# NORTHERN ELEPHANT SEAL (*MIROUNGA ANGUSTIROSTRIS*) COLONY ESTABLISHMENT AND GROWTH IN THE KING RANGE NATIONAL CONSERVATION AREA, CALIFORNIA

By

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# ABSTRACT

## NORTHERN ELEPHANT SEAL (*MIROUNGA ANGUSTIROSTRIS*) COLONY ESTABLISHMENT AND GROWTH IN THE KING RANGE NATIONAL CONSERVATION AREA, CALIFORNIA

Emma Levy

The King Range colony is the northernmost successful and expanding breeding site for northern elephant seals (*Mirounga angustirostris*). To evaluate the composition and growth of this colony, I conducted systematic surveys recording counts, age classes, births, and resighting seals with individually identifiable flipper tags. The timing of life-history events (breeding, molting, and resting) of all elephant seal sex and age groups at the King Range was consistent with observations at other colonies. Colony counts during breeding and molting have increased steadily over the 4-year study period (2018-2021), and pup production has increased by 87% since the first year of monitoring. The main driver of colony growth was juvenile elephant seals dispersing from colonies in central California, as revealed by the majority of tag resights being of juveniles from Point Reyes. Juvenile seasonal haul out behavior differed with a higher percentage of 'new' juveniles seen in the fall than in the spring and higher variability in seasonal arrival date, tenure, and number of visits in the fall resting haul out than during the spring molt. This difference may be due to the extreme physiological demands on elephant seals during their spring molt, which is absent during the fall. This growing northern elephant seal colony will likely become a seed colony for further northern dispersal as this species continues to be impacted by global climate change. By documenting juvenile dispersal and colony growth, I provide information to managers and the public for use in preparing and managing conflicts that might arise with the predicted expansion and redistribution of this species.

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# CHAPTER 1: SUMMARY AND PRESENT STATUS OF THE KING RANGE NORTHERN ELEPHANT SEAL COLONY

## INTRODUCTION

Northern elephant seals (*Mirounga angustirostris*) are a conservation success story. They survived the brink of extinction and recolonized large portions of the west coast of the United States over the last 100 years. Throughout the late 1800s, this species was deemed extinct on three separate occasions (Townsend, 1912). In the early 1900s, their population size was estimated to be fewer than 100 individuals, with speculation that there could have been as few as 20 northern elephant seals alive in Mexico (Bartholomew & Hubbs, 1960). In 1922, the Mexican government established Isla Guadalupe as a biological reserve to protect the remaining individuals from harassment and poaching (Hanna, 1925). In conjunction with protections under the 1972 U.S. Marine Mammal Protection Act, northern elephant seals were able to recolonize many historical breeding areas (Rick et al., 2011, Lowry et al., 2014). The most recent population-wide estimates compiled in 2010 estimated the northern elephant seal population size to be between 210,000 and 239,000 individuals in the United States of America and Mexico (Lowry et al., 2014).

During recolonization, northern elephant seals initially dispersed and colonized island habitats in Mexico, southern California, and central California (Table 1). Over time, island colonies became space limited, thus initiating the colonization of mainland breeding sites at Año Nuevo and many other areas (Table 1). After colonizing the mainland site in Point Reyes in 1981, small breeding sites began developing in northern California, Oregon, Washington, and British Columbia (Fletcher, 2009; Hodder et al., 1998; Jeffries et al., 2000). However, these small breeding sites have shown little growth due to space limitations or winter storm activity (Hodder et al., 1998).

Table 1. Timing of recolonization throughout the northern elephant seal range and description of origin of individuals that fueled each colony's growth (Fletcher, 2009; Hodder et al., 1998; Le Boeuf & Laws, 1994; Lowry et al., 2014).

| **Colony** | **First occurrence of pupping** | **Island or Mainland** | **Origin of Colonizing Individuals** |
|---|---|---|---|
| *Isla de Guadalupe, MX* | Origin colony | Island | - |
| *Islas de San Benito, MX* | 1930s | Island | Isla de Guadalupe |
| *San Miguel Island, CA* | 1950s | Island | Isla de Guadalupe |
| *San Nicolas Island, CA* | 1950s | Island | Isla de Guadalupe |
| *Santa Barbara Island, CA* | 1950s | Island | Isla de Guadalupe |
| *Año Nuevo Island, CA* | 1961 | Island | San Miguel Island, San Nicolas Island |
| *Isla de Cedros, MX* | 1960s | Island | Isla de Guadalupe, Islas de San Benito |
| *Isla Coronado, MX* | 1971 | Island | Isla de Guadalupe, Islas de San Benito |
| *Farallon Islands, CA* | 1972 | Island | San Miguel Island, San Nicolas Island, Año Nuevo Island |
| *Año Nuevo Mainland, CA* | 1975 | Mainland | Año Nuevo Island |
| *San Clemente Island, CA* | 1977 | Island | Isla de Guadalupe |
| *Cape San Martin/Gorda, CA* | 1981 | Mainland | Not described |
| *Point Reyes, CA* | 1981 | Mainland | Farallon Islands, Año Nuevo Island/Mainland |

| **Colony** | **First occurrence of pupping** | **Island or Mainland** | **Origin of Colonizing Individuals** |
|---|---|---|---|
| *Santa Rosa Island, CA* | 1985 | Island | Isla de Guadalupe, other Channel Islands |
| *Castle Rock, CA* | 1985 | Island | Not described |
| *Piedras Blancas, CA* | 1992 | Mainland | Not described |
| *Shell Island, OR* | 1993 | Island | San Miguel Island, Año Nuevo Island/Mainland, Farallon Islands |
| *Point Conception, CA* | 2005 | Mainland | Not described |
| *Race Rocks, BC* | 2009 | Island | Año Nuevo Island/Mainland, Farallon Islands, Point Reyes |
| *Vandenberg Air Force Base, CA* | ~2017 | Mainland | Not described |

Currently, 27 northern elephant seal breeding sites are located between Natividad Island, Mexico, and Race Rocks, British Columbia (Figure 1). Breeding sites observed over the last 5-35 years vary in pup production and growth status (Table 2). The Mexico breeding sites are stable or declining in growth (Figure 1) (García-Aguilar et al., 2018). Isla Guadalupe and Islas de San Benito have the highest pup production for the Mexico sites (Table 3) (García-Aguilar et al., 2018). California breeding sites vary in growth status; increasing, stable, or declining (Figure 1) (Lowry et al., 2014). The California sites with the highest pup production are in the Channel Islands (Table 2). All breeding sites north of California have shown little to no growth and produce fewer than 30 pups per year (Hodder et al., 1998; J. Hodder, pers. comm.; Jeffries et al., 2000) (Table 2).

Table 2. Northern elephant seal birth estimates for breeding sites in British Columbia, Washington, Oregon, and California.

| **Breeding Site** | **Birth estimates** | **Year** | **Data Source** |
|---|---|---|---|
| *Race Rocks, BC* | 4 | 2020 | Townley, 2020 |
| *Smith/Minor, Protection, and Whidbey Islands, WA* | Not available | 2000 | Jeffries et al., 2000 |
| *Shell Island, OR* | 8 | 1997 | Hodder et al., 1998 |
| *Castle Rock, CA* | 11 | 1994 | Hodder et al., 1998 |
| *Point Reyes* | 1,153 | 2021 | National Parks Service, 2021 |
| *Farallon Islands* | 120 | 2010 | Lowry et al., 2014 |
| *Año Nuevo Island/Mainland* | 2,144 | 2010 | Lowry et al., 2014 |
| *Cape San Martin/Gorda* | 101 | 2010 | Lowry et al., 2014 |
| *Piedras Blancas* | 4,469 | 2010 | Lowry et al., 2014 |
| *Vandenberg Air Force Base* | ~18 | 2017 | Dudley, 2017 |
| *Point Conception* | 8 | 2010 | Lowry et al., 2014 |
| *San Miguel Island* | 16,208 | 2010 | Lowry et al., 2014 |
| *Santa Rosa Island* | 5,946 | 2010 | Lowry et al., 2014 |
| *San Nicolas Island* | 10,882 | 2010 | Lowry et al., 2014 |
| *Santa Barbara Island* | 51 | 2010 | Lowry et al., 2014 |
| *San Clemente Island* | 57 | 2010 | Lowry et al., 2014 |

Table 3. Northern elephant seal birth estimates for breeding sites in Mexico.

| **Breeding Site** | **Birth estimates** | **Year** | **Data Source** |
|---|---|---|---|
| *Isla Coronados* | 27 | 2012 | García-Aguilar et al., 2018 |
| *Isla Todos Santos* | 10 | 2009 | García-Aguilar et al., 2018 |
| *Isla de San Martín* | 3 | 2009 | García-Aguilar et al., 2018 |
| *Isla San Jerónimo* | 1 | 2009 | García-Aguilar et al., 2018 |
| *Isla Guadalupe* | 2,037 | 2015 | García-Aguilar et al., 2018 |
| *Islas de San Benito* | 1,317 | 2016 | García-Aguilar et al., 2018 |
| *Isla de Cedros* | 339 | 2010 | García-Aguilar et al., 2018 |

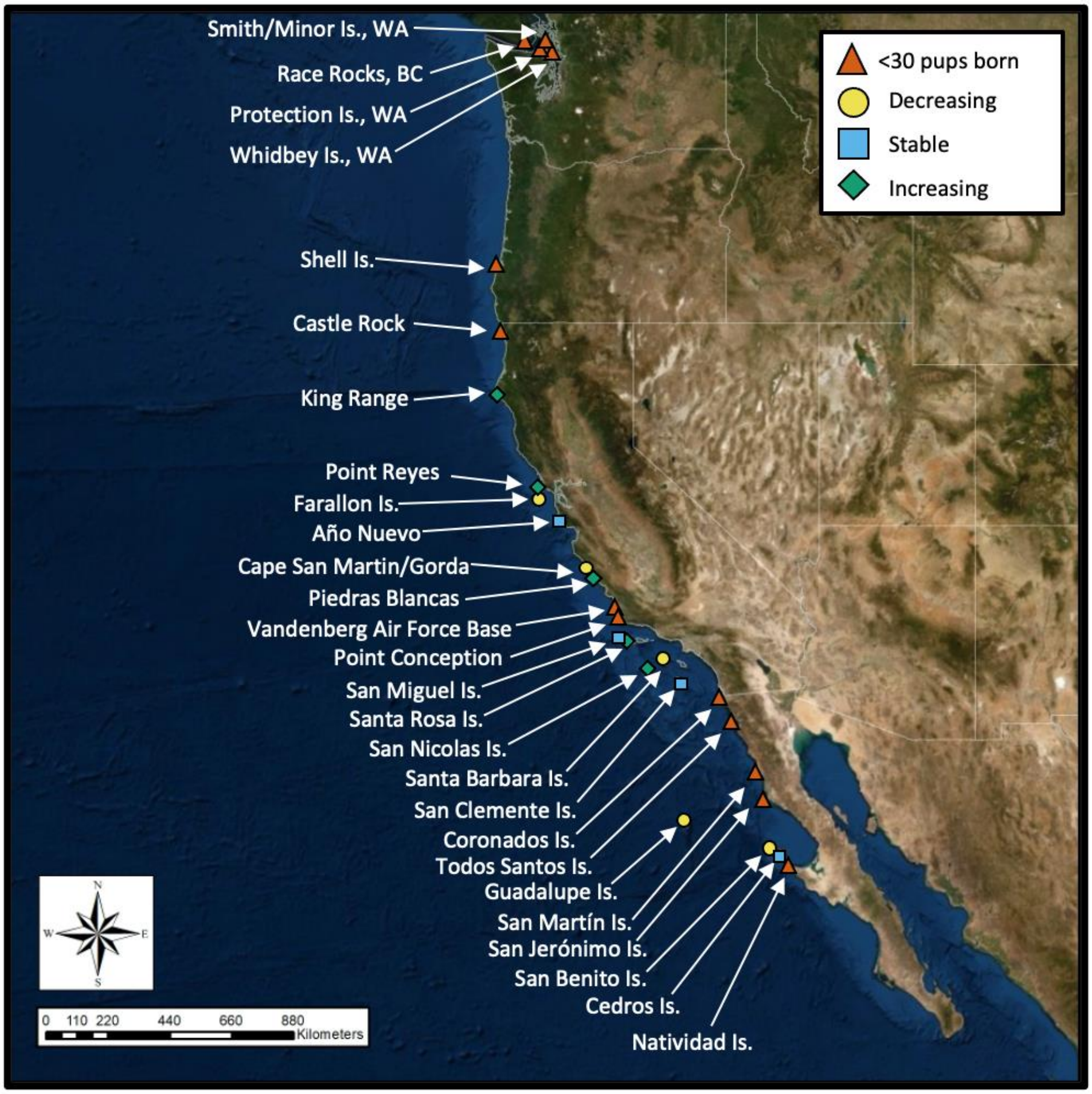

Figure 1. Map of northern elephant seal colonies in British Columbia, Washington, Oregon, California, and Mexico indicating colony growth status of each site (declining, stable, increasing, or under 30 pups born) (Dudley, 2017; Esri, 2019; García-Aguilar et al., 2018; Hodder et al., 1998; Lowry et al., 2014; Jeffries et al., 2000; Townley, 2020).

Northern elephant seals exhibit a predictable annual natural history pattern with two periods of hauling out on land separated by two at-sea foraging trips (Le Boeuf & Laws, 1994). On land, seals come ashore to breed, molt, or rest, the timing of which depends on age and sex. The breeding season is defined by the presence of breeding males, adult females, and pups (December 16 - March 15). The timing of the molting season varies for different sex and age classes, ranging between March 16 and August 15. Juveniles and adult females molt in the spring (March 16 - June 15), and subadult and adult males molt in the summer (June 16 - August 15). Lastly, during the fall resting haul out (August 16 - December 15), juveniles of many ages (7 months – 3 years old) and subadult males (4 to 5-years-old) are on the colony (Figure 2) (Le Boeuf & Laws, 1994; Le Boeuf et al., 2011). Each season transitions into the next, with some overlap between the sex and age classes. A small number of juveniles are observed year-round (Figure 2). Thus far, this pattern has shown no temporal variation with latitude, as seen in some other pinniped species (Temte et al., 1991).

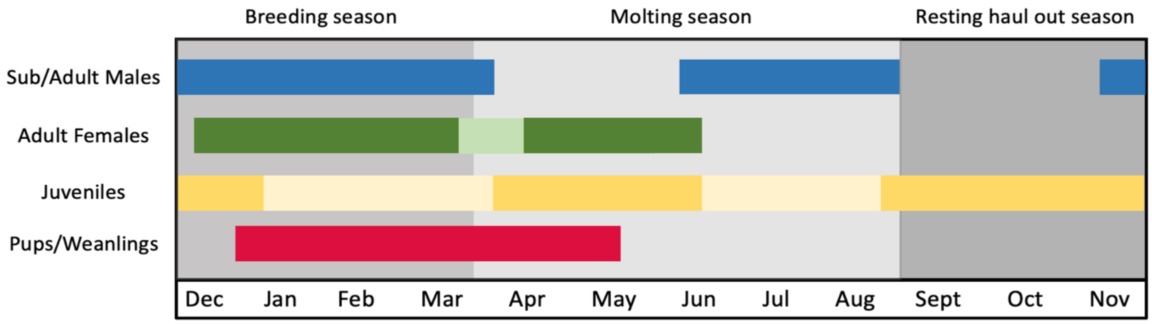

Figure 2. Generalized northern elephant seal annual haul out cycle for each sex and age class at a breeding colony. Dark-colored bars represent usual haul out periods for each age class. Light-colored bars indicate a time of low presence for an age class (adult females and juveniles).

In 2011, the first observation of a juvenile northern elephant seal was recorded in the King Range National Conservation Area, Humboldt County, California (40.2500° N, 124.3523° W). The first observations of pups being born were in 2015 and increased to ~60 pups born annually by 2017 (J. McAbery, pers. comm.). The King Range colony is ~300 km north of Point Reyes, the closest established breeding site, and is in a remote area that provides many kilometers of sandy beach space suitable for potential colony growth. The King Range colony has the potential for continual growth and may become a vital seed colony for northern elephant seal continued colony formation northward. This site also offers the opportunity to track the colony's growth over time as it is small enough to track all known individuals.

This study is the first description of the status and growth of the King Range northern elephant seal breeding colony. I documented from 2017 to 2021 (1) northern elephant seal total abundance, (2) seasonality in abundance of each sex and age class, (3) yearly pup production and mortality, and (4) the origin colony of immigrating individuals.

