Ontogenetic niche partitioning in southern elephant seals from Argentine Patagonia

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Abstract
Elephant seals, Mirounga spp., are highly dimorphic, having different energetic requirements according to age and sex, and foraging in various ecological and oceanographic contexts. Resource partitioning has been shown for the sub-Antarctic populations of southern elephant seals, M. leonina, where colonies are surrounded by narrow shelves that deepen abruptly. In contrast, seals from Peninsula Valdés (Argentina), in the northernmost extent of the breeding range, face an extended, shallow, temperate, and productive continental shelf. We integrated tracking data from 98 animals (juveniles and adults, males and females) gathered over more than two decades, and found that although all available habitats were used, individuals segregated by age and sex. Juvenile males favored shelf habitats, whereas subadult and adult males also used the shelf break. Juvenile females preferred the shelf and the more distant Argentine Basin.
used by postbreeding and postmolt adult females. Males showed the highest proportion of area-restricted search locations, suggesting more spatially concentrated feeding activity, and likely reflecting a preference for foraging habitat and prey. Our results are consistent with those from other populations, implying that elephant seals show remarkable similarities in habitat use by age and sex classes, despite broad differences in the offshore habitats between sub-Antarctic and temperate ecosystems.

**KEYWORDS**
elephant seals, *Mirounga leonina*, niche partitioning, ontogeny, Peninsula Valdés, South Atlantic Ocean

1 | **INTRODUCTION**

Ontogenetic shifts in niche are changes in resource or habitat during the course of an individual’s lifetime (Olson, 1996) that may be related to changes in predation risk, growth, energy needs, and foraging ability with age (Polis & McCormick, 1986; Werner & Gilliam, 1984; Woodward & Hildrew, 2002). Intraspecific differences in feeding ecology among age and sex groups may be manifest in foraging behavior and diet specialization (e.g., ontogenetic shifts in distribution, with a direct effect on foraging habitats and prey choice) (Field, Bradshaw, Burton, Sumner, et al., 2005; Field, Bradshaw, van den Hoff, et al., 2007; Olson, 1996; Polis, 1984). Such resource partitioning is a way of reducing intraspecific competition and enhancing the foraging success for individuals in each age class (Field, Bradshaw, Burton, Sumner, et al., 2005; Field, Bradshaw, van den Hoff, et al., 2007; Polis, 1984; Takimoto, 2003).

Ontogenetic niche partitioning has been reported in many species including green sea turtles (*Chelonia mydas*; Brand-Gardner et al., 1999), South American fur seals (*Arctocephalus australis*; Vales et al., 2015), South American sea lions (*Otaria byronia*; Drago et al., 2009), sperm whales (* Physeter macrocephalus*; Mendes et al., 2007), and the two species of elephant seals (*Mirounga angustirostris* and *M. leonina*; Bailleul, Authier, et al., 2010; Field, Bradshaw, Burton, Sumner, et al., 2005; Le Boeuf et al., 1993; Stewart, 1997). Both species of elephant seals are highly sexually dimorphic (Le Boeuf & Laws, 1994) and experience ontogenetic physiological and behavioral changes during matura-
tion (Field, Bradshaw, Burton, & Hindell, 2005). These changes involve diving ability, foraging capacity, movement patterns, foraging habitat, and diet (e.g., Bailleul, Authier, et al., 2010; Chaigne et al., 2013; Davis, 2019; Irvine et al., 2000; Orgeret et al., 2019; Stewart, 1997).

The annual cycle of southern elephant seal (SES) juveniles (defined here as 1–4 years of age) differs from that of adults. Adults spend 10 months at sea, divided into a 2-month postbreeding (PB) foraging trip and an 8-month post-
molt (PM) foraging trip. Juveniles start molting earlier than adults (November versus December to March) and some incorporate a facultative mid-year time ashore (April–August) (Hindell & Burton, 1988; Lewis et al., 2004). As individuals mature, they engage in longer trips to sea, migrate further from natal rookeries, and delay and shorten haul-out time. Older seals are therefore able to exploit a larger foraging area, which is unavailable to younger age classes (Field, Bradshaw, Burton, Sumner, et al., 2005). While the mechanisms that drive intraspecific resource partitioning are not well understood in this species, it has been proposed that the haul-out patterns of juvenile SES may act as a temporal regulator for the time spent at sea, reducing foraging competition (Field, Bradshaw, Burton, Sumner, et al., 2005).
During their first year at sea, juvenile SES feed at a lower trophic level than older animals (Lübcker et al., 2017; Newland et al., 2009, 2011; Walters et al., 2014). This is consistent with constraints associated with a smaller body mass, diving (breath-hold) capabilities, hunting skills, and foraging ranges. In addition, older animals are able to disperse further and access deeper and more abundant prey (Chaigne et al., 2013; Field, Bradshaw, Burton, Sumner, et al., 2005; Field, Bradshaw, van den Hoff, et al., 2007; Irvine et al., 2000). The diet of juveniles, as revealed by stomach content (Field, Bradshaw, van den Hoff, et al., 2007) and stable isotopes analyses (Bailleul, Authier, et al., 2010; Chaigne et al., 2013; Eder et al., 2010), does not differ between males and females, possibly due to similar body size (Field, Bradshaw, van den Hoff, et al., 2007). Thus, changes in the diet seem to be a function of ontogenetic changes in foraging ability and range, which may be controlled by physiological limitations and the haul-out pattern (Field, Bradshaw, Burton, Sumner, et al., 2005; Field, Bradshaw, van den Hoff, et al., 2007).

