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Range-wide movement patterns of Hawaiian monk seals

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The Hawaiian monk seal (*Monachus schauinslandi*) is critically endangered (IUCN 2012) and numbers approximately 1,200 seals scattered throughout the Hawaiian Archipelago (Fig. 1, Carretta *et al.* 2012). Most seals reside in the Northwestern Hawaiian Islands (NWHI) where abundance is declining; however, a small and growing number of seals also occur in the main Hawaiian Islands (MHI, Baker *et al.* 2011). Until recently, it was thought that there was essentially no movement of seals between the NWHI and MHI. However, recently, with more identified seals and an increasingly effective MHI sighting network, we have found increasing evidence of connectivity between these regions. Connectivity is important for monk seal conservation, as it influences genetic population structure (Wright 1943), metapopulation dynamics (Hanski and Simberloff 1997), and the probability and speed of potential infectious disease transfer (Fulford *et al.* 2002).

Previous Hawaiian monk seal movement studies focused on the six most-studied NWHI sites (defined here as single islands or atolls), from Kure Atoll southeast to Midway Atoll, Pearl and Hermes Reef, Lisianski Island, Laysan Island, and French Frigate Shoals (Wirtz 1968, Johnson and Kridler 1983, Schultz *et al.* 2011). Little information has been available on movement within the MHI or between the NWHI and MHI. Here, we present a new analysis of range-wide movements of tagged seals, based on sighting data collected over a 30 yr period (1981–2011). We provide preliminary descriptive results with some statistical analysis. A more robust quantitative analysis that attempts to estimate movement rates by accounting for spatial and

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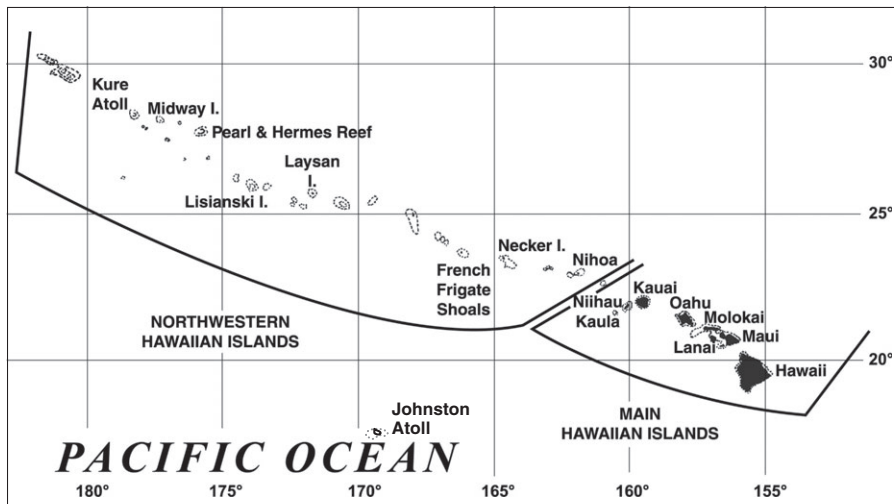


Figure 1. The Hawaiian Archipelago (spanning *ca.* 2,500 km) is grouped into two regions, the Northwestern Hawaiian Islands (NWHI) and the Main Hawaiian Islands (MHI). Johnston Atoll is situated approximately 850 km southwest of French Frigate Shoals, its closest neighbor in the Hawaiian Archipelago.

temporal variation in marking and resighting effort, as well as other confounding factors, may be undertaken in the future. In the interim, it is important to publish our current results to inform current and future conservation strategies.

