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Cassin's Auklet (*Ptychoramphus aleuticus*) Population Size, Reproduction, and Habitat Management on a Recently Colonized Island in California, USA

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Abstract.—Responses to climate change by seabirds in the North Pacific may include range restrictions and require colonizing new habitats. To inform conservation actions supporting climate adaptations, we examined the colonization of Año Nuevo Island, a nearshore island in central California, by Cassin's Auklets (*Ptychoramphus aleuticus*). We quantified population growth, reproduction, band returns, mortality, and habitat metrics from 1995-2017 and described habitat management that facilitated colony persistence. Cassin's Auklet breeding population grew to 136 birds by 2014, despite population declines during 2005-2007 and 2016-2017 concurrent with reproductive failures and die-offs that affected Cassin's Auklets regionally. Annual productivity of this small colony was similar to larger populations in the region at 0.72 ± 0.23 SD chicks fledged per pair from 1999-2017 ($n = 15$ years). Band returns indicated population connectivity with the Farallon Islands, California. Annual rates of burrow damage were $14 \pm 8\%$, with up to 30% damaged a year. Habitat management to prevent erosion damage to nesting burrows included sea lion exclusion, erosion control, and ceramic artificial burrows. Describing conditions that facilitated the colonization and growth of this Cassin's Auklet breeding site can inform actions that support other locations and multiple burrowing seabird species. *Received 10 January 2019, accepted 22 July 2019.*

Key words.—Año Nuevo Island, burrow erosion, California Current, climate change adaptation, habitat restoration, Rhinoceros Auklet, seabird, Western Gull

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Climate change adaptation is important for the survival of top marine predators, including seabirds (Sydeman *et al.* 2012; Hazen *et al.* 2013; Frederiksen and Haug 2015). While there is uncertainty in global and regional predictions of ocean warming impacts to seabirds, populations will be forced to adapt to significant ecosystem alterations (e.g., Grémillet and Boulinier 2009; Oro 2014; Bakun *et al.* 2015). In the North Pacific, seabirds may adapt to ocean warming and other changes by restricting their ranges northward and selecting nesting sites more favorable for successful reproduction as distributions of prey resources shift (Bakun *et al.* 2015; Sydeman *et al.* 2015). However, redistribution of seabird populations is constrained by specific requirements for breeding sites protected from terrestrial predators, located close enough to prey resources, and with appropriate nesting conditions (Nelson 1980), as well as behavioral traits such as high fidelity to nesting areas (Grémillet and Boulinier 2009). Although some studies have gained valuable insight into mechanisms of colony formation in seabirds (e.g., Kildaw *et al.* 2005; Munilla *et al.* 2016),

such study opportunities are infrequent due to high fidelity to natal colonies, limited unoccupied habitat free of mammalian predators, and general declines in many species. Conservation practitioners can support adaptation strategies by protecting, restoring, and managing suitable nesting habitat (Oro and Ruxton 2001). Success in such management requires understanding conditions necessary for species survival and population persistence.

Cassin's Auklet (*Ptychoramphus aleuticus*) is a north Pacific seabird predicted to be significantly negatively impacted by climate change in its southern range. Cassin's Auklets forage and breed from Alaska, USA to Baja California, Mexico with roughly half of the breeding population located in the California Current Ecosystem (CCE; i.e., southern British Columbia, Canada, to Baja California, Mexico; Ainley *et al.* 2011). Predicting climate change impacts in eastern boundary upwelling systems such as the CCE is complicated, with potential for both positive and negative impacts on seabirds (Hazen *et al.* 2013; Bakun *et al.* 2015; Garcia-Reyes *et al.* 2015). However, for planktivorous Cassin's

Auklets, models and observed trends suggest that climate change impacts will be negative due to decreased abundance and re-distribution of preferred zooplankton prey (Lee *et al.* 2007; Wolf *et al.* 2009, 2010). Additionally, increased competition for prey by recovering baleen whale populations may negatively affect Cassin's Auklets concurrently with climate change impacts (Ainley and Hyrenbach 2010). Though the Cassin's Auklet world population is roughly estimated at 3.5 million individuals (Ainley *et al.* 2011), long-term declines have been documented at major breeding colonies and at sea (Lee *et al.* 2007; Ainley and Hyrenbach 2010; Rodway and Lemon 2011), leading to a recent uplisting to "Near Threatened" by the IUCN (Birdlife International 2018). At the Farallon Islands, California, in the central CCE, Cassin's Auklets are predicted to experience declines due to prey changes that would lead to extirpation from this major breeding colony by the end of the century (Wolf *et al.* 2010). Despite model uncertainties, range restrictions in the CCE portion of the Cassin's Auklet population are likely (Wolf

et al. 2009, 2010). We had the opportunity to study a new colonization event by Cassin's Auklets at Año Nuevo Island (ANI), an island located 1 km offshore of the mainland in central California in the central CCE (Fig. 1). Insight from describing the patterns and conditions of site selection and persistence can inform our facilitation of seabird movements to new locations.

ANI is located 90 km south of the Farallon Islands (Fig. 1), which is the largest breeding colony of Cassin's Auklets in California (i.e., > 100,000 breeders in the 1970s; Manuwal 1972). California hosts approximately 3.7% of the world breeding population of Cassin's Auklets, with the majority (76%) of the world population occurring in British Columbia, Canada (Ainley *et al.* 2011). While ANI is not numerically significant to the global Cassin's Auklet population, it is one of the few long-term research sites in the CCE (the others being: Triangle Island, British Columbia, Canada; the Farallon Islands, California, USA; and San Benito Island, Mexico). In recognition of the value of such long-term studies, Cassin's Auklet