SES have a circumpolar distribution, dispersing mostly from sub-Antarctic Islands, with some smaller breeding populations in the Antarctic Peninsula (Laws, 1994). Outside this region, the largest breeding colony occurs at Península Valdés (PV) (Campagna & Lewis, 1992; Lewis et al., 2004). About 15,000–16,000 pups per year are born in this area (Ferrari et al., 2013). A smaller population in the Southwest (SW) Atlantic breeds in the Falkland/Malvinas Islands (Galimberti & Boitani, 1999; Laws, 1994), and an incipient group occurs in the Almirantazgo Sound, in the Magellan Strait (Acevedo et al., 2016). All populations of SES, including that of Patagonia, show foraging area segregation between sex and age classes (e.g., Campagna et al., 1998, 1999, 2006, 2007; Field, Bradshaw, Burton, Sumner, et al., 2005; Hindell et al., 1991, 2016). The generic description of the annual cycle applies to Patagonia (Lewis et al., 2004); adult females forage mostly in the deep waters of the Atlantic Basin, while adult males distribute along the continental shelf and over the shelf break (Campagna et al., 1998, 1999; Goulet et al., 2020; McGovern et al., 2019). Juveniles disperse in the open ocean as well as along the shelf break and on the continental shelf (Campagna et al., 2007). In deep, pelagic waters, juveniles remain in close association with transient oceanographic features, such as extended eddies, created by currents, which may serve to aggregate prey (Campagna et al., 2006).

**FIGURE 1** Individual tracks of elephant seals from Península Valdés derived from hierarchical state-space models (hSSMs) color-coded by age/sex groups. Dark red: adult females (both postmolt and postbreeding); Red: juvenile females. From dark to light blue: adult, subadult, and juvenile males respectively. Shaded in gray, going from light to dark gray, are the continental shelf, shelf break and oceanic waters, respectively.
The SW Atlantic is a large ocean system with several ecological regions (Martinetto et al., 2020) and oceanographic profiles (Campagna et al., 2000). It is broadly characterized by three ecosystems: the continental shelf, the shelf break, and the deep ocean basin (Figure 1; see Piola & Falabella, 2009; Piola & Matano, 2001). These temperate water masses merge close to the latitudes where seals reproduce (Piola & Matano, 2001) and provide distinct habitats with particular animal communities that have a clear isotopic signature (Eder et al., 2010).

During the pelagic phases of their annual cycle, elephant seals from both sexes and all age classes, cross or spend time in these oceanic environments (Campagna et al., 2000, 2006, 2007). The distinct habitats allow individuals to exploit different prey available within their diving abilities. Fish and squid species found in neritic waters generally differ in kind and energetic density from those found in oceanic waters (Brunetti et al., 1999; Cherel et al., 2008; Eder & Lewis, 2005). Seals from PV that forage on the shelf or shelf break have more demersal and mesopelagic fish in their diets, which are trophically closer to neritic rather than pelagic oceanic fish (Eder et al., 2010; Lewis et al., 2006; McGovern et al., 2019).

The migration pattern of SES across their range show interpopulation similarities in their foraging behavior and annual cycle, and intrapopulation differences related to sex and age class. Research on the PV colony has been conducted over more than three decades and was more recently expanded with the deployment of state-of-the-art biologists (Goulet et al., 2020; McGovern et al., 2019). In this study we integrate 25 years of tracking data from animals that breed and molt at PV, reviewing and expanding results across age classes and for both sexes. The purpose of this work was to analyze for the first time comparative and ontogenetic evidence for spatial segregation between sexes and among age groups for SES of Patagonia. Specifically, we examine (1) the at-sea behavior of the sexes and age classes (juvenile, subadult, adult), (2) identify geographic areas of time-intensive use, and (3) determine whether areas of high use differ among the sexes and age classes.

2 METHODS

2.1 Study area

The PV breeding colony is located on the Patagonian shelf, one of the largest (~1,000,000 km²), shallowest (<100 m in most of its extension), and productive marine plateaus in the Southern Hemisphere (Figure 1; Acha et al., 2004; Campagna et al., 2000; Piola & Falabella, 2009). Travel distance to deep waters varies among SES colonies, with PV having deep waters the farthest from the coast. At the latitude of PV, the edge of the continental shelf, delimited by the 200 m isobath, is located 300–400 km off the coast, in contrast to 20–50 km from South Georgia, and 10–100 km off the shores of most other large reproductive locations for the species (Kerguelen, Macquarie, and King George Islands). Thus, narrow continental shelves that deepen abruptly (>1,000 m) surround all major sub-Antarctic Islands where the largest colonies occur.

The SW Atlantic is dominated by two marine currents that flow in opposite directions. The Falkland/Malvinas Current flows northward, along the shelf break and the western boundary of the Argentine Basin and carries cold, sub-Antarctic, nutrient-rich waters. The Brazil Current flows southward, along the continental margins. It carries oligotrophic subtropical warm and salty waters. These currents meet at approximately 38°S, creating an intense thermohaline front known as the Brazil/Malvinas Confluence. This collision generates one of the most energy-rich (currents >1 m/s) and eddy-rich field regions in the world, affecting both oceanic waters and the shallow shelf (Piola & Matano, 2001; Saraceno et al., 2004).

Based on physical variables such as surface temperature, salinity, vertical stratification, and circulation, the SW Atlantic has several distinct oceanographic regimes (Piola & Matano, 2001). The continental shelf can be divided in the open shelf waters, of sub-Antarctic origin, diluted due to continental discharge, and the Magellan waters related to coastal fronts associated with low salinity and tidal mixing. The shelf break front is a transition zone between the shelf and sub-Antarctic waters of the Falkland/Malvinas Current. The meeting of these waters creates a permanent
thermohaline front with maximum concentrations of chlorophyll-a (>3.5 mg/m³) in spring/summer. Finally, the Argentine Basin may be divided into four systems, the: (1) Subtropical waters under the effect of the warm (>20 °C), high salinity (>35; all salinities are reported in the Practical Salinity Scale) Brazil Current, that is poor in nutrients, (2) Subpolar or sub-Antarctic, temperate (<15 °C) and nutrient rich waters, under the effect of the low salinity (<34.2) Falkland/Malvinas Current, (3) Mixed Subtropical-Subpolar regime, a transition zone associated with intense eddy activity produced by the collision of the Brazil and Falkland/Malvinas Currents, characterized with average chlorophyll-a values (<1.5 mg/m³) and, (4) Polar regime, cold (<4 °C), low salinity (<34) and high nutrient waters, close to the Antarctic Polar Front (for further treatment of these regimes see also Campagna et al., 2006, 2007; Eder et al., 2010, 2019; Piola & Fallabela, 2009).

