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Home Range Analysis of Hawaiian Monk Seals (*Monachus schauinslandi)* Based on Colony, Age, and Sex

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Abstract

Low survival rates of juveniles in populations of the endangered Hawaiian monk seal (*Monachus schauinslandi*) in the Northwestern Hawaiian Islands are believed to be the leading cause of the species' decline. One hypothesis is that younger seals are starving due to poor foraging success. Because high mortality of young seals poses a significant risk to population-level survival, increased knowledge of the specifics of weaned pup and juvenile foraging is of paramount importance. We used telemetry data and the most recent movement modeling techniques to compare monk seals' home ranges across various age and sex groups among five of the six primary breeding colonies in the Hawaiian Islands. We found significant differences in size and spatial patterns of home ranges at the regional and colony level, following a decreasing productivity gradient from the northwest to the southeast. Home range size was significantly smaller in the three northwestern colonies than the two central-northeastern colonies. Adult seals in one colony at the lower end of the productivity gradient had smaller home ranges than younger seals, perhaps indicating that lower levels of prey abundance are forcing younger seals to forage further away from the colony where larger adult seals outcompete them. Uniqueness in seal movement on Pearl & Hermes Reef might be associated with increased southerly latitudinal movement of the Transition Zone Chlorophyll Front, which brings nutrient rich waters and a potential surge in productivity, supporting the theory that better prey availability reduces home range size. The wide variability in home range sizes and locations suggests that a universal approach to managing monk seals on different colonies would be unsuccessful. Results here suggest that animals from different colonies may perceive habitat differently; these differences should be taken into account when translocating animals to new habitat.

Key Words: Hawaiian monk seal, *Monachus schauinslandi*, home range, space use, utilization distribution, kernel density estimates

Introduction

Despite being monitored since the 1950s and listed as endangered under the Endangered Species Act since 1976, very little is known about how the Hawaiian monk seal (*Monachus schauinslandi*) uses its environment. Specifically, we lack baseline information on the habitat preferences and space use of Hawaiian monk seals across the species' range. Several studies have used movement data to make inferences about foraging behavior and spatial use, but these have typically focused on short-duration CRITTERCAM use on seals at one colony (French Frigate Shoals) (Parrish et al., 2000, 2002, 2005, 2008). Though the temporal extent of these tags is limited, the efforts have provided insight into seal foraging activities (Parrish et al., 2000, 2002, 2005, 2008), prey species preference (Parrish et al., 2000), and interspecies interactions (Parrish et al., 2008). One study made use of longer-term telemetry data to look at movement (Brillinger et al., 2008); however, that study was based on a single monk seal.

Numbering approximately 1,100 monk seals (Carretta et al., 2010), the majority of the extant population is found in the isolated Northwestern Hawaiian Islands (NWHI), which are comprised of coral reefs and atolls, seamounts, banks, and shoals. In the NWHI, there are six major monk seal breeding colonies located at Kure Atoll, Midway Atoll, Pearl & Hermes Reef, Lisianski Island, Laysan Island, and French Frigate Shoals (FFS) (Stewart et al., 2006). Monk seals forage primarily on the barrier reefs of the atolls as well as along the seamounts and on submerged reefs and banks farther away from the atolls (Antonelis et al., 2003; Parrish et al., 2005; Parrish & Abernathy, 2006; Stewart et al., 2006).

While the whole population in the NWHI has been steadily declining at about 4%/y since 1998

(Carretta et al., 2010), each individual colony has experienced different rates of growth and decline over the past several decades (Craig & Ragen, 1999; Antonelis et al., 2003; Baker & Thompson, 2007). Survival rates among young seals vary among the colonies, but at all colonies these rates are significantly lower than rates achieved by adults (Baker & Thompson, 2007). One year's estimate at FFS approached 80% mortality (Baker & Thompson, 2007). Research on large-scale oceanographic features and events shows possible links between ocean productivity and variable survival rates (Antonelis et al., 2003; Baker et al., 2007) or seal abundances (Schmelzer, 2000), possibly due to a lack of prey abundance (Craig & Ragen, 1999). Some of this between-colony variation in survival might be due to a productivity gradient. Schmelzer (2000) used chlorophyll, sea surface temperature (SST), vertical water column structure, and the variability associated with these variables as proxy indicators of primary production, and thus as a proxy for prey availability, and found a latitudinal gradient in productivity in the NWHI decreasing from northwest to southeast. Additionally, Schmelzer identified a synchronous variation in abundances among proximate monk seal colonies, suggesting both that environmental conditions influence the survivability of the monk seal and that the colonies may be grouped together into three regions that experience similar environmental conditions: (1) northwestern (Kure, Midway, and Pearl & Hermes), central-northeastern (Lisianski and Laysan), and southern (FFS, plus the smaller populations of Nihoa and Necker Islands).

In addition to the environmental challenges, the monk seals experience, or have experienced, an array of threats, including human disturbance (Gerrodette & Gilmartin, 1990), competition with other apex predators (Parrish et al., 2008), shark predation (Alcorn & Kam, 1986), entanglement (Henderson, 2001; Boland & Donohue, 2003; Donohue & Foley, 2007), and mobbing (Starfield et al., 1995). Because juvenile survival is so low, and thereby poses a significant risk for population-level survival, increased knowledge of the specifics of juvenile seal foraging is of paramount importance to assessing the survivability of the population (Craig & Ragen, 1999; Baker & Thompson, 2007). Differences in foraging habitats between age and sex groups have been explored (Parrish et al., 2000, 2005; Schick, 2009) and to date have yielded evidence of differences in depth and slope preferences between adults and juveniles.