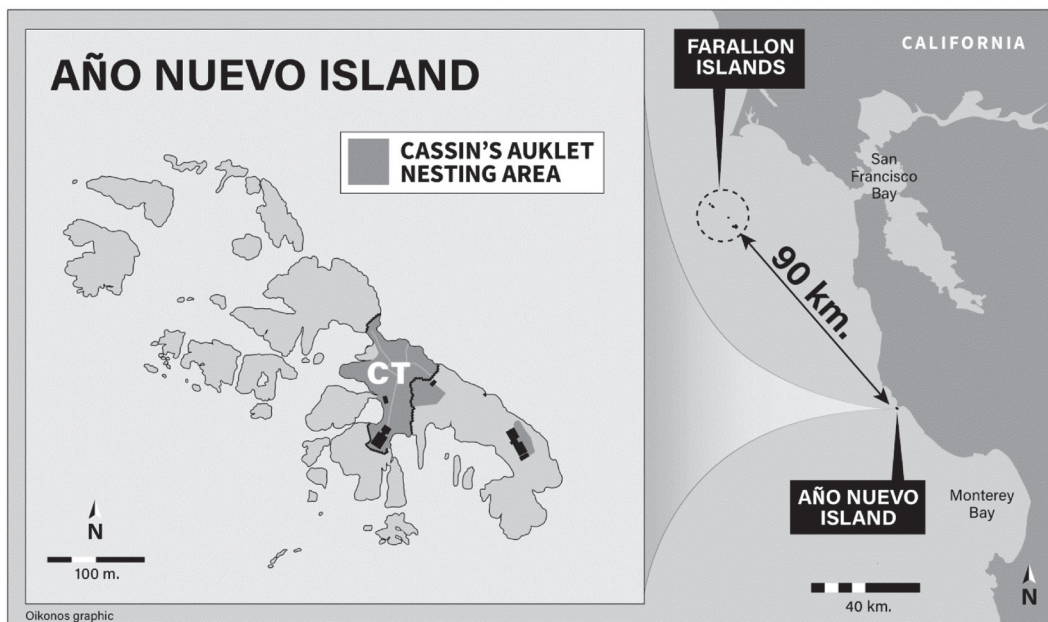


Figure 1. Locations of Año Nuevo Island and the Farallon Islands off the western coast of California, USA (right) and location of Cassin's Auklet (*Ptychoramphus aleuticus*) breeding colony on Año Nuevo Island (left). The central terrace is labelled "CT." The "south terrace" is located to the right (southwest) of the central terrace. Historic lighthouse station structures are shown in black. The sea lion exclusion structure is outlined in black on the edges of the central terrace.

breeding metrics were selected as one of only a few climate metrics by the state of California (Office of Environmental Health Hazard Assessment 2018).

Cassin's Auklets are adapted to nest on islands free of mammalian predators (Ainley *et al.* 2011). Following the removal of non-native mammalian predators, Cassin's Auklets re-colonized breeding sites from which they were extirpated on Langara Island, British Columbia, Canada, Anacapa Island, California, USA, and multiple islands in Baja California, Mexico (Regehr *et al.* 2007; Whitworth *et al.* 2015; Bedolla-Guzmán *et al.* 2019). There are no published examples of colonization of new sites not previously occupied by Cassin's Auklets. A recent colonization event on ANI, where there were no historical records of Cassin's Auklets nesting, provided an opportunity to document population growth and inform potential management strategies for multiple species and other locations.

At ANI, we began conducting seabird monitoring in 1993 and were present to document the Cassin's Auklet colonization event in 1995. Since 1995, we monitored various Cassin's Auklet metrics on ANI, with the objective of understanding the ecology and management needs of this newly established population. We quantified Cassin's Auklet breeding population, reproductive success, mortality, immigration and recruitment, and habitat quality metrics annually using standardized protocols. Adding further range-wide relevance to this local study, we actively managed the island with innovative techniques to specifically support burrow-nesting auklets. We designed and employed techniques to stabilize soil burrows and promote nesting that included seabird-safe erosion control, sea lion exclusion structures, native plant restoration, and durable artificial burrows. This combination of restoration techniques used at ANI is unique and addresses seabird habitat issues that have seldom been addressed elsewhere, such as slowing erosion of burrowing habitat and preventing crushing of burrows by marine mammals and other wildlife. Here, we focus on the Cassin's Auklet on ANI as a case study of successful colonization and retention

of a new breeding site by a seabird that is generally declining and regionally threatened by climate change.

METHODS

Study Area

Año Nuevo Island (ANI; 37° 06' 30" N, 122° 20' 09" W) is approximately 9 acres in size (Bischoff 2009) and is composed of a relatively flat terrace standing approximately 5-10 m above sea level, with steep bluffs on its edges. This terrace contains a relatively deep (approximately 1.5 m) soil profile suitable for burrow-nesting auklets, whereas smaller islets surrounding the main island are composed of bedrock. The majority of Cassin's Auklets on ANI nest in the "central terrace" portion of the island (Fig. 1). Currently, seven species of seabirds nest on ANI (Beck *et al.* 2017). Those most likely to interact with Cassin's Auklets or overlap in breeding habitat are burrow-nesting Rhinoceros Auklets (*Cerorhinca monocerata*) and Pigeon Guillemots (*Cepphus columba*), and surface-nesting Western Gulls (*Larus occidentalis*) and Brandt's Cormorants (*Phalacrocorax penicillatus*). In addition, Brown Pelicans (*Pelecanus occidentalis*) seasonally roost on the island in numbers that can exceed 1,000 at a time (Carle *et al.* 2016). Up to > 9,000 California sea lions (*Zalophus californianus*) also haul out seasonally on ANI (Lowry *et al.* 2017), overlapping with areas where Cassin's Auklets nest.

ANI was a peninsula until at least 1603, and had become an island by 1798 (Weber 1981). A lighthouse station with multiple buildings operated on ANI from 1872 to 1948 (LeBoeuf 1981). In 1949, brush rabbits (*Sylvilagus bachmani*) were introduced (Zoloth 1969) and caused plant community alterations. Rabbits may have excluded prospecting burrow-nesting seabirds via competition, although there are no records of either auklet species existing on the island prior to 1982. The rabbit population was extirpated from the island by the early 1980s (Steve Davenport, UC Santa Cruz, pers. commun.). In 1967, the island was included in Año Nuevo State Reserve, protected as a wildlife sanctuary, and closed to public visitation (LeBoeuf 1981). In the 1990s, with the establishment of nesting Rhinoceros Auklets on ANI, boardwalks were constructed to prevent trampling by researchers (Thayer *et al.* 2000).

