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Influence of intrinsic variation on foraging behaviour of adult female Australian fur seals

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ABSTRACT: Phenotypic variation and individual experience can create behavioural and/or dietary variation within a population. This may reduce intra-specific competition, creating a buffer to environmental change. This study examined how intrinsic variation affects foraging behaviour of Australian fur seals. Foraging movements of 29 female Australian fur seals were recorded using FastLoc GPS and dive behaviour recorders. For each individual, body mass, flipper length and axis length were recorded, a tooth was sampled to determine age, and milk was collected for diet analysis. Clustering of fatty acid dietary analysis revealed 5 distinct groups in the population. Behaviour was described using 19 indices, which were then reduced to 7 principal components (>80% of the behavioural variation). Bayesian mixed effect models were developed to describe the relationship between these components and intrinsic variation. No association was found between diet and age or body shape; however, age had a negative relationship with component 1 (27% of variation). Older females spent less time at-sea and foraged nearer to the colony. Age had an effect on component 5 (7% of variation), which represented haul-outs and dive depth; older females made fewer visits to haul-out sites and dived deeper to the benthos. This suggests that as animals age they are able to utilise prior knowledge to exploit nearby foraging sites that younger animals are either unaware of, or have yet to gain the experience required to efficiently utilise. Mass had a negative effect on components representing the directedness of a foraging trip, suggesting heavier individuals were more likely to travel directly to a foraging site.

KEY WORDS: Intrinsic variation · Foraging behaviour · Age effects · Phenotypic variation

INTRODUCTION

Traditionally, ecological studies have pooled individual data to measure population level effects, or effects defined by large-scale phenotypical differences such as sex and reproductive status, in order to describe a species' behaviour or diet (Boyd et al. 1994, Page et al. 2005, Breed et al. 2006, Kurle & Gudmundson 2007, Villegas-Amtmann et al. 2011). However, this approach may overlook additional sources of variation that exist within a population (Bolnick et al. 2002, 2003), whereby individuals may differ in traits that lead to varying efficiencies when capturing, manipulating or detecting forage items (Van Valen 1965). To optimise foraging success, individuals should choose food items that maximise energetic returns by balancing their ability to acquire the item and the energetic gains made from the food (Van Valen 1965).

Variations in foraging efficiency and resource use between individuals can be driven by small- or large-scale morphological differences (Smith & Skulason 1996). Large-scale variations, such as the switch from juvenile phase into adulthood, can cause shifts in an animal's behaviour or in the niche it occupies (ontogenetic niche shifts; Claessen & Dieckmann 2002, Kim et al. 2012). Smaller scale morphological differences, such as minor body shape variations, may affect an individual's ability to capture, manipulate

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or detect certain food types, causing it to focus more on those prey items it is most efficient at acquiring (Swennen et al. 1983, Smith & Skulason 1996). For example, the foraging efficiency of individuals within a population of perch *Perca fluvatis* feeding in 2 different habitats (littoral and pelagic zones) is determined by their body shape (Svanback & Eklov 2004). Narrower, more streamlined animals are more efficient at foraging in the pelagic zone than broader, deeper bodied individuals who are most efficient within the littoral zone (Svanback & Eklov 2004).

Furthermore, as individuals age, their experience and knowledge of their environment increases. Older individuals, having more experience, may have learned the locations of the most profitable foraging grounds and/or efficient capture techniques that younger animals have yet to learn (Orians 1969, Cresswell 1994). Thus, with experience, individuals may be able to shift their foraging areas to better regions or learn to capture more elusive but more profitable prey. For example, older European blackbirds *Turdus merula* are more successful at acquiring large prey (Desrochers 1992); 1 yr old birds are half as successful as 2 yr old individuals, with older (3 to 5 yr) birds being slightly more successful than the 2 yr olds (Desrochers 1992).

Additionally, animals may be limited in their capacity to learn multiple complex capture techniques or remember the locations of different profitable foraging grounds (Bélisle & Cresswell 1997). As such, the successful behaviours that an individual learns during the initial phases of its life will be continued throughout adulthood (Micheli 1997). These successful behaviours will depend on the environment in which the animal lives during those initial phases (Micheli 1997). As different individuals encounter novel environments due to spatial and temporal heterogeneity in resources, distinct groups of specialised individuals will form (Araújo et al. 2011). Concurrently, individuals will continue to exploit a food source or area so long as the energetic returns are good. Time spent exploring new areas or different foraging techniques will mean time lost that could have been used exploiting predictable resources (Bolnick et al. 2002, 2003). Thus, once an animal has learned to focus on certain prey items or feeding areas, they may continue to do so rather than invest in exploring potentially less profitable methods or regions (Bolnick et al. 2002, 2003).

The Australian fur seal *Arctocephalus pusillus doriferus* is a species endemic to the shallow continental shelf region of Bass Strait in southeastern Australia (Arnould & Hindell 2001, Littnan & Arnould 2002, Arnould & Kirkwood 2007, Kirkwood & Arnould 2011). Studies have shown Australian fur seal females to be almost exclusively benthic foragers, feeding on a wide range of prey including bony fish, cephalopods and elasmobranchs (Arnould & Hindell 2001, Kirkwood et al. 2008, Deagle et al. 2009). During pup-rearing, adult females adopt a central place foraging strategy and are constrained to forage within approximately 315 km of the colony (Arnould & Kirkwood 2007), returning to feed young on average every 5.41 to 8.67 d in the summer and winter, respectively (Arnould & Hindell 2001).

Several benthic communities exist within Bass Strait including dense and sparse sponge beds, rocky reefs and open sandy areas (Williams & Leach 1999). Data from animal-borne video data loggers have revealed that Australian fur seals forage within several benthic habitats found within Bass Strait (J. P. Y. Arnould unpubl. data), and consequently, there is opportunity for individuals to specialise their foraging behaviour to suit particular habitats or prey types. Diet studies based on faecal analysis have documented that a wide range of prey are consumed by the population, but it is not known whether this variation is reflected within individuals (Page et al. 2005, Kirkwood et al. 2008). Stable isotope analysis of blood, however, has indicated a degree of both intra-specific and inter-annual variation in the diet of Australian fur seals (Arnould et al. 2011) suggesting that there may be a degree of individual specialisation in diet within the population. In addition, satellite tracking and dive behaviour studies have revealed that different foraging trip strategies exist within the population (Kirkwood & Arnould 2011, Hoskins & Arnould 2013). It is not known, however, whether individual variation in diet is associated with individual variations in behaviour, or whether behavioural variations can be attributed to differences in morphology or age.

