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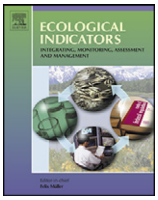

Foraging distribution overlap and marine reserve usage amongst sub-Antarctic predators inferred from a multi-species satellite tagging experiment

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ABSTRACT

Satellite telemetry data was used to predict at sea spatial usage of five top order and meso-predators; Antarctic fur seals (*Arctocephalus gazella*), macaroni penguins (*Eudyptes chrysolophus*), king penguins (*Aptenodytes patagonicus*), black browed albatross (*Diomedea melanophrys*), and light mantled albatross (*Phoebetria palpebrata*). All were tagged at Heard Island in the Southern Ocean over a single summer season collecting over 5000 tracking days for 178 individuals. We aimed to predict areas of likely high foraging value from tracking environmental data and also to quantify overlap in foraging range between species. Hidden Markov models were used to differentiate between bouts of Area Restricted Search (ARS) assumed to be associated with areas of higher foraging value, and transit behaviours. Oceanographic and distance metrics associated with ARS activity were then used to calculate a habitat electivity index. A combined bootstrap/Monte Carlo scheme was employed to propagate uncertainty from the Hidden Markov models into the habitat prediction scheme. Distinct differences were predicted in the spatial distribution of foraging locations in different species, reflecting different dispersive abilities and foraging strategy. The extent of usage and foraging distribution was largely contained within Australian the Economic Exclusion Zone (EEZ). In comparison, the smaller Australian Commonwealth Marine Protected Areas (MPAs) contained <20% of the predicted foraging distributions.

1. Introduction

1.1. Significance and impediments to predicting at-sea usage

Prediction of at-sea distribution and habitat preference of marine predators is an important task for estimation of abundance (Sharples et al., 2009), design of reserves (Ballard et al., 2012), calculating the risk of interactions with fisheries (Thaxter et al., 2012), other anthropogenic activities (*e.g.* Richardson et al., 1987; Desholm and Kahlert 2005) and also in assessing the role of competition in driving ecosystem change (Trites et al., 2007). Ballard et al. (2012) state that “designation of effective Marine Protected Areas (MPAs) requires substantial knowledge of the spatial use of the region by key species, particularly those of high mobility”. Advances in telemetry technology (McConnell et al., 2010) have now provided the observational capacity to assess the extent of that mobility for species that forage at sea and are difficult to observe directly. However, analytical methods that infer usage directly from those data (*e.g.* kernel density methods) require tracks from large numbers of individuals so that they are not unduly influenced by any one individual’s track. More advanced modelling methods may be better able to address some of the limitations that are typical in real-world data, such as limited sample sizes and deployments made at different times on different individuals.

These limitations necessitate a prominent role for spatial and usage distribution models which predict beyond the observations at hand (Ballard et al., 2012). However, there are two complex and

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inter-related impediments to predicting at-sea usage or distribution:

(1) mere presence of a species in an area may be insufficient to infer the value of that area (Bestley et al., 2008), thus, methods capable of discerning relatively high value regions are required.
(2) These must also be capable of predicting, with associated uncertainty, the spatial occurrence of similar locations based on a sample of individuals from a large population.

Determining how animals use space from tracking data generally requires inference of likely behaviour (often “transit” vs “searching” or “foraging”) purely from observed movement patterns. Many studies have noted that animals move in at least two modes; one, variously labelled “extrinsic”, “ballistic” or simply “transit”, corresponds to relatively fast travel in a consistent direction. This is contrasted with intensive or Area Restricted Search (ARS) (Fauchald and Tveraa 2003) behaviour which is associated with low speed and high turning rate (Kareiva and Odell 1987; Knell and Codling 2012). These movement behaviours are related to the patchiness of the environment and when prey are located: slower movements with higher turning rates increase the likelihood of encountering further prey resources (Boyd 1996; Le Boeuf et al., 2000). Stochastic models of individual movement and behaviour (Patterson et al., 2008) provide a statistically robust approach by which periods of residence and likely foraging behaviour can be estimated from satellite telemetry data (Jonsen et al., 2005; Dragon et al., 2012). An emerging challenge in movement studies is combining these models (with their associated uncertainty) with other sources of information, such as environmental parameters, to develop habitat usage models (Bestley et al., 2013)