By the mid-2000s, ANI had become denuded of plants due to drought conditions and trampling by increasing numbers of California sea lions and Brown Pelicans. These combined disturbances resulted in high rates of erosion damage to Rhinoceros Auklet burrows (Carle *et al.* 2016) as well as direct crushing of burrows by sea lions, and a general loss of topsoil burrowing habitat. To reduce burrow damage and erosion, in 2010 we began to pro-actively manage Rhinoceros and Cassin's auklet habitat using multiple techniques including sea lion exclusion, native plant restoration, deployment of erosion control fabric, and installation of ceramic artificial burrows (Fig. 2). In fall 2010, we constructed two 2.1 m tall



Figure 2. Cassin's Auklet (*Ptychoramphus aleuticus*) chick at Año Nuevo Island, California, USA, and multiple habitat management methods: ceramic artificial burrow designed specifically for Cassin's Auklets, restored native vegetation, and the custom sea lion exclusion fence in the background.

exclusion fences out of eucalyptus logs to prevent California sea lions from entering the central terrace auklet colony (Fig. 2). Simultaneously in 2010, we planted native grasses to help stabilize soil in nesting areas (Fig. 2) and covered the central terrace in tight-woven coconut fiber erosion control fabric. We installed erosion control fabric every 3-5 years from 2010-2017. To encourage burrowing, we cut holes in the fabric at existing burrow entrances and cut additional holes throughout the material for prospecting auklets. Ceramic artificial burrows, safe from erosion and crushing, were installed in multiple phases beginning in 2010 (Fig. 2).

Nest Sites

Breeding Cassin's Auklets on ANI dug natural burrows in soil that were often associated with historic lighthouse station infrastructure (i.e., wood and concrete waste). The majority of natural burrows were located in the central terrace, with smaller numbers on the southwest side of the island (Fig. 1). To facilitate handling the birds with minimal disturbance, researchers installed artificial burrows in multiple phases: 1) wood boxes with plastic tunnels existed from 1999-2010 (7 sites 1999-2001, 26-28 sites 2002-2010), 2) ceramic artificial burrows designed for larger Rhinoceros Auklets but suitable for Cassin's Auklets (95 sites 2011-2017; Hester *et al.* 2013), and 3) ceramic artificial burrows designed specifically for Cassin's Auklets (Fig. 2; 8 sites 2015-2017). To protect birds from heat, the artificial sites were either buried underground or designed with a thick clay heat shield to cover the nest chamber (Fig. 2).

Breeding Population Size

Burrow counts. We defined a potential nesting site as "viable" if the entrance was accessible and the tunnel was ≥ 30 cm long for three consecutive weeks during the peak incubation period. In a given season, we considered peak incubation as the period between the median lay and hatch dates (see Reproduction section below). In the central terrace core burrowing area (Fig. 1), we censused burrows weekly to determine viability. During 1995-2010, we applied an extrapolated estimate to account for one dangerous cliff area that was not monitored weekly (CT-Cliff; see *Total breeding abundance* sub-section below). During 2006 and 2007, we took only opportunistic notes on Cassin's Auklets and did not estimate the breeding population. When Cassin's Auklets started increasing substantially we allocated more resources to the species and installed ropes to allow safe monitoring of this cliff area from 2011-2017. On the south terrace, which contained $< 10\%$ of burrows annually (Fig. 1), we counted burrows before (March-April) and after (September-November) peak breeding season to limit disturbance to sea lions and nesting cormorants. We averaged these pre- and post-breeding counts to estimate the total annual number of viable burrows on the south terrace.

Burrow occupancy rates. To determine burrow contents and breeding attendance, we used miniature cameras with infra-red illumination and considered a viable site "occupied" if an adult was observed in a burrow for two consecutive weeks during peak incubation. We calculated an annual natural burrow occupancy factor (%)

of viable burrows occupied by breeding pairs) derived from the weekly monitored nests ($n = 20\text{--}59$ burrows monitored annually). While the majority of burrows had known contents from weekly camera monitoring, some were too fragile, dangerous to check, or inaccessible during the breeding season. Therefore, we applied the annual occupancy rate to estimate the number of breeding pairs in unmonitored burrows. Annually, the sample of unmonitored sites was 1–3 burrows in the central terrace and in 3–11 burrows on the south terrace.

Artificial burrows. From approximately March to July, we checked the contents of artificial burrows (wood or ceramic) weekly by lifting a lid or removing a tunnel to see inside the nest chamber. If an egg or chick was observed the site was considered “occupied.”

Total breeding abundance. To estimate the annual breeding abundance of Cassin’s Auklets on ANI, we combined the following:

- 1) The number of breeding pairs in occupied natural and artificial burrows in the central terrace from weekly monitoring, and
- 2) The number of breeding pairs in occupied natural sites in the south terrace estimated from two annual surveys.

To obtain total number of individuals, we multiplied number of breeding pairs by two. To estimate population for early years in which the dangerous CT-Cliff area was not checked weekly, we extrapolated based on nest distributions. The average annual proportion of total island breeding pairs in the CT-Cliff area (derived from 2011–2017 when this area was monitored weekly) was $41 \pm 0.07\%$ SD (range of 12–29 total breeding pairs). Therefore, for years in which the CT-cliff was not censused (1995–2010) we extrapolated total island population by adding 41% to the occupied burrow count.