Therefore, the aims of the present study were to (1) identify dietary groups in Australian fur seals using fatty acid signature analysis, and (2) identify the relationship between foraging behaviour and intrinsic variation in diet, morphology and age.

MATERIALS AND METHODS

Study site and field procedures

Field work was conducted at the Kanowna Island breeding colony in central northern Bass Strait, southeastern Australia (39° 09′ S, 146° 18′ E). Kanowna Island is a 30 ha granite island containing the third largest breeding colony of Australian fur seals, with an estimated annual production of 3400 pups (Kirk-

wood et al. 2010). Adult females nursing pups were selected at random and captured using a modified hoop net (Fuhrman Diversified). Upon capture, they were injected intramuscularly with the sedative Midazolam (ca. 0.1 mg kg^{-1}, Hypnovel®; Roche Products) before full anaesthesia was induced using isoflurane gas via a portable gas anaesthesia machine (Stinger™, Advanced Anaesthesia Specialists; Gales & Mattlin 1998). A FastLoc™ GPS (100 × 28 × 52 mm, 117 g; Sirtrack), dive behaviour recorder (74 × 57 × 36 mm, 120 g, Mk10; Wildlife Computers) and VHF transmitter (Sirtrack) were glued in series along the dorsal pelage using quick-set epoxy (Accumix 268; Huntsman Advanced Materials) and plastic flipper tags (Super Tags®; Dalton Supplies) were inserted into the trailing edge of each fore flipper.

Subsequently, individuals were transferred to a board and secured before being weighed on a suspension scale (±0.5 kg). After weighing, morphometric measurements (straight-line length, flipper length, axillary girth and axis length) were measured to the nearest 0.5 cm (Bonner & Laws 1993). The first post-canine from the individual's right mandible was extracted using dental elevators after the area was injected with a local anaesthetic (10 mg lignocaine hydrochloride, Xylocaine; AstraZeneca). Extracted teeth were stored in 70% ethanol until analysis. An intramuscular injection of oxytocin (1 ml, 10 IU ml^{-1}; Heriot Agvet) was administered and a small (10 ml) milk sample for fatty acid signature analysis was collected via manual expression of the teats.

Upon recovery from anaesthesia, individuals were left to return to the colony and resume natural behaviours. After a minimum of 1 foraging trip, individuals were recaptured following the methods detailed above and the data loggers were recovered by cutting the fur beneath them.

Laboratory procedures

To measure dietary variation between individuals, milk fatty acid signatures were analysed following the methods of Wheatley et al. (2008). Milk lipids were first extracted using a modified Bligh & Dyer (1959) 1 phase methanol/chloroform/water extraction (2:1:0.8, v/v/v). To make a biphasic system with a final solvent ratio of 1:1:0.9 (v/v/v, methanol/chloroform/water), chloroform and water (0.9% NaCl) were added. Total lipids were concentrated from their lower chloroform phase via rotary evaporation at 40°C. To produce fatty acid methyl esters, a small subsample was transmethylated at 80°C for 2 h using a methanol/chloroform/hydrochloric acid reagent (10:1:1, v/v/v). Samples were analysed using a gas chromatograph (6890N; Agilent) equipped with a HP-5 cross-linked methyl silicone-fused silica capillary column (50 m × 0.32 mm internal diameter), flame ionization dector, split/splitless injector and an Agilent 7683 auto-sampler with helium used as the carrier gas. Fatty acid peaks were quantified using Gas Chromatograph ChemStation software (Agilent Technologies).

Age was determined from the collected teeth following the methods of Gibbens & Arnould (2009). Teeth were removed from ethanol and rinsed in flowing water for ≥6 h to remove residual ethanol before being immersed in a hydrochloric decalcifying agent (RED; Apex Engineering Products) until flexible to the touch (8 to 24 h). Teeth were rinsed in deionised water for ≥6 h before being embedded in a mounting compound (Tissue-tek O.C.T compound; Sakura Finetek). A freezing microtome was used to cut at least 6 sections at a thickness of 25 µm. Sections were stained with haemotoxylin and fixed in a 5% ammonia solution. The 6 sections with the best definition were mounted onto glass slides using a mounting compound (DPX; Sigma-Aldrich) and a glass cover slip. Sections were viewed using a light transmission stereo-microscope with a rotatable polarizing filter and a magnification of 4 to 10×. Pairs of individual light and dark bands were identified and counted to determine the age at previous year. A total of 5 blind readings were made for each tooth, and the median value was used as the age. A single experienced person performed all readings to standardise any bias introduced from reader experience.

Data analysis and statistics

Downloaded dive behaviour and GPS data were processed using custom routines and the 'diveMove' package (Luque 2007) in R (R Development Core Team 2012). Dive behaviour data were summarised into individual basic dive statistics (dive duration, maximum depth, descent rate, ascent rate, post-dive duration) using diveMove. Furthermore, dives were classified as either benthic or pelagic using a custom written routine whereby individual dives were scored based on the proportion of time spent at the bottom of the dive multiplied by the maximum depth achieved during the dive. A density estimate of the resulting score revealed a bimodal distribution, with values to the left of the minimum value between the 2 modes representing pelagic dives, and values to the right of this minimum representing benthic dives.

Concentrations of individual fatty acids were converted into a proportion (%) of total fatty acids by mass, with any fatty acids present in trace amounts (<0.5%) being removed from subsequent analyses. A clustering analysis was run on the proportional fatty acid data to assess whether different groupings existed in the seals' diets. An agglomerative hierarchical clustering analysis was used with Euclidian distance and Ward's linkage criterion. Clusters were defined using the dynamic tree cutting algorithm in the R package 'dynamicTreeCut' (v.1.21; Langfelder et al. 2008). Variations in the mean proportions of fatty acids within these groups were compared visually.

