



Protected area use by two sympatric marine predators repopulating their historical range

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ABSTRACT: As large carnivores recover from over-exploitation, managers often lack evidence-based information on species habitat requirements and the efficacy of management practices, particularly where species repopulate areas from which they have long been extirpated. We investigated the movement and habitat use by 2 semi-aquatic carnivores (Australian fur seals *Arctocephalus pusillus doriferus* and New Zealand fur seals *A. forsteri*) at the northern end of their distributions in Australia, where after a long absence both are recolonising their historic range. We also assessed male fur seal habitat use overlap with terrestrial and marine protected areas (PAs). While at the margin of the range during winter and early spring, the males remained inshore close to terrestrial sites and where interactions with humans often occur. From early spring, the males from the range margin showed uniform movement toward colonies in the core of the species' range prior to their breeding seasons. This contrasts with males tracked from the core of the species' range that returned periodically to colonies during the year, and highlights the importance of range-wide monitoring of a species to inform conservation planning. Habitat use by some males included over 90 % of a marine PA at the margin of the species' range. Most terrestrial haul-outs used were within terrestrial PAs, while sites not protected were on the margin of the range. Despite wide-ranging habits, their dependence on coastal sites, where human access and activities can be regulated and more readily enforced, suggests that terrestrial and marine PAs will continue to play an important role in managing the recovery of these fur seals.

KEY WORDS: Fur seal · *Arctocephalus* · Habitat use · Distribution · Population recovery · Recolonisation · Human–wildlife interaction

1. INTRODUCTION

Conservation efforts have increased the population sizes of many large carnivores, and have either expanded their ranges or allowed recovery into histori-

cal ranges (Chapron et al. 2014, Gompper et al. 2015, Karamanlidis et al. 2015, Martínez Cano et al. 2016). These changes often result in increased conflicts between humans and carnivores and among humans (e.g. conservationists and industries) (Treves & Karanth

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2003, Miller et al. 2013). Interactions at expanding range margins can be challenging for humans, who are more often ill prepared to manage such change (Ciucci & Boitani 1998, Trouwborst et al. 2015, Morehouse & Boyce 2017). While lethal methods are often deployed to alleviate conflict, they are counter-productive for conservation of recovering species and do not necessarily reduce conflicts (Stahl et al. 2001, Treves 2009). Non-lethal management alternatives (e.g. Shivik 2004) are important to resolve human–carnivore conflicts and create a future where humans and competing wildlife coexist (Woodroffe et al. 2005). Accordingly, there is growing interest in identifying habitat selection by large carnivores and locating potential ‘conflict hotspots’ (Miller 2015). This can help prioritise limited management resources into areas with high-risk human–carnivore interactions. In this study, we investigated the movements of individuals from recovering populations of large semi-aquatic carnivores, fur seals, which are often seen by fishermen as competitors. We focussed on a region where 2 species have recently greatly expanded their geographic ranges after a long absence resulting from sealing in the 19th and early 20th centuries. We quantified habitat use and compared marine and terrestrial areas in relation to their protected status for conservation planning.

Protected areas are a widely used, multi-purpose management tool (J. E. Watson et al. 2014). Protected areas may conserve biodiversity and ecosystem functions, protect natural and cultural features, preserve human assets (e.g. forests and water resources) and minimise human impacts. By regulating human access and activities, protected areas can play a role in mitigating negative interactions with wildlife and aid the recovery of large carnivores (Linnell et al. 2005, Chapron et al. 2014, Santini et al. 2016). Protected areas are used in terrestrial and marine contexts, and when located along a coastline, they can assist in managing human impacts on adjacent marine and terrestrial habitats (Stoms et al. 2005). These areas are typically not designed specifically to mitigate interactions between humans and wide-ranging species, because their small boundaries do not sufficiently capture the species’ large foraging ranges (Hooker et al. 2011). However, despite many large carnivores ranging widely to feed, they often use discrete areas for essential activities such as breeding, moulting, resting and avoiding predators; for these activities, discrete protected areas may have beneficial effects (Huon et al. 2015, McAllister et al. 2015, Pérez-Jorge et al. 2015).

Protected area design often includes multiple use zoning where human activities are restricted to dif-

ferent extents depending upon intent. For example, within Australia’s marine park network, there may be 4 or more tiers of protection zones, ranging from no-take zones to areas where only certain types of fishing (e.g. commercial) are prohibited (Roberts et al. 2018). These zones can focus human activities into areas where they will cause the least disruption to animals, whilst allowing compatible activities to continue. With effective mitigation of negative human–carnivore interactions, protected areas can help sustain populations (Barnes et al. 2016), directly improve their demographic parameters (Gormley et al. 2012) and support ecosystem recovery (Prato et al. 2013). This suggests that conservation management of carnivores moving back into their historical ranges could be improved if existing protected areas with suitable habitat for essential activities by these carnivores could be identified.

Semi-aquatic species have a strong reliance on coastal habitats where we now also have high-density human populations, so it is not surprising that they have a long history of interactions with humans. Many species have been harvested, or culled to reduce fisheries and aquaculture interactions, but are now recovering (Gerber & Hilborn 2001, Kirkwood & Goldsworthy 2013, Magera et al. 2013). In Australia, the New Zealand fur seal *Arctocephalus forsteri* (also called long-nosed fur seal, Shaughnessy & Goldsworthy 2015) and the Australian fur seal *A. pusillus doriferus* are both recovering from past exploitation (Shaughnessy et al. 2015, McIntosh et al. 2018b). Both species are protected by national law under the Environmental Protection and Biodiversity Conservation Act 1999 and are the subjects of a national strategy to minimise adverse interactions with human activities (National Seal Strategy Group 2007). As with other semi-aquatic species, interactions between fur seals and humans occur on land and at sea, with fisheries, aquaculture and tourism industries and the general public (Kirkwood et al. 2003, Shaughnessy et al. 2003, Robinson et al. 2008b), and are likely to increase as seal populations continue to recover and industries develop (Schumann et al. 2013). These interactions can result in economic loss or injury to humans, and stress, changed behaviour, injury or death of seals. Therefore, it is important to have accurate information to correctly assess seal–human interactions and their consequences as seal populations recover (Costalago et al. 2019).