Reproduction

To determine reproductive success of Cassin’s Auklet pairs, we monitored nest sites every 7 days during the breeding season (March to July) from 1999–2017. We monitored natural burrows with a miniature camera with infra-red illumination, and artificial nest burrows by visual inspection. In artificial burrows we handled adults once during incubation to apply or re-sight metal bands, after which we stopped checks until hatching was expected. For reproductive success, we calculated productivity, defined as the number of chicks raised to fledging per breeding pair. We considered a chick fledged if it survived to ≥ 35 days of age in natural burrows or ≥ 35 days of age and ≥ 135 grams in artificial burrows (based on values from Ainley *et al.* 1990). In natural burrows, if we could not determine age precisely due to skipping a weekly check, fledging was defined as a mostly- or fully-feathered chick. Cassin’s Auklets will sometimes initiate a second-brood after successfully rearing a first chick (hereafter referred to as “double-brooding”) or lay new clutches after a failed first clutch (hereafter referred to as “re-lays”; Ainley *et al.* 1990); thus, maximum possible annual productivity was 2.0

chicks per pair. We considered breeding attempts a re-lay if a second egg appeared alongside an un-hatched first egg, an adult was seen two weeks in a row (indicating incubation behavior) after being absent for two or more weeks, or a newly hatched chick was seen late in the season after an incubation period > 3 weeks longer than expected. We defined double-broods as instances when an adult was seen two weeks in a row in the burrow after a chick had reached fledging stage and departed. We summarized annual productivity for first clutches only, double-broods only (excluding re-lays), and all clutches together (first clutches, double-broods, and re-lays).

From 1999–2012, the population was small enough that it was possible to follow every pairs’ reproductive success (with the exception of the dangerous CT-Cliff area that was not monitored by camera 1999–2010, and south terrace areas that were not monitored by camera in any year). Beginning in 2016, due to the increased population size of Cassin’s Auklets, we switched to weekly monitoring of reproductive success in a sub-sample of 35–40 natural burrows. We randomly chose nests in the reproductive sub-sample from occupied burrows in mid-June (after which we did not expect new pairs to initiate breeding), excluding sites that were too fragile or dangerous to check safely. We chose a sub-sample of 35–40 nests because this was a reasonable amount for one person to check with a burrow-camera in a single day.

Immigration and Recruitment

To document immigration, recruitment, and information about known-age Cassin’s Auklets we used four methods: 1) banding chicks from artificial burrows (chicks were not accessible in burrows), 2) re-sighting and banding adults in artificial burrows, 3) re-sighting and banding adults in standardized mist netting sessions, and 4) re-sighting banded birds found dead in the colony. We used mist nets from 1993–2017 to capture Rhinoceros Auklets for a separate study and opportunistically banded Cassin’s Auklets when they were captured. Standardized net positions were intended to optimize Rhinoceros Auklet capture, and were located in low density Cassin’s Auklet breeding areas. We conducted capture events four times a year in June and July for 3-hr intervals from 21:00–00:00 (Carle *et al.* 2015). Netting occurred every one to two weeks, and nights with full moons were avoided. We banded all captured Cassin’s Auklets with aluminum United States Fish and Wildlife Service bands and recorded all band numbers of previously banded birds.

Habitat Quality

Burrow damage. We quantified the incidence and severity of direct damage to Cassin’s Auklet nesting burrows by soil erosion annually. We recorded erosion type (i.e., damaged by erosion only, damaged by animal trampling, or damaged by human trampling) and severity codes (i.e., minor damage to entrance, major damage to entrance/minor damage to tunnel, or major damage to tunnel/any damage to nest cavity) on a

weekly basis for a sample of 20-46 burrows in the central terrace area from 1 April to 1 September each year, 2011-2017. We considered burrows to be "damaged" if they sustained major damage to the entrance or any damage to the tunnel or nest chamber, and we calculated the annual percent of occupied burrows damaged, excluding those damaged only by human activity (e.g., researchers or other visitors to the island).

Proximity to Western Gull nests. Western Gulls are the main predator of Cassin's Auklets at the Farallon Islands in central California (Ainley *et al.* 1990). Western Gulls actively prey on Cassin's Auklets and will also kill auklets out of territorial defense (e.g., we found many Rhinoceros and Cassin's Auklet fledglings killed by being pecked in the head near gull territories, but these birds were not eaten). We assumed that greater gull densities on nesting colonies result in greater relative risk of mortality for Cassin's Auklets. As a metric of predation risk, we annually recorded the number of Western Gull nests within a 1-m radius of each Cassin's Auklet natural burrow entrance in the central terrace area during peak gull incubation (end of May to beginning of June). Although gulls may depredate Cassin's Auklets throughout the breeding colony, we chose this 1-m radius from burrow entrances metric based on observational evidence from night-time trail cameras on ANI that Western Gulls nesting in close proximity to Cassin's Auklet burrows were frequently interacting with Cassin's Auklets around burrow entrances.

Mortality

Annually from March-September 1995-2017, we checked the accessible central terrace part of the island, including coves and beaches, for dead birds. We examined all dead Cassin's Auklets for bands, age (after hatch year or chick), and potential causes of death. Apparent causes of death were coded as bird of prey predation (i.e., wings and stripped keel only), gull predation (i.e., pecked in the head or regurgitated carcass), interaction with human infrastructure (e.g., a bird that entered a human structure and died when it could not get out), or unknown. For this mortality survey, we excluded chicks that died inside their nests because their mortality was assumed to be unrelated to interspecific interactions. We removed all dead auklet carcasses from the island to avoid double-counting.

Data Analysis

To describe the trend in Cassin's Auklet breeding population size we used a Generalized Linear Model with a Poisson distribution (to account for non-normal distribution of the data) and a log link function, with year as the independent variable and Cassin's Auklet population as the response variable. Years with no standardized census (2006 and 2007) were excluded from this analysis.

We used linear regressions to test trends over time in burrow damage, number of dead Cassin's Auklets found per year (2005-2017), and proportion of Cassin's Auklet burrows within 1 m of Western Gull nests, with year as the independent variable and each metric as the

response variable. With the exception of the number of dead Cassin's Auklets found per year, these datasets met test assumptions of normal distribution (tested using Shapiro-Wilk Goodness of Fit tests for the normal distribution), homoscedasticity (tested by visually examining normal quantile plots of the data), and lack of autocorrelation (tested using Ljung-Box Q tests). The number of dead Cassin's Auklet found per year metric was not normally distributed, so we log-transformed the data, after which it met test assumptions. We tested the impact of proximity to Western Gull nests on Cassin's Auklet reproductive success during 2011-2017 using a likelihood ratio chi-squared test with presence of a Western Gull nest within 1 m as the independent variable and whether the Cassin's Auklet pair fledged at least one chick (including re-lays and double-broods) as the response variable. We included all Cassin's Auklet breeding attempts with associated Western Gull proximity data and excluded nesting attempts in which chick fledging status was unknown for one or both clutches. We used the software JMP (version 14; SAS Institute, Cary, North Carolina, USA) to conduct all statistical tests. We present results as mean $\pm$ standard deviation (SD) unless otherwise specified. We considered statistical analyses significant at $\alpha = 0.05$.