Since many marine animal species are not directly observable for large portions of time, satellite-based tagging mechanisms are frequently employed to track their movements (e.g., Austin et al., 2003; Eckert, 2006; Schorr et al., 2009). Here, we use a large telemetry dataset (Stewart, 2004a, 2004b; Stewart & Yochem, 2004a, 2004b) of monk seal movement to examine, analyze, and compare monk seals' home ranges at five of the six primary breeding colonies in the NWHI. We use movement data to create kernel utilization distributions that show the home ranges of seals at the colony level, and by age and sex groups within each colony. We then compare the home range sizes of combined age and sex groups between the northwestern and central-northeastern regions, among the five colonies of these two regions, and between groups within colonies to test our assumptions regarding how home range sizes are expected to differ among these groups. Finally, we compare the colony-level home ranges with the Papahānaumokuākea Marine National Monument (PMNM) boundary.

Starting from first principles, we assume that higher levels of prey abundance near a colony will result in smaller home ranges for monk seals as most of their traveling excursions are foraging bouts. Conversely, we postulate that when there are limited resources based on population size, adults are able to outcompete the smaller subadults for local resources, forcing subadults to travel farther and have larger home ranges than adults.

Materials and Methods

Data Source and Processing

During a 5-y period, researchers at the Pacific Island Fisheries Science Center (PIFSC) attached *Argos* satellite-based Platform Transmitter Terminal (PTT) tags to monk seals on the six primary breeding colonies in the NWHI (Stewart, 2004a, 2004b; Stewart & Yochem, 2004a, 2004b; Parrish & Abernathy, 2006). In this paper, we use data from five of the six colonies, listed from westernmost to easternmost: Kure Atoll (2001-2002, $n = 9$), Midway Atoll (2000-2001, $n = 12$), Pearl & Hermes Reef (1997-1998, $n = 13$), Lisianski Island (2000-2001, $n = 19$), and Laysan Island (2001-2002, $n = 25$). Tagged seals ranged in age from as young as 4 mo to as old as 17 y and are classified into three age groups: (1) weaned pups less than 1 y old, (2) juveniles between 1 and 4 y, and (3) adults over 4 y (Table 1). Tags remained on each seal for up to 1 y before falling off, failing, or being shed during the annual molt. To conserve power, the tags were programmed to transmit only during hours of the day that were likely to have good satellite coverage and only while the tag was out of the water. They were programmed to stop transmitting when the seal was hauled out for more than 70 min (Stewart et al., 2006). Further details of how each tag was programmed may be found in Stewart (2004a, 2004b) and Stewart & Yochem (2004a, 2004b).

The accuracy of calculated locations from the *Argos* system is dependent on the number of messages sent during the connection. Fewer sent messages and increased length of time between satellite uplinks both result in increased error ranges associated with the determined location (Austin et al., 2003; Collecte Localisation Satellites [CLS], 2007). Monk seals spend large portions of their time below the water's surface, minimizing the time the transmitter is able to connect to satellites and reducing the number of messages sent when connected. This decreased satellite access results in satellite telemetry data that are recorded sporadically in time and space (Hays et al., 2001; Vincent et al., 2002), with higher levels of location error (CLS, 2007). Traditional filtering mechanisms use *a priori* criteria such as swimming speed or turning angle to remove improbable locations (Austin et al., 2003; Freitas et al., 2008). In comparison, state-space models (SSM) use a data model for the observed telemetry data. Together with a separate process model, the SSM provides evenly spaced tracks with daily estimates (with uncertainty) of the animal's true position (Jonsen et al., 2003). Most of the monk seal movement analyses to date (Stewart, 2004a, 2004b; Stewart & Yochem, 2004a, 2004b; Parrish & Abernathy, 2006; Stewart et al., 2006) have employed some type of subjective data filtering algorithm that eliminated presumably spurious location data. This study is the first to use SSM-filtered telemetry data to generate kernel home range estimates for seals in each age class/sex combination within each of five colonies.

Spatial Analysis

To find areas of high-use habitat, we used the SSM daily position estimates to create fixed kernel home range utilization distributions (Worton, 1989) with an *ad hoc* smoothing parameter (Silverman, 1986). We created polygons of the 25, 50, 75, and 95% utilization distributions (UD) for all individual seals, and then for groups of seals based on colony, age class (adult, juvenile, weaned pup), sex, and age class and sex combinations (e.g., adult males). We used the 95% UD as the delineator of the home range (Worton, 1989) and the 50% UD as the "core use" area and calculated corresponding areas for each. We performed a Kolmogorov-Smirnov (KS) test to determine if the home range sizes of groups of seals were significantly different. We tested for differences in home range size between various groups within each colony, between colonies, within two of the three regions noted by Schmelzer (2000) (northwestern region comprised of Kure, Midway, and Pearl & Hermes and the central-northeastern region comprised of Lisianski and Laysan), and between the two regions. Due to limited sample sizes in some groupings, we only performed the test with groups that had three or more seals. We also considered p values < 0.1 as showing some level of significance given the small population and small sample sizes.