2.2 Deployed instruments

From the 1990s up to 2018, SES from PV were equipped with a variety of ARGOS satellite (PTTs) and GPS tags (Campagna et al., 1998, 1999, 2000, 2006, 2007; Goulet et al., 2020; McGovern et al., 2019). This study synthesizes PTT tracking data obtained from 93 seals of both sexes and a range of age classes (Table 1). It also incorporates one animal equipped with a CTD tag (conductivity-temperature-depth data logger, Wildlife Computers) and four with archival Dtags deployed in 2018, which included snapshot GPS positioning (Table 1). Anesthesia protocols used to deploy and recover instruments were described in previous work (Campagna et al., 1998, 1999, 2006, 2007). Seals were anesthetized with a 1:1 combination of tiletamine and zolazepam administered by hand as a deep intramuscular injection in the gluteal region.

2.3 Location data

For the PTT-equipped animals, at-sea movements were determined using the ARGOS satellite tracking system (Argos, 2016). All location estimates were initially speed filtered to exclude positions that would require an unrealistic travel rate >10 km/hr (McConnell et al., 1992). We identified the start and end date of the foraging trips for each animal to exclude on-land locations and short movements near the coast, which would otherwise increase the relative importance of the colony in subsequent analyses. Animals with two (n = 11) or three (n = 1) consecutive foraging trips were also included.

Hierarchical state-space models (hSSMs) were used to filter the tracks, to provide location estimates at six-hourly periods, and to infer behavioral modes along the seals' tracks (Jonsen, 2016; Jonsen et al., 2006). These models account for errors around Argos derived locations, and estimate the most likely position at regular time intervals as well as the probability of the seal being either in an area-restricted search (ARS) or transit behavioral mode, determined by a move-persistence parameter (Jonsen, 2016; Jonsen et al., 2005). This parameter combines persistence in both direction and speed and indicates how similar (on average) each move step (displacement in the longitude and latitude direction) is to the previous one. The ARS behavior consists of relatively slow movements with little persistence between consecutive displacements, while transit includes relatively fast and more directionally persistent movements (displacements are very similar to the previous one) (Jonsen, 2016).

Not all instruments were of the same type or had the same settings, so there was considerable variability in their performance and the quality of the data. Fourteen satellite tags were duty-cycled (programmed 1–2 days off between each day of transmitting; Table 1). The database contained 34 incomplete trips because the tags stopped transmitting while still at sea. Other gaps in the data from poor transmissions ranged from one to more than 10 days between consecutive locations. When possible, tracks with long gaps were split into sections and reassembled after fitting separate hSSMs. Trips (n = 13) with few positions and many consecutive gaps were removed. We used a total
of 98 tracks from 86 seals (Table 2). The hSSMs were also applied to the GPS tracks. In order to combine GPS and PTT derived locations in the same model, we set all GPS locations to have Argos location quality 3.

**Table 1** Seals used in this study ($n = 98$) summarized by age/sex group, year of deployment of instruments, phase of the annual cycle (summer or winter, for juveniles and subadult males; PB: postbreeding or PM: postmolt, for adults), and number of animals on which tags were deployed each year. The total of individuals from each group is also shown.

<table>
<thead>
<tr>
<th>Age/sex group</th>
<th>Year</th>
<th>Phase of annual cycle</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile females</td>
<td>2003</td>
<td>Summer</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>Winter</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>Winter</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>Summer</td>
<td>6$^a$</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>16</td>
</tr>
<tr>
<td>Juvenile males</td>
<td>2003</td>
<td>Summer</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>Winter</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>Winter</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2005</td>
<td>Summer</td>
<td>4$^a$</td>
</tr>
<tr>
<td></td>
<td>2006</td>
<td>Summer</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>Summer</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>18</td>
</tr>
<tr>
<td>Subadult males</td>
<td>2006</td>
<td>Summer</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>Summer</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>Adult males</td>
<td>1994</td>
<td>PB</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>PB</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>1996</td>
<td>PB</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2001</td>
<td>PM</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>PM</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>10</td>
</tr>
<tr>
<td>Adult females</td>
<td>1996</td>
<td>PB</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1997</td>
<td>PM</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>PB</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>2008</td>
<td>PM</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>PB</td>
<td>4$^a$</td>
</tr>
<tr>
<td></td>
<td>2012</td>
<td>PB</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>PB</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>2013</td>
<td>PM</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>2015</td>
<td>PB</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>2016</td>
<td>PB</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2016</td>
<td>PM</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>PB</td>
<td>9$^b$</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>46</td>
</tr>
</tbody>
</table>

$^a$Denotes animals within the set with duty cycled satellite tags.

$^b$Five of these seals had GPS tags while the remainder in the table had Argos PTTs.

Age was estimated from body length, shape, and secondary sexual characters. Four age and sex groups were defined: 2–3-year-old juveniles (males and females; mean standard length ± SD = 2.05 ± 0.67 m), 5–6-year-old
subadult males (mean standard length $\pm SD = 3.16 \pm 0.24$ m), adult males (mean standard length $\pm SD = 3.84 \pm 0.32$ m), and adult females (mean standard length $\pm SD = 2.57 \pm 0.19$ m). Adult females were also classified as PM and PB according to the period in their annual cycle (Table 2). For adult males, trips were not divided into migration periods as there was a small sample size (Table 2) and many tracks were incomplete.

### TABLE 2

Samples used for the hierarchical state-space models (hSSMs) fitting and further analysis. The number of individuals in each age/sex group and the total sample size is shown. The number of animals within the set with consecutive trips is given in parentheses.