Currently, little information is available on the movements and habitat use by the 2 fur seal species in Australasia on which to base management plans, as most information is focussed on females (Harcourt

et al. 2001, Kirkwood & Goldsworthy 2013, Hoskins et al. 2017). Most studies on male movements and habitat use are from the core of the species' range (Kirkwood et al. 2006, Page et al. 2006, Knox et al. 2017). These studies have focussed on foraging behaviour and at-sea habitat use: Australian fur seals occupy mostly shelf waters (Kernaléguen et al. 2015, Knox et al. 2017), and New Zealand fur seals occupy a combination of shelf and pelagic waters (Page et al. 2006). Their at-sea movements can be strongly associated with fishing activities, such as fish farms, which generate a predictable source of food (Robinson et al. 2008a). While there is some segregation in behaviour and foraging niche between these 2 fur seal species (Page et al. 2005, 2006, Hardy et al. 2017, Hoskins et al. 2017), both interact similarly with human activities and accordingly management practices tend not to differentiate between them. With studies focussed on the foraging behaviour and broader habitat use (e.g. benthic versus pelagic) of seals, there is limited information on how they use discrete terrestrial haul-out sites and the waters adjacent to those sites, where interactions with tourism and recreational activities often occur, and can have lethal consequences (Back et al. 2018). Importantly, movements and habitat use by male fur seals at the periphery of both species' geographic range are unknown: this is the case in New South Wales, along the east coast of Australia, where the population is growing and a breeding population recently established (Warneke 1975, Irvine et al. 1997, Hardy et al. 2017). This continuing expansion along the margin of their range is therefore likely to see an increase in human–wildlife conflict, and humans appear to be less experienced and prepared for this type of conflict (Shaughnessy et al. 2008).

The east coast of Australia is subject to significant coastal development and human use of marine resources. Networks of marine protected areas have been established to protect representative marine habitats and biological diversity, and to maintain ecosystem processes (Lynch et al. 2013), but have not been designated specifically to protect seals. As fur seals have expanded northward along the east coast, they have established haul-outs within one of these marine protected areas: Jervis Bay Marine Park (JBMP). The seals are now seasonally abundant in JBMP (Burleigh et al. 2008), but it is unclear what habitats they require and whether these habitats are within existing marine and terrestrial protected areas.

We investigated the on-land and at-sea movements and habitat use by 2 species of fur seals that reside in the expanding margin of their range. By evaluating

the frequency of visitation to different habitats, we identified areas likely to be important to the seals and where interactions with humans could be most acute. By overlaying haul-out site use and foraging ranges with the distribution of terrestrial and marine protected areas, we assessed whether important areas used by seals at the margin of their range are receiving protection. The seals at this range margin are seasonally abundant, so the tracking study also aimed to determine how long the seals are in residence and where they go when they leave. This may help conservation managers to identify habitats into which the population might expand; thus, connectivity between core and peripheral populations was also investigated.

2. MATERIALS AND METHODS

2.1. Animal handling and data collection

The movements of male New Zealand fur seals (NZFS) and Australian fur seals (AuFS) from Lamond Head, Jervis Bay, Australia (35° 3' S, 150° 50' E) (Fig. 1) were recorded with Mk10-AFs Fastloc-GPS devices (Wildlife Computers; 105 × 60 × 20 mm, 240 g). Individuals were selected based on their proximity to a suitable access point to their rocky platform terraces at the base of a 30 m high cliff face. Species were distinguished by their pelage, facial structure and cusps on their post-canine teeth (Kirkwood & Goldsworthy 2013). To attach the device, each seal was sedated with a light intra-muscular injection of zoletil (dose rate based on estimated seal weight was 1 to 1.5 mg kg⁻¹) that was delivered remotely with the aid of a pneumatic dart-gun, then approached and restrained in a catch net before being maintained under sedation with a mix of oxygen and isoflurane (approximately 1.5 to 2% isoflurane; adjusted as required) delivered via a portable vaporiser (Gales & Mattlin 1998). While sedated, seals were measured using standard methods (Kirkwood et al. 2006), and the telemetry device was glued to the dorsal midline of each seal with a quick-setting epoxy (Araldite® K-268, Huntsman Advanced Materials; Quick Set Epoxy Resin 850-940, RS Components). Measurements were used to approximate the life stage of individuals (juvenile or adult) (Warneke & Shaughnessy 1985, Arnould & Warneke 2002, McKenzie et al. 2007a,b). Deployments occurred in 2011, 2012 and 2013 from June to August, when seal numbers ashore tend to increase (Burleigh et al. 2008). The devices transmitted GPS location (collected at 2 min intervals,

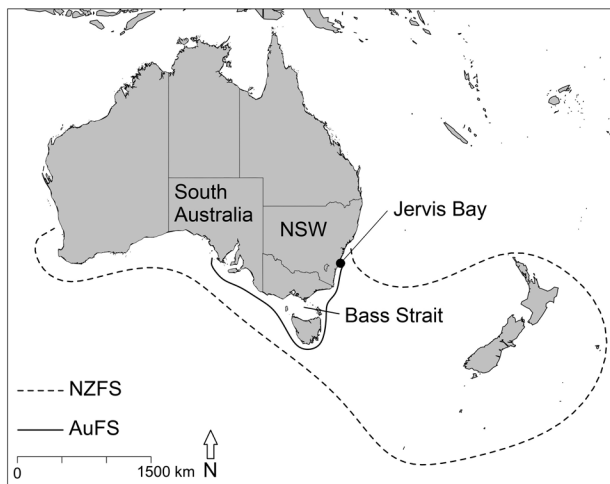


Fig. 1. Approximate range of New Zealand fur seals (NZFS) *Arctocephalus forsteri* and Australian fur seals (AuFS) *A. pusillus doriferus* (dashed line and solid line, respectively) and the site of deployment (Lamond Head, Jervis Bay; solid circle) in New South Wales, Australia (NSW Marine Parks Authority 2010). NSW is at the margin of both species' range (i.e. the edge of their breeding range and where several haul-out sites are established), and Bass Strait and the South Australia coast are the core of the range (where large breeding populations occur) for AuFS and NZFS species, respectively