# METHODS

I conducted this study in the King Range National Conservation Area (KRNCA), California. The KRNCA extends along 56 km of shoreline in southern Humboldt County between the Mattole River and Sinkyone Wilderness State Park and encompasses the Lost Coast Trail, a popular wilderness backpacking trail (Figure 3A). Within the KRNCA, northern elephant seals currently utilize ~3.05 km of coastline adjacent to the Punta Gorda Lighthouse and Lost Coast Trail (40.2494° N, 124.3502° W) (Figure 3B). I collected this data under the National Marine Fisheries Services permits #19108 (2015-2020) and #23188 (2020-2025) and approved by Humboldt State University Institutional Animal Care and Use Committee (IACUC) protocol #17.18.B.72.A.

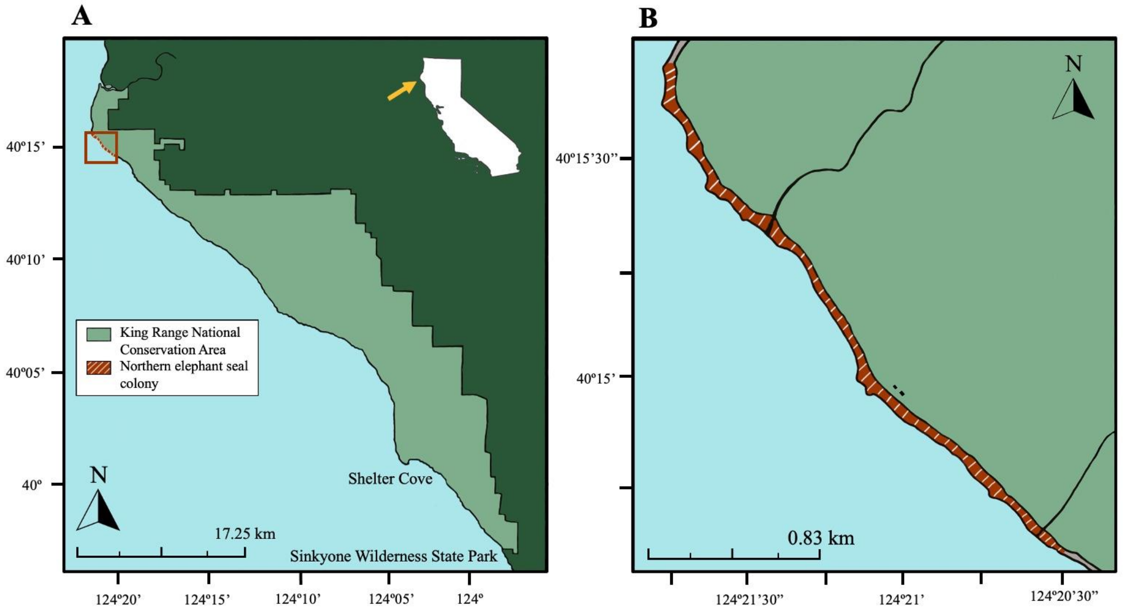

Figure 3. **(A)** Location of the northern elephant seal colony in King Range National Conservation Area, California. **(B)** Inset: Map of King Range northern elephant seal colony and the Punta Gorda Lighthouse location.

Long-term systematic monitoring of the King Range colony began in the 2017 – 2018 breeding season (late November – February). Year-round monitoring began in November 2018 and continued through August 2021. We conducted surveys every two weeks in the fall of 2019 (September – October) and the summer of 2019, 2020, and 2021 (June – August). I and prior field technicians conducted weekly surveys during 2018, 2019, and 2020 breeding seasons (November – March), May 2020, and from October 2020 to August 2021. Data gaps occurred from mid-March through April 2020 due to Covid-19 restrictions. In addition to surveys missed due to Covid-19, I and prior field technicians did not conduct three due to harsh winter weather conditions that made it unsafe to travel to or conduct surveys on the colony.

## Field Counts, Tag Resights, and Marking

During systematic surveys, one to two observers visually counted and photographed all northern elephant seals on land and in the rocky intertidal zone at the King Range colony. Each observer determined the sex and age class of individuals in the field based on external morphological characteristics, life history, flipper tag history data, and temporary dye marks. I compiled the numbers of northern elephant seals of known sex and age class based on this information.

I identified northern elephant seal pups by their dark brown coat and a close association with an adult female during their first four weeks of life. After weaning, the pup/weanlings molt their dark pup coat and develop a light silver coat. Weanlings were present between January and May. I classified weanlings after their first foraging trip as juveniles upon their return to the colony. Juveniles ranged in age from 7 months to potentially 3 years old, were smaller than adult females, and were mostly absent during the breeding season. Adult females (ages 3+) have no nose development and a brown or dark silver coat. Additionally, during the breeding season, they are closely associated with a pup (Reiter, 1984). Subadult 1 males (SA1), 4 years old, were the same size as adult females but had a wider nose than females with no elongation as seen in older males. Subadult 2 males (SA2), 5 years old, had a proboscis that extended down to the mouth, and wrinkles were present on the chest. Subadult 3 males (SA3), 6 years old, had a proboscis that extended past the mouth with wrinkling and scarring development on the chest. Subadult 4 males (SA4), 7 years old, had a proboscis that folded onto the ground while lying down and had a pink chest shield scarring that extended up to their eye. Adult males', 8+ years old, proboscis extended to the ground when laying down and folded under their mouth. They had a calloused pink chest shield that extended up above their eye (Casey et al., 2020).

Due to observer error in visually determining an elephant seal's age class, I combined age classes that showed the most variability in Figure 8 to ensure the data was comparable across all years. The 'juvenile' category combined juveniles (all ages and sexes) and SA1 males. Subadult males at the King Range do not exhibit the same intensity of chest shield development described in Casey et al. (2020), making age class determination less reliable. Therefore, I grouped SA2 and SA3 males together and SA4 and adult males together (Objectives 1 & 2).

I inspected the rear flippers of each seal to document the presence of color-coded plastic tags (Figure 4). Historical data from these tags (natal colony, sex, and age at tagging) provided known sex and age class information for each tagged seal. For each tagged seal, we recorded the tag color, number, and position on the flipper (Objectives 2 & 4).

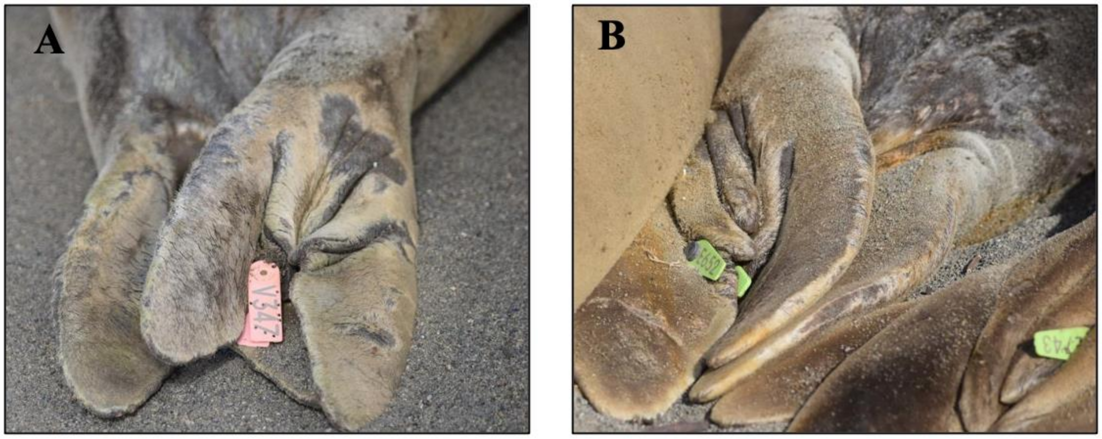

Figure 4. **(A)** Pink flipper tag from Point Reyes and **(B)** green flipper tags from Año Nuevo resighted during surveys at the King Range colony. Photos taken under NMFS 19108.

In addition to resighting flipper tags, I also applied temporary hair dye marks to tagged and untagged elephant seals to facilitate age class count accuracy, track known individuals, and minimize daily disturbance of the colony during surveys (Le Boeuf & Panken, 1977). In January 2020, I applied individually specific dye marks to tagged and untagged individuals. I deployed dye marks using Clairol® black or blonde hair dye to either write a flipper tag number (e.g., PV157) or a unique alphanumeric code (e.g., KF10) on an 11-inch wooden stamp that I applied to one or both sides of the seal (Figure

5). I applied black dye to juveniles and adults and blonde dye to pups due to the dark coloration of their fur (Figure 6). The seals shed the hair dye marks during their annual molt, so I re-applied the dye marks each subsequent year.

Figure 5. Example of the hair dye marking process using a wooden marking stick. Photo taken under NMFS 19108.

Figure 6. Example of a blonde hair dye mark on a northern elephant seal pup and a black hair dye mark on an adult female. Photo taken under NMFS 19108.

## Field Count Accuracy

I paired two or more field counts with a whole colony confirmation photo count to accurately determine the total number of elephant seals present during high abundance periods. During the spring and fall seasons, elephant seals congregate in large piles (>50 individuals). I processed the photo counts in Adobe Photoshop Elements 14, where colored dots were assigned to each seal and totaled for comparison to visually-estimated field counts. This method confirmed ± 5% under- or over-estimates of counts conducted in the spring and fall. On the few occasions when the photo count exceeded 5% of the field count, I chose the photo count to represent the final count for the survey. I confirmed field counts matched photo counts with 100% accuracy during the breeding and summer molting seasons when the elephant seals were less abundant or more spread out on the colony. Seals resting in large piles during the fall resting haul out and spring molting season also made age class determination challenging. Therefore, if adult females were resting in large groups of juveniles, observers could have misidentified them.

## Flipper Tag Deployment

To identify pups born on the King Range colony in the future, I attached light blue Allflex™ sheep ear tags to the rear flippers of weaned pups using tagging shears (Le Boeuf et al., 1972). We tagged in February and March of 2018, 2019, 2020, and 2021 a total of 66, 33, 101, and 173 weaned pups (Objectives 3 & 4).

## Pup Mortality

We counted and photographed deceased pups during each breeding season survey to document pup mortality (Objective 3). I noted the location and condition of each carcass to avoid double counting in subsequent surveys during the 2020 and 2021 breeding seasons. In 2021, I deployed blonde identifying marks on pups early in the season and tracked them weekly to identify if pups were missing from the colony after storm and king tide events.

# RESULTS

## Northern elephant seal abundance and seasonal age class variation

I observed northern elephant seals present year-round at the King Range colony. There were consistently three seasonal peaks in elephant seal abundance at the King Range between 2017 and 2021 that reflected their well-documented life-history patterns (Figure 7). The fall resting haul out and winter breeding seasons had a maximum of 344 and 370 elephant seals, respectively. The spring adult female and juvenile molting season had a maximum of 710 elephant seals over the study period (Figure 7).

During the fall resting haul out (August 16 – December 15), the maximum number of seals was higher at 344 in 2019 than 260 in 2020. The attendance pattern differed between years, as I observed a concentrated peak abundance in the fall of 2019 in mid-October and a less concentrated and more prolonged period of high attendance between October and mid-November in the fall of 2020 (Figure 7). Juveniles (7 months – 3 years old) started returning to the colony in mid-August for the resting haul out and were largely absent by mid-December. The juvenile age class accounted for over 84% of the weekly counts. Subadult and adult males began arriving in late November and early December in all years as the colony transitioned into breeding season (Figure 8).

The maximum number of seals present on a survey during the winter breeding seasons (December 16 – March 15) varied by ~9% during 2018, 2019, and 2020 but increased significantly (51%) in 2021. The timing of attendance was similar across all years, with peak abundance occurring in the first week of February (Figure 7). We observed a small number of juveniles present in January. Adult females began to arrive in late December and became abundant in January. I observed the peak pupping and the beginning of pup weaning occurring in the last week of January. Most adult females left the colony by the beginning of March, except for females that gave birth in mid-February (Figure 8). The age class composition in the breeding season across all four years for pups, weanling, juveniles, and adult females stayed constant. Yet, subadult and adult male age composition varied between years (Figure 8).

The following description of male age class presence during the breeding season excludes the 2019 season due to inconsistency in age class determination between observers. During the 2018 breeding season, SA2 males were the highest in attendance at an average of 76% ± 13% per survey, followed by SA3 males at 17% ± 13%, and SA4 males at 7% ± 5%. In 2018, research technicians observed no adult males present at the King Range. In 2020, SA2 male presence during the breeding season dropped to an average of 24% ± 30%, whereas SA3 and SA4 males average increased to 41% ± 19% and 28% ± 13%. Adult males held all the large harems and were present at an average of 7% ± 5%. In 2021, the male composition of the breeding season continued to shift towards the older age classes, with SA2 present at 14% ± 24%, SA3 males at 31% ± 14%, and SA4 at 45% ± 17%. Adult males continued as alphas, and their average presence increased to 11% ± 5% by 2021 (Figure 9). The average number of subadult and adult males present from mid-December to mid-March declined from 36 ± 7 in 2020 to 27 ± 4 in 2021.

The highest number of seals recorded at the King Range throughout all years occurred during the third seasonal peak, the spring adult female and juvenile molting season. The difference between spring maximum counts in 2019 and 2020 was 4%, and between 2020 and 2021 was 14%. The attendance pattern was similar during all years, with a steep peak in abundance in the second week of May (Figure 7). Weanlings remained present at the colony until the end of April or the beginning of May during the spring molting season (March 16 – June 15). During April and May, juveniles and adult females returned to the King Range to molt. Juveniles were the most abundant age class throughout all years (Figure 8). During the peak week of abundance in 2020 and 2021, weanlings made up 1-2%, juveniles 60-76%, adult females 23-37%, and subadults males <1% of the total daily count (Figure 8). Due to the number and density of seals during this season, older juveniles and adult females could have been misidentified by observers when unable to confirm sex and size due to seals resting in large packed groups.

During the summer subadult and adult male molting season (June 16 – August 15), there was no peak in abundance of elephant seals at the King Range. The attendance pattern was consistent across 2019, 2020, and 2021 and showed an abundance of 42 ± 9 individuals from mid-June through late August (Figure 7). The start of the summer male molt overlapped with the end of May and the beginning of June, with SA2/3 males returning first to molt. Subadult 4 and adult males were present mainly in July and August. Juveniles continued to be present during the summer months in small numbers. We observed them either molting late or returning early for the juvenile resting haul out season (Figure 8).

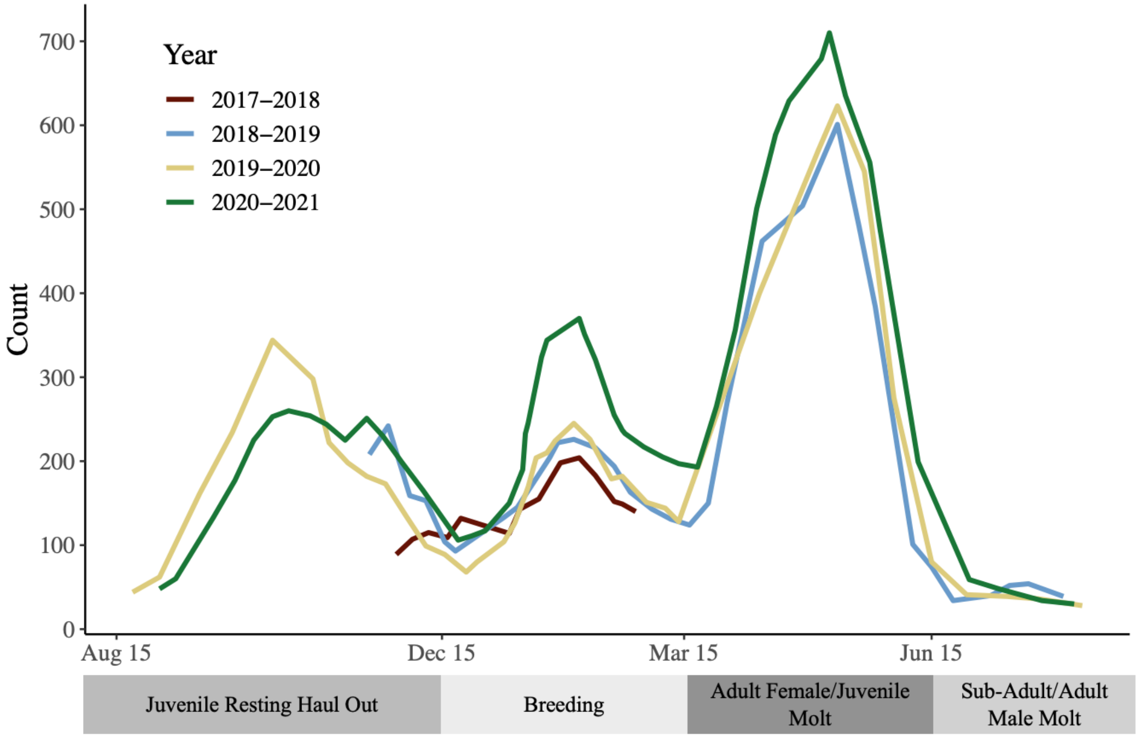

Figure 7. Northern elephant seals total colony counts at the King Range colony 2017 – 2018 (27 November 2017 – 25 February 2018), 2018 – 2019 (17 November 2018 – 14 August 2019), 2019 – 2020 (15 August 2019 – 15 August 2020), and 2020 – 2021 (30 August 2020 – 8 August 2021).