To describe the foraging behaviour of female seals, a total of 19 movement statistics were calculated for each individual foraging trip from the combined diving and GPS data. These included 8 variables describing dive behaviour: number of dives occurring within a trip, modal depth (m), mean dive duration (s), maximum dive duration (s), proportion of benthic dives, modal descent and ascent rates (m s^{-1}), and modal post-dive duration (s). GPS tracking data were described using 7 statistics, including foraging trip duration (s), total distance travelled (km), maximum straight line distance from the colony (km), mean travel speed (m s^{-1}) and mean direction of travel from the colony (bearing; °). In addition, the shape of the foraging trip route was described using 2 statistics based on the bearing from the colony to each at-sea location (Zar 1996). The first was an indicator of how directed a foraging trip was (r); this statistic describes the degree of fidelity between the mean bearing and other bearings in the distribution, returning a score between 0 (no fidelity) and 1 (high fidelity). The mean $\boldsymbol{x}$ ($\bar{x}$) and $\boldsymbol{y}$ ($\bar{y}$) vector components of the distribution were calculated using Eqs. (1) and (2), where a_i is the ith bearing and n is the number of observations; r is then calculated using Eq. (3):

$$\bar{x} = \frac{1}{n}\sum_{i=1}^{n}\sin(a_i) \quad (1)$$

$$\bar{y} = \frac{1}{n}\sum_{i=1}^{n}\cos(a_i) \quad (2)$$

$$r = \sqrt{\bar{x}^2 + \bar{y}^2} \quad (3)$$

The second indicator, s, is a measure of the angular deviation from the mean (in degrees) with a range of 0 to 81.03°. This gives an indication of how dispersed a foraging trip was (0 is highly directed and 81.03 is highly dispersed) and was calculated as follows:

$$s = \frac{180°}{\pi}\sqrt{2(1-r)} \quad (4)$$

The spatio-temporal distribution of foraging effort was calculated using a modified version of first-passage time analysis (FPT; Fauchald & Tveraa 2003), which included diving behaviour (first-passage diving, FPD; Hoskins 2014, Hoskins et al. 2015). An intensive foraging zone (IFZ) was defined as an area along a foraging track with a scaled FPD foraging score greater than 0.8. Included in the foraging behaviour statistics were the number of IFZs that occurred within a trip, the duration of these trips, and to give an indication of the degree of tortuosity with these IFZs, the mean fractal dimension was calculated (fractaldim v.0.8-1) for each zone.

Preliminary investigations revealed a high degree of collinearity between some of the calculated foraging behaviour statistics. To account for this, the dimensionality of foraging behaviour statistics was reduced using a Principal Components Analysis (PCA). Components with eigenvalues >1 were retained for further analysis and a varimax rotation was used on the retained components to reduced ambiguity within the loadings.

Bayesian regression analysis was used to investigate the effects that individual variations in diet and body shape had on foraging behaviour, as well as the effects that body shape had on diet. Prior to analysis, model assumptions were checked using histograms, boxplots and q-q plots. Collinearity between predictors was assessed, pairs of variables where the correlation was >0.7 were identified and one member of that pair was removed prior to analysis. Three sets of predictor variables were developed from the remaining variables. Firstly (to assess the influence variations in body shape may have on foraging behaviour and diet), mass, right flipper length (RFL; an indicator of an individual's flipper stroke power) and axis length (an indication of an individual's turning ability/manoeuvrability) were used. Secondly (as a proxy of experience), individual age was used as a predictor within the models. Finally, the relationships between different diets and foraging behaviour were investigated using the groupings determined by the clustering of the fatty acid data.

Bayesian mixed effects models with a Gaussian distribution were used to investigate the effects of the 3 predictor groups (body shape, age and diet) on the behaviour of Australian fur seals. This was achieved by comparing them to the principal component scores obtained from the PCA of behavioural statistics. Furthermore, the effects of variations in body shape and age on the diet of individual seals were

assessed using Bayesian mixed effects models with an unordered multinomial distribution with fatty acid groupings as the response variable. These were compared against the predictor groups of body shape and age. All models were fitted using the 'MCMCglmm' package (v.2.17) in R. Models had the year of deployment and individual seals included as random effects and used weakly informative priors for both the residual distribution and the random effects.

RESULTS

A total of 56 individual fur seals were sampled; of these, milk (for fatty acid analysis) and a tooth (to determine age) were successfully collected from 49 individuals. Seal ages ranged from 3 to 13 yr (average: 7.6 ± 3.0 yr); mass and length ranged from 51 to 101 kg (75.9 ± 11.6 kg) and 134 to 171 cm (152.5 ± 8.1 cm), respectively. There was a moderate positive relationship between age and body mass (t_{47} = 6.92, $p < 0.001$, $R^2 = 0.49$). Due to failure or loss of equipment at sea, concurrent GPS and dive behaviour data were recovered from only 29 individuals; of these, 22 also included age data and 23 included diet data (Table 1).

Deployment durations ranged from 2.4 to 138.3 d (mean: 21.0 ± 27.8 d), with individuals completing 2.7 ± 3.0 foraging trips (range: 1 to 19 trips; see Table S1 in the Supplement at www.int-res.com/articles/suppl/m526p227_supp.xls). Foraging trips lasted 5.9 ± 2.7 d, with individuals travelling 103.5 ± 41.3 km (range: 16.4 to 207.1 km) from the colony (Table S1). During these foraging trips, the seals spent 40.4 ± 7.0% of their time underwater during dives that lasted 189.4 ± 32.2 s; 83.7 ± 12.6% (range: 37.6–99.3%) of these dives were at the seafloor (Table S1). Intensive foraging behaviour periods (areas along a foraging track with FPD foraging score >0.8) lasted 177.7 ± 104.3 min (range: 30.9 to 428.3 min) and occurred 9.7 ± 6.4 times per foraging trip (Table S1).