<table>
<thead>
<tr>
<th>Age/sex group</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>All juveniles</td>
<td>26 (3)</td>
</tr>
<tr>
<td>Juvenile females</td>
<td>13 (1)</td>
</tr>
<tr>
<td>Juvenile males</td>
<td>13 (2)</td>
</tr>
<tr>
<td>Subadult males</td>
<td>7 (3)</td>
</tr>
<tr>
<td>Adult males</td>
<td>9</td>
</tr>
<tr>
<td>Postmolt adult females</td>
<td>11 (4)</td>
</tr>
<tr>
<td>Postbreeding adult females</td>
<td>33 (1)</td>
</tr>
<tr>
<td>Total</td>
<td>86</td>
</tr>
</tbody>
</table>

2.4 **Statistical analysis**

We used generalized linear models (GLMs) to compare the proportion of locations in an ARS behavioral mode between the different age and sex groups. The behavioral state of each of the estimated locations was determined using the $b$ parameter (state) of the hSSMs (Jonsen, 2016).

We also used location estimates derived from the hSSMs to compare the maximum distance traveled from the deployment site among age and sex classes using a GLM. In this, and in the following analysis, we used all the locations regardless of the behavioral mode.

To identify the regions that were used most intensively by different age and sex classes, we produced relative utilization maps based on the number of six-hourly locations in $50 \times 50$ km grid cells. We did this for each individual and then calculated the average relative utilization for each age and sex group. We used the top 50% of cell values in this average utilization distribution to identify the core areas for each group.

Finally, we employed GLMs to test for differences in habitat use between the age and sex groups. We calculated the number of locations recorded from each individual within three main SW Atlantic habitats: continental shelf (water depth 0–200 m), shelf break (>200–2,000 m) and oceanic waters (>2,000 m) using GEBCO14 bathymetry data (30 arc-second resolution; distributed by the British Oceanographic Data Centre). The bathymetric limits of these habitats respond to ecological considerations that can differ from geological definition (Dogliotti et al., 2014; Piola & Falabella, 2009; Violante et al., 2010). These were expressed as a proportion of the individual’s total number of locations to standardize for the different lengths of the tracks. Unless otherwise indicated, mean values $\pm$ standard deviations are reported.

### RESULTS

3.1 **Distribution and at-sea behavior**

Seals from PV ranged widely across the SW Atlantic, from the shallow waters of the continental shelf to the deep waters of the Argentine Basin, reaching to the Southeast Pacific Ocean (Figure 1). Juveniles of both sexes were capable of long-distance travel (maximum distance traveled from PV = 2,850 km) reaching both South Georgia and the SE
ARS behavior for juveniles occurred at the continental shelf, the shelf break, in oceanic waters, and even in the Chilean fjords (Figure 2). In contrast, subadult and adult males remained closest to the colony and did not migrate to oceanic waters (Figures 1 and 2). Their ARS locations were concentrated on the shelf and along the shelf break (Figure 2). Both PB and PM adult females used deep waters (>200 m; Figures 1 and 2) and, like the juveniles, were able to travel long distances reaching South Georgia and the Pacific Ocean (Figure 2). ARS locations for PM females were almost exclusively in the oceanic waters, whereas 17 PB females also used the shelf break (Figure 2).

The proportion of locations in each behavioral state varied among the age and sex classes (Table 3). Particularly, age and sex had a significant effect in the proportion of locations in ARS mode ($F_{5,80} = 9.90, p < .0001$). Juvenile males allocated on average 49% ± 24% of their time to ARS while juvenile females spent 34% ± 28% of their time in this behavior. Subadults and adult males had the highest proportion of ARS locations of all groups (68% ± 12% and 70% ± 19%, respectively), consistent with the relatively short travel distances to their foraging areas. This contrasts with adult females where only 23% ± 18% and 24% ± 25% of locations were allocated to ARS mode for PM and PB.
respectively. Fourteen tracks showed no ARS behavior. Of these, 4 were juveniles (1 male and 3 females) and 10 were adult females (2 PM and 8 PB).

There were significant differences in the maximum distances traveled from the deployment sites by the different age and sex groups \((F_{5,80} = 10.07, p < .0001; \text{Figure 3a})\). On average, PM adult females traveled the farthest \((2,173.0 \pm 736.7 \text{ km})\) followed by PB adult females and juveniles of both sexes (Figure 3a). In contrast adult males traveled the shortest distances \((869.3 \pm 323.8 \text{ km})\), covering less than half the distance of PM adult females.

### 3.2 Core habitats used by age and sex groups

Male and female juveniles were associated with all habitats described for the SW Atlantic and with many of the oceanographic regimes described for the region (Figure 4; see Methods). Juvenile females used the outer shelf close

<table>
<thead>
<tr>
<th>Age/sex group</th>
<th>n</th>
<th>No. of trips</th>
<th>No. of estimated locations</th>
<th>%ARS</th>
<th>%Transit</th>
<th>%Uncertain</th>
</tr>
</thead>
<tbody>
<tr>
<td>All juveniles</td>
<td>26</td>
<td>29</td>
<td>421 \pm 217</td>
<td>41.6 \pm 26.9</td>
<td>48.9 \pm 26.6</td>
<td>9.5 \pm 6.3</td>
</tr>
<tr>
<td>Juvenile females</td>
<td>13</td>
<td>14</td>
<td>400 \pm 228</td>
<td>33.7 \pm 28.0</td>
<td>56.1 \pm 28.8</td>
<td>10.2 \pm 8.3</td>
</tr>
<tr>
<td>Juvenile males</td>
<td>13</td>
<td>15</td>
<td>442 \pm 213</td>
<td>49.4 \pm 24.2</td>
<td>41.7 \pm 23.1</td>
<td>8.9 \pm 3.7</td>
</tr>
<tr>
<td>Subadult males</td>
<td>7</td>
<td>10</td>
<td>640 \pm 294</td>
<td>68.1 \pm 11.5</td>
<td>24.1 \pm 8.9</td>
<td>7.8 \pm 6.0</td>
</tr>
<tr>
<td>Adult males</td>
<td>9</td>
<td>9</td>
<td>352 \pm 171</td>
<td>70.4 \pm 19.0</td>
<td>24.0 \pm 19.7</td>
<td>5.6 \pm 4.6</td>
</tr>
<tr>
<td>Postmolt adult females</td>
<td>11</td>
<td>16</td>
<td>761 \pm 331</td>
<td>23.4 \pm 17.5</td>
<td>59.0 \pm 18.6</td>
<td>17.6 \pm 7.7</td>
</tr>
<tr>
<td>Postbreeding adult females</td>
<td>33</td>
<td>34</td>
<td>264 \pm 79</td>
<td>24.1 \pm 24.7</td>
<td>66.0 \pm 24.6</td>
<td>9.9 \pm 7.0</td>
</tr>
</tbody>
</table>