We performed all home range calculations and statistical analyses in *R* (R Development Core Team, 2009) using the packages *adehabitat* (Calenge, 2006) and *Matching* (Sekhon, 2009). Both the estimates of seal positions from the SSM output and the home range UDs were mapped in a geographical information system (*ArcGIS*, Version 9.3; ESRI, Redlands, CA, USA) overlaid on a 2,000-m contour derived from the 2004 bathymetry dataset (Marks & Smith, 2006). Additionally, we mapped the boundary coordinates for the PMNM in the GIS system and overlaid the UDs for the colonies to determine if the extent of the seals' home ranges fell entirely within this management domain (Figure 1).

Table 1. Data summary for individual colonies, ordered from westernmost (Kure) to easternmost (Laysan); population numbers are from 2006. For each colony, the number of tracks precedes a breakdown by age (Adults = Ad; Juveniles = J; Weaned Pups = WP) and sex (Male = M; Female = F). Duration indicates the mean number of days the tags lasted in each of the colonies. Also included are the start of the tagging and the last day with a successful satellite fix.

Colony	Population	#	Ad (M/F)	J (M/F)	WP (M/F)	Sex (M/F)	Duration	Start	End
Kure Atoll	118	9	5 (4/1)	3 (2/1)	1 (0/1)	6/3	133	31/10/01	22/9/02
Midway Atoll	60	12	3 (1/2)	7 (4/3)	2 (2/0)	7/5	84	1/1/01	21/9/01
Pearl & Hermes Reef	177	13	10 (6/4)	3 (3/0)	0	9/4	114	26/10/97	4/10/98
Lisianski Island	194*	19	9 (4/5)	6 (5/1)	4 (2/2)	11/8	81	15/10/00	9/7/01
Laysan Island	221	25	8 (3/5)	8 (5/3)	9 (4/5)	12/13	113	7/10/01	29/8/02
Totals	770	78	35	27	16	45/33			

* Total enumeration; other population numbers are minimum estimates (NMFS, 2007).

To show spatial variation between groups within colonies, we calculated and plotted a spatial intersect of the 95% kernel UD of each age and sex group to visualize space that is shared vs space that is distinct and to discuss possible resource partitioning causes. To quantify the area of overlap, we calculated the $PHR_{i,j}$ index of overlap (Fieberg & Kochanny, 2005), which gives the probability of finding animal *j* in animal *i*'s home range. In addition to simply enumerating the spatial overlap of home ranges, the PHR index accounts for the density of points/locations that comprise the calculated UD. Ecologically, this allows for directional comparisons across groups. For example, the likelihood of finding an adult female in an adult male home range vs the likelihood of finding an adult male in the adult female home range. On Kure and Midway, small sample sizes of juveniles and weaned pups led us to merge these two age classes when comparing home range overlap with adults.

Results

Regional and Intercolony Differences

Home range sizes of individual monk seals were significantly different between the northwestern and central-northeastern regions (KS test: $p < 0.01$). Quantitative comparisons of these home range areas via KS tests showed the following significant differences for colonies between the two regions: (1) Lisianski and each of the three westernmost colonies of Kure ($p = 0.07$), Midway ($p < 0.05$), and Pearl & Hermes ($p < 0.01$); (2) Laysan and Midway ($p = 0.09$); and (3) Laysan and Pearl & Hermes ($p = 0.05$). No significant intraregional differences in home range area were seen among the three westernmost colonies nor between Lisianski and Laysan in the central-northeastern region.

Among colonies, differences in size and spatial extent of the 95% UD home range likely reflect the topography and habitat surrounding each of the colonies (Figure 1). For example, the spatial extent of each colony highlights how monk seals on four of the five colonies visited nearby seamounts and atolls. Seals from Pearl & Hermes were the exception and did not visit surrounding seamounts or atolls (Figure 1). Lisianski seals had the largest home range area at 16,872 km^2, followed by Laysan (14,001 km^2), Kure (8,736 km^2), Midway (6,742 km^2), and Pearl & Hermes, which had the smallest home range at 1,291 km^2 (Table 2; Figure 1).

Significant differences in home range size were found between juveniles in the northwestern and central-northeastern regions ($p < 0.01$), and also between weaned pups in the northwestern and central-northeastern regions ($p < 0.05$). Home range sizes of males and females between the two regions were significantly different (male: $p = 0.06$; female: $p = 0.05$). When broken down into age and sex combinations (e.g., adult male), the only group that showed a significant difference between the regions was juvenile females ($p < 0.05$).

Significant differences in home range size were found between several age groups within each of the two regions. In the northwestern region, adults differed significantly from juveniles ($p < 0.01$) and from weaned pups ($p < 0.05$). Gender-specific home range size differences were also found to be significant in the northwestern region between male adults and male juveniles ($p = 0.09$), and female adults and female juveniles ($p < 0.05$); and in the central-northeastern region between male adults and male juveniles ($p = 0.07$). No significant differences were found between genders within either region (though see "Intracolony Differences" below).

On Kure, the seals' home range extended past the PMNM management boundary (Figure 1). Adult male seals visited Helsley Seamount to the northwest of the atoll.

Intracolony Differences

Kure Atoll—Adult seals on Kure had much larger home ranges than juveniles and weaned pups (Table 2). The 50% UD core use area for the adult males and the adult female were both on Kure Atoll, but the 95% UD showed that the home ranges of the adult males and the adult female differed (Figures 2a & 2b). The adult female spent time to the east, making use of nearby Midway Atoll and Ladd Seamount, while adult males traveled to seamounts in the northwest and to the southeast (Figures 2a & 2b). Juveniles and weaned pups spent most of their time directly within the atoll (Figure 2c). Home range sizes of the sexes of each age group were similar (Table 3).