Inter-individual variation in diet

Hierarchical clustering of the dissimilarity matrix created from the proportions of different fatty acids within Australian fur seal milk samples produced a dendrogram of several well-defined groups (Fig. 1). Application of the dynamic tree-cutting algorithm determined the presence of 5 unique dietary clusters within the dendrogram, stemming from 2 primary branches of the tree (Fig. 1). Each cluster contained

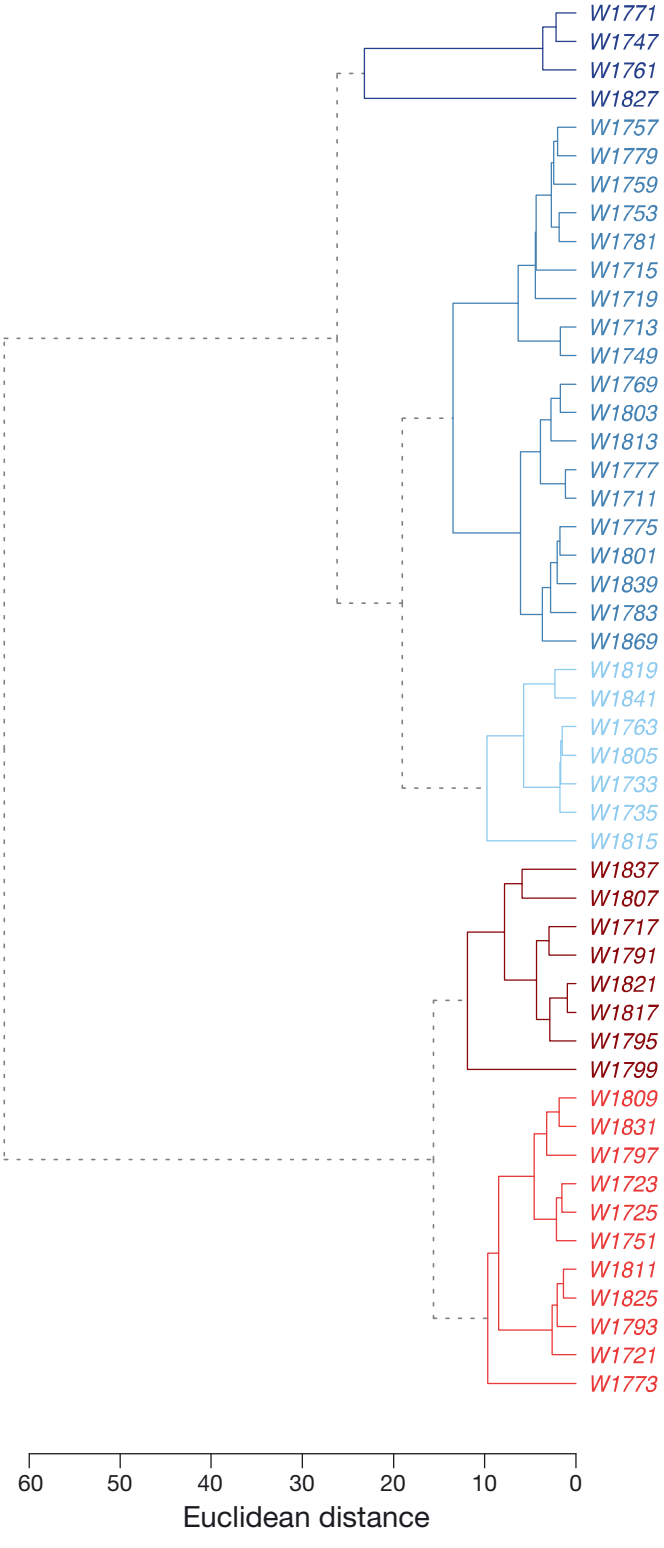

Fig. 1. Hierarchical clustering of different fatty acid profiles from milk samples of individual female Australian fur seals. Leaves of the tree represent each individual while the 5 groupings defined by a dynamic tree cutting algorithm are differentiated by colours. Group 1: red; Group 2: dark red; Group 3: light blue; Group 4: blue; Group 5: dark blue; n = 49

Table 1. Summary age, body shape, tracking and diving statistics for female Australian fur seals from the Kanowna Island breeding colony, Bass Strait, Australia. Data are presented as means ± SD (where appropriate). Where a difference exists, values of deployment duration and no. of trips are those where concurrent GPS and TDR data were available, whereas values in parentheses represent total duration/number

ID	Age (yr)	Mass (kg)	Axis length (cm)	Right flipper length (cm)	Deployment duration (d)	No. of trips	Trip duration (d)	Total distance covered (km)	Max. distance from colony (km)	No. of dives trip^{-1}	Modal depth (m)	Average dive duration (s)
W1717	13	86.5	62	42	4.01	1	4.01	252.75	88.84	702	85.26	195.16
W1721	12	91.5	72.5	43.5	40.93	5	6.66 ± 1.34	72.9 ± 410.17	126.22 ± 23.08	1034.2 ± 220.05	82.41 ± 2.53	175.19 ± 10.26
W1751	8	77	60.5	45	47.11 (86.05)	9 (17)	4.28 ± 2.01	130.61 ± 269.34	73.94 ± 41.36	732.44 ± 337.38	81.07 ± 2.45	166.88 ± 17.01
W1759	8	82	65	47.5	57.26 (62.22)	13 (15)	2.58 ± 1.33	85.47 ± 188.62	58.63 ± 20.78	533.08 ± 299.27	74.04 ± 13.21	169.68 ± 23.59
W1763	10	75	61.5	39.5	3.74	1	3.74	320.97	121.79	556	83.03	249.94
W1771	4	59.5	61.5	41	6.22	1	6.72	310.48	93.52	872	85.48	184.63
W1777		90.5	66.5	43.5	4.24	1	4.24	109.41	53.35	369	79.99	232.71
W1779		87	61	42.5	4.26	1	4.26	249.44	117.33	577	74.24	189.02
W1781	13	86	65.5	45.5	9.42	3	1.87 ± 1.13	71.22 ± 125.68	53.87 ± 28.32	320.67 ± 219.6	79.87 ± 0.73	238.66 ± 7.1
W1783		91.5	64.5	41	14.21	2	6.51 ± 0.62	6.26 ± 309.12	130.28 ± 16.39	874.5 ± 41.72	80.93 ± 3.72	228.55 ± 4.55
W1787	12	89.5	69	43.5	41.49 (54.61)	12 (19)	3.01 ± 3.04	155.33 ± 137.1	46.91 ± 52.5	381.08 ± 392.77	80.9 ± 0.33	201.81 ± 10.48
W1789		84.5	64.5	48.5	25.5 (42.87)	4 (9)	5.53 ± 4.54	175.34 ± 244.44	104.02 ± 69.26	712.75 ± 635.31	83.48 ± 3.84	251.29 ± 15.63
W1791	5	71	58	39	5.24 (4.73	1 (5)	5.27	54.42	16.36	871	38.12	189.98
W1793	4	59	62.5	41	5.91	1	5.91	276.1	121.08	643	85.17	165.96
W1795	5	68	63.5	41	4.61	1	4.61	311.33	131.14	714	81.47	185.48
W1807	4	69	62	39	17.19 (54.2)	2 (7)	7.64 ± 5.93	272.07 ± 430.47	146.1 ± 70.64	1361 ± 1187.94	66.4 ± 25.91	161.09 ± 26.2
W1809	6	80	64	42.5	35.02 (51.65)	3 (6)	10.5 ± 1.9	40.97 ± 579.08	198.21 ± 3.67	1655.67 ± 597.1	72.24 ± 1.44	154.72 ± 11.59
W1811	8	72	69.5	44.5	38.84 (38.84)	4 (6)	9.46 ± 4.53	199.83 ± 411.95	88.64 ± 9.01	1582.25 ± 900.34	81.14 ± 0.64	157.61 ± 11.01
W1817	12	80	72.5	41.5	4.06	1	4.06	264.27	112.07	708	79.71	215.21
W1819	6	63.5	64.5	40.5	4.07 (7.35)	1 (2)	4.07	253.83	98.63	582	83.48	168.04
W1823		77	68	42.5	7.53	1	7.53	408.42	93.96	1031	85.3	208.43
W1825	10	80.5	66.5	43.5	5.37	1	5.37	222.9	89.38	665	83.96	196.92
W1827		55	59	40.5	5.65	1	5.65	245.91	93.7	1043	79.06	184
W1829	11	86	68.5	43	10.12	1	10.12	578.09	196.7	2188	76.69	135.85
W1833	4	51	58.5	40	27.78 (122.98)	2 (17)	13.29 ± 0.21	36.49 ± 620.24	127.06 ± 95.45	2225 ± 308.3	59.78 ± 2.4	156.38 ± 2.57
W1835	8	56	65.5	41.5	10.61 (22.56)	3 (6)	3.34 ± 3.58	136.15 ± 131.48	43.25 ± 34.69	576.67 ± 567.92	78.41 ± 1.38	171.21 ± 33.46
W1837	4	62.5	60	43.5	8.66 (13.21)	1 (3)	8.7	255.47	101.17	1932	26.35	144.55
W1839		101	73	44	27.85 (35.65)	3 (4)	10.65 ± 3.85	164.56 ± 469.84	145.16 ± 71.99	1424 ± 610.94	75.62 ± 11.39	255.72 ± 6.15
W1841	7	71	64	41.5	25.9 (138.26)	3 (19)	7.81 ± 0.63	94.67 ± 419.58	154.64 ± 44.28	1345 ± 223.98	82.46 ± 1.85	182 ± 10.34
Mean	7.9	76	64.6	42.5	21.8	5.5	5.97	298.23	103.5	942.91	76.17	189.38
SD	3.2	12.6	4.1	2.3	27.5	5.9	2.78	143.63	41.28	536.28	13.08	32.23