RESULTS

Breeding Population Size

Cassin's Auklets were first recorded breeding on ANI in 1995 (2 pairs; Fig. 3). Cassin's Auklet population grew slowly from a population of 6 birds in 1995 to 58 in 2004 (Fig. 3). Cassin's Auklets were not detected breeding in 2005 and were detected breeding in very small numbers in 2006 and 2007 (at least 2 birds in 2006, at least 4 in 2007; Fig. 3). Breeding in greater numbers resumed in 2008 (14 birds), followed by growth to 136 birds in 2014, a decrease to 88 and 96 birds in 2015 and 2016 respectively, and another increase to 126 birds in 2017 (Fig. 3). There was a significant increasing trend in population between 1995 and 2017 ($P < 0.0001$; $\beta = 0.119 \pm 0.005$ SE; likelihood-ratio $\chi^2_1 = 602.9.2$, $n = 21$ years; Fig. 3). Occupancy rates of natural burrows ranged from 65-95% ($\bar{x} = 85 \pm 12\%$) during 2011-2017.

Reproduction

Cassin's Auklets bred in wooden artificial burrows at ANI from 1999-2006 (0-6 pairs a year, mean = 2.3 ± 1.8 pairs) and

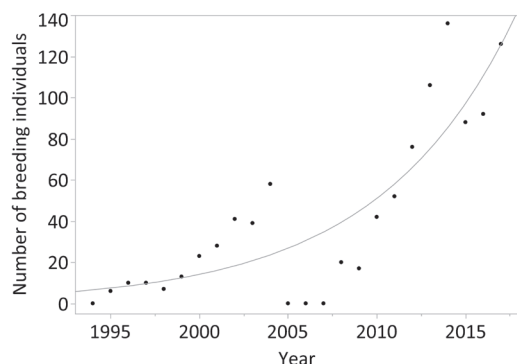


Figure 3. Population of individual breeding Cassin's Auklets (*Ptychoramphus aleuticus*) at Año Nuevo Island, California, USA, from 1994-2017. Cassin's Auklets were not documented nesting on ANI prior to 1995. Population estimates from 1995-2010 are based in-part on extrapolation, whereas all habitat was checked in 2011-2017. Population was not estimated for 2006 and 2007. Trend line shows the result of a Generalized Linear Model with a Poisson distribution and a log link function, with year as the independent variable and population as the dependent variable ($P < 0.0001$; $\beta = 0.119 \pm 0.005$ SE; likelihood-ratio $\chi^2_1 = 602.9.2$, $n = 21$ years).

in clay artificial burrows from 2013-2017 (2-7 pairs, mean = 3.5 ± 2.4 pairs). Average productivity in all breeding sites from 1999-2017 (excluding 2005-2007 and 2009, for which there were insufficient data) was 0.72 ± 0.23 chicks fledged per pair ($n = 15$ years, 4-44 nests per year; Fig. 4). Annual productivity ranged from highs of 1.00 chick fledged per pair (± 0.00 in 1999 and ± 0.63 in 2010) to a low of 0.21 ± 0.43 chicks per pair in 2004 (Fig. 4). In some years with high productivity, birds had second broods after the first chick had fledged. Double-brooding occurred in 2002, 2010-2014, 2016, and 2017 (8 of 15 years with data; Fig. 4). Second-brood productivity was 0.55 ± 0.26 chicks per pair ($n = 8$ years, 1-7 nests per year; excludes re-lays after failed first attempts) compared to 0.70 ± 0.21 for first-broods in the same years ($n = 8$ years, 6-42 nests per year). Average productivity for all sites combined in years with double-broods was 0.83 ± 0.10 chicks per pair, indicating double-broods and re-lays after failed attempts contributed 0.13 chicks fledged per pair to annual productivity.

Immigration and Recruitment

From 1999-2017, we banded 27 chicks and 65 breeding adults at artificial burrows. In addition, we banded 39 after-hatch-year individuals of unknown breeding status at mist nets. Two birds banded as chicks in 2001 were re-sighted as breeders in artificial burrows: one in 2006 and one in 2016. One bird banded as a chick in 2015 was caught in mist nets in 2017. We were unable to confirm whether this bird was breeding. All other re-sighted birds at artificial burrows and mist nets were banded as after-hatch-years on ANI, except for two birds banded as chicks on the Farallon Islands. One of these birds was banded on the Farallon Islands in 2010 and bred in an artificial burrow on ANI in 2014. Another was banded on the Farallon Islands in 2009, bred in an artificial burrow on ANI in 2016, and was caught in mist nets on ANI in 2017. In 2016, this known-age bird from the Farallon Islands (age 7 years) mated on ANI with a known-age bird from ANI (age 15 years).

Habitat Quality

From 2011-2017, on average $86 \pm 4\%$ of Cassin's Auklet nests were located in the central terrace area of the island (range = 81-91%; Fig. 1). Throughout ANI, the majority of nests were located in and around historic infrastructure such as the crumbling edge of a concrete cistern, the wood planks of an abandoned tramway, and under the edges of building foundations. The percent of occupied Cassin's Auklet burrows with burrow damage from erosion ranged annually from 6-30%, averaging $14 \pm 8\%$ from 2011-2017 ($n = 7$ years; Table 1). There was no significant trend in damage of occupied burrows over time ($P = 0.24$, $F_{1,5} = 1.70$, $R^2 = 0.25$). The percent of occupied Cassin's Auklet natural burrows that had at least one Western Gull nest within 1 m of the entrance averaged $22 \pm 9\%$ from 2011-2017 (range 10-36%; Table 1). There was no significant trend in this metric over time ($P = 0.12$, $F_{1,5} = 3.53$, $R^2 = 0.41$). Having a Western Gull nest within 1 m of a Cassin's Auklet entrance did not significantly impact the number of chicks fledged

