, i.e. cows that had either moulted or had weaned their pups, and which subsequently returned to the island, after a period at sea, to breed or moult (enabling the retrieval of the recorders), were included in the investigation. This study has, however, shown that the differing diel diving responses of the cows, the probable role and function of the ESIs, the proportional use of the various dive types, their specific depths, durations and frequencies of distribution and lengths of post-breeding and post-moulting pelagic periods, can potentially be used as measures of the cows' performances at sea. The marked individual variation in the diving behaviour of these and other cows therefore needs to be scrutinised more closely as it is likely to vary seasonally and geographically in response to physical and biological environmental factors.

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