and median fix rate received via satellite transmission was 1 fix per 1.5 h), behaviour data (e.g. dive and surface interval events, including their duration) and histogram summary data (e.g. percentage time at different depths and performing dives in 6 h intervals) via the Argos satellite network (Collecte Localisation Satellites) until the battery failed or the tag fell off the seal. Fastloc-GPS locations were post-processed with satellite ephemeris and almanac data (Fastloc-GPS Solver version 1.0.56, Wildlife Computers), which retained locations with at least 4 satellite acquisitions and an accuracy typically within 10s of metres (Dujon et al. 2014).

2.2. Movements on land and at sea

To distinguish when a seal was at sea (i.e. on a 'trip') or on land (i.e. hauled out), we used a combination of data sources from the telemetry device to complete gaps in individual data sources. First, locations were pre-defined as wet or dry by the device, based on the conductivity sensor. Second, between location time-stamps, we used behaviour data on single dives (movements below 2 m for greater than 10 s), post-dive surface intervals (i.e. an interval when the tag was at the surface and wet) and surface

intervals ashore (i.e. an interval when the tag was at the surface and dry for 20 consecutive minutes and ceased when wet for >30 s of a minute). Third, between location time-stamps and in the absence of behaviour data, we used histogram data summaries of time spent in dive and surface behaviours and periods hauled-out. A seal was indicative of being at sea between time-steps where the device was recorded as wet, dives or post-dive surface intervals were recorded, and 100% of a 6 h histogram summary was spent in dive and surface behaviours. A seal was indicative of being on land when the device was recorded as dry and where 100% of a 6 h histogram summary was spent hauled out. To better estimate the time on land and at sea, the transition between land and water was estimated to occur at the mid-point between an interval on land and at sea. If no location was recorded while a seal was defined as being on land, a haul-out location (or 'site') was assigned based on the proximity of recent locations to known haul-out sites.

On-land locations were pre-processed to account for variance in location accuracy when quantifying terrestrial habitat use. Locations were visually clustered into groups or 'sites', based on known site locations and applying a maximum 200 m diameter per group (which was the size of most point clusters and consistent with the size of known haul-out sites, (M. Salton pers. obs.)). We then calculated the length of time on land, or 'visits' ashore, the frequency of visits to each site and the number of individuals visiting each site. Sites were defined as being either a non-breeding site or breeding site based on a recent pup census throughout the species' range (McIntosh et al. 2014) and knowledge from experienced observers (R. Kirkwood pers. obs. and A. Irvine pers. comm.).

At-sea habitat use was quantified using 2 parameters: trip duration and foraging range. Trip duration was the time elapsed between a departure and a return to land. The foraging range was quantified using permissible home range estimation (Tarjan & Tinker 2016). This method incorporates underlying environmental information into probability estimates to define a permissible foraging range. Land was used as the environmental predictor (i.e. proximity to coast/land). Distance-from-land values were measured as the Euclidean distance from the closest shoreline feature (GEODATA Coast 100K 2004, Geoscience Australia). Areas on land were assigned a distance value of 0. The distance-from-land values were log-transformed to normalize the empirical data distribution. The smoothing parameter was calculated using the

univariate plug-in selector of Wand & Jones (1994) for the distance-from-land values, employed in the R package 'ks' v1.8.13 (Duong 2013). Probability values were estimated across 2 scales depending on location as a compromise between resolution and processing time: (1) a 500×500 m grid for areas <40 km from shore, and (2) a 5000×5000 m grid for areas >40 km from shore. The at-sea distribution for each individual was quantified at the margin of the range (i.e. New South Wales, at the edge of the breeding range and where several haul-out sites are established) and core of the range (where numerous breeding sites are located) using the 90% utilisation distribution (home range; HR) and 50% utilisation distribution (core range; CR). To test change in foraging trips and the size of the distributions between the margin and core of their range, we used a Student's *t*-test and a Wilcoxon's test, respectively, with the latter based on paired individuals (i.e. those for which we recorded distributions in both parts of the range) and accounted for non-normal distributions and unequal variance. The variability among individuals was assessed by calculating the total area used by all individuals and the percentage of that area used by 2 or more individuals (e.g. the area where at least 2 distributions overlapped).

2.3. Overlap with protected areas

We used different approaches to assess whether terrestrial and at-sea habitat used by the seals overlapped with protected areas, because haul-out sites were discrete locations while at-sea areas were spatial areas (i.e. polygons). Haul-out sites were classed as inside or outside a protected area, where a protected area is any spatial management area listed under the IUCN global protected area programme (Dudley 2008). The primary interest was at the margin of the range, but we also assessed how seals used sites and the overlap of sites with terrestrial protected areas when the seals dispersed from the margin of the range. For at-sea habitat use, we quantified how much of a fur seal's foraging range overlapped with the marine protected area that was consistently occupied by the seals at the margin of the range, i.e. JBMP. All data were processed and analysed

with R v2.15.1 (R Development Core Team 2012). Means are presented \pm SE.

3. RESULTS

Eleven adult male NZFS were tagged (4 in 2011, 2 in 2012, 5 in 2013) and 4 adult male AuFS were tagged in 2013. NZFS weighed 95 ± 6 kg and AuFS weighed 160 ± 39 kg (Table 1). The 15 seals were tracked for 129 ± 51 d (range: 21–204 d), and the period of tracking covered 21 June to 25 January in 2011, 2012 and 2013 (Table 1). We recorded 865 trips (range: 17–91 trips per seal), and from these we calculated that individuals spent $70 \pm 7\%$ of their time at sea (range: 58–82%) (Table 1) and otherwise they were on land.