The directional comparison of home range overlap probabilities (PHR) between the adult males and the adult female and between juvenile males and the juvenile female were very similar though reversed (Table 4). The adult female on Kure was more likely to be found in the male home ranges than males were to be found in the female home range (Table 4). Juvenile males were more likely to be found in the juvenile female home range than vice versa (Table 4). Younger seals were always in the adult home ranges, and adults were less likely to be found in the younger seals' home ranges (Table 4).

Midway Atoll—Midway is the smallest seal colony, with roughly 60 resident monk seals (Table 2). Adult home range areas were significantly larger than juvenile home range areas ($p = 0.07$). Adult seals of both sexes made use of nearby

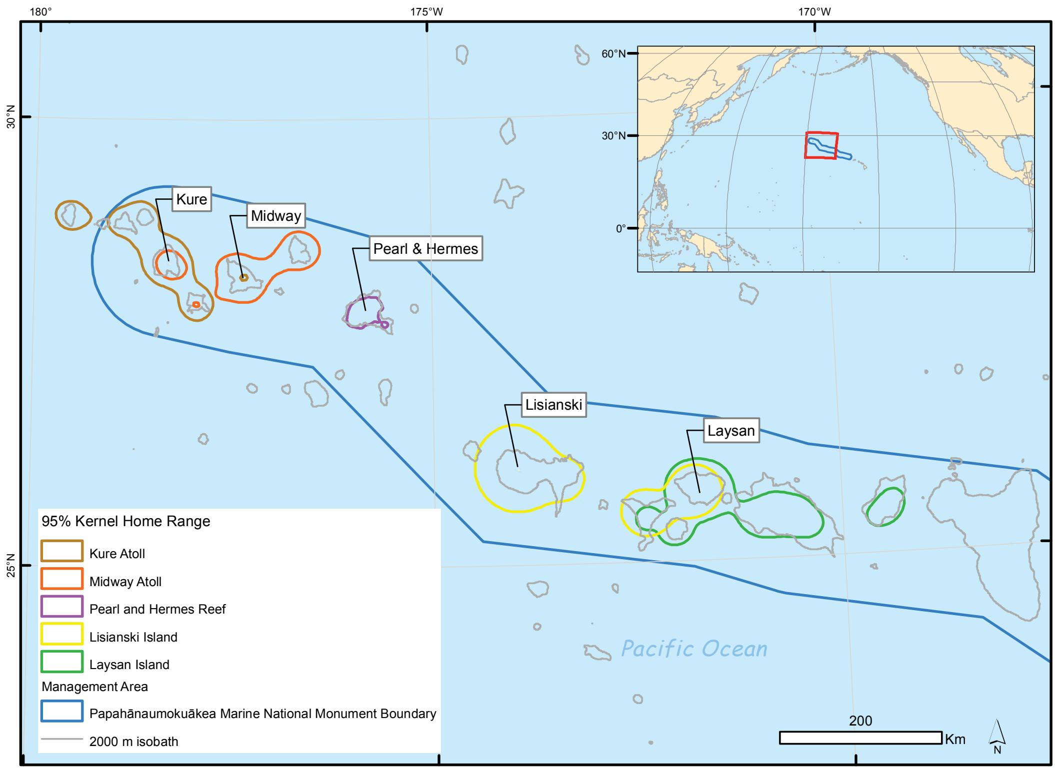

Figure 1. Summary map displaying the 95% Utilization Distribution (UD) home ranges of the five study area colonies; the Papahānaumokuākea Marine National Monument (PMNM) boundary is shown, with the 95% UD of Kure Atoll extending beyond the management jurisdiction of the monument. Intercolony movement can be seen between Kure and Midway, and between Lisianski and Laysan, as well as the use of seamounts beyond all colonies except Pearl & Hermes.

Table 2. Home range area summaries; for each colony, the 95% UD is given for the colony as a whole, for all the seals of each gender (Male = M; Female = F), and for all the seals of each age group (Adults = Ad; Juveniles = J; Weaned Pups = WP). N/A indicates no tracks were available.

	95% home range area (km^2)					
Colony	All seals	M	F	Ad	J	WP
Kure Atoll	8,736	9,163	3,413	12,458	444	488
Midway Atoll	6,742	8,039	5,453	9,919	2,209	420
Pearl & Hermes Reef	1,291	1,300	1,103	1,301	819	N/A
Lisianski Island	16,872	12,854	25,448	3,742	48,155	4,749
Laysan Island	14,001	4,327	19,201	26,678	6,301	2,748

Ladd Seamount, and one of the adult females visited Nero Seamount to the southwest (results not shown). The adult male actually made more use of Ladd Seamount than of Midway during the 256 d it was tracked. Overlap statistics (Table 4) showed high probabilities of finding adult seals of both sexes in the same area.

Only one of the four juvenile males left Midway Atoll. It spent enough time on Kure Atoll to have part of the 75% UD located there (results not shown); it also traveled to Nero Seamount. The other three juvenile males stayed almost entirely within the atoll. Because of the one male juvenile who left Midway Atoll, the 95% UD of that group is much larger than the female group, with the probability of finding a male in the female's home range low and the reverse probability high (Table 4).