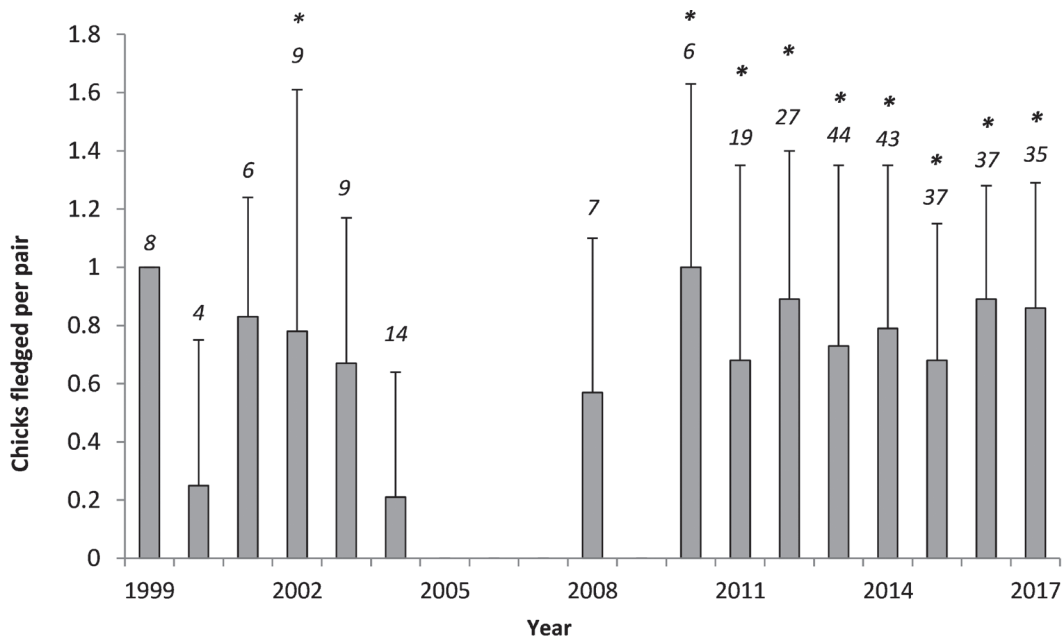


Figure 4. Annual productivity (chicks fledged per breeding pair, all clutches $\pm$ SD) of Cassin's Auklets (*Ptychoramphus aleuticus*) at Año Nuevo Island, California, USA, 1999-2017. Asterisks above bars indicate years when at least one double-brood (second clutch laid after a successful first chick was fledged) was recorded. Number of pairs followed each year is shown above bars. No breeding was recorded in 2005 and there were insufficient data to determine productivity in 2006 and 2007 ($n \leq 1$ occupied nest) and 2009 (breeding was documented but nests were not checked for reproductive success).

per pair by Cassin's Auklets ($P = 0.55$, $\chi^2_1 = 0.36$, $n = 185$ breeding attempts).

Mortality

From 1993-2017, we recovered a total of 42 dead Cassin's Auklets outside of burrows on ANI. No adult Cassin's Auklets were found dead inside burrows. Of the 42 dead birds found, 50% were after-hatch-year, 29% were hatch-year (chicks), and 21% were un-

known age. Three dead after-hatch-year Cassin's Auklets were found in March 1993, two years before nesting was first documented in 1995. Of the recorded mortalities, 28% were attributed to predation by Western Gulls, 12% to birds of prey, 5% to interactions with human infrastructure, and 55% to unknown causes. Deaths associated with human infrastructure were two after-hatch-year birds that died after becoming trapped in a historic lighthouse station building when a

Table 1. Percent of occupied Cassin's Auklet (*Ptychoramphus aleuticus*) burrows annually damaged by erosion and/or animal trampling, % of burrows < 1 m from Western Gull (*Larus occidentalis*) nests, and total number of active Cassin's Auklet natural burrows on Año Nuevo Island, California, USA, 2011-2017. Sample size (n burrows followed) is shown in parentheses.

Year	% burrows damaged (n)	% burrows < 1 m from Western Gull nests (n)	Total number active Cassin's Auklet burrows
2011	30 (20)	10 (10)	26
2012	6 (33)	17 (18)	38
2013	19 (42)	21 (34)	51
2014	9 (33)	18 (28)	60
2015	15 (33)	33 (33)	40
2016	10 (39)	36 (39)	44
2017	11 (46)	19 (47)	60

section of roof blew off and was temporarily missing during 2011. Of the 12 deaths of Cassin's Auklet chicks, 58% (7 birds) were attributed to attack by Western Gulls and 42% to unknown causes. The number of dead after-hatch-year Cassin's Auklets made up on average $1.5 \pm 2\%$ of the annual estimated breeding population of Cassin's Auklets during 2011-2017 (range 0-5% per year). There was no significant trend in the number of dead Cassin's Auklets found per year ($P = 0.71$, $F_{1,15} = 0.14$, $R^2 = 0.009$).

DISCUSSION

The colonization of ANI by Cassin's Auklets in 1995 and the persistence of the population over the subsequent 22 years demonstrates that Cassin's Auklets will naturally create new breeding colonies given appropriate conditions. At ANI, a potential prerequisite for colonization by burrowing auklets was removing competition for burrows from introduced rabbits. Promptly after the extirpation of rabbits, Rhinoceros Auklets bred for the first time in 1982 (Thayer *et al.* 2000) and Cassin's Auklets in 1995. Other important factors for colonization were that no predatory mammals were present on the island and there was a suitable soil profile for burrowing. Additionally, hetero-specific social attraction has been shown to attract certain animals (Putman and Blumstein 2019), and the presence of nesting Rhinoceros Auklets may have played a role in attracting nesting Cassin's Auklets to ANI. Similarly, Cassin's Auklets have been attracted to multiple islands from which they were extirpated in Baja California using a combination of eradication of introduced mammals and social attraction (Bedolla-Guzmán *et al.* 2019). Persistence of the colony at ANI is likely also related to factors we did not measure, including oceanographic conditions and prey availability in the region. However, protection of the habitat from human visitation and exclusion of sea lions from the main auklet breeding area reduced acute and chronic disturbances and supported colony persistence. The successful colonization by Cassin's Auklets of ANI and other

islands from which the species had previously been extirpated (Regehr *et al.* 2007; Whitworth *et al.* 2015; Bedolla-Guzmán *et al.* 2019) suggests that habitat management of potentially suitable islands throughout the Cassin's Auklets' range may be a viable conservation strategy for increasing adaptation opportunities for the species.