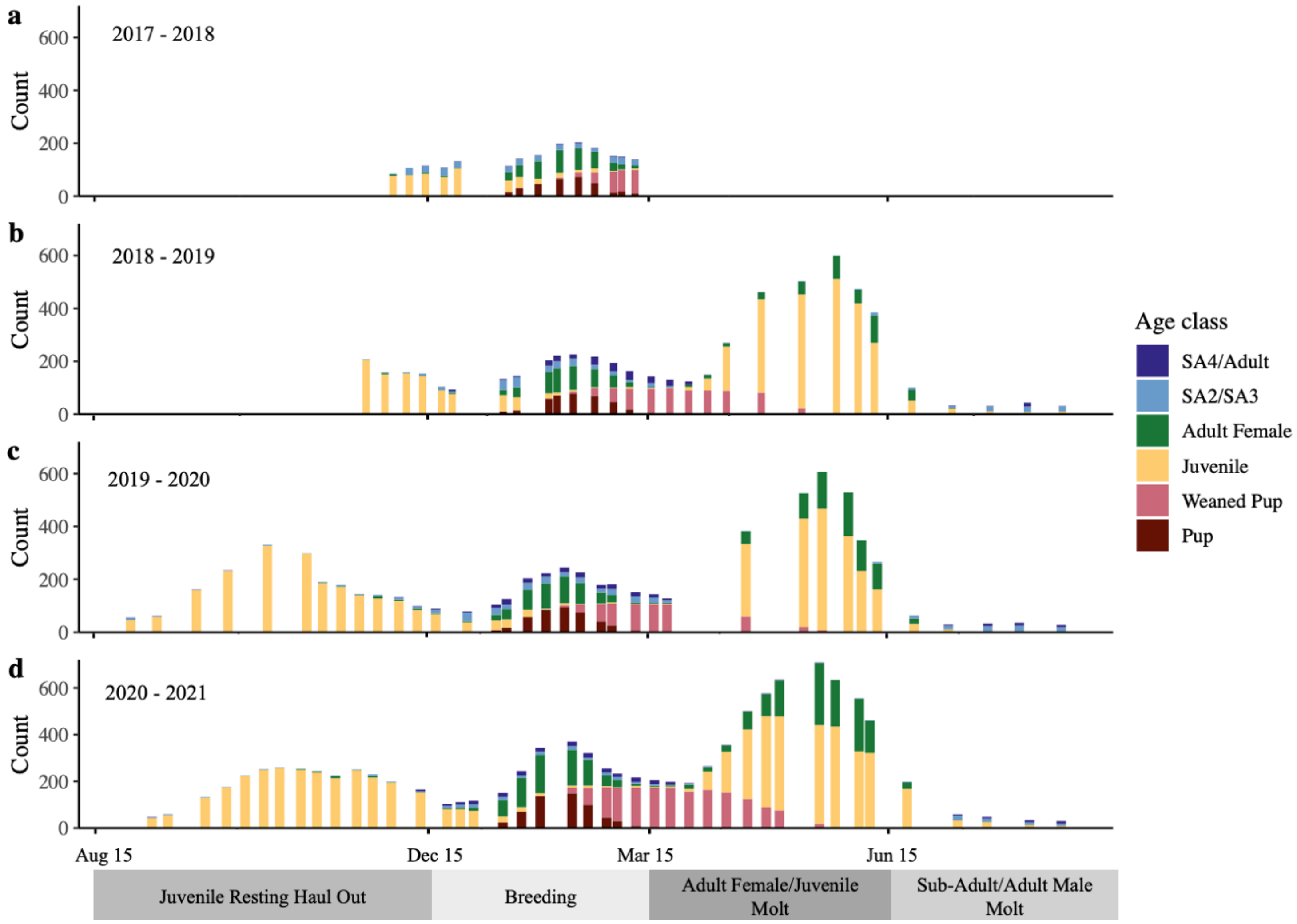

Figure 8. Northern elephant seal age class counts at the King Range colony during (a) 2017 – 2018 (27 November 2017 – 25 February 2018), (b) 2018 – 2019 (17 November 2018 – 14 August 2019), (c) 2019 – 2020 (15 August 2019 – 15 August 2020), (d) 2020 – 2021 (30 August 2020 – 8 August 2021).

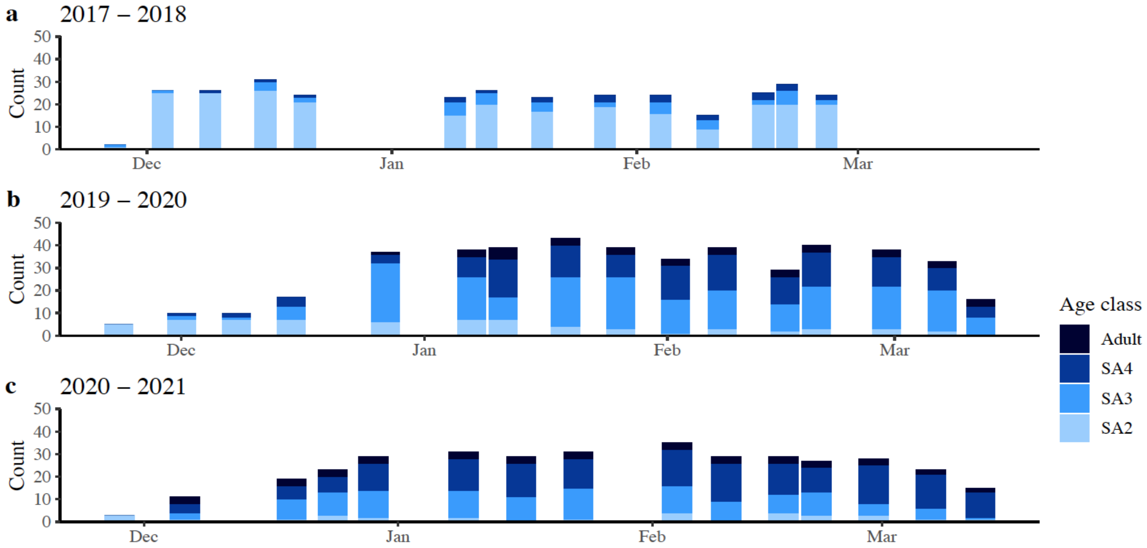

Figure 9. Northern elephant seal breeding male age class counts at the King Range colony during (a) 2017 – 2018 (27 November 2017 – 25 February 2018), (b) 2019 – 2020 (23 November 2019 – 12 March 2020), (c) 2020 – 2021 (28 November 2020 – 13 March 2021) breeding seasons. Data from the 2018 – 2019 breeding season was excluded due to high variation in observer age class determination.

## Pup production and mortality

Anecdotal evidence from local observers estimated that elephant seal pupping started on the King Range colony in 2015. Local observers estimated ~40 pups in 2016 and ~60 pups in 2017 (J. McAbery, pers. comm.). Systematic surveys began during the 2018 breeding season when the number of pups born rose to 99. Pup production between 2018 and 2019 showed no change; between 2019 and 2020 increased by 13%, and between 2020 and 2021 increased considerably by 65%, with 185 pups born in 2021 (Table 4). When I observed pup mortality during the 2020 and 2021 breeding seasons, 5-6% of the total pups produced died before weaning on the beach or washed offshore during storm events and king tides periods. These are likely conservative estimates of mortality, as there are many scavengers and large terrestrial mammalian predators in the KRNCA (ravens, turkey vultures, coyotes, mountain lions, and black bears). We did not observe pup predation events, so I assumed pup death on the colony was likely caused by crush injuries from large male seals or bite injuries from adult females. I did find one pup carcass dragged above the beach, so there is the potential that large scavengers (coyotes) are visiting the colony. During the 2021 pupping season, hair dye marks added soon after birth aided in estimating mortality after a large storm and king tides in January. After that event, I did not observe three of our marked pups again.

Table 4. Northern elephant seal birth, weaning, and pup mortality estimates during the 2017–2018, 2018–2019, 2019–2020, and 2020–2021 breeding seasons at the King Range colony.

| **Year** | **Pups born** | **Pups weaned** | **Pup mortality** |
|---|---|---|---|
| *2017 - 2018* | 99 | 99 | 0* |
| *2018 - 2019* | 99 | 99 | 0* |
| *2019 - 2020* | 112 | 106 | 6* |
| *2020 - 2021* | 185 | 173 | 12 |

An asterisk (*) indicates that pup mortality events could have been missed (carcass washed away before observation).

## Flipper tag observations

Between November 2017 and June 2021, I recorded a total of 350 individual flipper-tagged elephant seals visiting the King Range colony. Each known individual visited the colony during one to seven seasons. Seventy-eight percent of these seals emigrated from breeding colonies south of the King Range, with the remainder being seals born at the King Range (Figure 10). The highest proportion of tagged elephant seals was from Point Reyes (38%) and Año Nuevo (27%), the two closest and most productive breeding colonies in central California.

We first observed the majority (89%) of these tagged individuals as juveniles (3 years old or younger), yet there were older individuals seen for the first time in the first few years of the study. This was likely because the survey efforts focused on the breeding season, and during the first surveys of the molting and resting seasons, we likely resighted tagged individuals that would have been present on the colony before this study began. Of the 200 King Range-born seals tagged between 2018 and 2020, 38% returned to the King Range within their first or second year. Of the seals observed prior to the spring of 2021, 70% (n = 237) visited the King Range more than once, and 74% (n = 176) of those seals were immigrants.

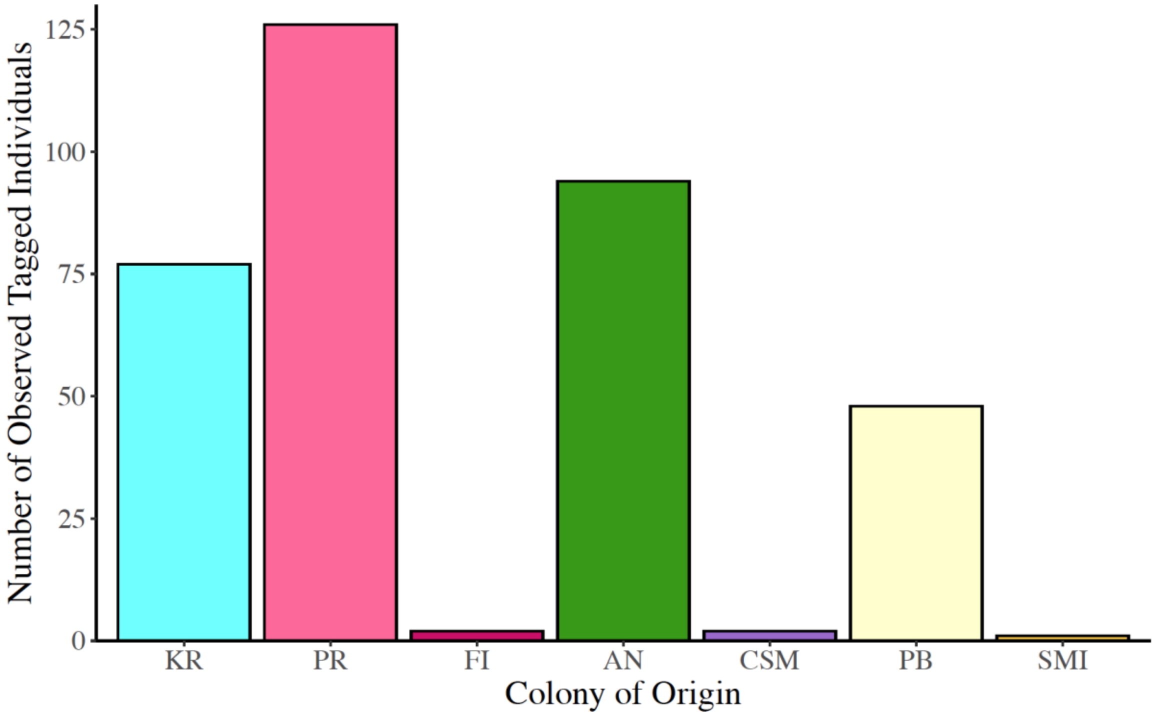

Figure 10. The total number of tagged northern elephant seals observed at the King Range colony in order of colony location in California, North (left) to South (right) (n = 350). KR (King Range), PR (Point Reyes), FI (Farallon Islands), AN (Año Nuevo), CSM (Cape San Martin/Gorda), PB (Piedras Blancas), SMI (San Miguel Island). Tag resights from 27 November 2017 – 10 May 2021.

# DISCUSSION

The most recent successful colonization of a breeding site for northern elephant seals at the northern end of their range was in 1981 at Point Reyes National Seashore (Allen et al., 1989). While there have been a few colonization events north of Point Reyes, these breeding sites have been unsuccessful at becoming large established colonies. The King Range colony provides the first example of successful breeding range expansion of this species north of Point Reyes.

Seasonal abundance patterns at the King Range are similar to those observed at Shell Island and Año Nuevo Island during early colony development (Hodder et al., 1998; Le Boeuf et al., 1974). Because northern elephant seals are pure capital breeders — fast while nursing their pup — they do not need to rely on local food resources during lactation like other California seal species (e.g., harbor seals, *Phoca vitulina*) (Costa & Maresh, 2022; Holser et al., 2021; Stephens et al., 2014; Temte et al., 1991). The reliance on local food resources is likely the cause of breeding season latitudinal variation in harbor seals (Temte et al., 1991). Northern elephant seals' breeding system could influence why we have not observed latitudinal variation in the timing of breeding throughout their range. There was no difference in the timing of seasonal peak abundance, not only at a colony in early development (King Range) nor at an established colony (Año Nuevo Island) (Le Boeuf et al., 1974). I expected some variation in this timing, given that the King Range colony is ~425 km closer to the northern elephant seal foraging areas (the Aleutian Islands and far offshore waters of Oregon and Washington), giving seals the ability to return earlier or later to spend more time foraging. The seasonal presence of each sex and age class at the King Range is consistent with early studies conducted at Shell Island, the Farallon Islands, and Año Nuevo Island (Hodder et al., 1998; Le Boeuf et al., 1974). The King Range confirms that northern elephant seals' timing of abundance and presence of each age class does not vary latitudinally between colonies in central California and Oregon.

Between 2018 and 2021, there was a transition from a breeding colony dominated by young subadult males to a colony controlled by a few adult males. Because of the King Range’s small size, young subadult males likely faced little competition in 2018, thus allowing them to hold harems at a young age. This is uncommon at large established colonies with higher male competition (Le Boeuf & Laws, 1994; Le Boeuf, 1974). This pattern of young males successfully holding harems at newly developing colonies was also observed on the Farallon Islands, Point Reyes, and Channel Island colonies (Allen et al., 1989; Le Boeuf et al., 1974; Le Boeuf & Laws, 1994). Over the 4-year study period, subadult males who had developed site fidelity to the King Range likely developed into mature adults, thus shifting the breeding hierarchy to be dominated by a small number of adult males.

Since the inception of pupping at the King Range in 2015, pup production has followed similar trends to those observed at Año Nuevo Island and the Farallon Islands colonies, increasing from a small number of pups to over 100 pups by year 7 of breeding (Lowry et al., 2014). If the King Range stays on the same pup production trajectory as

Año Nuevo Island, the number of pups born in 2025 will likely be double that seen in 2021.

As pup production increased at the King Range, so did pre-weaning pup mortality. This mortality was often caused by pup abandonment and large swell and king tide events. Pup abandonment is more common in young adult females during their first few years of pup rearing (Reiter et al., 1981). As many of the breeding females at the King Range are young, this is not a surprising occurrence. Still, pup abandonment is likely at a lesser intensity in a smaller colony that is not densely packed because young females do not have to compete for space while keeping track of their pup. At the King Range, there is still beach space available during king tides for females and pups to retreat. Yet, when paired with large swells, sections of the colony can become inundated with water. Given the King Range's current size, king tides do not dramatically affect pup mortality because all females have space to retreat, but at larger colonies, space competition paired with king tides increases pup mortality. As the King Range colony continues to expand and becomes more dense, pup mortality will likely continue to increase (Le Boeuf & Panken, 1997; Le Boeuf & Briggs, 1977).