Pearl & Hermes Reef—The adult males and females and juvenile males all have very small home ranges that stay mostly within the reef

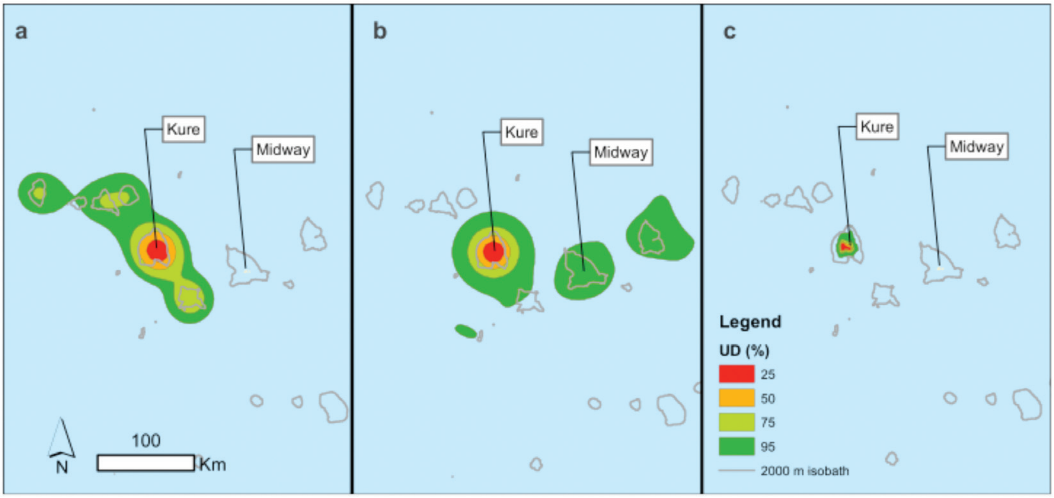

Figure 2. (a) Kure adult male ($n = 4$) home range with the 50% UD core use area within the atoll and the 95% UD home range encompassing seamounts to the northwest and southeast; (b) adult female ($n = 1$) home range also with the 50% UD core use area within the atoll, but the 95% home range encompassing geographic features to the northeast, including Midway Atoll; and (c) combined weaned pup and juvenile ($n = 4$) home range located entirely within the atoll.

Table 3. Home range areas by age and gender group combinations; for each colony, the 95% UD is given for the age and gender class combination (Adults = Ad; Juveniles = J; Weaned Pups = WP; Male = M; Female = F). N/A indicates no tracks were available.

	95% home range area (km²)					
Colony	Ad M	Ad F	J M	J F	WP M	WP F
Kure Atoll	11,303	12,529	334	526	N/A	488
Midway Atoll	7,867	12,491	3,912	548	420	N/A
Pearl & Hermes Reef	1,343	1,103	819	N/A	N/A	N/A
Lisianski Island	2,077	5,324	30,640	49,303	2,944	5,104
Laysan Island	3,794	29,809	2,406	9,727	4,763	897

(Table 3; Figure 3). (No weaned pups were tagged at Pearl & Hermes Reef.) This was the only colony for which the adult males showed a slightly larger home range than the adult females (Table 3). Adult males and females overlapped in their 50% UD core use area (results not shown); PHR values were similar in each direction (Table 4). The adult home range was about 60% larger than the juvenile home range (Table 2); the probability of finding a juvenile in the adult's home range was high, but the probability of finding an adult in the juvenile home range was much lower (Table 4).

Lisianski Island—Of the five colonies studied here, Lisianski Island had the largest colony-level home range (i.e., the home range based on all animals from the colony; Table 2). Unlike the other four colonies in this study, home range area did not increase with increasing age group (Table 2), and Lisianski Island was the only colony on which adults had the smallest home range (Table 2). The juvenile home range was an order of magnitude larger than that of the adults (Table 2; Figures 4a & 4b). Weaned pups had the second largest home range area, which was about 27% larger than the adults' home range area (Table 2; Figures 4a & 4c). Females as a group had almost double the home range area as the males (Table 2). The one juvenile female included here was tagged on Lisianski but then soon traveled to Laysan Island and remained there until the end of the transmissions. Because of this, the 50% core use area for this seal encompassed Laysan instead of Lisianski. The home range and core use area for the male weaned pups and adults were similar, mostly occupying the western half of the colony (results not shown). In contrast, the female weaned pups and adults had home ranges nearly double in size to their male counterparts, using more area on the colony (Tables 2 & 3).

Males of all ages on Lisianski were more likely to be found in female home ranges; this sex distinction is strongest for weaned pups (Table 4).

Table 4. Home range overlap probability estimates; $PHR_{i,j}$ is the probability of finding seal *j* in seal *i*'s home range, taking into account the UD of each home range (Adult = Ad; Juvenile = J; Weaned Pup = WP; Weaned Pup + Juvenile = WPJ; Male = M; Female = F). The first three columns compare home range overlap between genders within each age group; the second three columns compare home range overlap of age groups with genders combined.