Nearly three-fourths of Hawaiian monk seals reside on low-lying islands and atolls in the NWHI and utilize one of the six most-studied sites (Carretta *et al.* 2012, Fig. 1). The remainder occurs on Necker and Nihoa Islands, high rocky islands at the eastern end of the NWHI, which host a combined total of roughly 150 seals, and in the MHI. In contrast to the small and relatively far apart NWHI, the MHI consists of eight large islands, many of which are near each other (Fig. 1). Prior to the 1990s, monk seals were rarely seen in the MHI, but by 2010 the MHI subpopulation expanded to at least 150 seals (Baker and Johanos 2004, Baker *et al.* 2011). Rare monk seal sightings (including a single birth) have been confirmed at Johnston Atoll, which lies approximately 850 km southwest of French Frigate Shoals (Schreiber and Kridler 1969, Amerson and Shelton 1976).

Our analysis of range-wide movement patterns was based primarily on seals tagged as weaned pups at their natal sites, supplemented by seals tagged at older ages where noted. Weaned pups were marked with plastic tags on each rear flipper, and older seals were tagged or retagged opportunistically. Pups were tagged at all birth sites except privately-owned Niihau (MHI). In the NWHI, consistent tagging commenced in the early to mid-1980s, except at Midway where it was initiated in 1988. Because access to Necker and Nihoa Islands was limited, only sporadic tagging was possible. In the MHI, regular tagging has occurred at all accessible sites since 1988.

Tagged seals were resighted throughout their lifetimes using a combination of flipper tags, PIT tags, distinctive scars, natural markings, and temporary bleach marks, aided by a digital photography database (Harting *et al.* 2004). Only confirmed sightings of individual seals were used in analyses of movement patterns. Except where noted, data from seals subject to captive care or translocation were excluded

following the management action in case those manipulations affected subsequent seal movements.

Resighting effort was highly uneven over time and throughout the archipelago. Nearly every year since 1982, research field camps ranging from 2 to 5 mo duration were established at most NWHI sites. The main exceptions were Necker and Nihoa Islands, where surveys were limited to only 0–2 d/yr. Field observations typically were conducted within the March to August period, though data were occasionally available from other times of the year. During field seasons, systematic surveys to identify all seals on shore were conducted every 4–7 d on average, typically with partial surveys occurring daily (Baker *et al.* 2006). Capture-recapture analysis indicates that the probability that a tagged seal was seen at least once during a field season typically exceeded 90% (Baker and Thompson 2007). In contrast, the probability of detecting a seal at each island or atoll it may have visited, however briefly, during a given field season, was surely much lower and more variable among sites. Further, there was typically no field effort during the majority of each year, so that many (perhaps most) movements among NWHI sites were likely not detected. As such, we report minimum observed, rather than actual, movement rates.

There were few monk seal sightings in the MHI until the mid-1990s, after which sightings became increasingly common (Baker and Johanos 2004). Unlike in the NWHI, where a relatively large number of seals is concentrated on very small and mostly accessible islands, in the MHI a small number of seals is distributed over extensive and often inaccessible coastlines and offshore islets. Consequently MHI monitoring is spatially uneven but occurs year-round.

Sighting data for the MHI were mostly supplied by an informal network comprised of volunteers, collaborators, and the public, as verified by trained observers (Baker *et al.* 2011). Sighting data were also collected by NMFS, including occasional systematic surveys at remote sites not regularly covered by the sighting network. Aerial surveys of all MHI shorelines were conducted in 2000, 2001, and 2008 (Baker and Johanos 2004; NMFS, unpublished data); these and a limited number of single island aerial surveys included photographic identification and resightings of a few individual seals. MHI monk seal surveillance is biased toward accessible areas frequented by people. Further, no tagging and little resighting information was available from Nihoa, situated closest to the NWHI, which typically yielded the highest seal counts during aerial surveys. Similarly, Lehua (immediately offshore Nihoa) and Kaula, small inaccessible islands at the western end of the MHI, are regularly used by monk seals but were only very rarely surveyed.

Although the Hawaiian Archipelago comprises nearly the entire range of the Hawaiian monk seal, we also summarize confirmed sightings from Johnston Atoll. Johnston Atoll was populated by the US military, USFWS, and other government and civilian personnel since the beginning of our study until the completion of base closure in 2004 and has been infrequently visited since.