The King Range colony's growth is still heavily influenced by immigrant recruitment. Both Point Reyes and Año Nuevo — the largest and closest breeding colonies — contributed the most immigrant seals to the King Range. The Farallon Islands and Cape San Martin colonies are both in a declining state of pup production due to habitat changes, thus clarifying the small number of immigrants from those sites. Additionally, pups are no longer being tagged at the Cape San Martin colony. Piedras

Blancas and San Miguel Island are the furthest colonies from the King Range, as a result, they contribute fewer immigrants. To the best of our knowledge, elephant seal tagging efforts at San Miguel Island have declined, so fewer seals from that colony are tagged in the juvenile age class. Pup production at Castle Rock, Shell Island, and Race Rocks is small and not consistently successful. Thus, immigration from southern colonies is fueling growth at the King Range. This pattern of colony growth being driven by immigrants from the closest southern colonies is consistent with all other studies documenting early colony development in northern elephant seals (Allen et al., 1989; Hodder et al., 1998; Le Boeuf et al., 1974; Le Boeuf & Laws, 1994; Le Boeuf et al., 2011). Like Point Reyes and Año Nuevo, as the King Range colony grows, it will likely become an important seed colony for potential new breeding sites between northern California and British Columbia.

Even though this study did not track northern elephant seal presence before breeding started, anecdotal evidence shows that juveniles were present before pups were first observed (J. McAbery, pers. comm.). The recordings of tagged seals also support the fact that juveniles are the driver of growth at the King Range, given that 89% of tagged immigrants were first observed under the age of 3. Colony formation driven by juveniles has been documented at other colonies (Hodder et al., 1998; Le Boeuf et al., 1974). As pup production continues to increase and natal juveniles mature into adulthood in the coming years, the King Range colony will shift to internal rather than immigrant-driven growth.

A small proportion of tagged dispersing juvenile females have been tracked from their juvenile phase to their breeding phase at the King Range (n=9). This shows that females who first arrive at a new colony as a juvenile develop site fidelity that continues into adulthood. Additionally, many of the tagged breeding adult females at this colony are young, with over 50% in the 3 to 6-year-old category in 2021. At large colonies, many of these females would face high levels of space competition with older adult females and potentially get pushed into lesser habitable areas where storms and king tides are more impactful. Given that space competition at the King Range is low, these young females have a better chance of successful pup rearing (Le Boeuf & Panken, 1977; Reiter et al., 1981).

Currently, not all suitable habitat in the KRNCA is occupied by northern elephant seals. At this time, elephant seals mainly utilize the beach space, not the unoccupied marine terrace. As described at Point Reyes, many areas could be utilized for breeding in the future if the colony continues on a growth trend (Funayama et al., 2013). The terraces would provide more habitats safe from king tides and swell as the marine environment changes. The examination of the northern elephant seals' current range and potential expansion in the KRNCA was not included in this study. This would be important to explore in the future to understand how large the King Range colony could become and how that will impact the potential for human and seal interactions.

Northern elephant seals breeding on mainland beaches is not a new phenomenon. Many National and State Parks have had to enact management plans to preserve land for elephant seals and manage human visitation to those areas to reduce conflicts (Le Boeuf

& Campagna, 2013). The King Range colony poses a new management challenge to the Bureau of Land Management, which oversees the beach on which the colony persists. This site sits adjacent to the popular and remote 'Lost Coast Trail' used by day hikers and backpackers year-round. Currently, this site does not have a management plan for human and seal interactions. As a northern elephant seal colony grows, seals take up more space and potentially take over areas used for human recreation. Over the last four years, northern elephant seals have been using more of the available beach. This study and the continued monitoring at this site will provide informative data for future management of northern elephant seals at this growing colony.

Globally, species are seeing rapid changes in their environment due to climate change. The thick blubber layer of northern elephant seal pups makes them vulnerable to overheating, in some cases resulting in death from hyperthermia (Noren, 2002; Reiter et al., 1978). As air temperatures increase during the breeding months, northern elephant seals may abandon the southern reaches of their range and begin shifting northward to ensure pup survival (García-Aguilar et al., 2018). Additionally, a loss of beach habitat due to sea-level rise will cause a shift in this species’ distribution (Funayama et al., 2013). Breeding colonies with flat beaches backed by cliffs (i.e., Point Reyes and Piedras Blancas) are likely to have higher pup mortality during king tides and large winter storms in the years to come, in turn causing seals to spread to other surrounding habitats less impacted by sea-level rise. This move north will inundate currently growing colonies like the King Range that have refugia from rising sea levels and prompt seals to explore unoccupied areas. As observed with the formation of breeding colonies in central

California, successful emerging colonies play an essential role in serving as seed colonies for growth northward (Allen et al., 1989; Hodder et al., 1998; Le Boeuf et al., 1974; Le Boeuf et al., 2011). Models of potential but unused breeding habitats of northern elephant seals could allow managers to predict the range shift of this species in the coming decades.

# CHAPTER 2: JUVENILE NORTHERN ELEPHANT SEAL DISPERSAL AND TEMPORAL COLONY USE BEHAVIOR

## INTRODUCTION

Dispersal plays a vital role in shaping the composition and distribution of populations (Greenwood, 1980; Nathan, 2001). Dispersing individuals can be juveniles or adults, and dispersal can be permanent or impermanent (Greenwood, 1980). Many colonial mammalian and avian species exhibit natal dispersal, where juveniles move from their birthplace to a new site that could become their first breeding site (Greenwood, 1980). The evolutionary benefits of dispersal are to reduce inbreeding, resource competition, mate competition, and breeding space limitations. This typically results in a male-biased dispersal in mammals (Dobson, 1982; Greenwood, 1980). Many colonial breeding pinniped species – seals, sea lions, and walruses – are recovering after human exploitation and are colonizing new or historical breeding areas, making them ideal study species for dispersal. Few studies on pinniped colonization have investigated both dispersal and fine-scale temporal colony use behavior of juvenile individuals, which would provide insight into colony formation and growth.

Many pinniped populations were exploited to near extinction prior to the implementation of protective legislation, such as the U. S. Marine Mammal Protection Act (1972). Most populations have expanded in size and distribution since federal protection. The process of population recolonization or expansion is similar for many pinniped species. It has been described by Roux (1987) as four phases: survival, establishment, recolonization, and maturity. Many pinniped species have gone beyond the survival phase and have become established, with most currently in the recolonization phase. Pinniped recolonization is primarily driven by the movement of young non-breeding individuals rather than adults due to adult development of high site fidelity (Grandi et al., 2008; Pomeroy et al., 2000; Reiter et al., 1981; Roux, 1987). Natal dispersal has been documented in subantarctic fur seals (*Arctocephalus tropicalis*), South American sea lions (*Otaria flavescens*), New Zealand fur seals (*Arctocephalus forsteri*), grey seals (*Halichoerus grypus*), southern elephant seals (*Mirounga leonina*), and northern elephant seals (*Mirounga angustirostris*) (Brasseur et al., 2015; Dans et al., 2004; Dix, 1993; Grandi et al., 2008; Le Boeuf et al., 1974; Oosthuizen et al., 2011; Pomeroy et al., 2000; Roux, 1987). Pinniped species show varied sex biases in dispersal, with a male bias in northern fur seals (*Callorhinus ursinus*) and no sex biases in southern elephant seals and Cape fur seals (*Arctocephalus pusillus*) (Greenwood, 1980). Because many pinniped species exhibit natal dispersal, tracking the movements of juvenile individuals of a population is the key to understanding the mechanisms of colonization.

The juvenile phase provides young mammals time to learn and practice behaviors that support future reproductive success. The length of the mammalian juvenile phase ranges from 1-2 months in some rodents and bats to more than 7 years in elephants (Barclay et al., 2003; Sengupta, 2013; Smith & Buss, 1973). The average juvenile period for seals and sea lions lasts 2-6 years (Barclay et al., 2003; Boyd, 2009). In elephant seals and many other phocids (true seals), juveniles are independent of their mother after weaning (Le Boeuf & Laws, 1994). This results in typically high mortality during the first year of life, as juveniles learn how to find prey, avoid predators, and locate appropriate places to haul out on their own (Le Boeuf & Laws, 1994). Understanding the movement of juveniles during their first few years of life is vital to understanding the colonization process. Yet, juveniles are difficult to track due to their high mortality, erratic movement patterns, and difficulty resighting tagged individuals in large packed colonies. In a small, newly formed colony, known juveniles can be resighted on the haul out more easily due to lower densities than on large colonies.

The process of colonization through juvenile exploratory dispersal can be through: (1) spill-over; or (2) prospecting. Spill-over is a small-scale movement event that occurs when juveniles move from a densely packed breeding or haul out area to adjacent uninhabited areas. Over time, these new haul out areas develop into breeding sites through juvenile maturation or adult spill-over (Dans et al., 2004; Dix, 1993; Grandi, 2008; Pomeroy et al., 2000). I define prospecting as random long-range movement events of juveniles to new suitable resting and breeding sites. Prospecting events greater than 600 km have been observed in grey seals and southern elephant seals (Oosthuizen et al., 2011; Brasseur et al., 2015). The initiation of breeding at new haul out sites formed by prospecting occurs when these juveniles return to the new location after reaching sexual maturity. Prospecting promotes the expansion of a species' population range. Over time, it may increase more successful recolonization by creating many small seed colonies on northern or southern boundaries that supply increased exchange of juveniles.

Since the 1970s, northern elephant seals have recolonized southern and central California with continued expansion northward, forming new breeding sites in northern California, Oregon, and Washington (Lowry et al., 2014). This expansion has been primarily fueled by the natal dispersal of prospecting juvenile elephant seals during their first year of life (Le Boeuf et al., 1974). In some colonization events, there was a male bias in dispersing juveniles, and in others, no sex bias was reported (Allen et al., 1989; Hodder et al., 1998; Le Boeuf et al., 1974; Le Boeuf et al., 2011). Both sexes have been documented to colonize new breeding areas through spill-over and prospecting dispersal (Allen et al., 1989; Hodder et al., 1998; Le Boeuf et al., 1974; Le Boeuf et al., 2011).

Many northern elephant seal breeding sites were colonized through juvenile prospecting, where seals formed new breeding areas greater than 50 kilometers away from their natal site (e.g., The Channel Islands, Año Nuevo Island, Farallon Islands, Shell Island, OR, etc.) (Hodder et al., 1998; Le Boeuf et al., 1974; Le Boeuf & Laws, 1994; Le Boeuf et al., 2011). Additionally, spill-over dispersal of juvenile and subadult seals formed Año Nuevo Mainland and Point Reyes, where seals traveled less than 50 kilometers away from their natal site (Allen et al., 1989; Le Boeuf et al., 2011). Little is known about the behavior of juveniles and how they contribute to colony establishment once they disperse to a new area. Only one study investigated juvenile dispersal and temporal colony use at a new colony prior to the inception of breeding. This study confirmed that the youngest (<1-year-old) juveniles were the most common age in attendance at the pre-breeding stage. Juveniles stayed longer on the colony during the spring molting season compared to the resting haul out season (Le Boeuf et al., 1974).

Juvenile dispersal and colony use behavior has not been investigated in the context of comparing how natal and dispersing juveniles contribute to a colony's establishment.

Northern elephant seals become independent from their mothers at ~26 days old. Once weaned, they spend around two months fasting at the colony, where they learn to swim and dive near-shore before their first at-sea foraging trip (Le Boeuf & Laws, 1994). Juvenile survivorship is low, with only 50-60% of weanlings surviving to age 1 and only 31% reaching age 3 (Condit et al., 2014). Northern elephant seals of all ages haul out on a colony twice per year, once to rest/breed and once to molt. Juveniles haul out during the fall/early winter to rest (August – December) and during the spring to molt (March – June) (Le Boeuf & Laws, 1994). In spring, juveniles undergo a catastrophic molt over 4-6 weeks. During the molt, elephant seals are tied to the land, as they expend energy directing blood flow to their skin to shed their fur and the top layer of skin in large patches and regrow new fur (Le Boeuf & Laws, 1994).

During the fall resting haul out season, juveniles do not undergo an intensive physiological process that ties them to land. Little is known about why juveniles visit the colony at this time of year. One hypothesis is to avoid being present during the highly space-competitive breeding season (Le Boeuf & Laws, 1994). Another research found preliminary evidence of an increase in bone density in juveniles while on shore, suggesting that this could be another reason to return to the colony during the fall (P. Buckendahl, pers. comms.). Describing and quantifying the differences between how juveniles of each age use a colony could provide insight into the key times of year for dispersal and new colony formation. These two haul out periods offer an excellent opportunity to identify juveniles' colony of origin, age, and sex to describe the role they play in colony establishment and growth.

Northern elephant seals are ideal for investigating dispersal and colony establishment, as their population is expanding north into accessible mainland beach habitats. Their seasonal attachment to predictable and accessible terrestrial haul out sites makes them easy to observe year-round. The newly formed King Range colony in northern California provides the opportunity to investigate the role juvenile northern elephant seals play in colony establishment and growth as it is still small in size and heavily influenced by immigration from large established colonies.

In this chapter, the objectives are to (1) describe and quantify the temporal colony use behavior (peak abundance, arrival date, and tenure) of individually identifiable natal and dispersing juveniles during the fall resting haul out and spring molting seasons to define the key temporal stages of dispersal events, (2) describe the age and sex of juveniles dispersing or returning to the King Range, and (3) examine and categorize the movement strategies of individually identifiable natal and dispersing juveniles to and from the King Range colony.

# METHODS

## General

The first juvenile elephant seal was recorded at the King Range colony in 2011. The first occurrence of pupping occurred in 2015 (J. McAbery, pers. comm.). The study site, data collection, protocols, and permitting were the same as described in Chapter 1. Our collaborators contributed data from Point Reyes National Seashore and Año Nuevo State Park, California (Figure 11).

Prior field technicians conducted surveys at the King Range colony during the 2017 – 2018 breeding season (late November – February). Year-round surveys began in November 2018 and continued through August 2021, with a focused resighting effort beginning in the fall of 2020. Due to COVID-19 restrictions, there was a collection gap from mid-March through April 2020. Because of this data gap, only data from the 2021 molting season and 2019 and 2020 fall resting haul out seasons were robust enough for arrival date and tenure analysis.

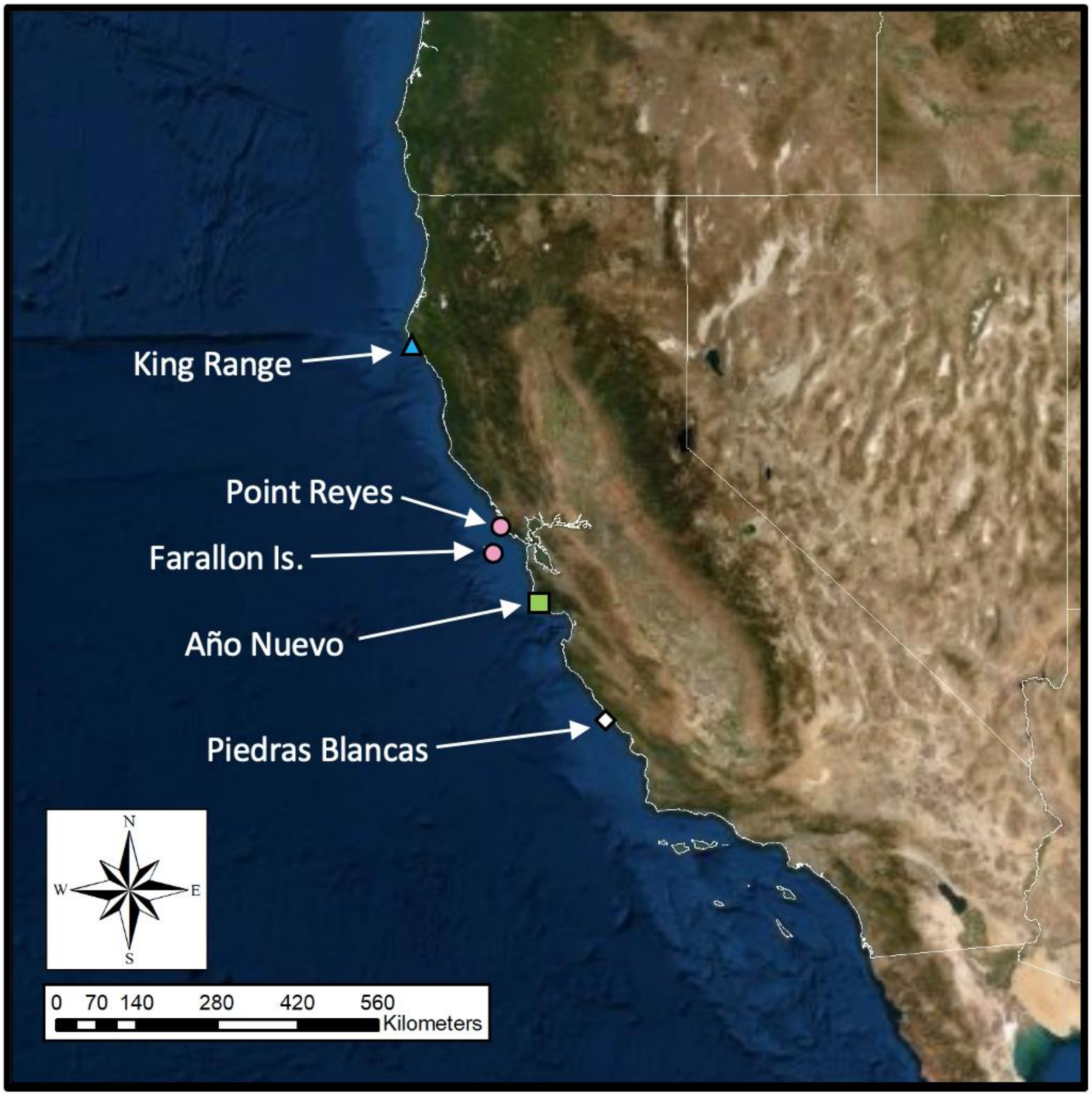

Figure 11. Map of California northern elephant seal breeding colonies discussed in this chapter. Colony location colors are affiliated with the flipper tag color deployed at those sites–King Range (blue, triangle), Point Reyes and Farallon Islands (pink, circle), Año Nuevo (green, square), and Piedras Blancas (white, diamond).