Colony group	$PHR_{F,M}$	$PHR_{M,F}$	Colony	$PHR_{Ad,WPJ}$	$PHR_{WPJ,Ad}$
Kure adults	0.74	0.86	Kure Atoll	1.00	0.28
Kure juveniles	0.95	0.82	Midway Atoll	0.93	0.37
Midway adults	0.98	0.87			
Midway juveniles	0.48	1.00	Colony	$PHR_{Ad,J}$	$PHR_{J,Ad}$
Pearl adults	0.87	0.92	Pearl & Hermes Reef	0.94	0.66
Lisianski adults	0.98	0.76	Lisianski Island	0.24	1.00
Lisianski juveniles	0.85	0.71	Laysan Island	1.00	0.54
Lisianski weaned pups	0.90	0.65			
Laysan adults	0.96	0.28	Colony	$PHR_{Ad,WP}$	$PHR_{WP,Ad}$
Laysan juveniles	0.92	0.57	Lisianski Island	0.85	0.95
Laysan weaned pups	0.53	1.00	Laysan Island	1.00	0.36

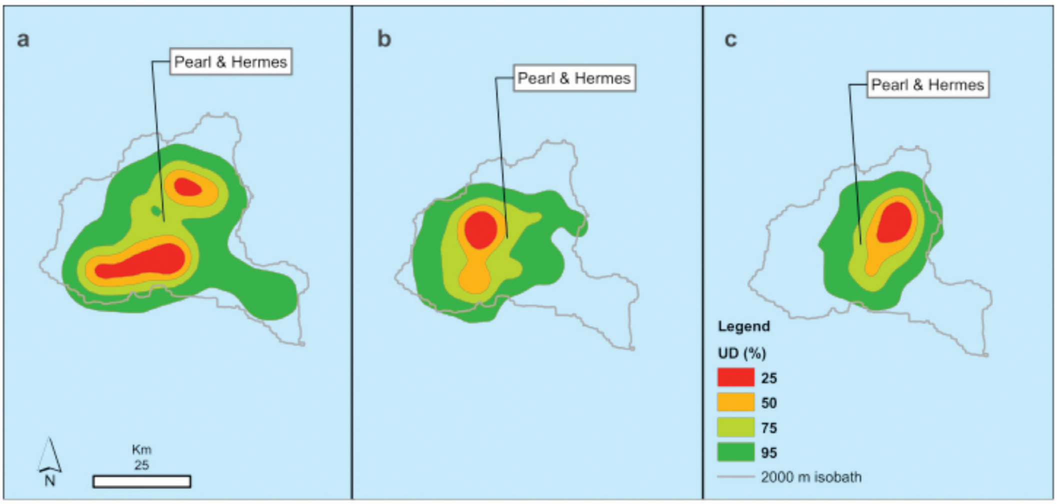

Figure 3. (a) Pearl & Hermes adult male ($n = 6$) home range with two 50% UD core use areas in the reef; (b) adult female ($n = 4$) home range, which is about 200 km^2 smaller than the males' home range, the only colony on which this occurs; and (c) juvenile male seals' ($n = 3$) home range.

The differences seen between adults and juveniles were even larger; there was only a 24% chance of a juvenile being located within the adults' home range, but there was nearly a 100% chance of finding an adult within the juvenile home range (Table 4). This contrasts with the probabilities between adults and weaned pups for which the directional PHR values are similar (Table 4).

Laysan Island—Laysan has the largest population of monk seals in this study (Table 1); however, at the colony-level, it had the second largest home range area. Laysan and Lisianski are the only two colonies on which the female group had a larger home range than the male group (Table 2; Figures 5a & 5b). Of the home range overlap statistics calculated for the five colonies, Laysan showed the most differences between age and sex groups. Sexes of the three age groups had low overlap probabilities in one direction: females of the two older groups had the larger home range; but for weaned pups, males had the larger home range. Between age groups, adults had larger home ranges than the two younger groups and, thus, the probability of finding an adult in either of the younger age groups' home ranges was low (54% for juveniles; 36% for weaned pups). Home range areas of adults were significantly larger than weaned pups ($p = 0.09$).

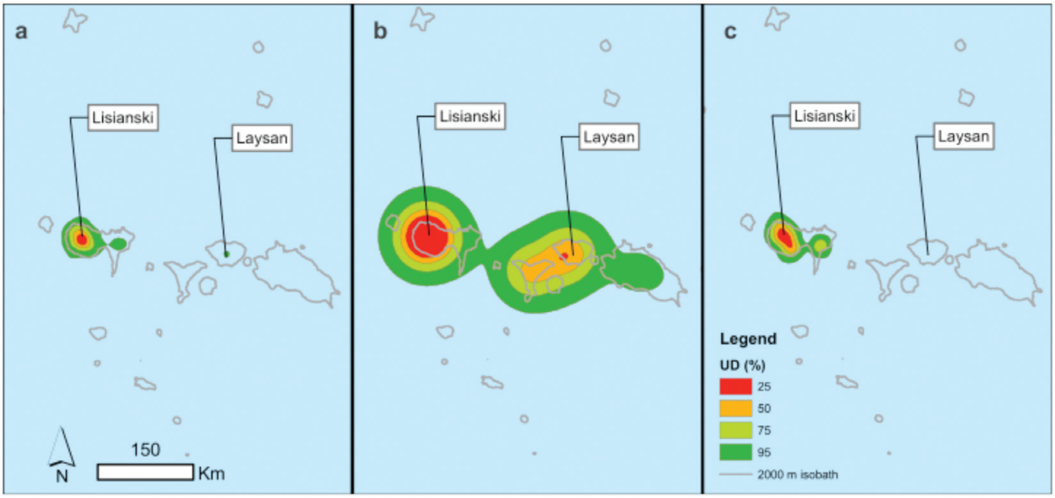

Figure 4. (a) Adult seals' home range on Lisianski Island, the only colony on which the adult home range is smaller than the juveniles' and the weaned pups' home ranges; (b) Lisianski juvenile seals' home range, encompassing Lisianski and Laysan Islands, Northampton Seamounts, and part of Maro Reef; there are two 50% UD core use areas around both islands and part of Northampton Seamount West; and (c) Lisianski's weaned pups' home range and core use area, restricted to Lisianski Island.