**Figure 3** Summary plots of: (a) maximum distance traveled (km) from deployment site, and (b–d) proportion of locations in different habitats. (b) Continental shelf, (c) shelf break, and (d) oceanic waters. Mean values and 95% Confidence Intervals for each age/sex group are shown. AM: adult males, JF: juvenile females, JM: juvenile males, PBF: postbreeding adult females, PMF: postmolt adult females, and SAM: subadult males.
to the shelf break front waters and the deeper subpolar oceanic waters (Figure 4), while juvenile males concentrated in the mid-shelf, although they also showed some core areas in polar waters near South Georgia Island, as did juvenile females (Figure 4). Core areas of subadult and adult males were restricted to the waters of the outer shelf and shelf break front (Figure 4). These animals distributed from approximately 35°–53°S. Core areas for adult females were located in the Argentine Basin under mixed subtropical-subpolar waters, and to a lesser extent in subpolar waters (Figure 4). However, PB female core areas also occurred at the shelf break and a small region in the Pacific Ocean used by only one of the 33 animals (Figure 4).

The proportion of locations in the three habitat types also varied significantly (Figure 3b–d). Juvenile, subadult, and adult males spent more than half of their time at-sea at the continental shelf ($F_{5,80} = 5.63, p = .0002$; Figure 3b). PM adult females spent only 11.0% ± 14.3% on the shelf, while PB females spent on average twice this time (22.1% ± 21.5% of locations; Figure 3b). The rest of the time, subadult and adult males were at the shelf break (46.2% ± 39.9% and 45.3% ± 37.8%, respectively; $F_{5,80} = 3.12, p = .01$; Figure 3c). In contrast, adult females spent most of their time in oceanic waters ($F_{5,80} = 10.94, p < .0001$; Figure 3d), and juvenile females spent a similar amount of time on the continental shelf (43.7% ± 40.5%; Figure 3b) and in oceanic waters (40.5% ± 40.1%; Figure 3d).

**FIGURE 4** Density/usage maps for the different age/sex groups inferred from location counts in 50 × 50 km cells. Tracks per age/sex category were: juvenile females ($n = 14$), postbreeding adult females ($n = 34$), postmolt adult females ($n = 16$), juvenile males ($n = 15$), subadult males ($n = 10$), and adult males ($n = 9$).
This study expands and integrates satellite tracking work conducted on SES from PV over more than two decades, from the 1990s to 2018. It provides the first analysis of ontogenetic changes and sex differences in the use of a variety of habitats in the SW Atlantic. Overall, our results confirm the at-sea behavior previously described for SES of this colony (Campagna et al., 1998, 1999, 2000, 2006, 2007), but our larger samples and more sophisticated analyses allowed us to statistically characterize the differences in behavior and habitat use among the different age and sex groups. Seals used all habitats available but displayed pronounced segregation by age and sex, most likely to optimize energetic and life-cycle requirements. Similar findings were reported for other populations of both the northern (e.g., Le Boeuf et al., 1993, 2000; Stewart, 1997) and southern species (e.g., Bailleul, Authier, et al., 2010; Field, Bradshaw, Burton, Sumner, et al., 2005; Hindell et al., 1991, 2016). Elephant seals across their range therefore show remarkable similarities in habitat use by sex and age classes, despite differences in geographical and environmental contexts.

4.1 | Shelf versus pelagic habitats

Foraging seals leaving PV encounter a variety of oceanographic and bathymetric regimes and ecological systems, from a shallow shelf to the deep waters of the SW Atlantic Ocean basin (Campagna et al., 2000). The transition between mixed coastal and shelf waters is quickly left behind, to either remain on the shelf or move towards the shelf break and further to the water masses of the Falkland/Malvinas and Brazil Currents, the confluence of these currents, and the deep waters of the Argentine Basin (Figure 1).

From a physical and oceanographic perspective, the Patagonian shelf is large, shallow, and a highly productive habitat. This is also reflected biologically with high chlorophyll-a levels, and also for the substantial fishery that it sustains (Acha et al., 2004; Alemany et al., 2014; Brunetti et al., 1999; Dogliotti et al., 2014; Lutz et al., 2010; Romero et al., 2006). This extended and shallow habitat for a deep diving seal provides an opportunity to test preferences between and within populations. In most places where elephant seals occur, shelves are relatively narrow and animals quickly access deep waters (1,000 m or more within 9–100 km from the coast; Campagna et al., 2007). We found that the shelf may be preferred by juvenile, subadult, and adult males and to a lesser extent by juvenile females but not by adult females.

Another distinct offshore habitat is the shelf break. The waters along the shelf slope have the most extended front of the SW Atlantic, the Shelf Break Front (Acha et al., 2004). This is an area of high biological relevance (Acha et al., 2004), associated with high concentrations of satellite chlorophyll-a (Romero et al., 2006), high primary production (Lutz et al., 2010), and a rich fish and squid fauna that attracts top predators (Acha et al., 2015; Alemany et al., 2014; Brunetti et al., 1999; Copello et al., 2011; González Carman et al., 2016). A large biomass of Argentine shortfin squid, *Illex argentinus*, occur here (Alemany et al., 2014; Brunetti et al., 1999). Mature squid migrate along the shelf and shelf break, and are likely prey for SES (Lewis et al., 2006; Rodhouse et al., 1992). The shelf break was the most common habitat for subadult and adult males.

Further offshore, the Argentine Basin is characterized by abyssal depths. Oceanic waters are affected by the Brazil/Malvinas Confluence, which produces intense eddy activity containing mixed subtropical and subpolar waters (Piola & Matano, 2001; Saraceno et al., 2004). This is a more ephemeral and less predictable habitat in terms of productivity, distribution, and availability of prey than the shelf and shelf break (Campagna et al., 2006; Figueroa et al., 1998; Lutz et al., 2010). This habitat was foremost common for some juveniles, especially females, and for PB and PM adult females.