ANI's current Cassin's Auklet breeding population is in the low hundreds of individuals, and is dwarfed by colonies such as the Scott Islands, British Columbia (estimated 2 million birds in the 1980s; Rodway 1992), Triangle Island (estimated 1.1 million birds; Rodway 1991), the Farallon Islands (estimated 38,274 in 1991; Carter *et al.* 1992), and San Jerónimo Island, Mexico (estimated 50,000-100,000 birds; Bedolla-Guzmán *et al.* 2019). However, many Cassin's Auklets breeding colonies throughout the species' range are of similar population size to ANI (i.e., in the hundreds of individuals; Vermeer and Lemon 1986; Carter *et al.* 1992). In the southern part of the Cassin's Auklet breeding range, from central California to Baja California, Mexico (Carter *et al.* 1992), ANI is one of six breeding islands with an estimated 100-1,000 individuals (as of the most recent published surveys; Carter *et al.* 1992; Bedolla-Guzmán *et al.* 2019). ANI could support a much larger nesting population of Cassin's Auklets than currently exists. The primary Cassin's Auklet nesting area on ANI in the central terrace (approximately 4,789 m² in area), had a peak density of 0.025 nesting pairs per m² in 2014. At the maximum reported burrow density for Cassin's Auklets of 1.1 pairs per m² (Manuwal 1972; Vermeer *et al.* 1979), the ANI central terrace alone could host > 5,000 pairs of Cassin's Auklets. Most of the central terrace area of ANI appears to be suitable habitat; thus there is available space for population growth at ANI, including in ceramic artificial burrows (e.g., in 2017, there were > 50 unoccupied ceramic artificial burrows on ANI, though occupancy varies by year).

After the colonization of ANI in 1995, Cassin's Auklet population grew slowly for 10 years. The population grew much more

rapidly from 2010-2014, peaking at 136 birds in 2014. Inter-annual variability in breeding effort became measurable when the population became large enough to discern patterns in the early 2000s. Years with low attendance of breeding birds at ANI in 2005 and 2015 coincided with unusual Cassin's Auklet mortality events in the region. Cassin's Auklet pairs did not attempt to breed on ANI in 2005, concurrent with breeding failures at other monitored Cassin's Auklet colonies at Triangle Island, the Farallon Islands, and San Benito Island (Sydeman *et al.* 2006; Wolf *et al.* 2009). Furthermore, an unusual mortality event of Cassin's Auklets occurred in 2005 in Monterey Bay, California, just south of ANI (Parrish *et al.* 2007). The observed regional impacts on Cassin's Auklets in 2005 were attributed in part to poor upwelling conditions and anomalously warm sea surface temperatures (Sydeman *et al.* 2006). These conditions apparently affected the Cassin's Auklet population at ANI, which did not begin to recover until 2008. During October 2014-March 2015, there was a large-scale mortality event of primarily hatch-year Cassin's Auklets throughout the west coast of North America, likely caused by starvation related to lowered prey availability or quality concurrent with unusually warm water conditions starting around July 2014 (Jones *et al.* 2018). This mortality event occurred after an above average reproductive year in 2014 for Cassin's Auklets throughout their range (Jones *et al.* 2018), including ANI. The decrease in breeding effort in 2015 at ANI was likely related to this mortality event, as the breeding population also declined by 15% (based on burrow occupancy as a proxy for population) at the much larger colony at Triangle Island, during 2015 (Jones *et al.* 2018).

Long-term reproductive success at ANI (0.72 ± 0.23 chicks fledged per pair) was relatively similar to values reported for other colonies across the range of Cassin's Auklets from British Columbia to Baja California, Mexico (ranging from 0.5-0.8 chicks fledged in most years; Ackerman *et al.* 2004; Wolf *et al.* 2010). The long-term reproductive mean at ANI was likewise similar to the 35-year mean at the Farallon Islands from 1970-2005

(0.70; Warzybok *et al.* 2006) suggesting that on a broad scale, environmental conditions at ANI may have been similar to those at the Farallon Islands. Double-brooding by Cassin's Auklets is a metric linked at least partially to environmental conditions favorable to Cassin's Auklet breeding (e.g., strong upwelling; Johns *et al.* 2017). Birds nesting at ANI produced double-broods in many, but not all, of the same years as birds at the Farallon Islands (e.g., double-broods occurred at both colonies during 2002, 2010-2014; Johns *et al.* 2017). Given the oceanographic differences between the Farallon Islands and ANI, there may be differences in inter-annual prey availability, as has been shown for chick-rearing Rhinoceros Auklets at the two colonies (Thayer and Sydeman 2007). The presence of two breeding colonies in central California (ANI and the Farallon Islands) with long-term data and standardized monitoring methods is valuable, warranting further analyses to learn the drivers of breeding variability among colonies in close proximity.