3.1. Behaviour at the margin of the range

All seals remained at the northern margin of the range (i.e. New South Wales, Australia) during the austral winter months. From 17 September, both species departed the margin of the range and moved south towards the core of the range where there are established breeding colonies (mean departure dates: AuFS 13 October \pm 10 d, NZFS 15 October \pm 6 d).

The seals used 26 haul-out sites while at the margin of the range and spent 14.8 ± 1.0 h ashore (range: 25 min to 4.2 d). Each individual visited between 4

Table 1. Deployment summary for male New Zealand fur seals (NZ) *Arctocephalus forsteri* and Australian fur seals (Au) *A. pusillus doriferus* at Lamond Head, Jervis Bay, New South Wales (Australia) in austral winters of 2011 to 2013. Dates are given as d/mo/yr

Seal ID	Length (m)	Girth (m)	Date attached	Deployment duration (d)	Time at sea (%)	GPS locations
NZ_1	1.56	1.05	21/06/11	194.5	74.3	1341
NZ_2	1.75	0.98	25/06/11	21.2	58.5	168
NZ_3	1.59	1.06	05/07/11	86.9	61.5	483
NZ_4	1.58	1.09	09/07/11	55.4	72.5	339
NZ_5	1.64	1.05	01/07/12	159.2	68.7	266
NZ_6	1.61	0.99	30/06/12	112.0	62.6	339
NZ_7	1.51	0.93	22/06/13	158.2	72.8	593
NZ_8	1.65	1.01	10/07/13	166.0	82.5	639
NZ_9	1.7	1.11	11/07/13	104.7	77.5	385
NZ_10	1.59	1.12	27/07/13	102.3	65.6	189
NZ_11	1.58	1.06	10/08/13	135.3	64.9	416
Au_1	1.49	0.99	19/06/13	204.3	73.1	441
Au_2	1.85	–	20/06/13	153.4	66.8	898
Au_3	1.42	0.9	11/07/13	112.5	75.4	481
Au_4	2.06	1.63	31/07/13	178.1	66.9	1204

and 10 sites (6.2 ± 1.9 sites). Most sites were non-breeding sites, with records of pups only on Montague Island (Fig. 2). The deployment site was revisited by 13 of 15 individuals (post-deployment): several sites were visited by 5 to 7 individuals (Fig. 2). Most sites were used by both species ($n = 16$ sites), with 9 visited by NZFS only and 1 by AuFS only. Generally, sites were visited infrequently, with some only visited once (5 sites) or fewer than 10 times (11 sites). The deployment site (Lamond Head) was the most frequented (a non-breeding site, 391 visits, or 59.3% of all visits to sites at the margin of the range). This may be indicative of high site fidelity or favourable site conditions (note that males tracked from Montague Island in 2012 and 2013 often visited this site when they came ashore in this area, R. Harcourt & D. Slip unpubl. data). The next most frequented sites had 38, 36 and 32 visits and were 145,

18 and 65 km away from the deployment site, respectively (Fig. 2).

While at the margin of the range, NZFS trips at sea were either on the continental shelf or in pelagic waters east of the shelf, and AuFS foraging trips were concentrated on the shelf (Fig. 3). Seals moved up to 250 km north of Jervis Bay to the coastline off the highly populated city of Sydney. The size of individual HR area at the margin of the range was 2467 ± 843 km², and was similar in size for both species (Table 2). The individual HR and CR areas overlapped, and the area of high overlap for CR areas was predominantly in the coastal waters within 20 km of the frequently used haul-out sites (Fig. 3). While at the margin of the range, at-sea trip durations were 1.7 ± 0.2 d (range: 38 min to 35.1 d) for individuals of both species, and approximately one-fifth of their at-sea trips were <0.5 d in duration (Table 2), during which time individuals remained within inshore waters adjacent to terrestrial sites (average individual mean maximum distance of 8 ± 6 km from site of departure).

3.2. Behaviour at the core of the range

After seals departed the margin of the range, 10 tags continued to transmit data (6 NZFS and 4 AuFS). During this period, the seals used 31 haul-out sites and spent 22.2 ± 2.6 h ashore (range: 25 min to 3.9 d). The sites used by the seals were spread across multiple jurisdictional boundaries, comprising 3 Australian states (Victoria, Tasmania and South Australia) and New Zealand (Fig. 3). Most sites were non-breeding sites, with only 10 of the 31 sites known for breeding activity. Individuals visited between 1 and 10 different sites throughout the core of their range. Eight of the 10 seals visited at least 1 breeding site, where they spent 21.5 ± 3.4 h ashore (range: 25 min to 3.9 d). Most sites were visited by only 1 individual (20 sites), but some sites were visited by up to 3 individuals (6 sites). Seven sites were visited by both species, 12 sites only by NZFS and 12 sites only by AuFS. Most sites were visited infrequently, either once (8