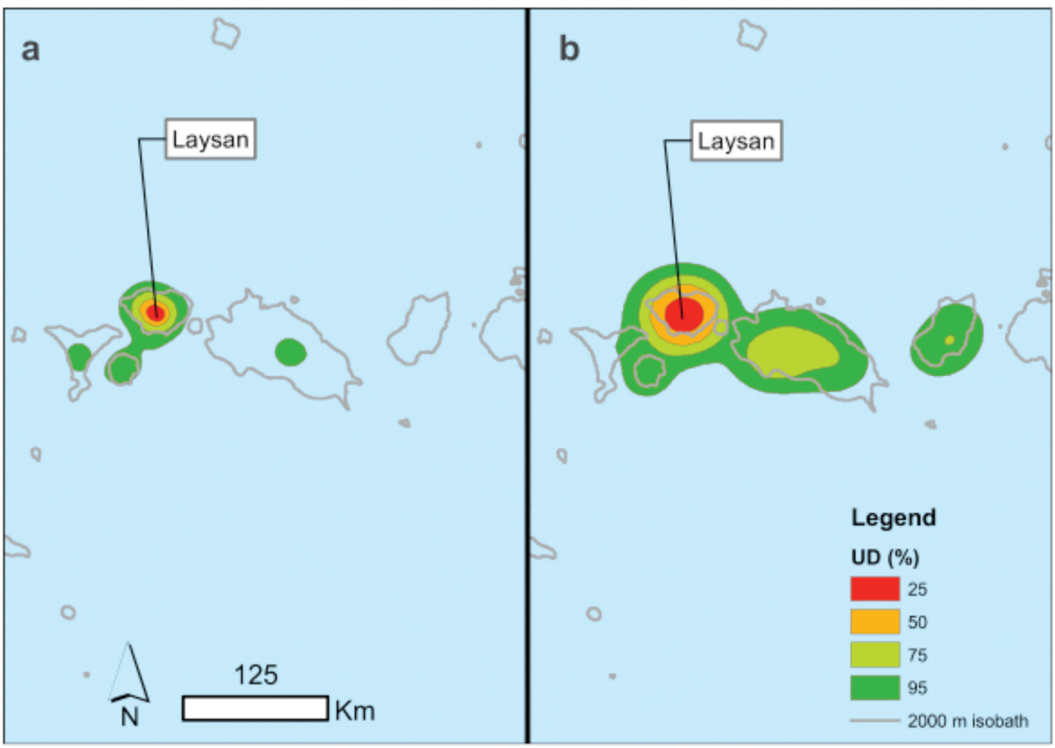

Figure 5. (a) Home ranges of all Laysan Island male seals; the adult males spent time on Northampton Seamount West, the juvenile males traveled to Northampton Seamount East, and the weaned pup males traveled to Maro Reef; and (b) home ranges of Laysan Island female seals, showing extensive time spent on Maro Reef and also time on Raita Bank, both to the east of Laysan Island.

Discussion

Hawaiian monk seals face an uncertain future and, as such, scientists and managers need as much quantitative information as possible on demography, movement, and overall space use across the entire range for this species. Such detail provides critical baselines in the face of climate change and possible translocation of individuals from the NWHI to the main Hawaiian Islands (MHI). Accordingly, we have examined a large dataset comprised of relocations of individual monk seals across all age groups, both sexes, colonies, and larger ecoregions within the NWHI. We have shown differences in spatial use by Hawaiian monk seals between and within two regions, among five colonies, and among the various age and sex groups within each colony. These differences reflect the landscape ecology of the individual colonies, past demographic and ecological within-colony patterns, and presumably the larger Pacific Ocean scale productivity patterns.

We examined spatial patterns in five of the six colonies that comprise two of the three ecoregions enumerated by Schmelzer (2000) and found that between the northwestern and the central-northeastern groups, juvenile and weaned pup seals had significantly smaller home ranges in the northwestern region (juvenile: $p < 0.01$; weaned pup: $p < 0.05$), but adults did not show a significant difference between the two regions. This could be indicative of the productivity gradient identified by Schmelzer, which is likely to have a greater influence on younger seals that are still learning to forage and might be unable to outcompete larger adults and other large apex predators (Parrish et al., 2005, 2008). In the more productive northwestern region, younger seals have smaller home ranges than their counterparts in the central-northeastern region, perhaps indicating greater prey availability closer to these colonies.

Another possibility is that differences in static physical characteristics, such as the depth, slope, and rugosity surrounding a colony, provide for more ideal foraging territory in one region vs another. If there is less available foraging habitat near a colony, this could be cause for seals to forage on more distant patches. Specifically, at the regional level, the monk seals on the three northwestern colonies of Kure, Midway, and Pearl & Hermes have significantly smaller home range sizes than the monk seals of the two central-northeastern colonies of Lisianski and Laysan. Our results are consistent with our initial two assumptions: (1) higher levels of prey abundance near a colony result in smaller home ranges for monk seals; and (2) when resources near a colony are limited, adults out-compete the smaller subadults for local resources, forcing subadults to travel further and have larger home ranges than adults.