## Colony of Origin, Sex, and Age

I confirmed juvenile age from the histories of plastic alphanumeric rear flipper tags deployed on the seals as weanlings at their natal colony. To track the presence and temporal distribution of juvenile elephant seals at the King Range colony, we resighted tagged seals during all surveys from November 2017 through May 2021. The historical data from these tags (natal colony, sex, and date of tagging as weaned pups) gave me the individual's known sex and age class information. We documented the tag color, number, and position on the rear flipper and used verification photos to confirm tag numbers. Once I determined age from an individual's tag history, I assigned them to an age group. Juvenile age groups were defined as follows: age 0 or yearlings (7-12 months old, first fall resting haul out), age 1 (first spring molt and second fall resting haul out), age 2 (second spring molt and third fall resting haul out), age 3 (third molt and fourth resting haul out).

## Age Group Seasonal Abundance

I determined the peak abundance of each juvenile age group during the fall resting haul out and spring molting seasons; the total number of tagged juvenile seals of each age group observed during each survey. I combined the total number of tagged elephant seals ages 0 (yearling), 1, and 2 for the resting haul out by week (2019 and 2020 data combined), and I totaled ages 1, 2, and 3 for the molt by survey date (only 2021 data). I only tracked seals up to 3 years old for this study due to many female elephant seals becoming breeding adults at age 4.

## Age at First Observation, Arrival date, and Tenure

I compared the age at first observation, the colony of origin, seasonal arrival date, seasonal tenure, and tenure attendance patterns for tagged yearlings (age 0), 1-year-olds, and 2-year-olds for the fall resting haul out and 1-year-olds, 2-year-olds, and 3-year-olds for the spring molt. I defined the age at first observation as the first date we observed a tagged seal on the King Range colony after its first foraging season. I defined seasonal arrival date for each seal as the first day we observed a tagged individual within a season. I defined seasonal tenure as the number of days between a seal's arrival date and the last day we observed that individual at the King Range within a season. Within each season, juveniles exhibited three different tenure attendance patterns:

1. Single sighting: we observed a seal on the colony during only one survey within a season.
2. Single bout: we observed a seal over multiple surveys with an estimated seasonal tenure between 2 - 49 days.
3. Double bout: we observed a seal over multiple surveys during two distinct periods–with a greater than a 6-week gap between sightings–within one season. The total estimated seasonal tenure was > 50 days.

I assumed the presence of tagged juveniles during extreme clumping periods of seals or when I observed many seals in the water during surveys, as it was unlikely that we would miss a tagged seal over multiple consecutive surveys.

## Movement Strategies

I described the movement histories for each tagged King Range juvenile (n=77) and for dispersing juveniles seen at least once at the King Range colony (n= 231). I complied these histories from the King Range records, public sighting reports, and sighting reports from Sarah Codde (Marine Ecologist, Point Reyes National Seashore) and Dr. Richard Condit (Database Manager, Año Nuevo State Park).

Additionally, I supplemented these histories with resight observations of untagged seals marked with hair dye during the 2020 fall resting haul out and resighted during the 2021 spring molt. During the 2020 resting haul out, I dye-marked 235 untagged juveniles with alphanumeric hair dye marks on their dorsal flanks during surveys to track their presence at the King Range and other colonies. Because marked individuals did not have a known birth year, we visually estimated age based on size and coat condition. I identified yearlings (7-12 months old, age 0) as being the smallest of the juvenile seals present and by coat characteristics (rough skin, lesions, and a patchy coat) (Le Boeuf & Laws, 1994). Because of these distinct coat patterns, I identified yearlings with the most confidence. Seals of both sexes, ages 1-2, were difficult to differentiate between, so I combined them in the juvenile category. This age group had a longer body length and was in better body condition compared to yearlings with no abnormalities in their coat condition. By collaborating with Point Reyes and Año Nuevo, I was able to compile histories of unmarked seals dispersing away from the King Range.

## Statistical analysis

I conducted all statistical analyses in RStudio using the R 4.0.2 stats package and the 0.6.0 rstatix package. These analyses included two resting haul out seasons (2019 and 2020) and one spring molting season (2021). Using an unpaired two-sample t-test I was able to determine that fall resting haul out seasonal arrival date for juveniles of ages 0, 1, and 2 were not different between years ($t(102) = -1.35$, $p = 0.18$; $t(90) = 1.76$, $p = 0.08$; $t(22) = -1.61$, $p = 0.12$). Therefore, I combined these data for analysis. Using the same test, I compared fall resting haul out seasonal tenure of all ages between years and found that the data were not significantly different for ages 0 and 2, but there was a significant difference between years in 1-year-old seasonal tenure ($t(156) = -0.52$, $p = 0.61$; $t(60) = -0.70$, $p = 0.49$; $t(95) = -2.00$, $p = 0.49$). Given that two of the three age groups showed no difference in seasonal tenure between years, I decided to combine the 2019 and 2020 fall resting haul out data for analysis.

I used a one-way ANOVA to determine age variation in seasonal arrival dates between the three juvenile age groups for the resting haul out and molting seasons. I found all data for juvenile seasonal arrival date to be normally distributed. I used Tukey's HSD test to further determine which age groups' seasonal arrival dates were different from one another. Due to a normality assumption violation in the seasonal tenure data, I used a Kruskal-Wallis test to determine age variation in seasonal tenure in both the resting haul out and molting seasons. I used Dunn's test to further determine which juvenile age groups' seasonal tenure were different from one another. To determine if natal and dispersing juvenile or male and female juveniles of each age group exhibited different colony use behavior, I used a Mann-Whitney U-test with a Bonferonni correction of 0.02, given that I was comparing three age groups. To determine if there were sex biases in natal and dispersing juveniles visiting the King Range colony, I used a one-sample proportions test to compare the number of female and male juveniles from each colony of origin and age of dispersal to the King Range colony.

# RESULTS

I observed juvenile elephant seals on the King Range colony throughout the year and noted their concentrated high abundance periods during the fall resting haul out and the spring molt (Figure 12).

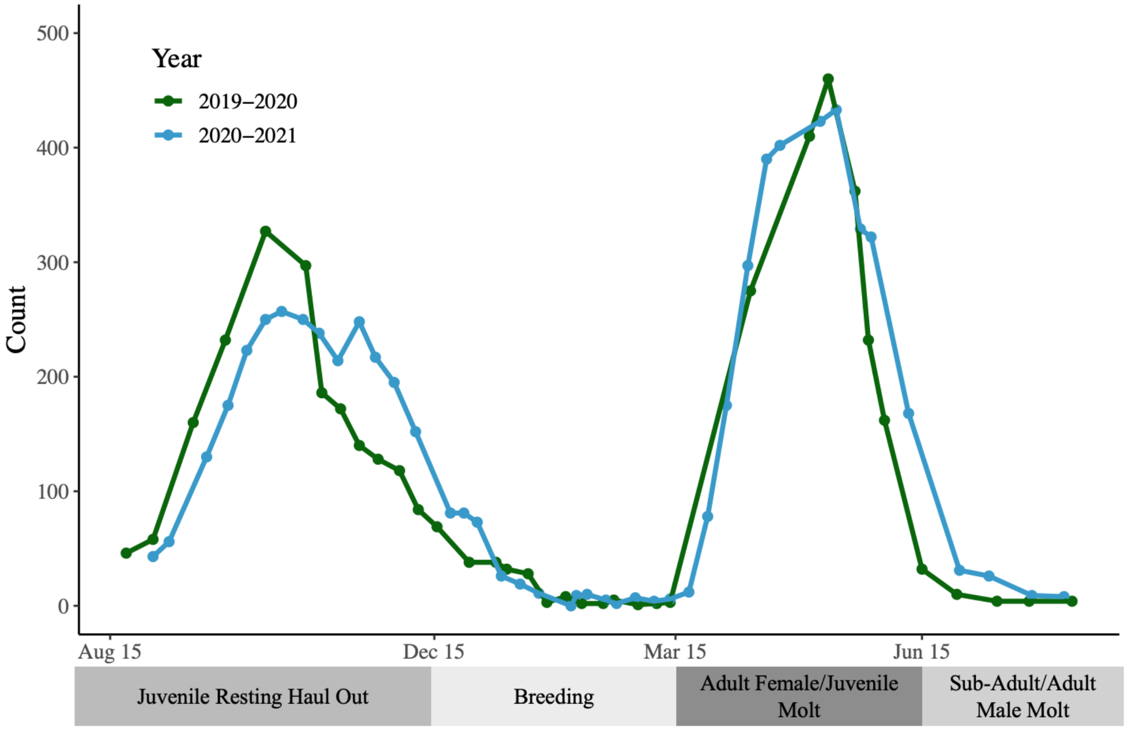

Figure 12. Juvenile northern elephant seal total counts at the King Range colony in 2019-2020 and 2020-2021. This figure includes counts of known-age (tagged) and visually estimated age (untagged) juvenile elephant seals.

## Temporal Colony Use Behavior

Over the study period, we observed 308 known-age tagged juvenile northern elephant seals (ages 0-3) at the King Range colony. We visually confirmed the sex of 266 of those individuals.

### Age Abundance

During the 2020 and 2021 fall resting haul out, I observed (158) age 0, (97) age 1, and (62) age 2 tagged elephant seals at the King Range colony. The timing of peak abundance differed between juvenile ages 0, 1, and 2, with their peaks occurring in late November, mid-October, and late October, respectively (Figure 13).

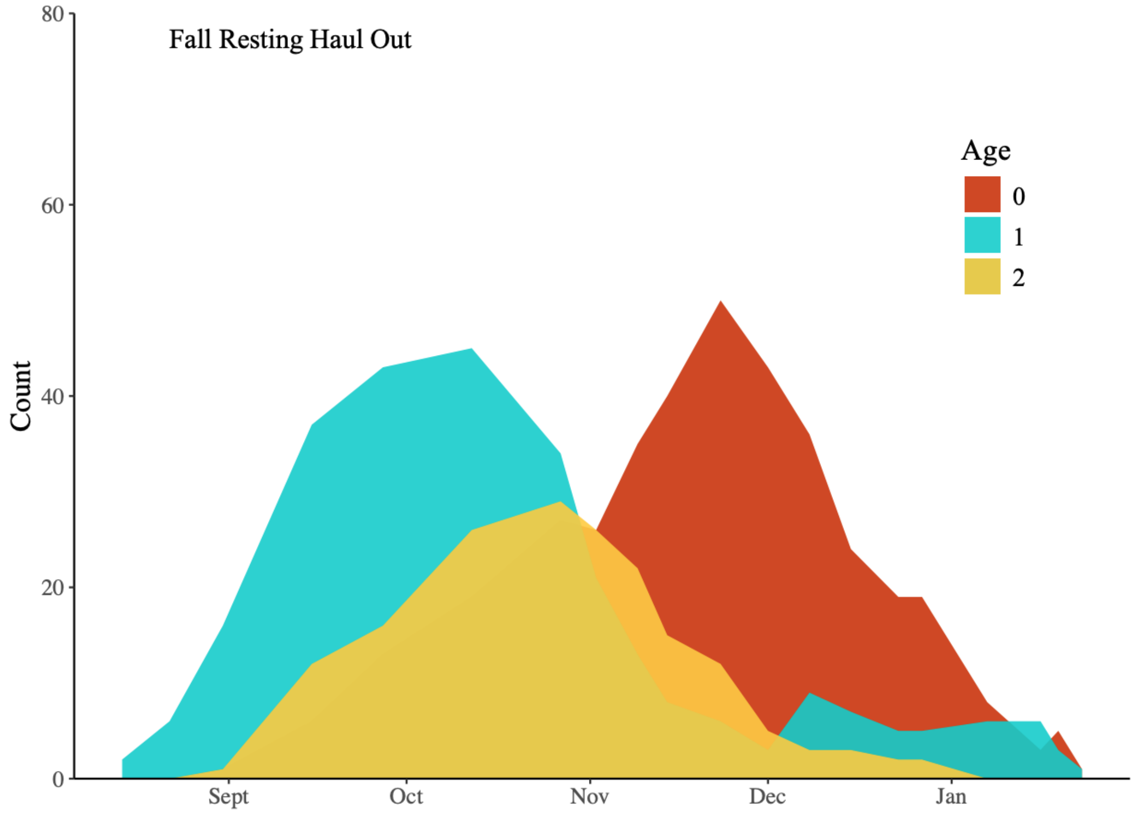

Figure 13. The total number of yearlings (age 0; orange), 1-year-old (blue), and 2-year-old (yellow) tagged northern elephant seals resighted during each survey for the 2019 and 2020 fall resting haul out seasons.

During the spring molting season, I observed (76) age 1, (19) age 2, and (50) age 3 tagged elephant seals. The timing of peak abundance differed much less between juvenile ages (1-3) than the fall resting haul out, with seals age 2 peaking in late April and seals ages 1 and 3 in early May (Figure 14).

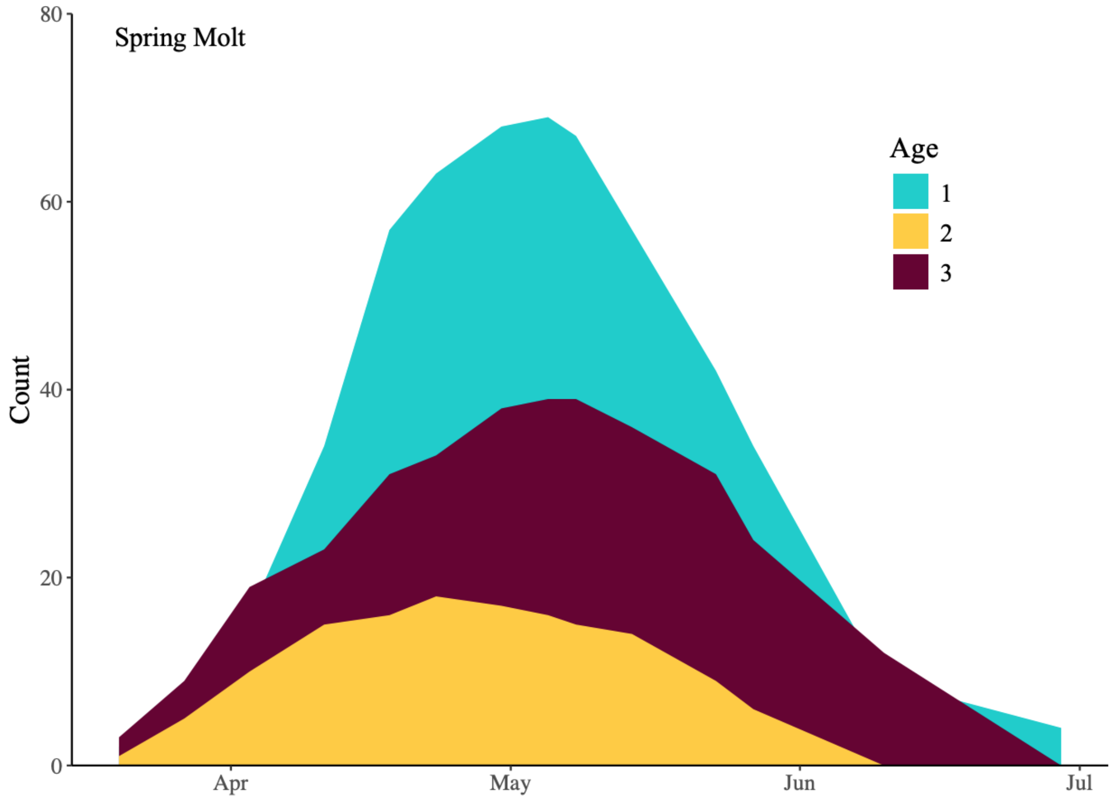

Figure 14. The total number of 1-year-old (blue), 2-year-old (yellow), and 3-year-old (purple) tagged northern elephant seals resighted during each survey in the 2021 spring molting season.