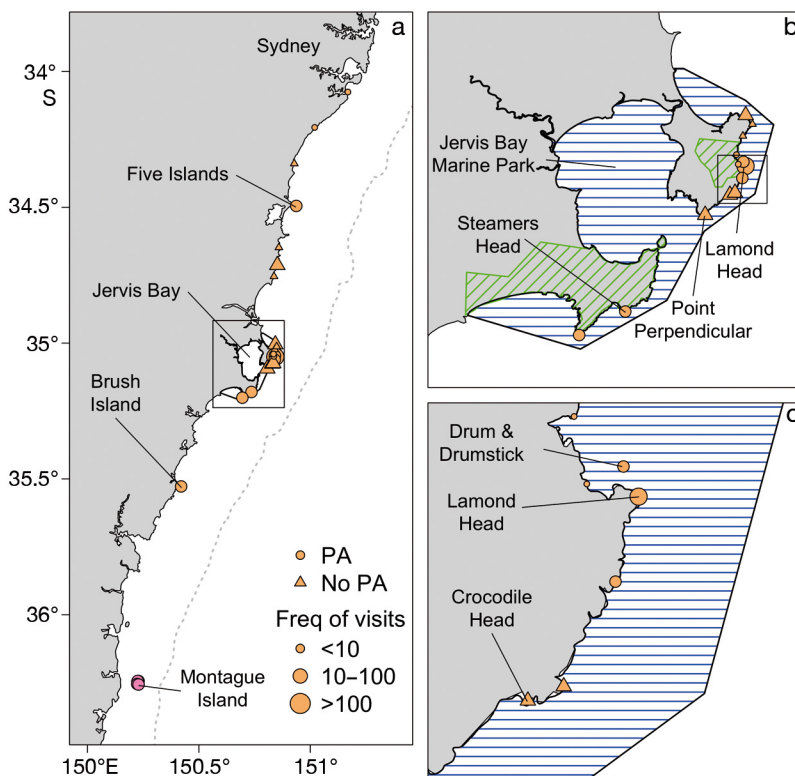


Fig. 2. (a–c) Sites visited by male fur seals and their overlap with a terrestrial protected area (PA); overlap (circle) or no overlap (triangle). Symbol size indicates the frequency of visits to a site and colour indicates non-breeding haul-out site (orange) or a colony (pink) (rare breeding attempts at Montague Island). The dashed line in (a) indicates the 200 m bathymetric contour and approximate edge of the continental shelf. (b) Enlargement of the marked area (rectangle) in (a). Diagonal hashed areas (green) indicate a terrestrial PA (southern Jervis Bay) and a naval exclusion zone (north Jervis Bay). (c) Enlargement of the marked area (square) in (b). Horizontal area (blue) in (b) and (c) is Jervis Bay Marine Park

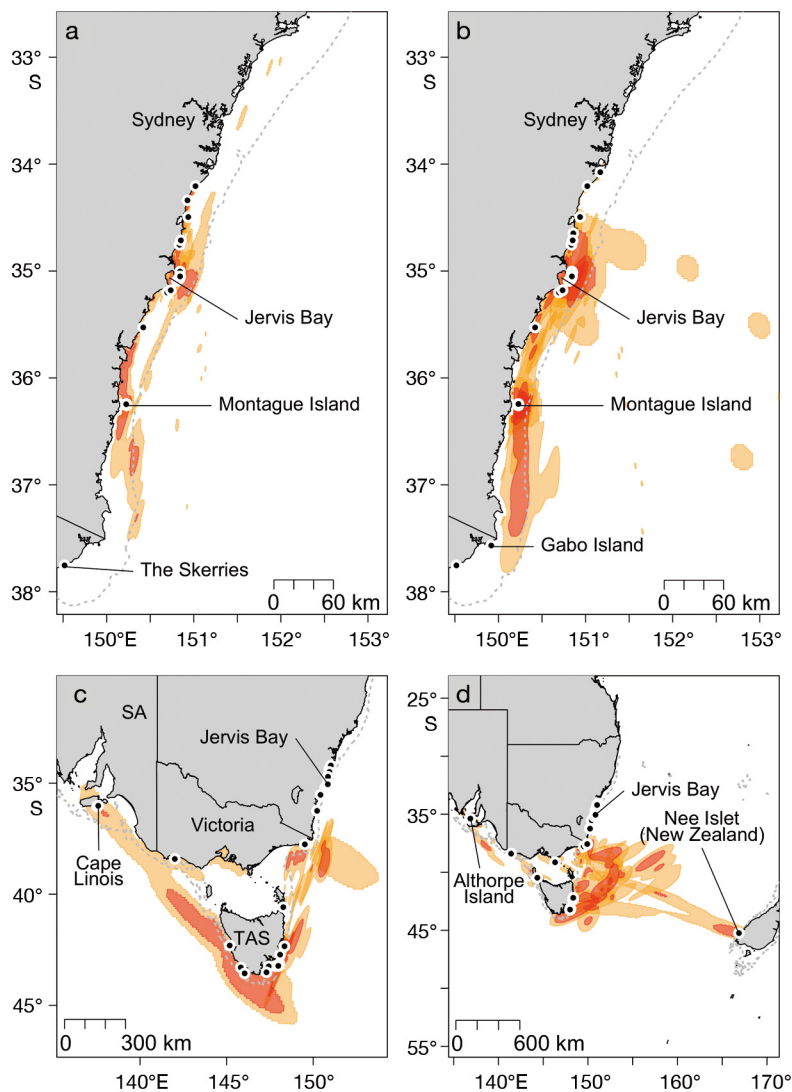


Fig. 3. Home range (orange) and core range (red) utilisation distributions of each individual male fur seal tracked from Jervis Bay in 2011 to 2013. (a) Australian fur seals *Arctocephalus pusillus doriferus* at the margin of the range ($n = 4$) and (c) core of the range ($n = 4$); (b) New Zealand fur seals *A. forsteri* at the margin of the range ($n = 11$) and (d) core of the range ($n = 8$). At the time of tracking, The Skerries was the north-eastern extent of the breeding sites for these fur seals (i.e. core geographic range), with rare breeding attempts at Montague Island. Darker shades indicate greater overlap among individuals. Dashed lines are the 200 m bathymetric contour and approximate edge of the continental shelf. SA: South Australia, TAS: Tasmania

sites) or fewer than 10 times (26 sites). The most frequently used site was The Skerries (breeding site, 79 visits, or 34.5% of all visits to sites at the core of the range). The next most frequently used sites were Althorpe Island (non-breeding site, 23 visits, or 10.0%), Gabo Island (non-breeding site, 18 visits, or 7.9%) and Cape Lino (non-breeding site, 15 visits, or 6.6%).