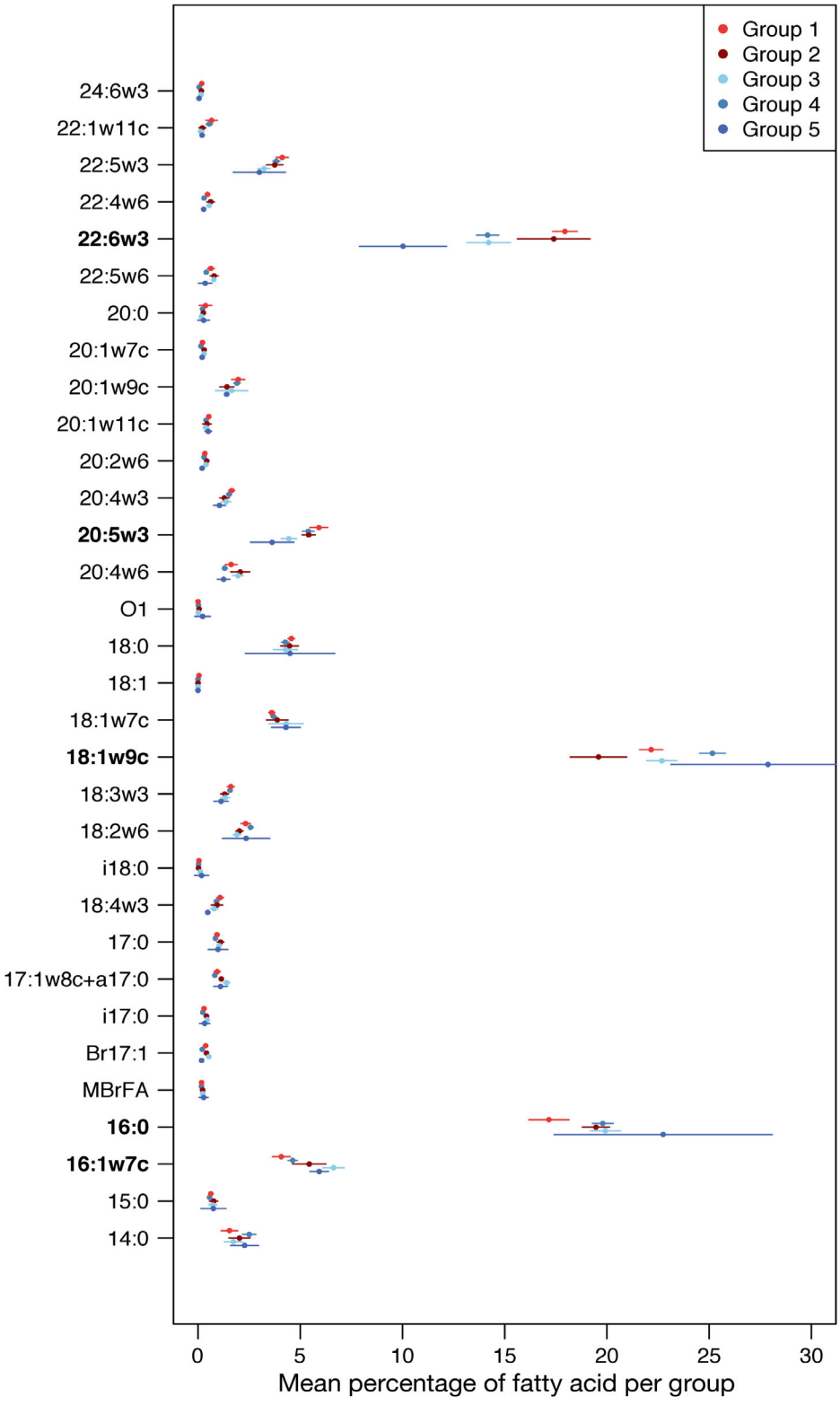

Fig. 2. The mean proportion (%) of different fatty acids found within the milk samples of 5 groups of female Australian fur seals differentiated by cluster analysis (see Fig. 1). Horizontal bars represent the 95% confidence intervals surrounding these means. Bold labeling indicates the 5 fatty acids where large differences between the groups were identified