### Arrival Date

Juvenile elephant seal age had a significant effect on mean arrival date during the fall resting haul out, with yearlings arriving primarily in mid-November, 1-year-olds in late September, and 2-year-olds in mid-October ($F(2,314) = 95.3$, $p < 0.001$) (Figure 15). The mean seasonal arrival date was significantly different between ages 0 and 1, ages 0 and 2, and ages 1 and 2 ($p < 0.001$, 95% C.I. = [-52.67, -36.90]; $p < 0.001$, 95% C.I. = [-38.76, -20.45]; $p < 0.01$, 95% C.I. = [5.23, 25.11]). In addition, age had a significant effect on the mean arrival date during the spring molt, with 2-year-olds primarily arriving in early April and 1-year-olds and 3-year-olds in mid-April ($F(2,142) = 3.6$, $p = 0.03$) (Figure 16). The mean seasonal arrival date was significantly different between ages 2 and 3 ($p < 0.05$, 95% C.I. = [1.05, 19.55]). There was no statistically significant difference in mean seasonal arrival date between ages 1 and 2 ($p = 0.06$) or between ages 1 and 3 ($p = 0.81$).

Natal and dispersing juveniles of all ages (0-2) showed no significant difference in seasonal arrival date during the fall resting haul out ($W = 3526.50$, $p = 0.02$; $W = 896.00$, $p = 0.69$; $W = 221.00$, $p = 0.05$). Additionally, I found no significant differences between natal and dispersing juvenile seasonal arrival date across all ages (1-3) during the spring molt ($W = 613.00$, $p = 0.46$; $W = 49.50$, $p = 0.74$; $W = 155.50$, $p = 0.02$).

There was no significant difference in fall resting haul out seasonal arrival date based on the sex of each juvenile age group (0-2) ($W = 2612.50$, $p = 0.06$; $W = 860.50$, $p = 0.12$; $W = 387.50$, $p = 0.90$). In the spring no significant difference in seasonal arrival date was found between sexes of ages 1 and 2 ($W = 455.00$, $p = 0.07$; $W = 33.00$, $p = 0.37$). There was a significant different in when 3-year-old males and females arrived to the colony, with males arriving later than females ($W = 96.00$, $p < 0.001$).

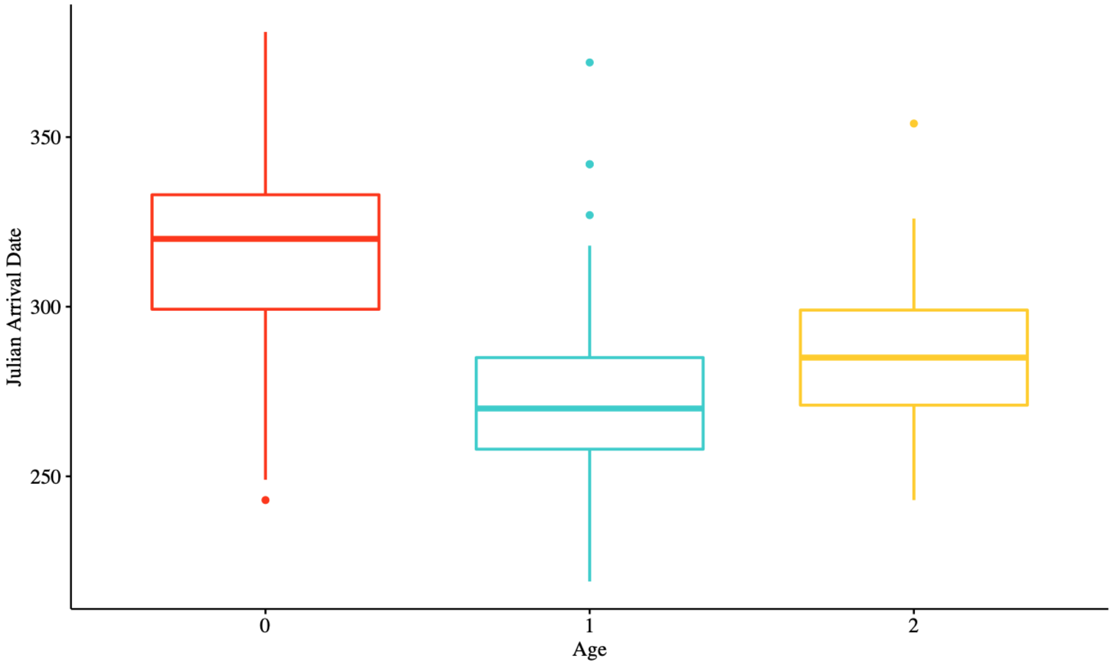

Figure 15. Juvenile northern elephant seal mean arrival date as a function of age (yearling (age 0), 1-year-old, and 2-year-old) at the King Range colony during the fall resting haul out in 2019 and 2020.

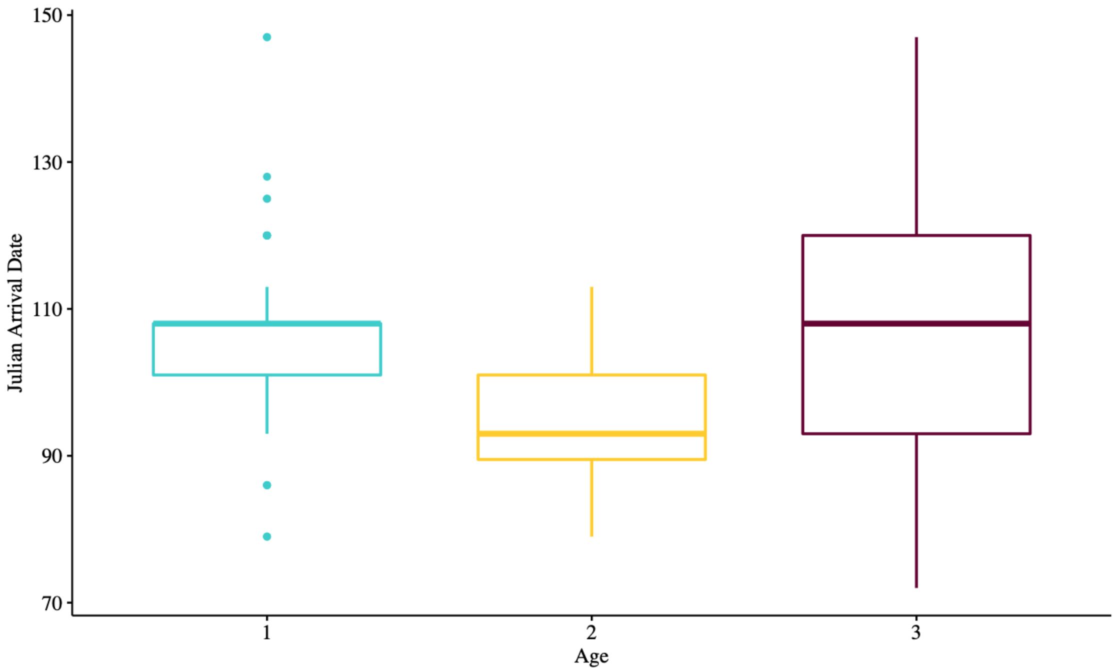

Figure 16. Juvenile northern elephant seal mean arrival date as a function of age (1-year-old, 2-year-old, and 3-year-old) at the King Range colony during the spring molting season.

Seasonal Tenure

Juvenile elephant seal age had a significant effect on seasonal tenure during the fall resting haul out ($H(2) = 21.33$, $p < 0.001$) (Figure 17). The mean seasonal tenure was significantly different between ages 0 and 1 and ages 0 and 2 ($Z = -4.52$, $p < 0.001$; $Z = -2.37$, $p < 0.05$). There was no statistically significant difference in mean seasonal tenure between ages 1 and 2 ($Z = 1.40$, $p = 0.16$). Based on the spread of the data point in Figure 17, yearlings and 1-year-olds showed much more variation in seasonal tenure during the resting haul out season than 2-year-olds (Figure 17).

During the spring molting season, juvenile age did not significantly affect seasonal tenure ($H(2) = 1.76$, $p = 0.41$) (Figure 18). There was no statistically significant difference in mean seasonal tenure between 1 and 2, ages 1 and 3, and ages 2 and 3 ($Z = -1.32$, $p = 0.6$; $Z = -0.48$, $p = 1$; $Z = 0.94$, $p = 1$). The juvenile mean seasonal tenure during the molting season was consistently longer for all ages than the mean seasonal tenure of juveniles during the fall resting haul out ($M = 37–40$, $M = 19–31$).

Natal and dispersing juveniles of age 0 showed a significant difference in seasonal tenure during the fall resting haul out ($W = 1923.00$, $p < 0.001$). Yet, natal and dispersing juveniles of ages 1 and 2 showed no significant difference in season tenure in the fall ($W = 797.00$, $p = 0.23$; $W = 248.00$, $p = 0.14$). No significant difference in seasonal tenure was observed for all natal and dispersing juveniles of age 1-3 during the spring molting season ($W = 735.50$, $p = 0.56$; $W = 41.50$, $p = 0.80$; $W =341.00$, $p = 0.10$).

Male and female yearlings and 1-year-olds showed no significant difference in seasonal tenure during the fall resting haul out ($W = 1865.50$, $p = 0.13$; $W = 833.50$, $p = 0.08$). Males and females of age 2 did show a significant difference in seasonal tenure during the fall resting haul out, with males having a longer tenure than females ($W = 181.50$, $p < 0.001$). During the spring molting season male and female juveniles ages 1 and 2 showed no significant difference in seasonal tenure ($W = 659.50$, $p = 0.52$; $W = 56.50$, $p = 0.32$). Yet, there was a significant difference in seasonal tenure for males and females of age 3, with females exhibiting a longer tenure than males ($W = 357.5$, $p = 0.01$).

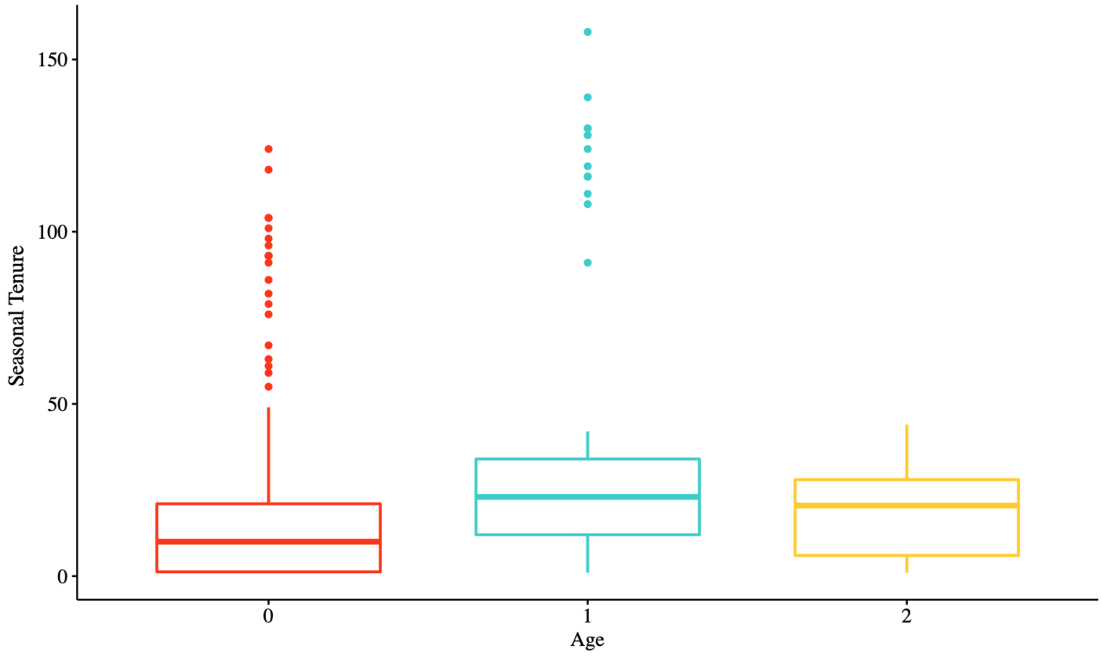

Figure 17. The effect of juvenile northern elephant seal age (yearling (age 0), 1-year-old, and 2-year-old) on mean seasonal tenure at the King Range colony during the fall resting haul out in 2019 and 2020.

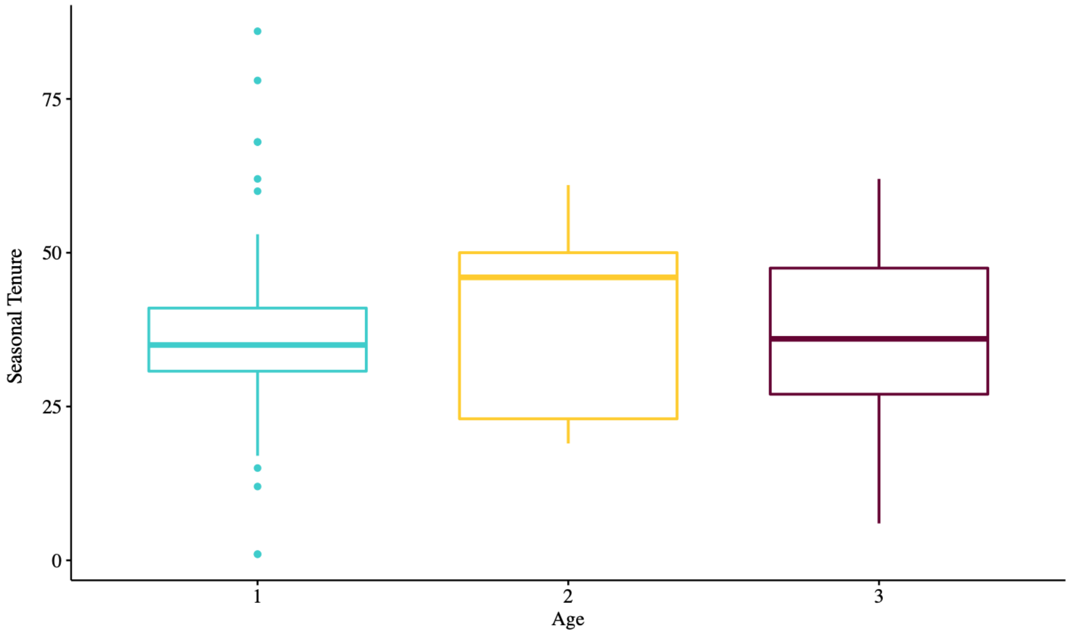

Figure 18. The effect of juvenile northern elephant seal age (1-year-old, 2-year-old, and 3-year-old) on mean seasonal tenure at the King Range colony during the juvenile molting season.

Attendance Patterns

I observed variable time spent hauled out (seasonal tenure) between juvenile elephant seals of different ages. I, therefore, further categorized tenure attendance patterns (single sighting, single bout, double bout). Overall, I observed all three patterns during the fall resting haul out season, whereas the single bout pattern (97.3%) was overwhelmingly the most common during the spring molting season (Figure 19).

I observed seals only seen during one survey (single sighting) more often during the fall resting haul out (22.5% of all tagged seals) than during the spring molt (1.4% of all tagged seals) (Figure 19). I observed single sightings in all ages and colonies of origin during the fall resting haul out. In contrast, I only saw this pattern in 1-year-old seals during the spring molt (Figures 20 & 21).

I observed single bouts as the most common attendance pattern for all ages and colonies of origin in both the resting haul out and molting seasons (Figures 20 & 21). Both natal and dispersing juveniles of all ages exhibited this pattern during the fall resting haul out and spring molting seasons. Seals ages 2 and 3 only exhibit this attendance pattern during the molting season (Figures 20 & 21).

