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Master of Science
in Life Sciences

Demographic parameters of the Black-vented shearwater (*Puffinus opisthomelas*) on Isla Natividad, Baja California Sur, Mexico

A dissertation
submitted in partial satisfaction of the requirements for the degree
Master in Science

By:

Johnatan Alejandro Estrada Padilla

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A Dissertation Presented by

Johnatan Alejandro Estrada Padilla

And approved by the following Committee

Dr. Cecilia Soldatini
Thesis co-supervisor

Dr. Yuri Vladimir Albores Barajas
Thesis co-supervisor

Dr. Horacio Jesús de la Cueva Salcedo

Dr. Oscar Sosa Nishizaki

Dr. Edgardo Alfredo Sepúlveda Sánchez Hidalgo
Coordinator of the Postgraduate Program in Life Sciences

Dr. Ana Denise Re Araujo
Director of Graduate Studies

Resumen de la tesis que presenta **Johnatan Alejandro Estrada Padilla** como requisito parcial para la obtención del grado de Maestro en Ciencias en Ciencias de la Vida

Parámetros demográficos de la Pardela Mexicana (Puffinus opisthomelas) en Isla Natividad, Baja California Sur, Mexico

Resumen aprobado por:

Dra. Cecilia Soldatini Codirectora de tesis	**Dr. Yuri Vladimir Albores Barajas** Codirector de tesis

Comprender la dinámica poblacional de aves marinas es fundamental para su gestión y conservación efectivas, especialmente aquellas con una distribución restringida durante la reproducción. La pardela mexicana (*Puffinus opisthomelas*, BVSH por sus iniciales del inglés, Black-vented Shearwater) es un ave marina endémica de México que se reproduce principalmente en Isla Natividad, Baja California Sur. A pesar de la importancia de su conservación, no existe información demográfica. Se proporciona la primera evaluación robusta de los parámetros demográficos de la BVSH utilizando datos de captura, marcaje y recaptura recopilados durante un periodo de ocho años, entre 2016 y 2025. Se evaluó la fidelidad a la pareja y al nido y se aplicó un modelo de Cormack-Jolly-Seber bajo un enfoque bayesiano para estimar supervivencia aparente y probabilidad de recaptura. Se actualizó el tamaño poblacional mediante censos aéreos con drones, complementados con evaluaciones terrestres de ocupación de madrigueras. Las estimaciones de supervivencia aparente resultaron ser más bajas comparadas con otros Procellariiformes, posiblemente debido a la escala temporal corta y la cobertura espacial limitada del área de estudio. Las aves mostraron una alta fidelidad a la pareja (98.13%) y al nido (99.38%) y una proporción elevada de individuos transitorios (40.98%), consistente con lo observado en otras aves marinas que anidan en madrigueras. Los modelos por sexo indicaron una supervivencia ligeramente mayor en hembras. La estimación poblacional actualizada sugiere un aumento en el número de madrigueras y en el porcentaje de ocupación de estas respecto a trabajos anteriores, aumentos atribuidos en gran medida a la cobertura espacial mayor y una resolución de imagen más grande utilizadas en este estudio Se proporciona una línea base demográfica valiosa para la BVSH y se enfatiza la importancia de mantener un monitoreo a largo plazo. Investigaciones futuras deberían evaluar el éxito reproductivo y cuantificar amenazas antropogénicas como la captura incidental, la contaminación lumínica y la degradación del hábitat local. Estos esfuerzos son fundamentales para promover la conservación de esta especie endémica frente a presiones ambientales y humanas latentes.

Palabras clave: Procellariiformes, Demografía, Aves marinas, Tamaño poblacional, Modelo Cormack-Jolly-Seber

Abstract of the thesis presented **by Johnatan Alejandro Estrada Padilla** as a partial requirement to obtain the Master of Science degree in Life Sciences

Demographic parameters of the Black-vented shearwater (*Puffinus opisthomelas*) on Isla Natividad, Baja California Sur, Mexico

Abstract approved by:

Dr. Cecilia Soldatini
Thesis co-supervisor

Dr. Yuri Vladimir Albores Barajas
Thesis co-supervisor

Understanding population dynamics is essential for the effective management and conservation of seabird species, especially those with restricted breeding distribution ranges. The Black-vented Shearwater (*Puffinus opisthomelas*, BVSH), a seabird endemic to Mexico, breeding mostly on Isla Natividad, Baja California Sur. Mexico. Despite its importance, demographic information for this species is lacking. This study provides the first robust assessment of demographic parameters for BVSH using capture–mark–recapture data collected over an eight-year period between 2016 and 2025. Mate and nest fidelity were evaluated, and a Cormack-Jolly-Seber model with Bayesian framework was applied to estimate apparent survival and recapture probabilities. The population size was updated using drone-based aerial surveys coupled with ground-based burrow occupancy assessments. Apparent survival estimates were lower than expected for Procellariiformes, potentially due to the short temporal scale and the limited spatial coverage of the study area. Results revealed strong fidelity to mates (98.13%) and nests (99.38%), and a high proportion of transients (40.98%), consistent with findings in other burrow-nesting seabirds. Sex-specific models indicated slightly higher survival in females. The updated population size indicates an increase in burrow numbers and occupancy relative to previous studies, largely attributable to the broader spatial coverage and higher image resolution used in this study. This work offers a valuable demographic baseline for BVSH, emphasizing the importance of continued long-term monitoring. Future research should assess reproductive success and quantify anthropogenic threats such as bycatch, light pollution, and habitat degradation. Future research on reproductive success and anthropogenic threats, such as bycatch, light pollution, and habitat degradation, will be critical for conserving this endemic seabird under increasing environmental and human pressures.