Areas used by other populations of elephant seals have habitats that differ from those of the SW Atlantic, off PV. The shelf at the Antarctic Peninsula is also extensive and accessible by seals, yet waters deepen to 1,000 m or more a few kilometers off King George Island. Adult males and females from this region predominantly forage on...
the Antarctic continental shelf (Hückstädt et al., 2012; Muelbert et al., 2013). The shelf at South Georgia is also narrow and while males can stay close to the colony, females travel longer distances with some reaching the continental shelf by the Antarctic Peninsula (McConnell & Fedak, 1996). At Macquarie Island, the shelf extends only a few kilometers from shore and is comparatively deep (over 1,000 km$^2$ of sea floor < 1,000 m deep). Here, the seals distribute over oceanic waters with adult male foraging areas being closer to the Antarctic continent than those of juveniles and adult females (Field, Bradshaw, Burton, Sumner, et al., 2005; Hindell et al., 1991). At Kerguelen Island, the Kerguelen plateau is large and deeper than that in Patagonia (~1,200,000 Km$^2$ of waters < 1,000 m). It is located in the vicinity of important frontal areas such as the Frontal Zone, between the Subantarctic and Polar Fronts and the Antarctic Zone close to the Antarctic continent (Bailleul, Authier, et al., 2010). These frontal systems, also present near the other sub-Antarctic colonies, are relatively productive (Moore & Abbott, 2000) and provide potentially accessible and predictable foraging resources. Main foraging areas of subadult males are over the Kerguelen-Heard Plateau and the Antarctic shelf, while adult females favor oceanic waters mainly within the Frontal Zone (Bailleul, Authier, et al., 2010). Marion Island is also surrounded by deep waters (> 1,000 m) and is relatively far away from any continental shelf as well as the Antarctic ice-edge. Seals here forage pelagically, over deep waters (McIntyre et al., 2010, 2012). Northern elephant seals that breed along the coast of Baja and Central California are also exposed to a narrow continental shelf, extending only 7 km and 27 km from Isla Guadalupe and Año Nuevo, respectively. Neither males nor females that leave Año Nuevo, remain close to the rookery (Le Boeuf et al., 1993, 2000).

4.2 | Ontogenetic changes in habitat use

4.2.1 | Males

Juveniles from PV preferentially used mid-shelf waters but then increasingly used the shelf break as they aged. Foraging in the shallow mid-shelf may confer some advantages to young males, prior to having to satisfy much greater energetic demands as they grow. Some benefits could be related to shorter travel distances from the colony and reduced diving effort to access habitats rich in food (Campagna et al., 2007; Eder & Lewis, 2005; Eder et al., 2011). Nonetheless, some juveniles also used oceanic habitats. Eder et al. (2011) suggested that foraging in distant areas may be related to intraspecific resource partitioning as this behavior seem to occur during the months when adult seals are also foraging at sea (January to August). As juveniles continue to grow, increasing the relative allocation of energy to growth, later correlated with social rank and mating success (Field, Bradshaw, Burton, et al., 2007; Le Boeuf et al., 1993), they increasingly used the outer shelf and shelf break, as did all adult males. Switching to the shelf break front may offer access to larger, more predictable food resources, necessary to sustain the energetics of larger body sizes.

Recently weaned pups from Macquarie Island (McConnell et al., 2002), as well as 1–4-year-old juveniles, disperse in oceanic waters of the Southern Ocean and show spatio-temporal segregation according to age (Field, Bradshaw, Burton, Sumner, et al., 2005). As seals grow, they travel farther from the colony and remain at sea for longer periods (Field, Bradshaw, Burton, Sumner, et al., 2005). There are also diet differences, in both species composition and prey size, among these juvenile classes (Field, Bradshaw, van den Hoff, et al., 2007). Older seals have greater proportions of larger squid species in their samples than smaller individuals, possibly related to an increase in diving ability, with increase body size and foraging range as seals grow. Age related changes in foraging and haul-out behavior, as well as diet composition, may be a way to reduce intraspecific food competition (Field, Bradshaw, van den Hoff, et al., 2007).

A similar pattern of dispersion to Macquarie was reported for Kerguelen Island: juveniles favor oceanic waters, while subadults forage almost exclusively over the Kerguelen-Heard Plateau and the Antarctic shelf (Bailleul, Authier, et al., 2010; Orgeret et al., 2019; O’Toole et al., 2014). Stable isotope analyses suggest that
young juveniles forage in pelagic environments, shifting to predominantly neritic shelf waters and increasing their trophic level when 3–4 years old. These habitats are also preferred by adult males (Bailleul, Authier, et al., 2010; Chaigne et al., 2013).

The oceanography and physical context of Marion Island results in males foraging in pelagic, deep waters since being were young (McIntyre et al., 2010, 2012; Tosh et al., 2012). However, juveniles travel farther from land than adults, and increase their dive duration as they age (McIntyre et al., 2012). Contrary to PV, South Georgia, Macquarie, or Kerguelen, and also to northern elephant seals, adult males do not forage benthically over shallow shelves or slopes (Bailleul, Authier, et al., 2010; Campagna et al., 1999; Hindell et al., 1991; Le Boeuf et al., 2000).

In summary, age-related spatial and dietary resource partitioning could be explained by changes in energetic requirements as juveniles mature, as well as to physiological capabilities and experience, which allows them to exploit different ecological niches (Bailleul, Authier, et al., 2010; Field, Bradshaw, Burton, Sumner, et al. 2005; Field, Bradshaw, van den Hoff, et al., 2007; Irvine et al., 2000; Orgeret et al., 2019).