4 (10%), 19 (38%), 7 (14%), 8 (16%) and 11 (22%) of the individuals, respectively. The clusters were defined by large variations in 5 of the 32 fatty acids identified within the samples (16:1w7c, 16:0, 18:1w9c, 20:5w3 and 22:6w3) (Fig. 2). On average, the milk of females within Groups 1 and 2 contained greater proportions of the fatty acid 22:6w3 and the lowest proportions of 18:1w9c than that from femals in Groups 3, 4 and 5 (Fig. 2). Individuals from Group 5 contained the greatest proportion of the fatty acids 16:0 and 18:1w9c, and the lowest proportions of 20:5w3 and 22:6w3 (Fig. 2).

In total, concurrent GPS, dive behaviour and fatty acid data was available from 24 seals. These individuals were assigned to the groupings determined by the fatty acid clustering analysis resulting in 6, 6, 6, 3 and 2 individuals within Groups 1 to 5, respectively. Data from seals within these groups accounted for a total of 22, 23, 7, 5 and 2 foraging trips. Due to the small number of seals contained within Group 5, these individuals were removed from subsequent analyses.

Individual drivers of Australian fur seal foraging behaviour and diet

Principal component analysis of the behavioural statistics calculated from the concurrent GPS and dive behaviour data resulted in 7 components with eigenvalues >1. These components accounted for a total of 81% of the variation within the dataset. Components 1 through 7 each represented 27, 13, 11, 10, 7, 6 and 5% of the variation

Table 2. Component loadings (after varimax rotation) of the resultant 7 principal components with eigenvectors >1, obtained from a principal component analysis performed on 19 different indices of female Australian fur seal foraging behaviour calculated from a tracking and dive behaviour dataset (n = 29). Values in **bold** represent those that have a strong positive or negative loading on their respective component. *r* is a measure of how directed a foraging trip is and *s* is a measure of angular deviation from the mean. IFZ is the zones of intensive foraging identified using first-passage diving analysis. fracDim is the fractal dimension of the Intensive Foraging Zones. See 'Materials and methods' for more detailed descriptions

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
No. of dives	**0.40**	0.05	0.06	−0.02	−0.10	0.00	0.08
Modal depth	0.05	0.17	−0.05	0.17	**0.66**	0.00	−0.06
Mean dive duration	−0.10	0.00	**−0.63**	−0.01	0.01	0.11	−0.08
Max. dive duration	0.16	−0.23	**−0.54**	0.05	0.08	−0.14	0.10
Proportion benthic dives	−0.13	**0.42**	**−0.39**	−0.11	−0.20	0.05	−0.09
Modal descent rate	0.04	**0.57**	0.11	0.00	0.14	0.06	0.04
Modal ascent rate	0.06	**0.60**	0.03	0.03	0.00	−0.09	0.01
Modal post-dive duration	−0.07	0.08	−0.22	−0.02	0.06	−0.08	**−0.50**
Trip duration	**0.41**	0.08	−0.04	0.01	−0.09	0.03	0.04
Total distance travelled	**0.48**	−0.01	0.04	0.01	0.09	−0.01	−0.05
Max. distance from colony	**0.45**	−0.12	−0.04	−0.09	0.13	0.11	−0.15
Mean travel speed	−0.07	−0.14	0.14	−0.02	0.26	−0.07	**−0.47**
Mean bearing	−0.19	0.00	−0.05	−0.07	0.25	−0.08	**0.64**
r	0.03	−0.01	0.00	**−0.67**	0.01	−0.04	−0.04
s	−0.03	−0.01	0.00	**0.67**	−0.02	−0.01	−0.05
Number of haul-outs	0.06	0.04	−0.01	0.18	**−0.56**	−0.04	−0.03
Number of IFZ	**0.32**	0.04	−0.18	0.07	0.03	**−0.47**	0.18
IFZ duration	0.17	0.04	0.01	−0.02	−0.05	**0.58**	0.02
IFZ fracDim	−0.03	0.05	0.15	−0.08	−0.11	**−0.60**	−0.15

within the dataset of 19 behavioural indices describing the foraging behaviour of Australian fur seals. Varimax rotation of the 7 retained components revealed strong loadings of different variables onto each component (Table 2). Inspection of the posterior distributions from the MCMCglmm output determined that several of the body shape, age and diet variables assessed had a relationship with the foraging behaviour components (Table 3). Behavioural PC1 (which contained variables describing the duration and distance travelled during a foraging trip as well as the number of times an animal performed intensive foraging behaviour) was influenced by both the age of individuals and their presence in dietary Group 2 (Table 3). This indicates that younger individuals tended to travel further and spend more time at sea than older individuals. Concurrently, individuals belonging to Group 2 were more likely to travel further and spend more time at sea than individuals belonging to other dietary groups (Table 3).

Behavioural PC3 had strong negative loadings for dive duration (mean and maximum), and the proportion of benthic dives was associated with dietary Groups 2 and 3 (Table 3). Individuals within these groups were more likely to have reduced mean and maximum dive durations and proportionately less benthic dives. A negative influence was found between behavioural PC4 (made up of indices representing the shape of the foraging track) and mass (Table 3), indicating that larger individuals made more directed foraging trips (i.e. high *r* score and low *s* score) than smaller individuals. Furthermore, a positive influence was found between individuals grouped into dietary Group 2 and behavioural PC4, indicating that individuals from this group were more likely to have less directed foraging trips (i.e. low *r* score and high *s* score) than individuals in other dietary groupings.

Behavioural PC5, with its strong positive loading on modal depth and negative loading on the number of haul-outs within a foraging trip, was influenced positively by axis length and age (Table 3). This indicated that older, longer individuals were more likely to forage in deeper waters than younger, shorter individuals. Concurrently, while foraging in shallower waters, younger individuals were more likely to haul-out onto land at locations other than the breeding colony. When assessing the influence of morphometric measures (body mass, flipper length and axis length) or age on diet, no effect could be detected in any of the models developed.