We defined movements as sequential sightings of an individual seal at two different island/atoll sites, and when a seal transited from one site to another, later returning to the first site, this was considered a “round trip.” In the NWHI, transits between the distinctly separate single islands or atolls were counted as movements, whereas much shorter transits along a single island shoreline or amongst islets within an atoll were excluded. As in the NWHI, we excluded within-island transits in the MHI but treated any trips between the eight MHI as movements. The following analyses do not address the duration of movements, such that a seal transiting to another site for a day is counted the same as one residing longer at the destination.

Spatial and temporal gaps in observation effort made the timing of movements highly uncertain. Therefore, if a seal moved sometime between its final sighting in the previous year and its first sighting in the current year, we assumed that the movement occurred in the current year.

We conducted limited statistical analysis to assess patterns for which unequal marking and resighting effort were not expected to be highly influential. Age-related natal site fidelity was investigated by calculating the proportion of seals that were observed at other than their natal site at each age. Minimum annual movement rates between specific sites were calculated as the proportion of all tagged seals (all ages pooled) per year observed to move from one site to another. Minimum annual movement rates by age class (weaned pups, juveniles aged 1–2 yr, subadults aged 3–4 yr, and adults aged 5 yr and over) were calculated as the proportion of seals that were observed to move between sites. The data were pooled over all years so that, for each age class, the sample consisted of all individuals that belonged to that class in one or more years. Accordingly, an individual seal could contribute to the sample for multiple age classes. Finally, we evaluated individual variability in movement histories for adult seals including the number of observed movements of individual seals per year, and the number of within-year round trips.

Study animals ($n = 4,438$ seals; 4,320 NWHI and 118 MHI) were resighted throughout their lifetimes, allowing detection of 1,161 movements by 373 individuals. The proportion of seals observed away from their natal sites varied with location but, in general, increased from weaning into adulthood (Fig. 2). Males and females did not differ in the proportion of seals at each age that were observed at nonnatal sites (paired t -test on arcsin square root transformed proportions, $t(25) = -1.57321$, $P = 0.13$). The pattern became more variable after age 20 likely due to small sample sizes. Overall, 14% of seals were not at their natal site at age 10 yr (94 of 694 surviv-

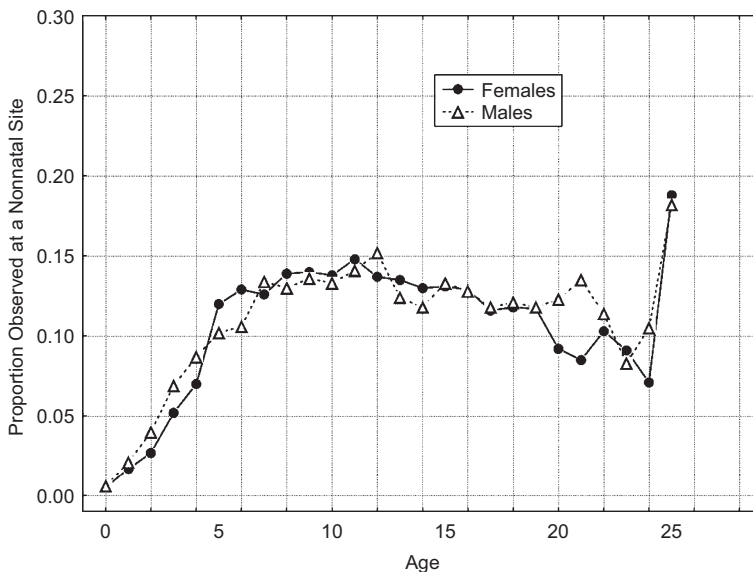


Figure 2. The proportion of Hawaiian monk seals observed away from their natal site at each age by sex, showing no differences between the sexes (n ranges from 4,438 seals to 12 seals for ages 0 to 26, respectively).