4.2.2 | Females

Juveniles from PV used the outer shelf as well as the more distant Argentine Basin, while adult females remained mainly over deep oceanic waters. One juvenile seal reached the South Pacific waters through the Drake Passage but returned to Valdés through the Magellan Strait (Figure 2). Young females exploit ephemeral temperature fronts created by the major currents of the SW Atlantic, which may represent alternative transient foraging areas where they can briefly benefit from reduced competition with more experienced seals and with other species of diving birds and marine mammals (Campagna et al., 2006). The use of eddies was also described for juveniles from Marion (Tosh et al., 2015) and adult females from Kerguelen Islands (Bailleul, Cotté, et al., 2010; Dragon et al., 2010).

The behavior at PV is similar to that at Macquarie Island (Field, Bradshaw, Burton, Sumner, et al., 2005; Field, Bradshaw, van den Hoff, et al., 2007), Marion Island (McIntyre et al., 2011; Tosh et al., 2012), and Isles Kerguelen (Bailleul, Authier, et al., 2010; Orgeret et al., 2019). Some adult females from South Georgia also concentrate over deep waters (McConnell & Fedak, 1996; McConnell et al., 1992).

Females at the Kerguelen Islands do not have a major dietary shift as they age, but they do broaden their trophic niche (Bailleul, Authier, et al., 2010; Chaigne et al., 2013). For adult females, the energy dense (when compared with prey such as squid) deep-living mesopelagic fish like myctophids represent a major proportion of their diet (Bailleul, Authier, et al., 2010; Cherel et al., 2008; Guinet et al., 2014).

At PV cephalopods may not represent a big proportion of adult female’s diet, although diet work was initially limited to the shelf and shelf break with no information from the Argentine Basin, where most of the foraging dives took place (McGovern et al., 2019). A more recent study based on prey capture attempts and antipredatory flashes emitted by bioluminescent prey suggested that PB females could possibly be feeding on nonbioluminescent midwater squid, but also that they may pursue dispersed, larger or more agile prey items, harder to catch (Goulet et al., 2020). Studies of the northern elephant seal based on quantitative fatty acid (Goetsch et al., 2018) and video analyses (Yoshino et al., 2020) showed that PB females feed mainly on fish (such as myctophids) rather than squid, in the mesopelagic zones across the eastern North Pacific.

4.3 | Sex differences in habitat use

The similar movement patterns of juvenile males and females is also reflected in their isotopic signatures (Eder et al., 2010). At Macquarie Island, 1–4-year-old juveniles do not show differences in the foraging behavior (Field, Bradshaw, Burton, Sumner, et al., 2005; McConnell et al., 2002) or diet (Field, Bradshaw, van den Hoff, et al., 2007) between sexes. At this age, seals have yet to become sexually dimorphic and both sexes have similar energetic
requirements that diverge as the animals grow (Field, Bradshaw, Burton, & Hindell, 2005; Field, Bradshaw, Burton, et al. 2007).

In adults, differences in foraging areas are likely related to their high sexual dimorphism (Le Boeuf et al., 2000). As males are four to five times heavier than females, they have larger absolute energy requirements that may result in different feeding strategies. As absolute energy requirements increase with mass, adult males must consume about three times more prey per day than females to recover mass loss (Le Boeuf et al., 1993). Our results indicate that PV adult females employ a different foraging strategy than males, consistent with Campagna et al. (1998, 1999, 2000) and Eder et al. (2019). Both PM and PB females traveled farther from the colony than males predominantly foraging in distant subpolar and mixed subtropical-subpolar pelagic waters. Adult males, however, spent time at sea in potentially stable environments associated with predictable seasonal frontal areas of the outer shelf and shelf break (Acha et al., 2004; Romero et al., 2006).

The different proportion of time spent in ARS is likely a reflection of the habitats, from the shallow continental shelf to the abyssal waters, that seals use to forage as well as prey preference. On the shelf and shelf break seals showed much more ARS behavior, indicating more spatially concentrated feeding activity. In the oceanic waters the seals displayed more cursive search behavior moving continuously from patch to patch, which suggests that they are targeting dispersed rather than discrete patches. Juvenile and adult females spent less time in an ARS behavior than subadult and adult males, and some females showed no ARS behavior at all. However, this does not imply that they were not feeding. There is evidence supporting that SES also target prey opportunistically while in transit (McGovern et al., 2019; Thums et al., 2011) without necessarily changing their trajectory or their diving behavior.

Stable isotope studies in this colony are consistent with the movement patterns of adult males and females, (Lewis et al., 2006). Nonetheless, more recent isotopic studies suggest that some females may forage on the shelf or shelf break as well (Eder et al., 2019). The shelf and shelf break were more important to the PB females, which used these habitats for almost 25% of their 70-day foraging trips. Furthermore, of the total ARS locations estimated for this group, more than 50% occurred at the shelf break (not shown). A study based on dive type classification (foraging, resting, and transit) inferred through 3-dimensional movements and video-recorded observations, indicates that over the shelf, foraging dives (in which prey were visually detected in the video and ingestion of prey was either viewed or heard on the audio) represents only 2% of the total dives made by PB females at this habitat. While, over the shelf break (200–3,500 m depth) and Argentine Basin, 80% of the dives are foraging dives (McGovern et al., 2019).

Males from South Georgia engage in shorter trips than females, remaining at or near the edge of the continental shelf 450–900 km from the island (McConnell & Fedak, 1996). Neither male nor female northern elephant seals that leave Año Nuevo, remain close to the rookery. Males travel to destinations as far as 4,000 km from the colony and there remain along the continental margins. Females, on the contrary, favor the open ocean over deep waters of the Northeast Pacific (Le Boeuf et al., 1993, 2000). Adult females from Kerguelen, Macquarie, Marion, and South Georgia Islands have comparatively little to no foraging over shelf habitats near the breeding colony, as indicated by the shape of the dives (Bailleul, Authier, et al., 2010; McIntyre et al., 2011) and ARS behavior (Hindell et al., 2016). However, adult females from the Antarctic Peninsula predominantly forage on the Antarctic continental shelf (Costa et al., 2010; Hindell et al., 2016; Hückstädt et al., 2012; Muelbert et al., 2013). Male and females from Elephant Island, located on the Antarctic continental shelf in the Northern Antarctic Peninsula, use the shelf habitats more than other populations, although some individuals still employ open-water, foraging strategies (Muelbert et al., 2013).