Several behavioural principal components were not associated with any of the measures of body shape, age or diet recorded in this study (Behavioural PC2, PC6 and PC7). Similarly, no relationships were found between any of the behavioural principal components and dietary FA Groups 1 and 4.

DISCUSSION

We found that in female Australian fur seals, differences in diet, morphology and age could predict different aspects of an individual seal's behaviour. Variation in experience, body shape and/or size can lead to differing efficiencies when foraging (Mittelbach 1981, Ehlinger 1990, Day & McPhail 1996, Svanback & Eklov 2004); hence, variation in dietary choices and/or foraging strategies may exist within popula-

Table 3. Bayesian generalised linear mixed effects models with Gaussian distributions run using the 7 behavioural principal components derived from principal components analysis of 19 behavioural indices calculated from the tracking and dive behaviour dataset collected from individual female Australian fur seals. The response of these 7 component scores was assessed using predictor variable groupings of body shape, age and diet. FA G1 to G4: fatty acid grouping identified from clustering analysis of individual's fatty acid signature profiles; post-mean: posterior mean; RFL: right flipper length; values in **bold:** significant relationship between that variable and a behavioural principal component

	Behavioural PC1			Behavioural PC2			Behavioural PC3			Behavioural PC4			Behavioural PC5			Behavioural PC6			Behavioural PC7		
	Post-mean	Lower 95% CI	Upper 95% CI	Post-mean	Lower 95% CI	Upper 95% CI	Post-mean	Lower 95% CI	Upper 95% CI	Post-mean	Lower 95% CI	Upper 95% CI	Post-mean	Lower 95% CI	Upper 95% CI	Post-mean	Lower 95% CI	Upper 95% CI	Post-mean	Lower 95% CI	Upper 95% CI
Predictor group 1: body shape (n = 29)																					
Intercept	16.7	1.7	31.8	0.3	−13.6	13.6	0.8	−11.7	13.4	−0.8	−13.1	12.1	−10.4	−22.4	2.0	1.3	−10.2	13.3	−10.1	−22.0	1.9
Mass	<0.1	−0.1	0.1	0.01	<0.1	0.1	<0.1	−0.1	0.1	**−0.1**	**−0.2**	**−0.1**	<0.1	−0.1	0.1	<0.1	−0.1	<0.1	<0.1	−0.1	<0.1
RFL	−0.2	−0.6	0.2	−0.2	−0.6	0.1	<0.1	−0.3	0.3	<0.1	−0.3	0.3	−0.1	−0.4	0.2	−0.1	−0.4	0.2	0.1	−0.2	0.4
Axis	−0.1	−0.3	0.1	0.1	−0.1	0.3	<0.1	−0.2	0.1	0.1	−0.1	0.3	**0.2**	**<0.1**	**0.4**	0.1	−0.1	0.2	0.1	<0.1	0.3
Predictor group 2: age (n = 22)																					
Intercept	3.1	0.9	5.5	−0.6	−2.7	1.4	0.7	−1.4	2.6	1.1	−1.0	3.1	−1.6	−3.5	0.3	−0.7	−2.5	1.3	−0.3	−2.2	1.5
Age	**−0.3**	**−0.6**	**−0.1**	0.1	−0.1	0.3	<0.1	−0.2	0.1	−0.1	−0.3	0.1	**0.2**	**<0.1**	**0.4**	0.1	−0.1	0.3	<0.1	−0.1	0.2
Predictor group 3: diet (n = 24)																					
FA G1	7.0	−54.0	72.0	−39.0	−101.2	18.5	3.2	−52.7	59.7	1.4	−53.6	58.7	−35.1	−91.0	18.0	−11.8	−64.1	40.7	−41.7	−93.6	9.9
FA G2	**2.0**	**0.3**	**3.8**	0.6	−1.2	2.1	**1.6**	**0.1**	**3.2**	**1.7**	**0.2**	**3.3**	0.3	−1.1	1.9	−0.6	−2.0	0.9	0.4	−1.0	1.9
FA G3	1.5	−0.2	3.6	0.2	−1.5	1.9	**1.9**	**0.4**	**3.6**	1.1	−0.5	2.8	−1.5	−3.1	0.0	−0.1	−1.6	1.3	−0.1	−1.6	1.3
FA G4	2.0	−1.5	5.1	0.2	−2.9	3.1	1.9	−0.9	4.6	0.8	−2.3	3.5	−0.3	−3.1	2.4	−0.7	−3.3	1.9	−0.8	−3.4	1.9

tions. Different components of a population may utilise different regions or prey types, and the existence of varying behaviours or dietary specialisations within a population may provide a buffer to environmental change. If behavioural or dietary variation is not maintained within a population, then its ability to respond to environmental change may be compromised. Consequently, identifying and understanding the drivers of behavioural variation within a population is important when making ecosystem management decisions, as measures implemented to protect the population should also protect this variation.

Variation in the diet of Australian fur seals

Several populations of generalist predators have been found to contain groups of individual specialists (Schindler et al. 1997, Woo et al. 2008, Villegas-Amtmann et al. 2008, Newsome et al. 2009). Individual dietary specialisation can help increase overall reproductive success within a population by reducing the degree of intra-specific competition (Van Valen 1965). Australian fur seals have previously been found to display some degree of inter-individual variation in diet (Arnould et al. 2011). The current study found 5 different groupings based on fatty acid dietary analysis, characterised by large differences in 5 individual fatty acids (DHA – 22:6w3, EPA – 20:5w3, 16:1w7c, 16:0 and 18:1w9c). Previous studies have identified that fish in the southeastern Australian region tend to have proportionately lower levels of DHA, EPA and 16:0 combined with higher levels of 16:1w7c and 18:1w9c, whereas cephalopods are the opposite (Baylis et al. 2009, Pethybridge et al. 2010). These studies included several species that are known to be prey of Australian fur seals, including some major prey items (i.e. Gould's squid *Nototodarus gouldi*, redbait *Emmelichthys nitidus* and barracouta *Thyrsites atun*). However, the fatty acid profile of cephalopods has been found to be biased toward their specific diets (Stowasser et al. 2006), therefore cephalopods consumed by Australian fur seals in our study may have had different fatty acid signatures than those in Baylis et al. (2009) and Pethybridge et al. (2010). If they are representative of prey in this region, then the profile of Group 5 would be characteristic of a diet dominated by fish, whereas Groups 1 and 2 would be consistent with a cephalopod-based diet. The combination of proportions of these 5

fatty acids in Groups 3 and 4 were less clear and may represent groups with mixed diets (Baylis et al. 2009, Pethybridge et al. 2010).