Keywords: Procellariiformes, Demography, Burrowing-nesting seabird, Population size, Cormack-Jolly-Seber

Dedication

To my parents, Mónica Padilla Bautista and Alejandro Estrada López, and to my brother Joseph Andrey Estrada Padilla.

For always being there, no matter how far from home I was, I always had your love and support throughout this project.

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I would like to thank Dr. Cecilia Soldatini for allowing me to join the laboratory, for trusting me with such valuable data, and for funding and making possible unforgettable trips to some of the most remote islands in our country. To Dr. Yuri Vladimir Albores Barajas, for his companionship in the field and the support he provided; I deeply appreciate the extra effort he made in helping me count burrows for this thesis.

My gratitude goes to the Cooperativa Buzos y Pescadores de la Baja California, who not only make research on the island possible but also always welcome us with great hospitality and kindness.

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Chapter 1. Introduction

Demography studies the size, territorial distribution, composition, and changes of a population (Hauser & Duncan, 1972). Demographic studies can be highly diverse; they can be global or focused on a specific area, can be applied to single populations or span multiple taxa (Salguero-Gomez & Gamelon, 2021). Demography was developed to forecast population growth; nowadays it is also used to estimate survival, fertility and population dynamics, which are used to define fitness (Metcalf & Pavard, 2007; Schreiber & Burger, 2002). Studying demographic processes entails knowing and understanding the elements and variables that influence population shifts, encompassing the environmental and anthropogenic factors conditioning mortality or dispersion (Arizaga et al., 2021).

For wildlife managers, evolutionary biologists and ecologists, estimating demographic parameters such as population size, fecundity, and mortality is an urgent need. These parameters provide information about population trends, needed for management and predicting extinction risks (Lebreton et al., 1992; McDonald & Amstrup, 2001; Metcalf & Pavard, 2007). However, in natural populations, such as marine species and large mammals, the estimation of these parameters is one of the most difficult challenges due to the lack of precision and accuracy derived from sampling errors in censuses, and incomplete data on the life history of the species (McDonald & Amstrup, 2001; Sanz-Aguilar et al., 2010). In large vertebrates, such as seabirds, population size and other demographic parameters are meaningful indicators of large-scale and long-term changes in marine ecosystems (Mercker et al., 2021).

Seabirds depend on marine ecosystems associated with islands, estuaries, coastal, and oceanic waters during their life cycle, developing physiological and morphological adaptations that allow them to spend weeks, months, and even years at sea (Schreiber & Burger, 2002). There are about 370 known species of seabirds, divided into four orders; Sphenisciformes, Procellariiformes, Pelecaniformes, and Charadriiformes (BirdLife International, 2025; Schreiber & Burger, 2002). Seabirds are one of the most studied bird groups due to their longevity, wide distribution, and colonial breeding, allowing the collection of large amounts of data from a specific site in relatively short-time surveys (Furness, 1997).

Given their dependence on marine environments, seabirds are highly sensitive to environmental changes, making them a suitable choice to act as sentinel and bioindicator species (Furness, 1997; Schreiber & Burger, 2002). Despite their importance, seabirds are one of the most threatened bird groups, with 116 species (31.4%) under some protection category on the International Union for Conservation of Nature

Red List (BirdLife International, 2025; IUCN Species Survival Commission, 2012). Their main threats are invasive species in nesting areas, habitat degradation and modification, and fishing bycatch (Croxall et al., 2012).

To assess the status of a wildlife population, such as a seabird, it is essential to estimate demographic parameters at key locations and understand the ecological processes influencing them; information that is critical for effective management and conservation (Sandercock, 2006; Sutherland & Dann, 2012). A variety of techniques and analytical approaches are available to evaluate demographic parameters in wildlife populations. Capture-Mark-Recapture (CMR) models have been used in seabird's studies to estimate parameters such as population size, survival probability, and mate and nest fidelity (Chao, 2001; Ellison, 2004; Oro & Doak, 2020). Population size estimates for surface and burrow-nesting seabirds can also be obtained from aerial imagery collected by Unmanned Aerial Vehicles (UAVs), such as drones (Albores-Barajas et al., 2018; Hodgson et al., 2016).

