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Segregation between the sexes: Antarctic fur seals, *Arctocephalus gazella*, foraging at South Georgia

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Antarctic fur seals show extreme sexual size dimorphism and their breeding strategies place very different constraints on the behaviour of males and females. Whereas the foraging behaviour of lactating females is well studied, very little is known about males. We tracked 14 adult males during a period when they are observed around South Georgia to compare their behaviour with that of 41 lactating females tracked from the same island. There was significant spatial segregation between the sexes in both the horizontal and the vertical dimensions. Female fur seals foraged near the surface, mostly at night, concentrating their efforts at the shelf break and in deeper off-shelf waters. Males foraged closer to the breeding beaches and their time at sea was concentrated in waters over the continental shelf. Males dived significantly deeper and longer and spent longer in the bottom phase of a dive than females. Females dived mostly at night, whereas males dived much more during the day and overall had greater variability in their behaviour within a trip. Sex was a better predictor of dive durations than mass when depth was considered. Categorizing dives into three types showed that males often foraged on or near the bottom, a behaviour not observed in females. We suggest that body size dimorphism causes sexual differences in foraging behaviour (e.g. dive depth, duration, etc.) but how this is manifested (i.e. trip distance, foraging location) is dependent on the local environment and the related prey resources.

Keywords: Antarctic fur seal; *Arctocephalus gazella*; diving; foraging; niche width; resource partitioning; sexual dimorphism; sexual segregation

Niche theory has been used to explain community structure and competition for resources amongst organisms (Pianka 1981). Whereas interspecific interactions are clearly very important, there is an increasing recognition of the role of intraspecific competition (Bolnick et al. 2003; Polis 1984). Populations tend to stabilize where competition between conspecifics is reduced by resource partitioning (Tschumy 1982). This partitioning can take the form of different diets, habitat use or foraging behaviour (Schoener 1986) and is driven by interference competition or exclusion from resources as a result of evolutionary selection (Polis 1984). The overall niche width of a species can be effectively increased if there are differences in resource use by different phenotypes (Bolnick et al. 2003). Ontogenetic niche shifts are important in many species and are often strongly related to body size (Field et al. 2005; Polis 1984; Woodward & Hildrew 2002). Sexual segregation in niche use has also been identified in a wide range of species (Mysterud 2000; Pearson et al. 2002; Ruckstuhl & Neuhaus 2005). Several hypotheses have been proposed to explain sexual segregation: forage selection (sexes requiring different food or water resources), predator avoidance, activity budgets and social affinity have been proposed as driving forces. Most hypotheses proposed to explain sexual segregation predict a positive correlation between body size dimorphism and degree of segregation (Mysterud 2000). The size of an animal has a strong effect on its behaviour compared to conspecifics. This is due largely to the increased maintenance costs of larger body sizes that translate into increased energy requirements. However, size can also affect several other important factors such as the susceptibility to predation and physiological constraints, for example, thermoregulation, travel speed and, in diving predators, their aerobic limits. Whereas the study of how and why the sexes

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segregate has been recognized as important, research has been restricted mostly to ungulates and terrestrial systems. Pinnipeds show some of the most extreme sexual size dimorphism within vertebrates (Staniland 2005). Male southern elephant seals, *Mirounga leonina*, can be over six times larger than females whereas male otariid seals attain at least twice the size of females. Their large size and aggressive nature, coupled with an unpredictable response to intravenous/muscular anaesthesia, has meant that few studies have investigated the at-sea behaviour of male otariids. In the few studies carried out, large differences between males and females have been observed. New Zealand fur seal, *Arctocephalus forsteri*, males, had longer foraging trips and dived deeper and longer than females and there was significant spatial separation between them at sea (Page et al. 2005, 2006). A single male Australian fur seal, *Arctocephalus pusillus doriferus*, was recorded diving to shallower depths than conspecific females and, unlike the typical nocturnal foraging behaviour of females, it had no diurnal pattern to its diving (Hindell & Pemberton 1997). However, this animal was part of a translocation experiment so that its behaviour may not have been typical. A few studies have managed to acquire at-sea locations for male otariids. Male South American sea lions, *Otaria flavescens*, undertook longer foraging trips and travelled farther than their female counterparts but there was some degree of overlap in their locations (Campagna et al. 2001). Adult male Australian fur seals foraged in the same area of the Bass Strait as females, although smaller males showed greater segregation and often foraged farther away (Kirkwood et al. 2006). Postbreeding, when there is no requirement for them to associate with females, male northern fur seals, *Callorhinus ursinus*, and Antarctic fur seals, *Arctocephalus gazella*, were observed to migrate long distances away from the breeding beaches (Loughlin et al. 1999; Boyd et al. 1998).