It should be noted that milk samples were collected at the beginning of the deployment period rather than at recapture, and thus reflect dietary input prior to the collection of behavioural data. In seals, milk fatty acids are representative of the most recent meals and/or previously stored lipid supplies (Iverson et al. 1997), so the results of the current study may not be completely representative of the subsequently recorded foraging behaviour. Arnould et al. (2011) have previously identified a degree of blood isotope consistency within Australian fur seals, suggesting diet remains similar for at least 28 d. Of the deployments in the current study, 79% were for periods of 28 d or less, providing a degree of confidence that these results may represent, in part, the types of prey being acquired during the subsequently recorded foraging behaviours. However, this study did not utilise serial samples of diet to establish how far beyond this window these dietary preferences were maintained. As such, until studies utilising repeat sampling of individual seals occur, it will be difficult to identify dietary specialisations within Australian fur seals.

Effects of individual differences on foraging behaviour

In pinnipeds, age has been found to affect both the diving behaviour (Austin et al. 2004, McDonald et al. 2009) and foraging movements (Beck et al. 2003) of adult grey seals *Halichoerus grypus* (diving and foraging movements) and Antarctic fur seals *Arctocephalus gazella* (diving behaviour). In the current study, age was found to have a dominant effect on the foraging behaviour of Australian fur seal females, with older individuals foraging nearer to the colony and spending less time at sea. The observed inter-individual differences in trip duration and distance travelled would suggest that different aged animals were encountering different prey densities. It is unlikely this is due to contrasting environmental conditions, as individuals were foraging from the same colony in the same years. Consequently, the findings suggest apparent prey availability must differ between individuals of different ages. This suggests that older seals are exploiting foraging grounds unknown or unavailable to younger individuals from the same colony.

Younger individuals spent more time within their foraging environment, possibly because they do not have the knowledge or experience to find more cryptic foraging grounds nearer to the colony, and are therefore travelling further to find prey. However, it is also possible that younger individuals are competitively excluded from nearby profitable foraging grounds by the older animals. Younger cohorts of many species are pushed into suboptimal habitats by older conspecifics, which allows the older, more dominant animals greater energetic gains and increased success (Ebenman 1987, Persson & Greenberg 1990). This competition and exclusion is one possible mechanism for density dependent control within a population. As a population grows, dominant animals control increasing amounts of optimal foraging habitat, reducing the foraging success and increasing mortality of the younger cohorts (Tschumy 1982). However, current population levels of Australian fur seals are at an estimated 50% of pre-sealing levels and increasing at around 5% per annum (Kirkwood et al. 2005), making density dependent effects unlikely in this population.

It is also possible that older individuals are able to exploit different prey species that are more difficult to locate and capture, and thus inaccessible to younger, less experienced animals. Whereas age was not found to influence the diet of seals in the current study, Arnould et al. (2011) found that age did have an effect on the plasma $\delta^{15}N$ values (an indicator of trophic level) of female Australian fur seals from the same colony. However, the sample size in our study was much smaller, and may not have had the power to detect an age effect. Consequently, a possible shift in diet of Australian fur seals with age leading to differential use of foraging regions (or vice versa) cannot be discounted.

Interestingly, no relationship was found between a female's mass and the behavioural component representing both mean and maximum dive duration (PC3). This is contrary to the results of studies on other species of seal that have found mass to be a significant predictor of dive duration (Horning & Trillmich 1999, Irvine et al. 2000, Costa et al. 2001, Lea et al. 2010, Staniland et al. 2010). Maturation in Australian fur seals is rapid, with individuals reaching 87% of their maximum body size in 3 yr (Gibbens & Arnould 2009). In the present study, females with concurrent age and behavioural data were at least 4 yr old, meaning that all were at least 87% of their maximum size (Gibbens & Arnould 2009). During development, dive duration is correlated with the mass/age of Australian fur seal pups (Spence-Bailey et al. 2007). However, the results of our study suggest that once animals reach maturity,

body mass, and by proxy aerobic capacity, is not a limiting factor during foraging. Gibbens & Arnould (2009) suggested that rapid growth in Australian fur seals might be adaptive and due to a benthic mode of foraging, allowing individuals access to prey on the seafloor sooner. The bathymetry within Bass Strait is extremely flat and shallow, averaging 86 m (Passlow et al. 2006). Thus, once animals reach a large enough size that they are able to efficiently exploit these depths, the benefits of additional aerobic stores may be minimal. A similar response has been found in adult female northern fur seals *Callorhinus ursinus*, whose body size does not appear to be a driving factor in the duration of dives (Skinner et al. 2012).

Australian fur seals exhibit a degree of inter-trip fidelity to foraging sites (Kirkwood & Arnould 2011), suggesting that individuals utilise prior knowledge when making foraging decisions. In the current study, heavier individuals tended to show greater intra-trip fidelity to a travel direction (high *r* value) and had foraging trips that were less dispersed (low *s* value). This suggests that heavier (presumably more successful) individuals may be utilising their prior knowledge to travel directly to areas where foraging success has been high on previous trips.

Conversely, the minimal influence of morphometric measures on foraging behaviour may be a result of the measures chosen, rather than the foraging behaviour of individuals seals themselves. The measures we used (mass, flipper length and axis length) only give an approximation of body shape and may lack the sensitivity to act as more specific predictors of foraging behaviour. Future work would benefit from the inclusion of higher resolution of body shape (i.e. through the use of 3D modelling) to determine the influence of morphology on fur seal foraging behaviour.

In summary, our study highlighted that even within a phenotypically similar group of animals, intrinsic variation exists and it is in part driven by morphological and age differences. Furthermore, we determined that adult female Australian fur seals can be differentiated into groups based on diet, and that some relationships can be elucidated between these dietary groups and behaviour. However, the lack of overlapping diet and behaviour data means that until further studies investigate this link further, our results should be viewed with caution. Considerations for the existence of different behavioural and/or dietary groupings and the processes (e.g. body size and age) that drive them, such as those found in the present study, should be investigated in other species, especially if management decisions are required. Future work would benefit by further cementing the links between diet and behaviour discovered here, and should extend these results to determine whether similar responses exist in adult male Australian fur seals.

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