Procellariiformes comprise albatrosses, petrels, storm-petrels, fulmars, and shearwaters, and are characterized by tubular nostrils and a specialized gland for excreting excess salts (Schreiber & Burger, 2002). The Black-vented Shearwater (*Puffinus opisthomelas*; BVSH) is a member of the Procellariidae family and is commonly distributed along the North American Pacific coasts from Washington State, USA, to the Mexican state of Oaxaca. Reported sightings also suggest a wider distribution extending south to Costa Rica and Panama (Everett, 1988; Keitt et al., 2024). Breeding is geographically restricted, with approximately 95% of the population nesting on Isla Natividad, while the remainder breeds on the San Benito Archipelago, Isla Rasa, and islets near Isla Guadalupe (Everett, 1988; Keitt et al., 2024; Velarde et al., 2015). BVSH is currently listed as "Endangered" under NOM-059-SEMARNAT-2010, reflecting its restricted breeding distribution in Mexico and its sensitivity to anthropogenic disturbance of its habitat. In contrast, the IUCN Red List classifies the species as "Near Threatened," as conservation strategies are considered to have stabilized its populations (BirdLife International, 2022; Secretaría de Medio Ambiente y Recursos Naturales, 2021).

The BVSH exhibits nocturnal habits on land, nesting primarily in burrows, with a small proportion of individuals nesting in rocky crevices; nests are maintained throughout the breeding season (Keitt et al., 2000, 2024). In the absence of tree cover and with access to sandy soils, BVSH typically dig burrows that end in chambers located 1–2 m below the surface (Albores-Barajas et al., 2018). At sea, BVSH feed by pursuit-plunging, dipping, and diving to depths of up to 50 m, mainly targeting schooling baitfish such as sardines (*Sardinops sagax*) and anchovies (*Engraulis mordax*), with squids (order Teuthoidea) comprising a smaller proportion of the diet (Keitt et al., 2000, 2024). No studies have yet assessed mate and nest fidelity in this species; however, as with most other shearwaters, BVSH are expected to be monogamous and highly philopatric (Warham, 1990).

Given that the BVSH is an endemic species with geographically restricted breeding sites, continuous monitoring of its population trends and the environmental threats it faces is imperative. Estimating key demographic parameters is essential for understanding population dynamics. However, for BVSH only a limited number of studies have been published, and these have focused almost exclusively on estimating population size on Isla Natividad using a variety of methodologies that have yielded inconsistent results. This study re-evaluates the burrow occupancy and population size on Isla Natividad and, for the first time, applies CMR methods to assess additional demographic parameters, including survival, mate and nest fidelity. By incorporating models that account for detectability biases in burrowing seabirds, this work provides more robust estimates, facilitates comparisons with related species, and clarifies the status of the BVSH population on Isla Natividad. These demographic insights are critical for conservation planning, particularly given the importance of Isla Natividad, which supports the vast majority of the species' global breeding population.

1.1. Background

A widely used parameter to understand how ecological processes influence wild populations is population size, a key factor in assessing the conservation status of a species (Rayner et al., 2007; Sutherland & Dann, 2012). To classify a species as threatened, organizations such as the IUCN apply specific criteria, including population trends over the last ten years, geographic range, and population size (IUCN Species Survival Commission, 2012). At a broader spatial scale, Important Bird and Biodiversity Areas (IBAs) are sites identified as globally significant for the conservation of birds and other biodiversity based on data-driven criteria, such as the presence of globally threatened species, restricted-range species, biome-restricted assemblages, or significant congregations (BirdLife International, 2006). Complementing these approaches, the Ramsar Convention identifies wetlands of international importance based on multiple criteria aimed at conserving biological diversity, including the presence and abundance of waterbirds, fish, and other taxa (Ramsar Convention Secretariat, 2010).

Seabirds offer unique insights into the status of the marine ecosystem, thus improving the understanding of how populations respond to environmental changes is crucial to take appropriate conservation actions

(Piatt & Sydeman, 2007; Schumann et al., 2013), but surveying cryptic species such as burrow-nesting or crevice-nesting seabirds is problematic. These species are typically nocturnal on land, and their breeding sites are often difficult to access; even when access is possible, detecting and counting individuals is challenging (Schumann et al., 2013). For burrow-nesting species, borescope inspections are commonly used to estimate population size (Jones et al., 2003). Recently, drones have been employed to reduce biases associated with extrapolations arising from the observation and sampling challenges (Albores-Barajas et al., 2018).

Demographic and ecological data are sparse for many threatened seabirds, making it difficult to reliably assess their conservation status (Bourgeois & Vidal, 2008). For example, Waugh et al., (2013), reviewed published scientific studies on population data from 350 colonies of nine taxa of shearwaters, *Puffinus,* in New Zealand. They found that despite approximately 125 years of research, sampling methods consisted of land and at-sea observations and ground counts, providing only rough estimates of population sizes for most taxa. Due to extended periods between estimations and the difficulty of assessing population sizes for highly numerous and widely distributed species, it was not possible to provide broad assessments of the status of New Zealand's shearwater populations. The study concludes that consistency in quantitative surveys is crucial for these species at key sites and highlights the need for standardized methodologies for species breeding in large colonies, such as shearwaters.

The population size of the BVSH has been little studied; early estimates can be found in Anthony's (1896) field notes, where he mentions a population of over 50,000 birds, and in Grinnel's (1897) observations, which reported "massive flocks" at sea, south of California and Baja California. A century later, Everett and Pitman (1993) reported a decline in the population of this shearwater, estimating between 2,500 and 5,000 breeding pairs based on visual counts around Isla Natividad. Keitt et al. (2003) conducted the first study to assess the population of the BVSH on Isla Natividad. Using circular plots, they determined the relationship between available and occupied burrows, extrapolating their findings to the entire colony area. For 1997, they estimated 76,570 (±18,411) breeding pairs, whereas in 1998, an El Niño year in the Eastern Pacific, the estimate dropped to 22,433 (±1,950).