While at the core of the range, NZFS trips to sea were primarily in pelagic waters east of the continen-

tal shelf between Australia and New Zealand, and AuFS trips remained on the continental shelf but also around the shelf break, with 1 individual venturing off the shelf. The fur seals displayed a change in foraging behaviour from the margin of the range to the core of the range; while their foraging trip duration was not significantly different (Student's paired t -test, $t = -2.23$, $p = 0.052$), they had significant expansion of their HR (Wilcoxon signed-rank test, $V = 0$, $Z = -3.3$, $p < 0.001$, $R = 0.99$) (Fig. 3, Table 2). There was high variability among individual HR and CR, and only a small percentage of the total area was used by 2 or more individuals (HR: 29.5% and CR: 11.0%).

During October, 1 NZFS (NZ_13) traversed the Tasman Sea. The seal left Montague Island (on 2 October) and reached Nee Islets, New Zealand, on 10 November. This seal spent 15 d around the Nee Islets and a total of 9.5 d hauled out there. The seal left the Nee Islets on 24 November, traversed the Tasman Sea and hauled out at Cape Hauy, Tasmania, on 18 December for 1.2 d.

3.3. Protected areas

Of the 57 sites used by the seals, most ($n = 47$) were within terrestrial protected areas (i.e. national parks, reserves, naval exclusion area) (Fig. 2). All 10 sites that were outside terrestrial protected areas were non-breeding haul-out sites at the margin of the range (Fig. 2). Six of the sites outside terrestrial protected areas were along the Jervis Bay coastline and the other 4 were north of Jervis Bay towards Sydney. There was no difference in the average number of visits to sites outside terrestrial protected areas (7.5 ± 7.6 visits) compared to sites inside terrestrial protected areas (7.3 ± 8.5 visits, excluding the deployment site, which was an extreme outlier). A total of 591 visits were recorded at 13 sites in JBMP (range: 1–391 visits per site). After the deployment site, the frequency of use of other sites in Jervis Bay was relatively low

Table 2. Foraging behaviour parameters (mean \pm SE) of male New Zealand fur seals (NZFS) *Arctocephalus forsteri* and Australian fur seals (AuFS) *A. pusillus doriferus* when they were at the margin of the range (i.e. New South Wales) and in the core of their range. Parameters include home range (HR; 90% utilisation distribution) and core range size (CR; 50% utilisation distribution). For seals at the margin of the range, we also investigated how much of Jervis Bay Marine Park (JBMP) was used, and the overlap of individual HR and CR with JBMP

Region and parameter	NZFS	AuFS
Margin of the range		
Number of seals	11	4
Haul-out duration (h)	14.2 \pm 1.3	16.4 \pm 1.5
Trip duration (d)	1.4 \pm 0.2	1.8 \pm 0.4
HR size (km ²)	2612 \pm 1133	2068 \pm 778
CR size (km ²)	587 \pm 266	427 \pm 208
Trips <0.5 d (% of individual's total no. trips)	23.9 \pm 5.6	19.9 \pm 2.9
JBMP area used (%)	28.1 \pm 7.2	41.4 \pm 19.6
HR overlap with JBMP (%)	10.1 \pm 3.7	9.9 \pm 5.3
CR overlap with JBMP (%)	12.5 \pm 8.2	16.4 \pm 15.8
Core of the range		
Number of seals	6	4
Haul-out duration (h)	18.9 \pm 2.3	28.7 \pm 5.3
Trip duration (d)	3.4 \pm 0.9	4.1 \pm 1.5
HR size (km ²)	153 140 \pm 40 517	88 394 \pm 57 877
CR size (km ²)	33 972 \pm 8607	22 039 \pm 14 816
Trips <0.5 d (% of individual's total no. trips)	43.1 \pm 8.4	28.3 \pm 16.4

and did not appear to be influenced by whether the site was inside or outside a protected area (Fig. 2).

While at the margin of the range, individuals of both species used a large percentage of JBMP (up to 93% of the park; Table 2, Fig. 4). As expected for a wide-ranging species, only a percentage of an individual's HR overlapped with JBMP; however, there was great individual variability with the CR of some individuals being almost entirely within JBMP (up to 92% of an individual's CR overlapped within the park; Table 2). When the home range or core range of a seal overlapped with JBMP, the overlap occurred mostly within the coastal waters adjacent to haul-out sites (Fig. 4).

4. DISCUSSION

We tracked the movements and habitat use of sympatric male AuFS and NZFS at the northern end of their distribution where both species are expanding their range, to identify areas important to these predators and determine if they are receiving protection there. Habitat use by the study males was similar to

that of males that reside at the core of the species' range, but they used much larger ranges and had consistent seasonal movements away from the margin to the core of their distribution. Despite being wide-ranging predators, the males consistently used discrete terrestrial sites and adjacent inshore waters while at the margin of the range, and these habitats were either coincidentally, or actively, selected for reduced disturbance, falling within established terrestrial and marine protected areas.

Many large marine carnivores, such as seals, crocodiles, turtles and seabirds, range widely at sea, but return periodically to land to rest, breed and moult, and this can bring them into close contact with coastal human populations. Consistent use of particular discrete inshore habitats makes terrestrial and marine protected areas a viable management option for mitigating human–carnivore conflict, at least where the 2 areas coincide. Protected areas are often designed with human and ecosystem values in mind (Thackway & Cresswell 1997), and not specifically

for wide-ranging carnivores, and yet in this study they appear to capture most of the terrestrial habitat used by the seals. The seals received protection throughout much of their range as a result of management of activities in protected areas, with the exception of some sites at the expanding northern margin of their range. Wide-ranging marine carnivores may opt to use protected areas specifically because of functions offered within their boundaries (e.g. less human activity or different activities, such as prohibited rock fishing). Alternatively, the areas humans zoned for protection have features that are coincidentally also favoured by the carnivores (e.g. remote areas, low human visitation, limited commercial activity). When marine carnivores are on land they can be disturbed by visual, aural and olfactory cues whether approached from land or sea (H. Watson et al. 2014, Cowling et al. 2015, Marcella et al. 2017) or from the air by piloted and remotely operated aircraft (Born et al. 1999, Bevan et al. 2018, McIntosh et al. 2018a), which at worst may have lethal consequence (Back et al. 2018). An effective way to reduce disturbance to marine carnivores on land is to restrict access and modify behaviour of humans, for example