Space-use patterns on Pearl & Hermes differ from all the other colonies in both regions. Notably, while seals of different age and sex groups from other colonies seem to range across large distances, all seals from Pearl & Hermes stay entirely within the 2,000 m isobath of the colony. One possible explanation for the lack of movement outside this colony is that during the time of tagging, the Transition Zone Chlorophyll Front (TZCF) was deflected strongly downward, thereby ostensibly producing favorable productivity conditions for colonies in the northwestern region (Baker, 2006). This would imply animals not having to range as far to find prey. Another possible explanation is the spatial arrangement of nearby foraging patches (Parrish et al., 2005), where it appears certain colonies have more seamounts and atolls in close proximity than others. Pearl & Hermes would appear to have fewer such foraging patches. Contrast Pearl & Hermes with Kure, where animals visit and exploit patches in many directions at large distances—for example, animals from Kure ventured northeast to Ladd Seamount, covering a distance of some 165 km. This transit would appear feasible for seals in Pearl & Hermes as the distance from Pearl & Hermes to Ladd is only 110 km. However, a critical difference is the intervening paths: between Kure and Ladd lies Midway—hence, an animal from Kure would not have to cover the same amount of open, deep water to reach Ladd as would an equivalently dispersing animal from Pearl & Hermes.

Even if either or both of these hypotheses are true, within Pearl & Hermes, space-use patterns also suggest habitat partitioning by age and sex. Moorcroft et al. (2006) showed how mechanistic home range analysis can help infer the determinants of individual space use—for example, they showed how space-use changes as a function of interactions with topographic constraints and interactions with conspecifics. This would be one way to test whether the patterns observed on Pearl & Hermes are driven by interaction with conspecifics, with habitat features, or both. Another way to test this hypothesis would be to employ the movement model of Schick et al. (2008). While Schick (2009) did not see group-level differences among animal-environment interaction within Pearl & Hermes, an alternative parameterization could include distance to conspecifics as a covariate to see if, for example, juveniles are actively choosing similar patches as adults in terms of habitat covariates but are located in different areas within the colony.

Of all the colonies, seals in Laysan appear to segregate the most by age and sex groups—that is, the skewed PHR values in each direction indicate the home range of one group is larger than the other. Specifically, the difference between the males and the females of all age groups was particularly striking. One possible explanation for larger female home ranges on Laysan is that mobbing has occurred here. Adult male seals congregate in the water and try to mount female seals and subadult seals of both sexes, causing injuries, some of which can be fatal (Hiruki et al., 1993; Starfield et al., 1995). Females might be spending their foraging efforts elsewhere, only coming back to Laysan to mate, pup, and molt. Males, on the other hand, can meet their energetic needs closer to the island. If true, the converse is that females bear increased energetic costs and possibly enhanced predation risk when traveling and foraging much farther from the colony. Interestingly, while we see some juveniles from Lisianski foraging at Laysan, we see no evidence of adult females foraging on Laysan.

Due to small sample sizes and unequally weighted tracks in the combined group home ranges, caution should be taken with any conclusions drawn from these results. Despite these small sample sizes, it is important to note that they represent roughly 10% of the population of each colony, which is a significant portion not normally achieved in wildlife studies. In addition to sample size considerations, we have not addressed interindividual variation in foraging. Home range size for each individual seal varied across an order of magnitude in certain colonies (results not shown). Such variation in light of small sample sizes might explain some observed differences in PHR values. Additional research would clarify whether these differences are related to true group-level differences (i.e., adult males vs adult females) or simply large individual differences within small groups. Lastly, shorter durations of tagging data on younger seals (due to smaller tags with shorter battery life) might underrepresent the true distribution of younger seals.

Future Work

Our analyses are nontemporal and do not take into account possible space-use differences in time of day or season. In the future, it would be interesting to look at movement differences between day and night, using a model that produces more than one fix per day. Also, generating more recent and precise movement data with GPS-based tags can significantly improve the level of confidence and specificity in observed animal movement paths. Lastly, looking at home range sizes and overlap of seals at French Frigate Shoals, the largest of the six primary breeding colonies and located at the lowest end of the habitat productivity gradient, would add value to this study as FFS has undergone the largest population decline of all the colonies.

Management Implications

There are implications for how this research could aid in protecting the small but healthy and growing population of monk seals that appear to be recolonizing the MHI (Baker & Johanos, 2004). Constructing robust conservation plans requires a better understanding of the foraging environment, of competition among age groups within monk seals, of prey distribution and abundance, and of fisheries' impact on monk seal prey. As the monk seal recovery team begins to look at relocating weaned pups that have near zero chance of survival on their natal colony (C. Littnan, pers. comm., 10 November 2010) to a more favorable environment, the information presented here can aid in those decisions. For example, weaned pups on Lisianski and Laysan have much larger home ranges than those in the northwestern region. While these differences may be due to biogeographic differences, it is clear that these animals are more accustomed to ranging over larger areas to forage. It is possible that this ability may assist them should they be translocated to a new foreign environment where it might take some extensive exploration to find preferred foraging patches. That is, animals that are comfortable ranging over larger distances may be free of search constraints that limit animals that search within spatially constrained areas. As these animals encounter and explore new habitat, those comfortable with ranging over larger distances may have an advantage.

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