Recent studies have revisited population estimates of BVSH on Isla Natividad. Albores-Barajas et al. (2018) used an unmanned aerial vehicle (UAV) to obtain a comprehensive overview of burrow numbers on the island and estimated their occupancy. Based on burrow counts and occupancy rates, they estimated 37,858 (±8,510) breeding pairs during the El Niño year of 2016 and 46,322 (±4,931) in 2017. More recently, Méndez-Sánchez et al. (2022), in a study of seabird population trends at the California Current Islands, provided a new estimate for BVSH on Isla Natividad. Using the plot-based methodology proposed by Keitt et al. (2003), they calculated average burrow density and extrapolated to the colony area, estimating 118,920 (±16,740) breeding pairs between the 2017 and 2019 breeding seasons. In 2021, the species was assessed as "Stable" after the eradication of feral cats, which had been a major cause of mortality. However, ongoing threats such as bycatch in fisheries, habitat loss, and habitat degradation have not yet been fully assessed, and may still be contributing to population decline (IUCN, 2021).

In the study of wildlife population dynamics, besides estimating the population size, it is also desirable to calculate the basic demographic parameters that influence it (*i.e.*, breeding success, immigration and emigration, mortality rate, etc.) (Pollock et al., 1990). Survival and fecundity rates are fundamental ecological parameters, as they, together with dispersal rates, drive changes in local population sizes (McCarthy, 2007). Due to the imperfect detection of individuals in free-living populations, monitoring survival requires Capture-Mark-Recapture (CMR) methods, which use individual samples on discrete occasions, at which they may or may not be detected (Cubaynes et al., 2021). In CMR studies, ringing is essential to model the observation probability of each individual as the product of its survival probability and the probability of detection, given survival (McCarthy, 2007). Repeated sampling generates capture histories that record whether an individual was detected (1) or not detected (0) during each sampling occasion (Williams et al., 2002).

The first report of ringed seabirds dates back to 1918, when Guillemots were marked as nestlings (Mead, 1974). However, the first study involving demography and migration was published by Mead (1974), which studied Razorbill (*Alca torda*) and Guillemot (*Uria aalge*), species that were used as shooting targets during autumn. However, during winter and spring, oiling was identified as an important source of mortality. Ringing recoveries of dead/dying birds were used to estimate annual mortality rates derived from hunting. Mead's study shows a very high survival rate for adults of both species, explained by the low recovery rate of rings at this stage; the rings used at that time were less effective, and ring loss or illegibility was common, causing bias in the estimates. During the same decade, Ashcroft (1979) estimated the survival of breeding adults of Puffins (*Fratercula arctica*) by yearly proportions of observed ringed individuals. For this species, between 1972 and 1977, the adult survival rate was between 90-94%; however, the author assumes that survival was underestimated due to the lack of sampling effort and that the actual survival for that decade was close to 95%.

Major advances in marking methods and the general analysis of CMR data have been made in recent years, along with the development of software capable of handling complex datasets, allowing the development of a large array of models that provide robust estimates of apparent survival and recapture probabilities of open populations (Lebreton et al., 1992). In ecological literature, the term apparent survival refers to the probability of survival in the interval between two sampling occasions; not referred as "survival" because it can be affected by permanent emigration of tagged individuals from the study site. In contrast, recapture is used as an estimator of detection of individuals previously seen during sample occasions (Cubaynes et al., 2021). Currently, studies estimate a variety of demographic parameters by applying CMR models for open and close populations under the Cormack-Jolly-Seber (CJS) approach (Cormack, 1964; Jolly, 1965; Seber, 1965).

The CJS approach is a suitable analytical framework to assess survival variability caused by factors such as time, environmental and individual covariates, or heterogeneity among individuals (Cubaynes et al., 2021). Pradel (2005) described the use of Hidden Markov Models (HMM) in capture-recapture models with multiple and uncertain states, proving useful for low-detectability birds, such as burrow-nesting species. Burrow occupancy has been studied in seabirds of the Procellariidae family, *e.g.*, Hamilton (1998), who compared methodologies for estimating nest occupancy in the sooty shearwater (*Ardenna grisea*); Jones et al. (2003), who applied capture-recapture models to assess occupancy in the same species; and Schumann et al. (2013), who optimized sampling strategies for burrow-nesting seabirds.

Few models have been developed for Procellariiformes regarding apparent survival estimates and multiple breeding parameters of adults, due to logistical challenges in monitoring even basic demographic rates (Hunter et al., 2000). There are no studies regarding BVSH demographic parameters, however demographic models have been successfully applied to several other species within the order, multiple species of storm petrels (Sanz-Aguilar et al., 2010; Soldatini et al., 2016), *Ardenna grisea* (Clucas et al., 2008; McKechnie et al., 2020), *Puffinus yelkouan* (Oppel et al., 2011), *Ardenna carneipes* (Lavers et al., 2019), *Puffinus mauretanicus* (Genovart et al., 2016), *Calonectris diomedea*, (Genovart et al., 2024) and *Puffinus puffinus* (Wood et al., 2021). These models range from simple assessments of species survival to more complex frameworks that incorporate variation among colonies, seeking to explain the influence of external factors including predation, environmental conditions, and fisheries interactions. Some of these studies also assess the effect of individual breeding status within colonies (Clucas et al., 2008; Sanz-Aguilar et al., 2010), searching for a more comprehensive understanding of the demographic dynamics of Procellariiformes.