ing seals), an age by which nearly all females have become parturient (Harting *et al.* 2007). Also, because seals ventured away from and then returned to natal areas, roughly twice as many (28%) had been observed at a nonnatal site at least once by age 10 yr. Of 1,621 births by females whose own natal sites were known ($n = 349$), 10% were females giving birth at sites other than where they were born. Although mating was rarely observed, some information on natal and breeding dispersal may be inferred from pupping sites: 11% of first pups were born to females at nonnatal sites, and 95% of subsequent pups were born at the same island or atoll as the female's first pup.

Due to minimal surveillance at Necker/Nihoa and outside the Hawaiian Archipelago we utilized all documented movements, including trips by seals tagged at older ages and one previously translocated seal, to describe relatively rarely observed cross-regional movements. From 1981 to 2011, 10 seals were observed to make 14 trips between the NWHI, the MHI, and Johnston Atoll. Eight trips were documented between Necker/Nihoa and the MHI. Five trips were made between more distant NWHI sites and the MHI, including a Midway Atoll-born female that transited nearly the entire Hawaiian Archipelago (*ca.* 2,400 km), produced the first recorded pup on Hawaii Island in 2001, and subsequently pupped on Niihau and Oahu for a total of eight MHI births recorded as of 2011. Finally, one French Frigate Shoals-born female traveled to Johnston Atoll as an adult and remained for about a year before disappearing. A Laysan-born male also traveled to Johnston Atoll during a previous study (Schreiber and Kridler 1969). Other than at Johnston Atoll, no sightings of Hawaiian monk seals have been confirmed on any Pacific island external to the Hawaiian Archipelago. Unconfirmed sightings of pinnipeds have been reported at Palmyra Atoll and Wake Atoll (Westlake and Gilmartin 1990, Ragen and Lavigne 1999) and in the Marshall Islands at Bikini Atoll and Mejit Island (NMFS, unpublished data); areas *ca.* 1,700–2,500 km away from the Hawaiian Archipelago.

While observed movements between the NWHI, MHI and Johnston Atoll were rare, movements among sites within the NWHI and within the MHI were more common (Table 1a, b). Seals moved between the atolls at the western end of the chain (Kure, Midway, and Pearl and Hermes) more than between other NWHI sites. Less movement was observed between Lisianski and Laysan Islands, and still less between Laysan and French Frigate Shoals (Table 1a). Relatively more movement was observed between islands in the MHI than between islands and atolls within the NWHI (Table 1b).

To evaluate the influence of proximity on movement among sites, we plotted the observed minimum movement rates against straight-line intersite distances. Observed annual movements declined rapidly with distance, with relatively high movement between sites separated by 100 km or less, and very little observed between locations separated by more than 400 km (Fig. 3). We considered whether the finding that seals tended to move more readily between nearby sites than more distant ones, while intuitive, could be influenced by sampling inequities among sites, particularly the year-round observations of seals that occur in the MHI. However, considering just the NWHI, the most proximate atolls (Kure Atoll, Midway Atoll, and Pearl and Hermes Reef) had relatively low field effort but high observed intersite movement; and we also saw a decline in movement with distance across the NWHI. Thus, while the precise shape of the declining curve in Figure 3 may be somewhat distorted by sampling bias, the finding that movement declined with increasing distance between sites is likely correct.

Table 1a. Minimum annual observed movement rates among eight Northwestern Hawaiian Islands (NWHI) sites and from the NWHI to main Hawaiian Islands (MHI). The n value is the number of tagged seals seen annually at each site, summed over all years. Proportions in individual rows sum to 1, whereas proportions in columns do not. Bolded values indicate the proportions of seals that were only observed at the site where they had been the previous year. Dashes indicate values of 0.0000. French Frigate Shoals and Pearl and Hermes Reef are abbreviated FFS and PHR, respectively. One seal from French Frigate Shoals was observed at Johnston Atoll (annual proportion = 0.0001).