I observed the double bout tenure attendance pattern most during the resting haul out and rarely during the molt (Figure 19). I found yearlings to be the most common juvenile age group to exhibit this pattern. In addition, 1-year-old seals exhibited this pattern during the spring molting and fall resting haul out. This behavior was most commonly displayed by natal (King Range) and dispersing juveniles from Año Nuevo. (Figures 20 & 21).

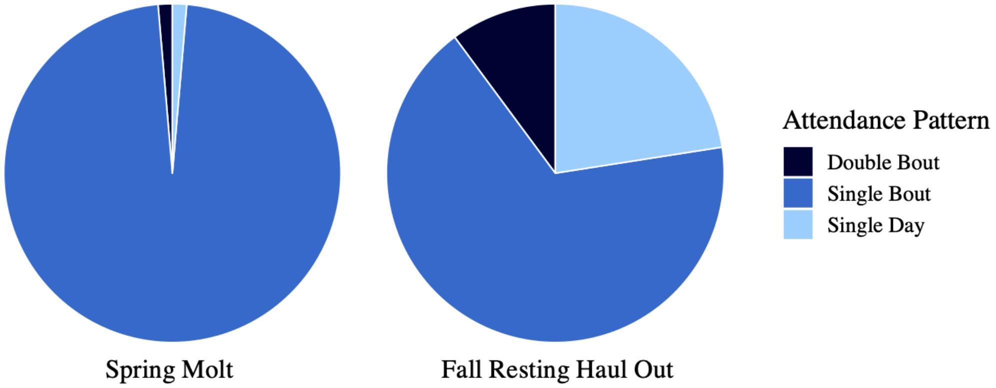

Figure 19. Juvenile northern elephant seal tenure attendance patterns observed during the fall resting haul out (n=317) and spring molting (n=145) seasons at the King Range colony.

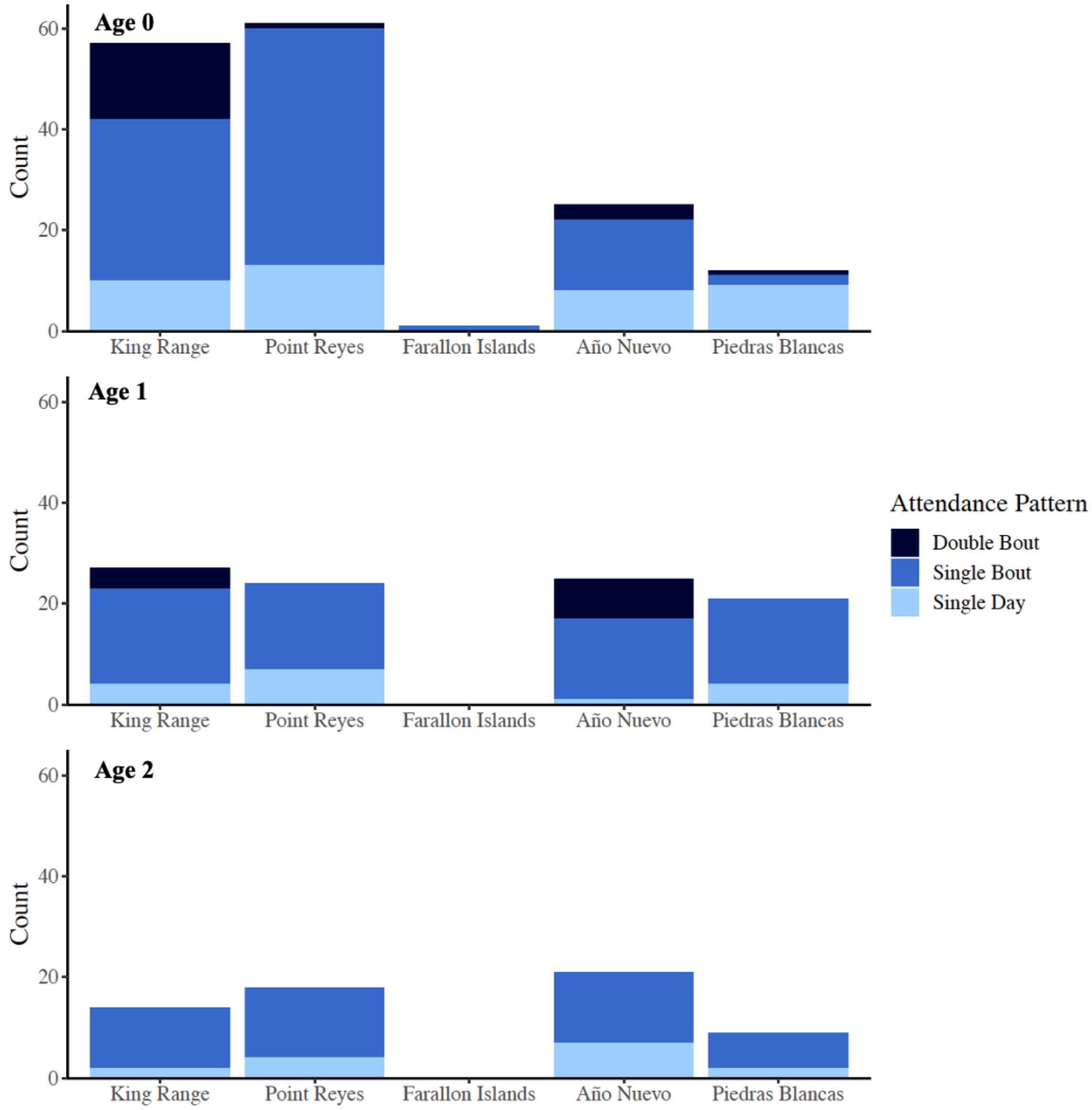

Figure 20. Fall resting haul out juvenile northern elephant seal tenure attendance patterns based on age and colony of origin.

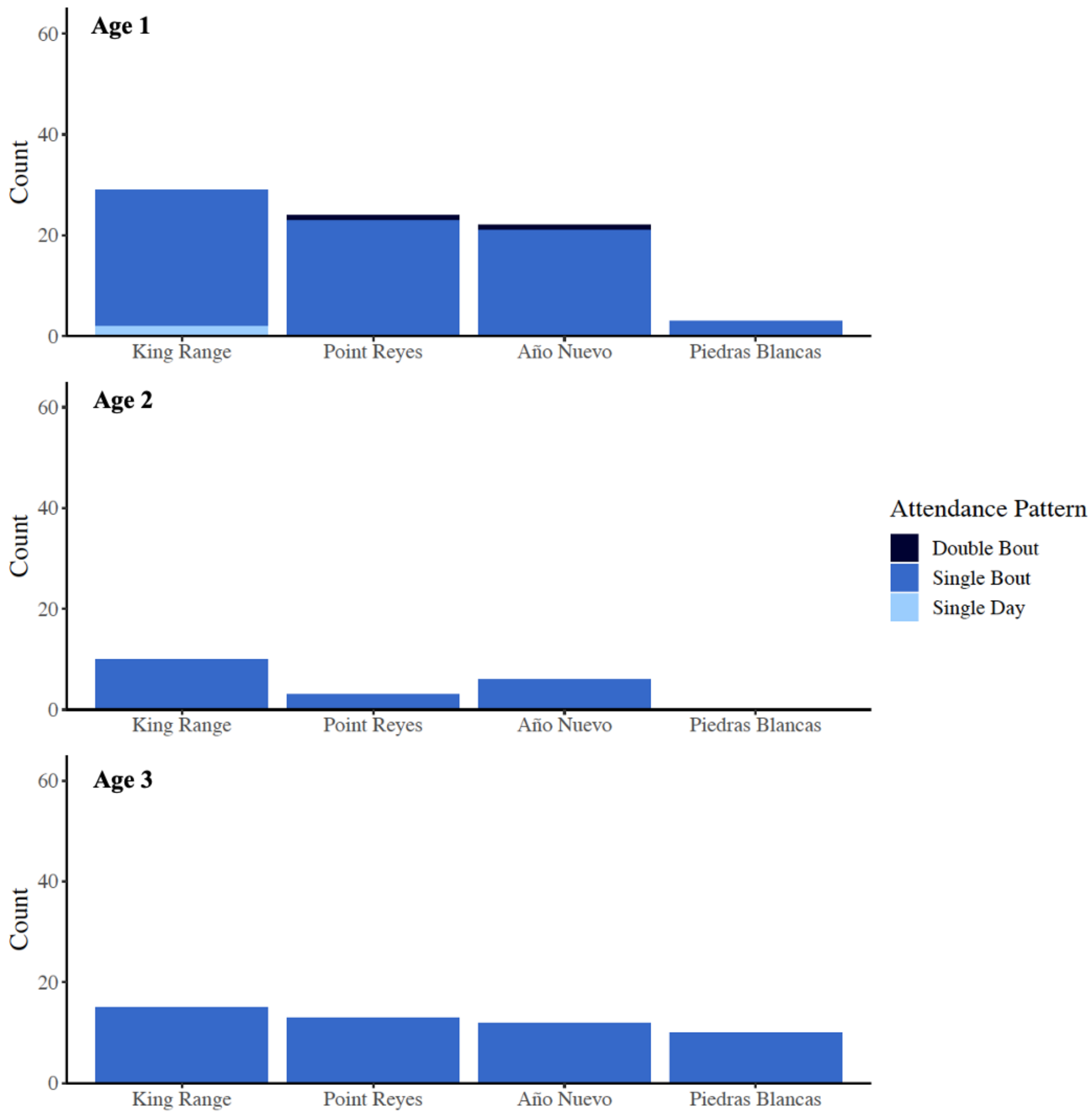

Figure 21. Spring molt juvenile northern elephant seal tenure attendance patterns based on age and colony of origin.

Given the number of outlier data points for seasonal tenure in ages 0 and 1, I decided to investigate seasonal tenure of the most common tenure attendance pattern, single bout. Compared to the seasonal tenure evaluation that included all attendance patterns above, this reevaluation of only the single bout tenure attendance pattern showed much less variability in seasonal tenure of all ages, and mean seasonal tenure for 2-year-olds increased (Figure 22). Juvenile elephant seal age significantly affected mean tenure during the resting haul out for the single bout tenure attendance patterns (*H*(2) = 54.36, $p < 0.001$). Removing the single sighting and double bout tenure attendance patterns from this analysis for the spring molt only affected the 1-year-old seasonal tenure with a slight reduction in variation. Juvenile elephant seal age did not significantly affect mean seasonal tenure (*H*(2) = 3.33, $p = 0.19$).

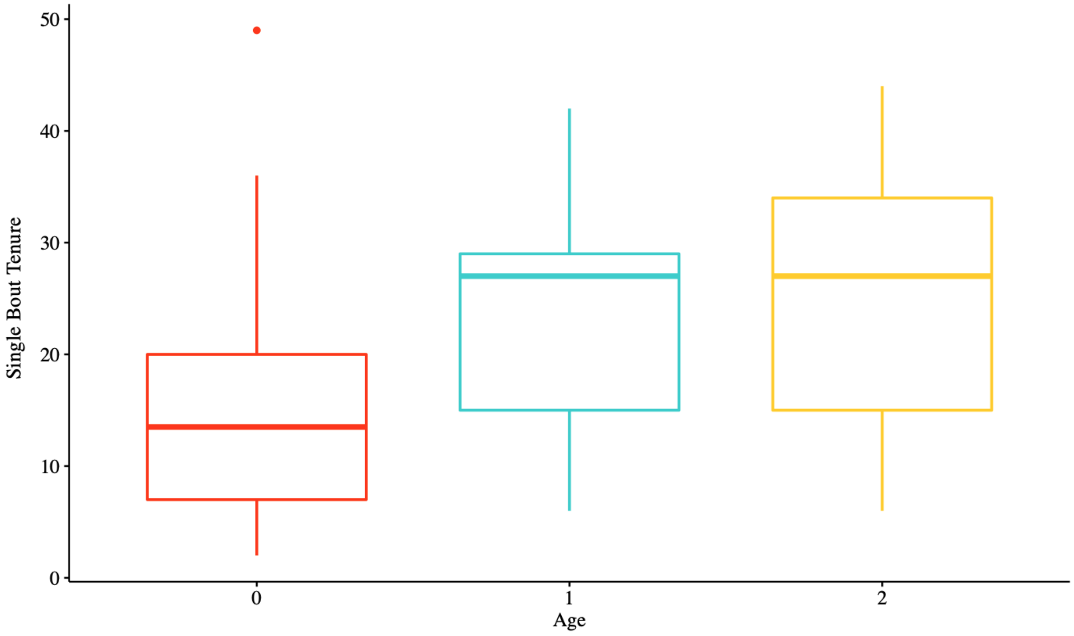

Figure 22. The effect of juvenile northern elephant seal age (yearling (age 0), 1-year-old, and 2-year-old) on the mean seasonal tenure of the single bout tenure attendance pattern at the King Range colony during the fall resting haul out in 2019 and 2020.

## Dispersal age/origin/sex composition

The majority of tagged juvenile elephant seals (75%; n=231) observed on the King Range between 2017 and 2021 were not born on the colony but dispersed from three larger colonies in central and southern California. I recorded most tagged elephant seals (68%) for the first time at the King Range colony during their first resting haul out (7-12 months old). Additionally, I recorded 25% dispersing during their first molting season or second resting haul out season. I observed a small proportion (7%) of elephant seals for the first time at ages 2 and 3 (Table 5).

Table 5. Age of tagged northern elephant seals when first observed as juveniles at the King Range colony separated by colony of origin from North to South (n=308).

| **Age** | **Season** | **King Range** | **Point Reyes** | **Farallon Islands** | **Año Nuevo** | **Piedras Blancas** | **Total** |
|---|---|---|---|---|---|---|---|
| *0 (7-12 mos.)* | 1st resting haul out | 63 | 77 | 1 | 48 | 20 | 209 |
| *1* | 1st molting | 8 | 8 | - | 21 | 11 | 48 |
| *1.5* | 2nd resting haul out | 5 | 10 | - | 7 | 7 | 29 |
| *2* | 2nd molting | 1 | 6 | - | 5 | 3 | 15 |
| *2.5* | 3rd resting haul out | - | 1 | - | - | - | 1 |
| *3* | 3rd molting | - | 4 | - | - | 2 | 8 |

Of the 308 tagged juvenile elephant seals, I observed, 266 were of known sex. While the sex ratio for natal juveniles at the King Range showed no significant bias ($x^2(1)$ = 0.64, $p$ = 0.42), I did find a significant female bias for all dispersing juveniles combined (M:F, 1:1.5, $X^2(1)$ = 7.6, $p$ < 0.01). However, when I evaluated the sex ratio of dispersing juveniles by colony of origin, I only found a significantly female skew for seals originating from Piedras Blancas (Table 6). Overall, the age of first observation did not have a significant effect on the sex ratio for natal and dispersing juveniles, except for dispersing juveniles first observed at age 1, who showed a significant female bias ($X^2(1)$ = 10.78, $p$ < 0.01) (Table 7).

Table 6. Sex ratio of tagged juvenile northern elephant seals observed at the King Range separated by colony of origin.

| **Birthplace** | **Male** | **Female** | **Sex Ratio** | **Chi-squared ($X^2$)** | **df** | **p-value** |
|---|---|---|---|---|---|---|
| *King Range* | 34 | 42 | 1 : 1.2 | 0.64 | 1 | 0.42 |
| *Point Reyes* | 31 | 44 | 1 : 1.4 | 1.92 | 1 | 0.17 |
| *Año Nuevo* | 36 | 44 | 1 : 1.2 | 0.61 | 1 | 0.43 |
| *Piedras Blancas* | 8 | 26 | 1 : 3.3 | 8.5 | 1 | **<0.01** |

Table 7. Sex ratio of tagged juvenile northern elephant seals observed at the King Range separated by the age of first observation of natal and dispersing seals.

| **Origin** | **Age** | **n** | **Sex ratio** | **Chi-squared ($X^2$)** | **df** | **p-value** |
|---|---|---|---|---|---|---|
| *Natal* | 0 | 63 | 1 : 1.25 | 0.57 | 1 | 0.45 |
| *Disperser* | 0 | 113 | 1 : 1.1 | 0.14 | 1 | 0.71 |
| *Natal* | 1 | 13 | 1 : 1.2 | 0 | 1 | 1 |
| *Disperser* | 1 | 58 | 1 : 2.6 | 10.78 | 1 | **<0.01** |
| *Disperser* | 2 | 13 | 1 : 1.6 | 0.31 | 1 | 0.58 |

## Movement Strategies

The 231 tagged juvenile elephant seals that I observed dispersing to the King Range showed a variety of movement strategies. I recorded 93% (n=214) only visiting the King Range after leaving their natal colony, suggesting permanent dispersal from their natal site. In the remaining 7% (n=17), I observed variable movement strategies by prospecting at multiple sites after leaving their natal colony, suggesting impermanent dispersal from their natal site. The most common movement strategy was for juveniles to leave their natal site and travel north to find a new haul out site (n=15). I recorded some instances of individuals moving south after first visiting a colony north of their natal site (n=6) (Figure 23, Appendix A 1).