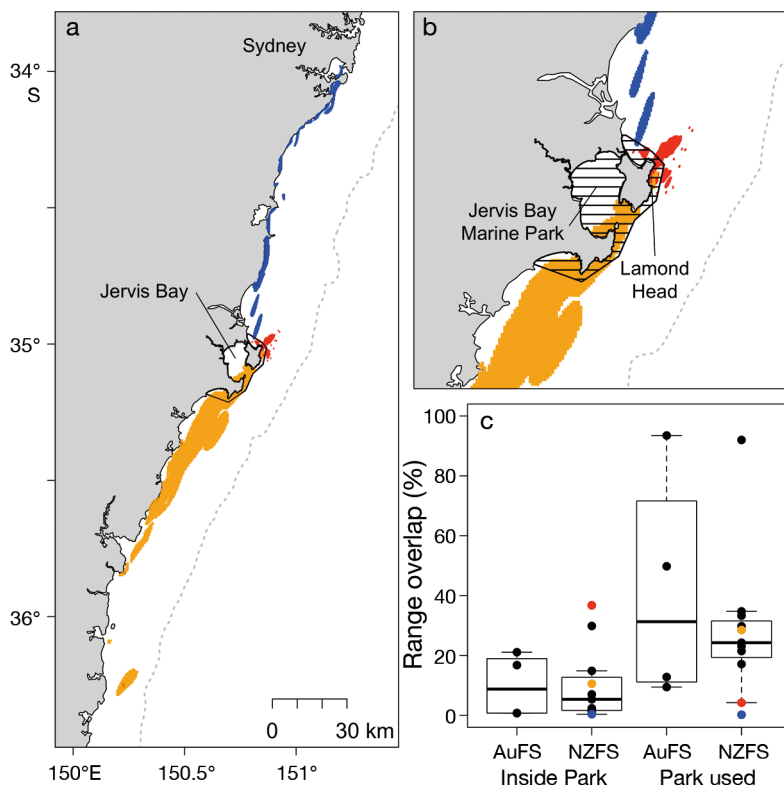


Fig. 4. Overlap of individual male Australian (AuFS) and New Zealand (NZFS) fur seal home ranges with Jervis Bay Marine Park. (a,b) Home ranges of 3 individuals are presented with different colours (red, orange, blue), and the same colours used to represent these individuals in the box plots in panel c. Dashed line is the 200 m bathymetric contour and approximate edge of the continental shelf. (c) Percentage of the range contained within the park (Inside park) and the percentage of the park utilised by each seal (Park used) (dot per individual). Minimum and maximum are delimited by the whiskers, the box represents the 25th to 75th percentile, and thick line represents the median. Dots represent each individual's value

by installing barriers and/or interpretive signage (Cassini et al. 2004, Granquist & Sigurjonsdottir 2014, Marschall et al. 2017) and regulating approach distances for different aircraft types with minimum height restrictions (Hodgson & Koh 2016). Protected areas allow strict regulation of human access and activities and have proven applicable for conserving large carnivores through reduced negative interaction with humans (Hooker & Gerber 2004, Barnes et al. 2016, Santini et al. 2016). Minimising human disturbance to provide refugia may be particularly important for low-density populations, such as those at the margin of a range where individuals may feel more at risk due to decreased vigilance and dilution effects (Stevens & Boness 2003). A network of established protected areas along the coastal fringe may enhance recovery and range expansion of wide-ranging carnivores, like these seals, by providing

important stepping stones of refuge as they expand their range (Kirkman 2010, Huisamen et al. 2011).

With tracking studies of wide-ranging marine carnivore focussing on foraging trips at sea, there has been less focus on what these carnivores are doing during short trips within inshore habitat. In this study, the considerable time spent on land and within inshore waters adjacent to terrestrial sites by all individuals of both species is indicative of the importance of this habitat to these marine carnivores at the margin of their range. Terrestrial sites are important to male fur seals for a variety of reasons (to breed, moult, rest, digest and seek refuge from marine predators), although at the margin of the range the benefit is unlikely associated with reproduction because there are no reproductively active females in the area. During the non-breeding period, social interactions between males are likely to play an important role in gaining experience that determines hierarchy and breeding success (Stirling 1970, Miller 1974, McCann 1980). Little is known about the importance of inshore waters adjacent to terrestrial sites. Male NZFS and AuFS move between land and inshore waters to thermoregulate (Mattlin 1978, Garlepp et al. 2014), which may be more important for seals in

warmer climates at lower latitudes (Stevens & Boness 2003). The inshore environment may also provide valuable foraging grounds, with the diet of both fur seal species at Jervis Bay having a high prevalence of benthic, demersal and reef-associated prey associated with inshore habitats (Hardy et al. 2017). Inshore habitats may also be selected for features (e.g. shallow reefs and kelp beds) that improve evasion from predators (Wirsing et al. 2007, Wcisel et al. 2015). Supporting these critical functions with protection of terrestrial sites and inshore waters will facilitate recolonisation of these habitats throughout their historic range. The coastal margin of the range of these seals, the focus of this study, supports a large and dense human population, with active fishing, aquaculture and tourism industries. Mitigating at-sea interactions with fur seals in the relatively discrete area found adjacent to terrestrial haul-out sites

would be challenging at this margin of their range, but would likely benefit the recovery of the seals by reducing disruption to critical on-land and inshore behaviours.