It seems likely that birds from the nearby, large breeding colony Farallon Islands breeding population initially colonized ANI, based on the two banded birds we recorded on ANI that hatched on the Farallon Islands. However, the region around ANI was an important non-breeding area for Cassin's Auklets that nest in British Columbia (Studholme *et al.* 2019), suggesting another potential source of recruitment. Also, as expected for this species with high natal philopatry (Pyle 2001), we documented recruitment into the ANI breeding population of two banded birds hatched on ANI. The current level of meta-population connectivity between ANI, the Farallon Islands, and other breeding populations remains unknown. A study of Cassin's Auklet genetics across their range indicated that two genetic populations exist, with a northern group found north of Point Conception, California, and a southern group breeding in the Channel Islands, California, USA and Baja California, Mexico (Wallace *et al.* 2014). ANI was not included in the study but is likely composed of birds from the northern genetic

population, based on the Point Conception geographical barrier and evidence of immigration from the Farallon Islands. ANI is the closest breeding colony to the north of Point Conception, suggesting it could represent a meta-population link currently or in the future between northern and southern genetic groups. Some flow of northern group genes was detected in the southern population by Wallace *et al.* (2014), though southern genes did not appear to flow north. Further genetic work on the Cassin's Auklets at ANI could shed light on sources of immigration to the colony and its relative importance as a link between different genetic groups (e.g., Munilla *et al.* 2016).

ANI has been managed since the 1990s to stabilize habitat for burrowing seabirds (Thayer *et al.* 2000) and prevent trampling of nests by high densities of California sea lions, Brown Pelicans, and Brandt's Cormorants, though the most active management occurred from 2010 on (Hester *et al.* 2013). Habitat management focused on Rhinoceros Auklets has benefitted Cassin's Auklets, given overlap of the two species' nesting areas on ANI and similar nesting requirements. In 2010, a sea lion exclusion fence was constructed around the central terrace seabird breeding area (approximately 0.47 hectares; Hester *et al.* 2013) that protected > 80% of Cassin's Auklet burrows on the island from being crushed by sea lions. However, trampling by Brown Pelicans and Brandt's Cormorants still occurred seasonally inside the sea lion exclusion area, especially when numbers of roosting pelicans peaked in late summer and fall, often overlapping with periods when Cassin's Auklets were present in burrows (Carle *et al.* 2016). During this study, up to 30% of occupied Cassin's Auklet burrows at ANI were severely damaged annually. The impacts of burrow damage vary, but in some cases have caused breeding failure due to parental abandonment or exposure of the chick or egg to predators. High winds and winter storms also cause erosion resulting in habitat loss. Re-vegetation efforts aimed at stabilizing soil and giving protective cover may have been a factor in Cassin's Auklets expansion into new areas of

the island's central terrace from 2011-2014. During that period, burrows were sometimes located in the cover of native vegetation planted during the habitat restoration, such as American dune grass (*Elymus mollis*). Plant cover declined during 2013 and 2014 due to damage from roosting pelicans and multi-year drought (Carle *et al.* 2016), and subsequently fewer Cassin's Auklets nested in flat, exposed parts of the central terrace. However, core Cassin's Auklet breeding areas currently have the greatest plant cover on the island (e.g., 56% plant cover in an area of high density Cassin's Auklet nesting in 2016; Carle *et al.* 2016), which may help reduce burrow damage and provide cover from predation. Cassin's Auklets are benefiting from the management of central terrace habitat, but many birds nest in a fragile bluff (the CT-cliff), which could be easily trampled by animals and/or erode away in the absence of ongoing habitat protection. To further support colony persistence, we initiated additional efforts to encourage breeders in this CT-cliff area to relocate into nearby clay artificial burrows designed specifically for Cassin's Auklets.

ANI also hosts a high density of breeding Western Gulls, a primary predator of Cassin's Auklets. We attributed 28% of Cassin's Auklet mortalities on ANI to Western Gull predation, though causes of the majority of mortalities were unknown. At the Farallon Islands, Western Gull predation accounted for mortality of 7-8% of the nesting population during one season (Nelson 1989), whereas mortality rates of birds found on ANI from all causes of death were $1.5 \pm 2\%$ of the breeding population during our study. Though proximity to Western Gull nests did not result in decreased reproductive success of Cassin's Auklets on ANI, we could not measure the brief period when chicks depart their burrows to fledge and are vulnerable to gull predation. The percent of Cassin's Auklet nests within 1 m of a Western Gull nests increased from 2010-2016, from 10% to 38% of nests, despite Western Gull nesting population declining by > 30% during the same period (Carle *et al.* 2016). This could be because Cassin's Auklets expanded from the

steep nesting area at the CT-cliff into flatter areas with higher densities of nesting gulls. However, the rate of proximity between Cassin's Auklet and Western Gull nests declined from 44% in 2016 to 19% in 2017, which was possibly related to a decrease of 36 Western Gull nests in the central terrace in 2017 (Oikonomos, unpubl. data). Regardless of the factors driving interactions between nesting Cassin's Auklets and Western Gulls at ANI, it does not appear that Western Gull density is currently a serious threat to the persistence of the ANI Cassin's Auklet colony, especially considering the decade-long decline of ANI's Western Gull nesting population (Carle *et al.* 2016).

Given the positive population trajectory, relatively high breeding success, and active habitat management of Cassin's Auklets at ANI, we expect this colony to persist, though modeling of the future population trajectory would be a useful future research direction. An immediate threat to the colony is the pace of soil erosion and burrow damage, especially if current management efforts at erosion control were to cease. Climate change poses a threat to Cassin's Auklets in general, including at ANI either through changes in prey availability related to oceanographic changes (Wolf *et al.* 2010; Jones *et al.* 2018) or through sea-level rise increasing the pace of habitat loss from erosion. Sea level in central California is predicted to rise by 0.48-3.04 m by 2100 (50% probabilities with different models and scenarios; Griggs *et al.* 2017). The elevation of the ANI central terrace where the majority of auklets nest ranges from 5-12 m. Thus, ANI is unlikely to be overtopped by the sea in the near future, but wave action with rising sea levels could severely erode top-soil burrowing habitat during the 21st century. Sea level rise also has the potential to create new islands suitable for colonization by Cassin's Auklets (e.g., Greyhound Rock, located 7 km south of ANI, which is currently a peninsula connected by a narrow isthmus about 2 m in elevation). The colony of Cassin's Auklets at ANI has potential to grow and shows the adaptive abilities of Cassin's Auklets to colonize new islands. ANI also can be used as a

case study for management issues and solutions, especially on small nearshore islands characterized by dense use of many species of wildlife. With the uncertain future facing Cassin's Auklets, it is important to continue protection, management, and study of recently established breeding colonies.

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