1.2. *An approach to predicting high value areas*

In this paper we combine state space models for categorising movement behaviour, with a habitat prediction approach which explicitly predicts areas of likely increased foraging effort. (*i.e.* ARS), such that uncertainty in the former is propagated into predictions of spatial distribution. We apply this to tracking datasets for five species; Antarctic fur seals (*Arctocephalus gazella* Peters, 1875), macaroni penguins (*Eudyptes chrysolophus*, Brandt, 1837), king penguins (*Aptenodytes patagonicus* Miller, 1778), black browed albatross (*Diomedea melanophrys*, Temminck, 1828), and light mantled albatross (*Phoebetria palpebrata*, Forster 1785) tagged concurrently at Heard Island in the austral summer of 2003-4. At this time of year, the adults of these species are central place foragers, interspersing periods ashore provisioning young with periods of at-sea foraging. However, there are contrasting energy requirements among the species, due to differences in life history, breeding schedules and diet, resulting in divergent foraging patterns. Nonetheless, individuals will seek to maximise energy gains by feeding in regions where prey are more abundant, densely aggregated or more predictable (Lea et al., 2006), and so there are likely to be regions utilised by two or more predator species simultaneously (Hindell et al., 2011) and these are likely to be areas of particular ecological significance.

1.3. *The significance of the study area, Heard Island*

Understanding the physical conditions which signify foraging habitat for top predators has been the focus of a great many studies (Boyd et al., 2006; Sydeman et al., 2006; Block et al., 2011). Our study area, in the vicinity of Heard Island and Iles Kerguelen, is situated on the Kerguelen Plateau, one of the World’s largest oceanic ridges. Being one of the few land masses in this region, this location, along with the nearby Iles Kerguelen, is an important location for land-based marine predators (Bost et al., 2000; Inchausti et al., 2003; Lea et al., 2006, 2008; Hindell et al., 2011); two species of seal breed on Heard Island along with four breeding and three non-breeding penguin species (Meyer et al., 2000a). Additionally, fifteen species of flying seabirds use the area as a breeding location (Meyer et al., 2000a). For these reasons, along with its diverse demersal habitat, and importance in fisheries management (Green et al., 1998; Lord et al., 2006), the area has been noted to have high conservation values and parts of the surrounding Australian EEZ have been designated an MPA. The Kerguelen Plateau area extends over 2000 km from the Antarctic continent into the Southern Ocean. The islands are situated amongst the convergence of temperate and polar waters – Heard Island is directly within the Antarctic Circumpolar Current and close to the Polar Front (van Wijk et al., 2010). As such, the fact that both Heard Is. and Iles Kerguelen are the only available land masses in the region and are within close proximity to significant oceanographic features, these features are crucial to understanding the foraging ecology of mobile predators in the region.

All animals in this study were tracked in the same austral summer season of 2003–2044. It is therefore important, at the outset, to consider the representativeness of this season against long run averages. One of the major sources of variability in oceanographic conditions in the region is the path of the polar front, which varies in its meridional position from year to year. The front has shown a southward trend in position since 1992 (Sokolov and Rintoul 2009), and may also exhibit marked changes in path where it interacts with the Kerguelen Plateau. While it is accepted that the southern branch of the polar front passes through Fawn Trough to the south of Heard Island, the northern branch has historically passed either to the north of the Kerguelen Plateau, or south of Heard Island also through Fawn Trough, nearly ten degrees of latitude further south (Sokolov and Rintoul 2009). The variations in frontal position are known to affect the foraging behaviour of king penguins breeding on Crozet Island and foraging to the west of the HIMI region (Péron et al., 2012). During the 2003/04 summer season (the focus of this paper) the polar front was in a southerly phase, which persisted until at least 2008 (Sokolov and Rintoul 2009; Péron et al., 2012). Thus, the foraging distributions reported here, although based on only a single study season we would expect to be typical of other years. The southward movement of Southern Ocean fronts is predicted to continue into the future (Péron et al., 2012). As this 2003/2004 season represents data collected in the southerly phase the behaviour recorded here could be expected to be representative for the years to come.

1.4. *Use of physical variables to represent areas of high productivity*

While many studies have linked physical variables to predator behaviour and distribution (*e.g.* Lea et al., 2006; Bailleul et al., 2007a; Biuw et al., 2007; Wakefield et al., 2009a), the physical state of the ocean, or even predictions of primary productivity, constitute only proximate predictors of the distribution of top predators. This is due to the many chains of trophic and non-trophic interactions which take place before influencing the behaviour of top predators, but typically, data on the density and distribution of prey species are unavailable. Accordingly, the responses of marine top predators are viewed as integrating across lower trophic levels (Croxall et al., 1992; Reid and Croxall 2001). Yet, direct effects of measurable physical variables are likely; simple measures such as distance from a haul-out location dictates accessibility of habitat (Aarts et al., 2008) especially during stages of rearing young; high ice concentrations may restrict some species’ access to otherwise productive habitat (Bailleul et al., 2007b; Pomerleau et al., 2011). Nonetheless, determining which habitat covariates to include in a spatial distribution