Original site	n	Destination site								
		MHI	Niihoo	Necker	FFS	Laysan	Lisianski	PHR	Midway	Kure
Niihoo	92	0.0218	0.8913	-	0.0870	-	-	-	-	-
Necker	69	-	-	0.5072	0.4928	-	-	-	-	-
FFS	7,035	0.0001	0.0024	0.0065	0.9888	0.0020	-	-	-	-
Laysan	4,909	0.0004	-	-	0.0037	0.9635	0.0312	-	-	-
Lisianski	3,145	-	-	-	0.0010	0.0471	0.9450	0.0054	0.0010	0.0006
PHR	3,022	-	-	-	0.0003	0.0030	0.0076	0.9500	0.0271	0.0119
Midway	887	-	-	-	-	0.0011	-	0.0676	0.7768	0.1545
Kure	2,067	-	-	-	-	-	0.0010	0.0155	0.0745	0.9090

Table 1b. Minimum annual observed movement rates among eight sites within the main Hawaiian Islands (MHI) and from the MHI to Northwestern Hawaiian Islands (NWHI). The n value is the number of tagged seals seen annually at each site, summed over all years. Proportions in individual rows sum to 1, whereas proportions in columns do not. Bolded values indicate the proportions of seals that were only observed at the site where they had been the previous year. Dashes indicate values of 0.0000. Kahoolawe and Molokai are abbreviated KAH and MOL, respectively. No seals were recorded moving between the MHI and Johnston Atoll.

Original site	n	Destination site								
		Hawaii Is.	KAH	Maui	Lanai	MOL	Oahu	Kauai	Niihau	NWHI
Hawaii Is.	38	0.7368	-	0.1053	0.0263	0.0526	0.0789	-	-	-
KAH	23	0.0435	0.6522	0.1304	-	0.1739	-	-	-	-
Maui	39	0.1026	0.1282	0.4103	-	0.3077	0.0513	-	-	-
Lanai	4	-	-	-	1.0000	-	-	-	-	-
MOL	208	0.0096	0.0096	0.0817	0.0096	0.7548	0.1154	0.0192	-	-
Oahu	100	0.0200	-	0.0100	-	0.2400	0.6500	0.0700	0.0100	-
Kauai	125	0.0160	-	-	-	0.0320	0.1120	0.8320	-	0.0080
Niihau	2	-	-	-	-	-	0.5000	-	0.5000	-

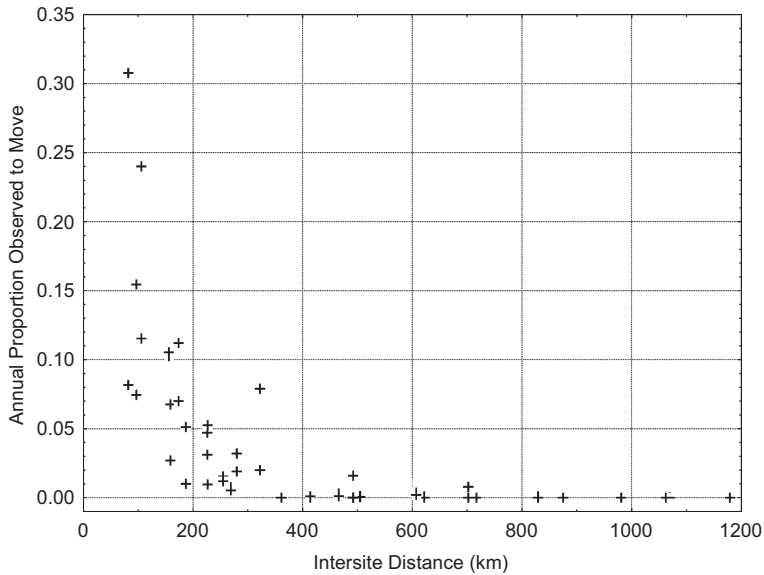


Figure 3. Relationship between intersite distance (km) and the annual proportion of Hawaiian monk seals observed to move between locations, with each point representing directional movement between a pair of sites. This plot excludes data from Necker, Nihoa, Niihau, Lanai, Kahoolawe, and Johnston Atoll due to very low field effort at these sites.