Spatial dynamics and life history traits, such as the behavior of individuals within a population and fidelity rates, can be used as indicators of population status (Bourgeois et al., 2014; Braby et al., 2012). Both mate and nest fidelity are known to influence adult demographic rates in long-lived seabirds (Braby et al., 2012; Leach et al., 2020). Birds select breeding territories based on characteristics that maximize reproductive output while minimizing energetic costs (Schreiber & Burger, 2002). Similarly, optimal mate choice ensures that each partner can successfully fulfil parental duties, thereby enhancing reproductive output (Bourgeois et al., 2014). In socially monogamous birds such as most seabirds, higher breeding success has been associated with maintaining both nest and mate, a strategy favored by their long-life cycles and high adult survival rates (Bried et al., 2003; Murray, 1969). High fidelity rates in seabird populations may be related to mate quality, defined as a partner's ability to contribute effectively to reproduction (e.g., provisioning chicks, defending the nest, or contributing to incubation), as well as to factors such as breeding habitat quality and food availability. Fidelity can also be shaped by age or breeding experience (Bourgeois et al., 2014; Bried et al., 2003; Wooller et al., 1990).

Procellariiformes have shown high nest, site, and mate fidelity, which are known to be higher for burrow nesting species (Bourgeois et al., 2014; Bried et al., 2003; Thibault, 1994). The few studies on this order conclude that an individual's fidelity to nest and mate is associated with breeding success (Bourgeois et al., 2014; Mariné & Bernard, 2020), and high survival rates (Bradley et al., 1990). Successful breeding increases the likelihood of individuals remaining faithful to their nest and mate for the next breeding season (Mariné & Bernard, 2020), while a low breeding success rate may be associated with a higher likelihood of nest change or divorce (Thibault, 1994; Weimerskirch, 1990). Multiple authors suggest that even though the nesting site is a relevant factor for mate fidelity in Procellariiformes, mate fidelity is not a side effect of nest-site tenacity but represents a response to different selective forces (Bourgeois et al., 2014; Bried et al., 2003; Mariné & Bernard, 2020).

1.2. Justification

The BVSH colony on Isla Natividad is located near the fishing village, exposing the species to persistent threats such as fishing bycatch, human disturbance, habitat loss, and chemical and light pollution. Isla Natividad is of particular importance because it supports approximately 95% of the global breeding population, making it a critical site for the long-term conservation of the species. Although several studies have estimated population size on the island, methodological differences have produced highly variable results, creating uncertainty about the specie's status. Moreover, demographic information beyond population size, such as survival, fidelity, and burrow occupancy, remains scarce. This study provides the first comprehensive demographic baseline for BVSH, integrating CMR data with aerial surveys to generate more robust estimates of population size and other vital rates. Establishing this baseline is essential for clarifying the status of the species, facilitating comparisons with related seabirds, and guiding future monitoring and conservation strategies.

1.3. Hypothesis

Demographic parameters of BVSH on Isla Natividad, including population size, adult survival, mate and nest fidelity, and burrow occupancy, are expected to be consistent with those reported for other burrow-nesting *Puffinus* species with stable populations.

1.4. Objectives

1.4.1. Main objective

Estimate the demographic parameters of population size, survival, recapture probability, nest and mate fidelity of the Black-vented Shearwater (*Puffinus opisthomelas*) on Isla Natividad in 2025, to establish a demographic baseline for the species.

1.4.2. Specific objectives

- Analyze the capture-recapture history of the Black-vented shearwater on Natividad Island during the period 2016–2025 to infer overall population demographic processes.

- Determine the total number of burrows on the Natividad Island colony using drone imagery to obtain a new estimate of the BVSH population at Isla Natividad.

- Estimate the burrow occupancy rate, nest fidelity, and mate fidelity of the Black-vented shearwater during the 2025 breeding season on the island to determine reproductive success parameters.

- Estimate the population size of the BVSH on Isla Natividad based on the burrow occupancy rate and total burrow count to update current population estimates.

- Model the probability of recapture and the apparent survival rate of the Black-vented shearwater during the breeding season on Natividad Island as a parameter of its population dynamics.