Protecting the entire foraging range of wide-ranging marine carnivores is often impractical. By understanding the movements of carnivores, it is possible to identify life stages or periods within a breeding cycle that are contained in discrete areas more suitable for protected area zoning. For example, this study showed that when male seals were at the expanding margin of their range they used relatively small at-sea areas, with a large percentage overlap with the existing marine protected area, JBMP, and the park captured the core range areas that were adjacent to terrestrial sites. Through spatial zoning within their boundaries, marine protected areas can be used to direct marine-based activities (fishing, aquaculture, tourism) and land-based fishing and tourism activities into areas away from sites important to species of conservation concern. JBMP is an example of a park that is internally zoned to spatially regulate activities throughout the park, and since its establishment, several predators have returned and established populations in the park (Lynch et al. 2013, Bruce et al. 2014, this study). By identifying the areas within the park that are important to each marine carnivore, management authorities can apply evidence-based information to improve zoning within the park (i.e. modify boundaries or activities within zones) to better mitigate interactions between users and the carnivores. In the absence of such information, our study suggests that zoning the coastal marine environment close to terrestrial sites could capture important inshore habitat for wide-ranging marine carnivores that regularly come ashore, and provide the opportunity to mitigate interactions between these carnivores and human activities which disrupt behaviours that occur in terrestrial and inshore habitats.

Factoring novel and consistent intraspecific variation in foraging behaviour into movement models for carnivores is an important consideration to accurately predict the habitat use by populations of interest, and is necessary to correctly inform conservation planning. In this study, the uniform movement of the male AuFS and NZFS from overwintering at the margin of the range towards colonies prior to breeding contrasts with males tracked within the core of the range in other studies. Long-range movements from the winter grounds have occurred in only a small number of individuals tracked from the core of the range in other studies (NZFS: Page et al. 2006; AuFS:

Kirkwood et al. 2006, Robinson et al. 2008a, Knox et al. 2017). This sort of intraspecific variation in movements is rarely seen in other otariids, with males either all migrating away from colonies post-breeding (Robertson et al. 2006, Staniland & Robinson 2008) or all showing high fidelity to a colony throughout the non-breeding period (Lowther et al. 2013, Baylis et al. 2018). This appears analogous to partial migrating species, where segregation in overwinter movement behaviour may be associated with individual characteristics such as age, body size, competitive ability and personality (Lundberg 1988, Chapman et al. 2011). Breeding status may explain the more consistent movement and colony fidelity of males tracked from the core of the range (Kirkwood et al. 2006), with those less involved in breeding in the subsequent season (e.g. holding or challenging for breeding territory) ranging more widely over winter. This idea is supported by our study, with all males on the margin of the range having minimal association with colonies in the subsequent breeding season and insufficient body size to be competitive for breeding territory (Lourie et al. 2014), although other strategies exist (Caudron et al. 2009). High intra- and inter-specific competition and local depletion of food resources at the core of a species' range, close to breeding areas, may be a strong motivation for some individuals to disperse from breeding colonies (Ashmole 1963, Boyd et al. 1998, Kuhn et al. 2014). As a trade-off, however, lower densities of peripheral populations are thought to reflect poorer quality habitat towards the margins of a range (Holt 1987, Lawton 1993, Guo et al. 2005), which is thought to explain divergent foraging behaviour from individuals at the core of the range (Augé et al. 2011). The movements of individuals at the periphery of a population's range can clearly diverge from the patterns identified in individuals at the core of their range. This study emphasises that caution is required when modelling habitat use of carnivores recolonising their historic range when using information derived from individuals at the core of their species' range.

This study identifies important considerations to improve conservation and management of recovering wide-ranging marine carnivore populations, based on analyses of movements and habitat use by males of 2 fur seal species occupying an expanding margin of their range. The dependence of many marine carnivore species on discrete habitats that are of similar size to existing protected areas means that recovering populations of marine carnivores can benefit from an established network of protected

areas, both terrestrial and marine, at the frontier of their range. Improvements can be made to the designation and zoning of protected areas by integrating specific habitat use information of individuals at expanding range margins into the review of management plans. This will help account for unique intra-specific behaviour of individuals at range peripheries. As marine carnivores recolonise their historic ranges, it is necessary to consider ecosystem consequences, and the utility of protected areas, where high-level predators become established and exert influence on trophic dynamics within protected areas (Hooker et al. 2011, Kelaher et al. 2015). Having a network of protected areas along the coastal fringe at the margins of a carnivore's range could help to minimise and mitigate adverse interactions between industry and recovering marine carnivores, and thereby support key conservation and management objectives for marine carnivore populations. For these protected areas, it is important to ensure enforcement of regulations, as activities can persist illegally and reduce the effectiveness of the protected area (Harasti et al. 2019). Given that wide-ranging marine carnivores will often move beyond discrete habitats, point-source management methods, such as seal exclusion devices on trawl nets (Shaughnessy et al. 2003), will likely continue to play a role in mitigating at-sea interactions between humans and recovering marine carnivore populations.

Despite promising recovery of populations for both fur seal species throughout their range (Kirkwood et al. 2010, Shaughnessy et al. 2015, Watson et al. 2015), recent population estimates based on pup numbers identified a reduction in the AuFS population at core breeding colonies (McIntosh et al. 2018b). The implications of population fluctuations within the core of a species' range for the colonisation of the margin by peripheral populations is still unknown. In this case, resource partitioning, on land and at sea, between 2 recovering, sympatric predators requires further investigation, and studying this at the expanding margin of both species' range, where neither species currently has apparent priority, may provide useful insights for carnivore population recovery and recolonisation (Hardy et al. 2017). Importantly, the implications for large-scale environmental change, such as strengthening of the East Australian Current (Suthers et al. 2011), on the recovery of large carnivore populations and changes in their distribution are still largely unknown, but potentially significant (Niella et al. 2020), and should be considered when planning for recovery and expansion of marine carnivore populations.

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