Of the untagged juvenile elephant seals (ages 0-2) that were dye-marked in Fall 2020 and observed again (n=139), I observed 91% back at the King Range and noted 9% at Point Reyes or Año Nuevo in Spring 2021 (Appendix A 2). Some dye marks could have been lost or faded beyond recognition between the fall and spring seasons. Still, the resighting rate of marked seals returning to or dispersing from the King Range was similar to that of the tag resighting rate. The majority of tagged/marked juvenile elephant seals (n=15 tagged, n=10 marked) who visited multiple colonies prospected during their first year of life (1st resting haul out or 1st molt). I documented only two tagged seals (1 Año Nuevo and 1 Point Reyes) moving between the King Range and other colonies past the age of 3.

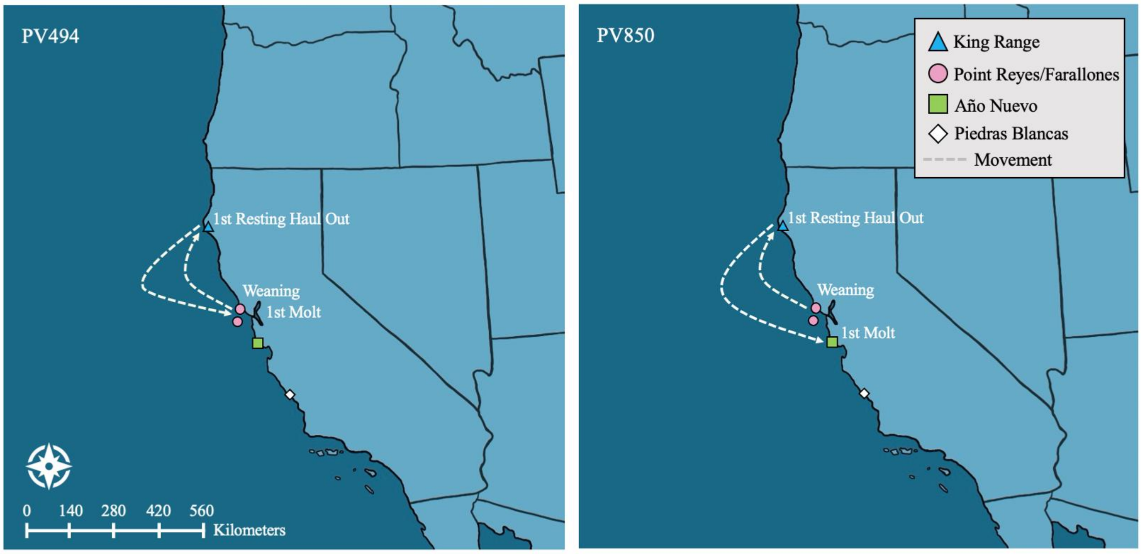

Figure 23. Examples of movement histories of two tagged juvenile northern elephant seals that dispersed to multiple sites during their first year of life.

Of the tagged natal elephant seals observed as juveniles after their first foraging season, I recorded 95% (n=77) only at the King Range and 5% (n=4) prospecting at other breeding colonies or public beaches. The juveniles observed by collaborators at different sites during their first year of life were not seen back at the King Range since their first foraging migration. I have not recorded these individuals prospecting at multiple sites. Collaborators observed these individuals at Resurrection Bay, Alaska, and Cannon Beach, Oregon (non-breeding sites), as well as Point Reyes, California, and Race Rocks, British Columbia (breeding sites).

# DISCUSSION

Juvenile northern elephant seals are the primary age class dispersing and colonizing new breeding sites today. The formation of northern elephant seal breeding colonies north of central California has been driven by long-range prospecting dispersal events of juveniles from their natal colony (Fletcher, 2009; Hodder et al., 1998). Juveniles haul out twice per year—in the spring to molt and fall to rest (Le Boeuf & Laws, 1994). While this pattern has been consistently recorded across their range, this is the first study to describe juvenile use of a colony in the context of colony establishment and growth.

The behavior of juveniles during the fall resting haul out season has not been well described, but it is significant to the colonization process for northern elephant seals. The fall resting haul out is the first season for seals born the previous winter to return ashore in large numbers and offers older juveniles a second yearly haul out before the breeding season begins. More dispersing tagged seals were first observed on the King Range colony during their first fall resting haul out season. This study confirms earlier findings that a large proportion of prospecting juvenile northern elephant seals disperse to new areas for their first resting season (Le Boeuf et al., 1974). Subsequently, if seals were returning to the King Range after being born there, they were still more likely to be first sighting in the fall than in the spring.

The behavior of juvenile seals on the King Range colony during the fall resting haul out (4.5 month period) differed from the spring molt (3 month period). The length of each season likely contributed to the variation in juvenile age group peak abundance that was observed during the fall and spring. In the fall, juvenile seasonal arrival date and tenure were much more variable than in the spring. The fall is a longer season with more variable behavior patterns is likely related to the lack of the time-sensitive and physiologically expensive catastrophic molt that occurs in the spring. In contrast to other seasons, the fall resting haul out is one of relatively low cost in relation to physiological processes (breeding and molting), competition with other seals, and harsh environmental conditions. The variability in juveniles' arrival and tenure may also be attributed to the length of their juvenile learning phase, described from weaning to age 2, where seals fine-tune their foraging and navigational skills near- and offshore (Le Boeuf et al., 1996; Zeno et al., 2008). Once juveniles reached age 2 at the King Range, their time spent on the colony became more consistent during both seasons. The fall resting haul out has shown to be a flexible time for young juvenile elephant seals (< 1-year-old) to explore new areas with little cost.

Juvenile tenure attendance patterns were more variable in the fall, with juvenile seals visiting the colony for a single-day, single bout, or multiple bouts. The single-day visits could reflect juveniles quickly prospecting at the King Rang before moving on to another colony, whereas the double bout visitation may reflect juveniles struggling to find adequate foraging areas during their first foraging trip or juveniles exhibiting a near-shore foraging strategy (Le Boeuf et al., 1996). In comparison, during the spring molt, the single bout pattern was the most common pattern observed, with only juveniles of age 1 exhibiting the other two attendance patterns. This was likely caused by elephant seals being tied to land for 5-6 weeks to undergo their catastrophic molt.

Sex differences in temporal colony use started to manifest as juveniles at the King Range reached ages 2-3. During the fall resting haul out, 2-year-old males had a significantly longer tenure than females. The transition from the juvenile phase to adulthood in male northern elephant seals is a much longer process compared to females, where males become sexually mature at 5 years old but are not socially mature until 8-years-old. As male elephant seals reach ages 3-4, they are present on a breeding colony in the late fall/early winter and are seen “play” fighting to develop their social and competitive skills (Casey et al., 2020). Therefore, social development could be playing a role in the long tenure of 2-year-old males on the colony in the fall. During the spring molting season, once juveniles reached age 3, males shifted to arriving later than females. As northern elephant seals mature, the sexes shift to molt during two different times of the year, females in the spring and males in the summer (Le Boeuf & Laws, 1994). This trend of 3-year-old males molting later in the spring is consistent with previous findings (Clinton, 1994). Yet, this study provides a comparison between both sexes.

Unlike other studies that found a male bias in juvenile elephant seal dispersal, I observed a slight female bias in juvenile dispersal to the King Range (Le Boeuf et al., 1974). The drivers of dispersal for each sex are different, with males likely dispersing due to mating competition and females dispersing due to space competition (Le Boeuf et al., 1974; Le Boeuf & Laws, 1994; Reiter et al., 1981). Due to our small sample size and short length of study, our findings on sex-biased dispersal are likely inconclusive.

A high proportion of the juveniles who dispersed to the King Range were only observed there after leaving their natal colony. High site fidelity (>90%) is often observed in adult females in this species, but less is known about the importance of site fidelity in juveniles (Reiter et al., 1981; Zeno et al., 2021). Zeno et al. (2021) reported that >80% of juvenile females that dispersed to a new site continued to return there throughout their lifetime. Studies of juvenile northern elephant seals homing behavior confirmed that 80% of juveniles return to the colony where they were captured after being translocated (Oliver et al., 1998). Similarly, a dispersing juvenile southern elephant seal’s presence on a new colony during their juvenile phase increases their likelihood of maintaining site fidelity to that new site into adulthood (Hofmeyr et al., 2012; Pistorius et al., 2002). The small proportion of juveniles that did not disperse to the King Range permanently, explored multiple colonies including the King Range before settling on a new colony or returning to their natal colony. This occurred primarily during their first two years of life, confirming that this exploratory dispersal behavior in northern elephant seals most commonly occurs early in life.

The King Range colony is currently growing due to the recruitment of juvenile seals dispersing from southern colonies. Over time this colony will mature to a point where natal juveniles will shift to driving the colony's growth. During this phase of growth, both dispersing juveniles and natal juveniles followed similar arrival and tenure patterns across all ages and seasons. Natal juveniles also showed higher site fidelity to the King Range compared to dispersing juveniles. As this colony is still small with little space and mate competition, there may not be pressure on natal juveniles to explore other sites.

Due to their reliance on terrestrial haul out sites for breeding and molting, northern elephant seals and other pinnipeds are particularly vulnerable to the effects of climate change; thus, we are likely to see many species' distributions and movements affected in the coming years (Harwood, 2001). A northward distributional shift has been reported in many fish and invertebrate species due to warmer water conditions as a result of climate change (Perry et al., 2005; Gregory et al., 2009). Increasing sea surface temperatures and more frequent terrestrial heat waves have contributed to declining northern elephant seal pup production in Mexico as pups have lower heat tolerance (García-Aguilar et al., 2018). Furthermore, sea-level rise projections for Point Reyes National Seashore reported that by 2050 much of the current breeding habitat could be inundated with water. This would likely push elephant seals into other areas of Point Reyes that are closer to human development or to different breeding colonies altogether (Funayama et al., 2013). These predictions are likely to be similar for all breeding colonies but would have the most impact on those colonies with limited haul out space. As the effect of climate change continues to impact the northern elephant seal population across their geographic range, juveniles and potentially adult seals will likely disperse northward to areas within a more suitable thermal range, such as the King Range. This study, combined with previous investigations on dispersal and colony use behavior, provides a baseline for future comparisons on how climate change may impact this species and provide managers with information to develop effective management plans (Le Boeuf et al., 1974; Zeno et al., 2021).

To further our understanding of northern elephant seal dispersal behavior and colony establishment, launching a much larger collaborative population-wide study on juvenile dispersal would provide a clear picture of the current level of exchange between colonies. To predict a colony's population growth, a state-space model (Clark 2007) could be used if juvenile female dispersal rates, number of breeding females, and female survival rates are known (Condit et al., 2014; Ferrari et al., 2013). Lastly, the King Range was established through the exploratory dispersal of juveniles and was not historically known to be a site for northern elephant seal breeding. Implementing species distribution models under differing climatic conditions for northern elephant seals from Mexico to Alaska could provide a future prediction of where prospecting juveniles might start new colonies (Jarvie & Svenning, 2018). Once those sites are known, the implementation of sea-level rise models could tell managers how successful those sites could be if colonized (Funayama et al., 2013).

Studying a northern elephant seal colony during its early growth presents challenges and benefits. The King Range is a small colony (producing less than 1,000 pups per year), so relative sample sizes are small compared to large breeding colonies. However, the benefit of working at a small site was that I was able to confidently document the presence and behavior of all known age individuals on the colony, which is difficult or nearly impossible to do at large established colonies. The King Range is remote with little human impact, which dictated weekly instead of daily surveys but offered uninterrupted access to the breeding colony during surveys. This study greatly benefited from close collaborations with researchers who shared observations of known individuals that visited both the King Range and other breeding colonies. These collaborations unlocked valuable insight into the exploratory dispersal behavior of juvenile northern elephant seals.

# SUMMARY

The King Range northern elephant seal breeding colony is an important new haul out site for both juvenile and breeding adult seals at the northern end of their breeding range. As more juveniles recruit to the King Range, we are likely to see this colony continue on its increasing population growth trajectory. Because the King Range is the only colony at the north end of the species range reliably producing pups, it has the potential to become a vital seed colony for continued growth north of California.

The behavior of northern elephant seals less than 1-year-old is challenging to understand. Yearlings have the highest mortality rate and are the least predictable of all age groups to return to their natal colony (Condit et al., 2014). The benefit of working at a small, isolated breeding colony is that I have been able to thoroughly track the haul out patterns of this challenging age group. Much of our understanding of northern elephant seals are about what they do at sea, their physiology, and the breeding behavior of adult individuals (Le Boeuf & Laws, 1994). This small and growing breeding colony can provide important insight into the role that the young juvenile age group plays in the establishment of new breeding colonies. They have held an important role in the recovery and range expansion of this species thus far and are likely to play an important role in the future as large colonies suffer from the impacts of warming temperatures, habit loss from sea-level rise, and competition with humans for coastal space.

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# APPENDICES

Appendix A 1. Observations of tagged northern elephant seals that visited the King Range and other colonies within their first two years of life. AN (Año Nuevo), FI (Farallon Islands), KR (King Range), PR (Point Reyes), and Race Rocks (Race Rocks Ecological Reserve, British Columbia).

| **Tag/Mark** | **Natal Colony** | **Birth Year** | **Sex** | **1st Fall** | **1st Winter** | **1st Spring** | **2nd Fall** | **2nd Winter** | **2nd Spring** |
|---|---|---|---|---|---|---|---|---|---|
| *GD149* | Año Nuevo | 2017 | F | - | - | AN | - | - | KR |
| *GD294_GE460* | Año Nuevo | 2018 | F | - | AN | KR | KR | - | - |
| *GD408* | Año Nuevo | 2018 | F | FI | - | FI | KR | - | - |
| *WN383* | Piedras Blancas | 2018 | F | - | - | AN | KR | - | - |
| *GE779_GG512* | Año Nuevo | 2019 | M | - | - | Race Rocks | KR | - | KR |
| *PV360* | Point Reyes | 2019 | F | KR | - | - | - | - | AN |
| *PV494* | Point Reyes | 2019 | Unknown | KR | PR | - | - | - | - |
| *GH170_GH171* | Año Nuevo | 2020 | M | KR | AN | - | | | |
| *PV347* | Point Reyes | 2020 | Unknown | KR | - | AN | | | |
| *PV562* | Point Reyes | 2020 | F | KR | - | AN | | | |

| **Tag/Mark** | **Natal Colony** | **Birth Year** | **Sex** | **1st Fall** | **1st Winter** | **1st Spring** | **2nd Fall** | **2nd Winter** | **2nd Spring** |
|---|---|---|---|---|---|---|---|---|---|
| *PV850* | Point Reyes | 2020 | F | KR | - | AN | | | |
| *PV959* | Point Reyes | 2020 | Unknown | KR | - | PR | | | |
| *PW 24* | Point Reyes | 2020 | Unknown | KR | PR | - | | | |
| *PW 79* | Point Reyes | 2020 | M | KR | - | AN | | | |
| *PV783* | Point Reyes | 2022 | F | KR | - | AN | | | |

Appendix A 2. Observations of marked northern elephant seals that visited the King Range and other colonies between Fall 2020 and Spring 2021. AN (Año Nuevo), KR (King Range), and PR (Point Reyes).

| **Tag/Mark** | **Natal Colony** | **Birth Year** | **Sex** | **Fall 2020** | **Spring 2021** |
|---|---|---|---|---|---|
| *KJ92* | Unknown | 2020 | M | KR | AN |
| *KJ136* | Unknown | 2020 | M | KR | AN |
| *KJ144* | Unknown | 2020 | F | KR | AN |
| *KJ148* | Unknown | 2020 | Unknown | KR | AN |
| *KJ163* | Unknown | 2020 | F | KR | AN |
| *KJ197* | Unknown | 2020 | F | KR | AN |
| *KJ202* | Unknown | 2020 | M | KR | AN |
| *KJ135* | Unknown | 2020 | M | KR | PR |
| *KJ183* | Unknown | 2020 | M | KR | PR |
| *KJ214* | Unknown | 2020 | F | KR | PR |
| *KJ13* | Unknown | 2019 or 2018 | Unknown | KR | AN |
| *KJ233* | Unknown | 2019 or 2018 | F | KR | AN |
| *KJ284* | Unknown | 2019 or 2018 | Unknown | KR | AN |