Chapter 2. Methodology

2.1. Study area

Isla Natividad (27° 52′ N, 115° 10′ W) is an arid island located 8 km northwest of Punta Eugenia, Baja California Sur, Mexico (Figure 1). The island measures approximately 7 km in length and 2 km in width, with a total area of about 728 ha (Keitt et al., 2002; Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, 2018). It lies within the core area of the El Vizcaíno Biosphere Reserve (Secretaría de Desarrollo Urbano y Ecología, 1988). The adjacent waters are characterized by strong upwelling and dynamic circulation patterns, resulting in high primary productivity with annual peaks in April and May (Keitt et al., 2002; Secretaría de Agricultura, Ganadería, Desarrollo Rural, Pesca y Alimentación, 2018). This productivity has supported the establishment of a fishing village of at least 400 permanent residents, most of whom are members of the cooperative "Sociedad Cooperativa Buzos y Pescadores de la Baja California" (Donlan, C et al., 2000). Adjacent to the village lies the largest known colony of BVSH worldwide, covering approximately 148 ha and supporting about 95% of the global breeding population, making it a site of critical importance for the conservation of the species (Albores-Barajas et al., 2018; Keitt et al., 2002).

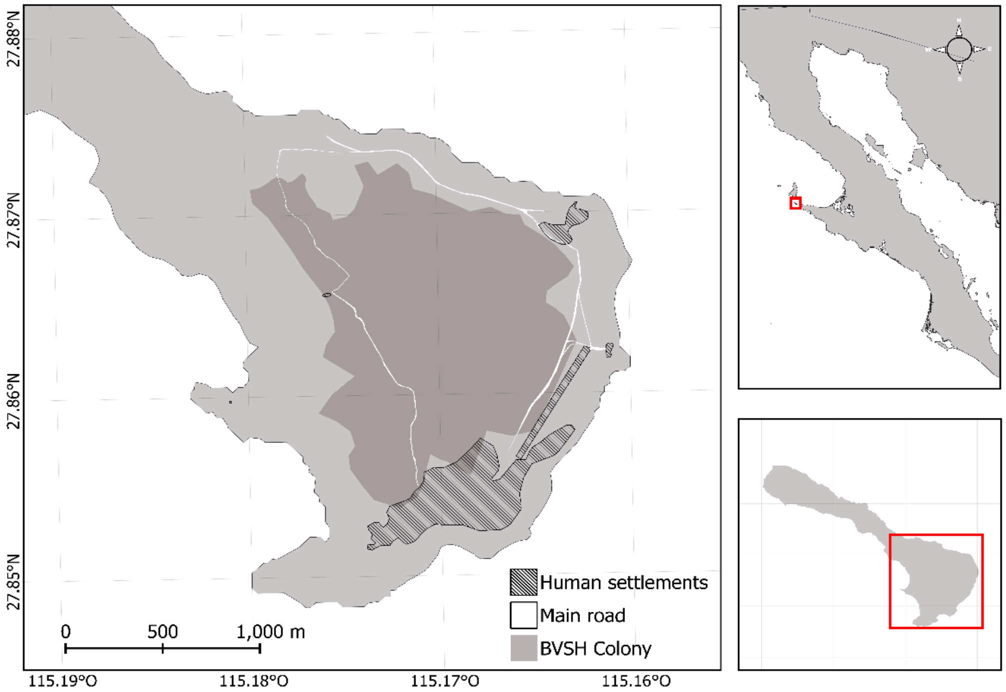

Figure 1 Isla Natividad map including main human settlements, roads and the BVSH colony

2.2. Field work

The BVSH colony was monitored intermittently from February to July each year since 2016, with at least one visit per breeding season, except in 2020 and 2021, when no data was collected due to the restrictions caused by the global COVID-19 pandemic. Due to the nocturnal terrestrial habits of BVSH, sampling was conducted at night during the new moon phase to maximize bird detection (Donlan, C et al., 2000). Monitoring activities involved ringing and recording recaptured individuals as described by Lebreton et al. (1992) with the intention of using Capture-Mark-Recapture (CMR) methods. Biometric data from each organism was recorded.

2.2.1. Capture-Mark-Recapture

The CMR methodology, as described by Lebreton et al. (1992), was implemented in a 0.35 ha plot (Figure 2). Three capture methods were employed. First, approximately 50 pre-selected burrows, modified for easy access by observers to the nest chamber, were monitored annually. Individuals in these burrows were captured; unringed birds received individually numbered rings, and previously ringed birds were recorded in a logbook. This method allowed year-to-year tracking of breeding individuals but was limited by the number of treated burrows and potential burrow destruction. Second, as BVSH often congregates in groups of 2-8 individuals near burrows, a net-capture method was applied, allowing a greater number of individuals to be captured and ringed (Keitt et al., 2000). Third, BVSH were occasionally captured and ringed outside the CMR area. Since 2016, captured individuals have been marked with alphanumerically coded metal rings on the right leg.

Biometric measurements included body mass (g), recorded using 500 g and 1000 g PESOLA® precision scales (Switzerland), and wing, tarsus, and bill lengths (mm), measured with a 150 mm caliper (150 mm 6-inch Dial Caliper Plastic Vernier Meter, China). Blood samples were also collected for molecular sexing. From 2017 to 2019 and 2022 to 2025, the same capture methods were applied; recaptured individuals were logged, and their biometrics were re-measured for longitudinal comparison.