The annual proportion of seals observed to move differed significantly among the age groups (Friedman ANOVA, chi-square [$n = 11$ sites, $df = 3$] = 28.418; $P < 0.001$), was progressively higher for older seals, and consistently higher in the MHI. Movements of pups were rare, whereas 8% and 53% of adults moved annually in the NWHI and MHI, respectively (Table 2). There was considerable individual variability among seals. In the NWHI, only a small number of adults made frequent trips, including round trips, while most had no or few annual movements. In the MHI, where distances are close, most adults were seen on multiple islands over the course of the year, with several seen on as many as four islands.

There was no significant difference between the sexes in the proportion of individuals that moved (chi-square, $P = 0.51$, $df = 1$), the mean number of annual movements per individual (t -test, $P = 0.53$, $df = 1,209$, $F = 1.099$), nor in the number of

Table 2. The proportion of seals that were annually observed to move, for four age classes in the NWHI and MHI. Movements were from a seal's current site to another location, irrespective of natal site. Sample sizes are in parentheses and refer to the number of tagged seals of each age class and region, summed over all years.

	NWHI	MHI
Pups (age 0)	0.46% (4,343)	2.44% (123)
Juveniles (ages 1–2)	1.88% (4,309)	17.09% (158)
Subadults (ages 3–4)	5.87% (2,796)	27.59% (87)
Adults (age 5 and older)	7.68% (9,778)	53.22% (171)

round trips per individual ($F = 1.43$, $P = 0.92$, $df = 1,209$). We are not aware of any spatial or age/sex class observability bias that might lead to erroneous conclusions regarding movements by age or sex.

Our findings of range-wide connectivity and movement patterns of Hawaiian monk seals based on tag sightings are consistent with Schultz *et al.* (2011), who found no genetic stock structure within the species range. Consistent with our results, satellite telemetry studies found that monk seal foraging ranges tend to increase with age, and foraging trips extend as much as 322 km from the island of origin (Stewart 2004, Stewart *et al.* 2006).

This study confirms that there is ample connectivity among monk seal subpopulations both within the NWHI and especially within the MHI. Further, we documented movements of seals *between* the NWHI and MHI, regions which were previously thought to be effectively isolated from one another. The relatively rarely observed movement of tagged individuals between the NWHI and MHI likely belies a greater actual level of connectivity. There have been very limited tagging and re-sighting effort at key locations (Necker, Nihoa, and Niihau) which, because of their geographic positions, are likely a nexus between the NWHI and MHI.

The now apparent connectivity between NWHI and MHI monk seals will profoundly influence conservation and research efforts. Movement of seals between these parts of the Hawaiian archipelago may significantly influence monk seal metapopulation dynamics. More surveillance is needed, especially at Necker and Nihoa Islands, to better characterize the level of interchange. The potential for infectious disease outbreaks are a recognized threat to monk seals, as the species is likely naïve to many pathogens affecting terrestrial mammals. This has been of particular concern in the MHI, where monk seals now coexist with a variety of nonnative terrestrial mammals, which may become vectors for spread of pathogens to seals (Littnan *et al.* 2006). Our results demonstrate that an epidemic in the MHI could spread to the NWHI through seal movements, with potentially devastating results. Disease outbreak response planning, including vaccination of monk seals against potential threats (morbillivirus and West Nile virus) is currently underway. These efforts will be informed by the observed movement patterns reported in this study.

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