If adult females can successfully exploit the shelf habitats elsewhere, it is unclear why those from PV do not make more use of it, considering it is resource rich. Foraging on the shelf may result in additional costs for females, that offset the energetic advantage of feeding there. The high-energy, dense but benthic prey on the shelf (Eder & Lewis, 2005), may require more energy for females to capture or to efficiently handle food. An additional cost of shelf foraging may be an increase in predation risk (Chaigne et al., 2013). For northern elephant seals predation risks from white sharks (*Carcharodon carcharias*) or killer whales (*Orcinus orca*) are higher near the coast, were males...
forage, than in the open waters (Le Boeuf et al., 2000). Shelf waters in Patagonia are also more likely to have larger numbers of killer whales (Iñíguez, 2001; López & López, 1985) and more diversity of potentially dangerous shark species (Irigoyen et al., 2015). Males in a highly polygynous mating system have fitness benefits from growing rapidly, which may offset the risk of predation. Their large body size may represent a greater defense against predators (van den Hoff & Morrice, 2008). Females, on the contrary, may give birth to a single pup per year thus maximize their fitness by living longer and producing more offspring over a longer life span (Le Boeuf et al., 2019).

Females might also be excluded from the shelf habitat by males and other species (Lewis et al., 2006). Interspecific competition for shelf resources may also be a factor promoting long-distance feeding trips (Campagna et al., 2007; Eder et al., 2019; Lewis et al., 2006). The Patagonian shelf and shelf break are also intensively used by commercial fisheries and many other top predators including: South American sea lions (Campagna et al., 2001), Magellanic penguins (Spheniscus magellanicus; Boersma et al., 2009; Gómez-Laich et al., 2015), southern giant petrels (Macronectes giganteus; Copello et al., 2011), dusky dolphins (Lagenorhynchus obscurus; Crespo et al., 1997), and other marine mammals and pelagic birds from the region (Copello et al., 2013; González Carman et al., 2016) and from more distant areas (Croxall & Wood, 2002). All these species are relatively shallow divers, although some of them, such as the South American sea lion, may dive to the bottom of the shelf in most of its extension (Campagna et al., 2001). The South American sea lion population has been expanding in the last decades, particularly in northern Patagonia (Dans et al., 2004).

Commercial fisheries target several shelf and shelf break species of fishes and squid known to be prey items for top predators (e.g., Alemany et al., 2014; Brunetti et al., 1999; Copello et al., 2014; Crespo et al., 1997). Although SES are able to forage deeper than all these other species, a similar isotopic profile has been found between adult SES males and South American sea lions (Lewis et al., 2006) that foraged over the continental shelf. Eder et al. (2019) also indicated that the high specialization found in the small percentage of PM adult females which exhibited a neritic foraging strategy, associated with the shelf or shelf break, does not rule out that adult females foraging in deep oceanic waters may be avoiding intra and interspecific competition.

The maintenance of two distinct foraging strategies in adult females, oceanic and, to a lesser extent shelf, has been reported in other studies (Bailleul et al., 2007, Bailleul, Authier, et al., 2010; Hindell et al., 2016). In general, females from Kerguelen and Macquarie Island focus their foraging activity on frontal systems in oceanic waters (Bailleul, Authier, et al., 2010; Bailleul, Cotté, et al., 2010; Hindell et al., 2016). During the beginning of winter, when the sea ice extent its minimum, PM females make the most use of the shelf habitat close to the Antarctic continent. As the winter progress, and sea ice extends northwards, they travel away from the shelf remaining along the sea marginal ice zone (Bailleul et al., 2007; Hindell et al., 2016). Females from Macquarie use the deep ocean habitat exclusively at this point. Adaptable and variable foraging patterns provide behavioral plasticity within the population that may help individuals buffer it from changes in one or the other of the habitats.

Throughout their range, both species of elephant seals, are far-ranging, deep-diving animals using a wide variety of geographic and oceanographic regions. The Patagonian shelf off PV is very different to others within the distribution of SES. Here, it is a shallow, extensive, highly productive, and competitive habitat where many other species (including humans) forage. However, there was a pattern of segregation between sex and age classes consistent with other SES populations. Juveniles, especially males, favored shelf waters but as females they were also able to disperse over deep oceanic waters far from the colony. Subadult and adult males traveled the shortest distances to exploit the resources found at the outer shelf and shelf break. In contrast, adult females traveled hundreds of kilometers further, perhaps in order to exploit the more ephemeral eddies, where there is less competition and predation. Young seals of both sexes have similar energetic requirements that diverge as they grow, and sexual dimorphism becomes more evident. Habitat partitioning between the sexes and age classes would benefit seals by decreasing competition. Additional factors, such as vulnerability to predators, may also shape behavioral differences. Thus, the Patagonian shelf may remain as an under-used productive habitat, where only a proportion of the seals, mainly males, make use of it. SES develop a fixed pattern of deep and distant foraging, segregating by age and sex, likely as a way to reduce intra specific competition and maximize foraging success for each age and sex class.
ACKNOWLEDGMENTS
This is a synoptic work that integrated data collected during many years. We are grateful to all the field personnel that assisted in the deployment and recoveries of data loggers, specially to Ricardo Vera, as well as the different institutions that provided financial support, particularly the Wildlife Conservation Society and the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) of Argentina. All animal handling procedures were performed in accordance with animal ethics standards and followed the guidelines approved by the American Society of Mammalogists (Gannon et al., 2007).

AUTHOR CONTRIBUTIONS
Julieta Campagna: Conceptualization; formal analysis; visualization; writing-original draft; writing-review and editing.
Mirtha Lewis: Funding acquisition; writing-review and editing. Victoria González Carman: Writing-review and editing. Claudio Campagna: Funding acquisition; writing-review and editing. Christophe Guinet: Funding acquisition; writing-review and editing. Mark Johnson: Funding acquisition; writing-review and editing. Randall Davis: Funding acquisition; writing-review and editing. Mark Hindell: Conceptualization; formal analysis; writing-original draft; writing-review and editing.

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