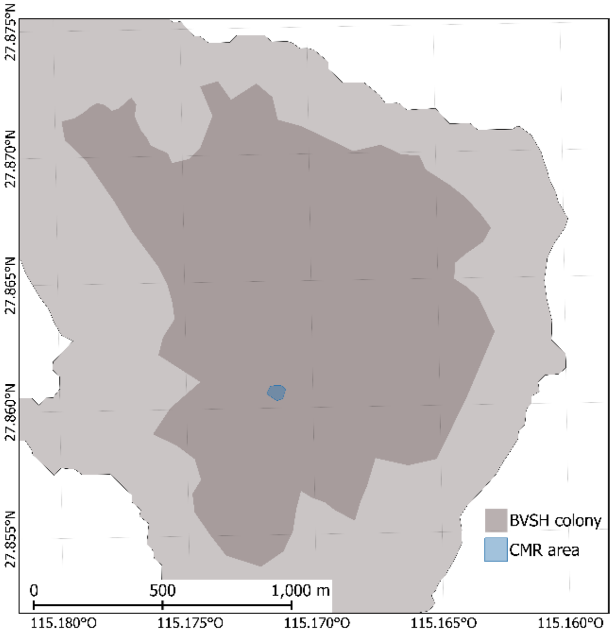

Figure 2 CMR area within the BVSH colony at Isla Natividad

2.2.2. Burrow occupancy

To determine the burrow occupancy rate, the barricade detection method and borescope inspections were used (see below). During the 2025 breeding season, burrow occupancy was estimated by ground-based methods conducted in late-April and early-May during the peak incubation period. Twenty-five 20m x 20m (400 mts^2) quadrants were monitored within the colony and classified into three categories based on burrow density: high-density zones with more than 0.15 burrows per m^2 (≥60 burrows per quadrant), medium-density zones with more than 0.10 and less than 0.15 burrows per m^2 (between 41 and 59 burrows per quadrant), and low-density zones with less than 0.10 burrows per m^2 (≤40 burrows per quadrant). The burrow occupancy methodology proposed by Albores-Barajas et al. (2018) was applied, assessing the same quadrants monitored in 2018 and separating them into the same categories based on Keit et al. (2003) to compare results.

2.2.2.1. Barricade detection

Barricade detection involves placing a small wooden piece vertically at the entrance of the burrow as a barricade. The displacement of these barricades indicates whether at least one individual has moved through the entrance of the burrow. This method is widely used in burrowing-nesting seabirds due to the complexity and depth of their burrows, avoiding invasive techniques to determine the presence of active nests (Gaston & CoIlins, 1988; Hamilton, 1998). In each quadrant, wooden barricades were placed at dusk when other species, *i.e.* crows and gulls, were less active in the colony. The barricades were removed soon after sunrise the following day, to minimize interference from other species. To assess burrow occupancy, the status of each barricade was recorded as either displaced or intact (Figure 3). This method provides only an apparent occupancy estimate, as there is intrinsic uncertainty about the occupant—it could be either a breeding individual or a transient visitor. To overcome accuracy issues, a borescope calibration was implemented (Hamilton, 1998).

For detecting actual occupancy of burrows in the BVSH colony, Albores-Barajas et al. (2018) methodology was followed, using the barricade method as the main occupancy methodology for population size estimate, and determined the detection error with the borescope. The implementation of these two methodologies allowed the estimation of the number of breeding pairs as well as the proportion of non-breeding BVSH on Isla Natividad.