Antarctic fur seals breed in large numbers at South Georgia. Females come ashore in late November/early December to give birth and, for the following 4 months, undertake foraging trips at sea (2–10 days) interspersed with periods ashore to suckle their pups (1–4 days). During this time they are a major consumer of Antarctic krill, *Euphausia superba* (Boyd 2002), but also impact the local fish species (Reid & Arnould 1996). As with many pinniped populations this causes a potential for competition with fisheries (Everson et al. 1999) and therefore information about Antarctic fur seal foraging has been used to define small-scale management units.

Male Antarctic fur seals can weigh up to four times as much as the largest females and provide no parental care. Thus, males have very different physiological constraints on their foraging and, unlike central place foraging mothers, have no need to return to land to nurse offspring. We might therefore expect large differences in the foraging behaviour of the sexes. Whereas the foraging behaviour of females is well described, at least during the breeding season (McCafferty et al. 1998; Boyd et al. 2002; Staniland & Boyd 2003), our knowledge of adult males is restricted mostly to their land-based breeding behaviour (Boyd & Duck 1991; Arnould & Duck 1997; McCann 1980). Postbreeding migrations of three males showed that they travelled south and dived slightly deeper than females (Boyd et al. 1998). However, male fur seals are observed on the beaches of South Georgia throughout the winter with numbers increasing during October–November to a peak in the main breeding season during December. During this period males lay down energy reserves to maximize their potential to fast ashore (Boyd & Duck 1991). Also males, being larger, have greater absolute energy requirements than females with a full-grown male (3.8 tons year^{-1}) requiring almost twice as much food as a breeding female (1.9 tons year^{-1}) (Boyd 2002). These requirements suggest that if adult males forage around South Georgia immediately prior to breeding they could consume in the region of 1200 tons of krill per day based on the conservative population size of Boyd (2002).

In this study, we investigated the foraging behaviour of adult male fur seals while they were resident at South Georgia and compared it to the corresponding female behaviour. We investigated the effects of different physiological and breeding constraints on the two sexes. We sought to determine which areas were important to male fur seals and to ascertain any overlap in the foraging areas of the two sexes during a time when they come together for breeding.

METHODS

Equipment and Tracking

Fourteen male fur seals were tracked on trips to sea from Bird Island, South Georgia (54°00′S, 38°02′W), during November and December 2004. Males were approached while asleep and restrained by placing a net over the head, as the animals moved away and into the net their movements became restricted by its tapering shape. At the end of the net a small reinforced opening held the animal's muzzle, closing the mouth but leaving the nostrils clear. Netted animals were physically restrained by two people and anaesthetized using an isoflourane (2–5%) – oxygen mix delivered by a mask from a portable vaporizing system. From initial netting until the mask was in position took on average (mean ± SD) 3 ± 1 min and animals were anaesthetized for 42 ± 2.5 min. Pure oxygen was given at the end of the procedure, until consciousness returned, to aid recovery (mean = 8 ± 1 min).

Once stable, the seals were weighed and measured before instruments were attached to the dorsal fur along the line of the spine using quickset two-part epoxy resin. Five seals were instrumented with Sea Mammal Research Unit satellite-relayed data loggers (SRDLs; SMRU, St. Andrews, U.K.; 370 g, 10.5 × 7 × 4 cm) programmed to prioritize the relay of depth, temperature and light data via the Argos (CLS, Saint-Agne, France) system. Platform transmitter terminals (PTTs; Sirtrack, Havelock North, NZ; Kiwisat 101; 245 g 13 × 6.5 × 1.9 cm) were deployed on the remaining nine seals and time depth recorders (TDRs; Wildlife Computers MK7; 50 g, 9.5 × 2.5 × 2.5 cm) were deployed on three of these individuals for the later part of their tracking period. Animals were recaptured in the same manner to remove the tracking equipment. However, the time of anaesthesia was considerably reduced,