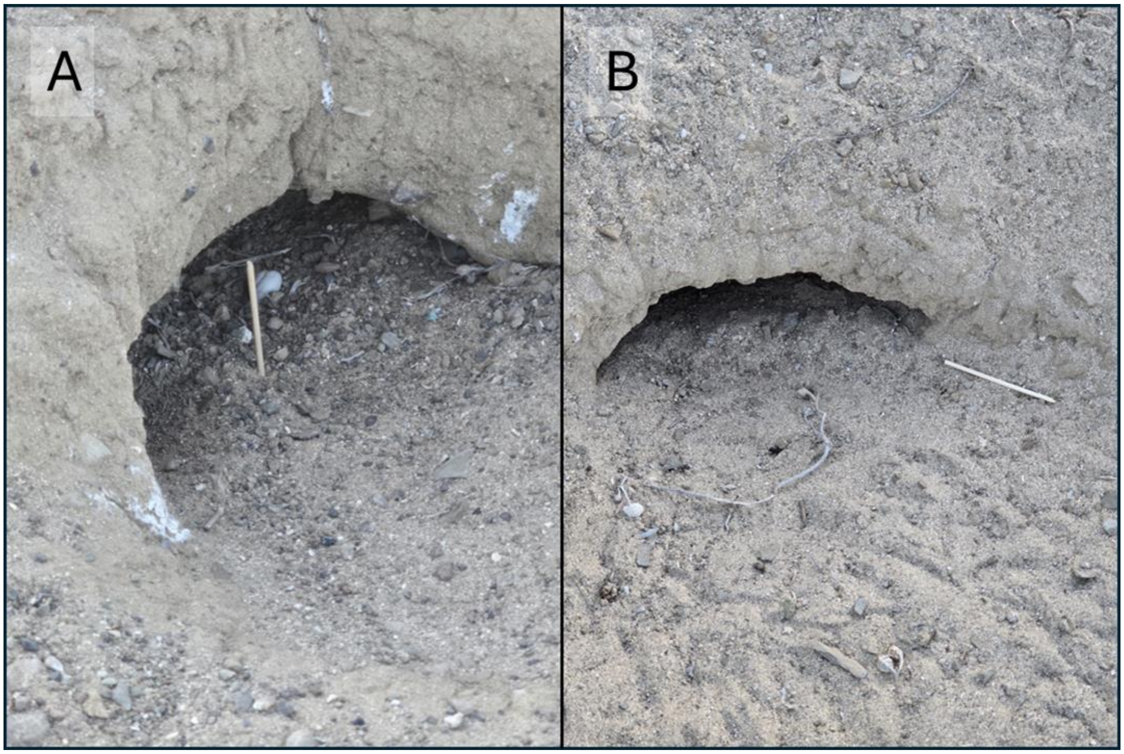

Figure 3 Barricade method to detect burrow occupancy in the BVSH colony. A) Intact barricade B) Displaced barricade

2.2.2.2. Burrow's real occupancy detection

The borescope detects reproductive signs within burrows through a small camera attached to an extension cord that allows inspecting nests in burrows and crevices, providing a measure of real occupancy by reproductive individuals (Dyer & Hill, 1991; Rexer-Huber et al., 2014). Being able to observe the presence or absence of adults, eggs or chicks inside a burrow, allows differentiating between empty burrows and those with breeding individuals, non-reproductive occupants, or transient visitors. The borescope method was used to calibrate the occupancy estimates obtained through the barricade method. The interior of 20 burrows in six of the 20m x 20m quadrants (120 burrows) were inspected; assessed burrows were selected within 6 quadrants, 40 burrows were assessed for each density category (see above); selection could not be random since there was range and mobility limitations using the borescope. Only burrows that had straighter access tunnels and were less than two meters in depth could be assessed. Burrow inspections were made using a generic 8 white LEDs borescope (China), with a high definition 2 MP camera (1920 x 1440 resolution), an 8.5 mm lens and a maximum length of three meters. The borescope was connected to a smartphone, and pictures were stored on the internal memory of the phone. The burrow was registered as unoccupied or occupied. If a burrow was occupied, it was classified into one of three categories: occupied by an adult, occupied by an egg (with or without an adult), or occupied by a chick (with or without an adult) (Figure 4). This approach allows to determine whether a burrow was truly occupied by an adult, and differentiate between burrows with active nests, confirmed by the presence of a chick or egg, and those occupied by non-reproductive individuals, prospectors, or accidental visitors (Rexer-Huber et al., 2014).

Figure 4 Image taken with borescope. It shows a nest occupied by an adult with its egg.

2.2.3. Data Preparation and Software

The data obtained during fieldwork was organized into a database referred to as *capture history*, represented by integer values of “0” and “1” on each sample year (Table 1). The first capture history is configured as follows: the first column for Ring ID, a column for each monitoring year, and additionally, all the data regarding ringed individual’s measurements. 1 indicates that the individual was either captured for the first time or recaptured if it was already ringed, while 0 means the individual was not recaptured. In the capture history of burrows, 1 means that the barricade was displaced or that an egg or chick was present inside the burrow, whereas 0 indicates that the barricade remained intact, or no egg or chick was detected. The data analysis involved designing multiple models with a Bayesian approach, using the MCMC algorithm through the Nimble package and a Goodness-of-Fit analysis in R2ucare within RStudio version 4.4.1 (Choquet et al., 2009; de Valpine et al., 2017; Gimenez et al., 2018; R Core Team, 2024).

Table 1 First three BVSH individuals ringed in 2016. The table shows how data is arranged and includes covariates such as sex and age.

RING ID	2016	2017	2018	2019	2022	2023	2024	2025	SEX	AGE	NEST
B00001	1	0	1	1	0	0	1	0	Male	Adult	17
B00002	1	1	0	0	1	0	0	0	Male	Adult	26
B00003	0	1	1	1	0	1	0	0	Female	Chick	26

1.4.4. Population Size

2.2.3.1. Burrow counts throguh drone images

The total number of burrows in the BVSH colony on Isla Natividad was manually counted as proposed by Albores-Barajas et al. (2018), using georeferenced aerial images captured by a DJI Phantom 4 Pro drone during the 2022 breeding season. This is a drone is 28.95 x 28.95 cm x 19.60 cm and weighs 1388 g. The camera used for the aerial pictures was the default camera for the DJI Phantom 4 Pro, with a f/2.8 focal point, exposure time: 1/2,000, and ISO = 100. Each photo is 5472 x 3648 pixels; it is stored on a Class 10, 32 Gb miniSD card and downloaded after completing each day's flight. The camera was pointed 90 degrees downwards, parallel to flat ground, and supported on a gimbal, to avoid vibration effects. Images were taken between 11 AM and 3 PM local time to avoid miscounts due to environmental shadows.

An aerial survey was conducted using a drone with a flight plan designed in DJI GroundStation Pro (GSPro) software with 80% photo overlap. The flight was set at an altitude of 100 m above ground level, covering a 358.87 ha. The UAV captured high-resolution images with sufficient overlap to ensure accurate photogrammetric processing.

The images were processed in the AgiSoft Metashape software (version 1.8, formerly Agisoft PhotoScan) to generate an orthomosaic. The orthomosaic was reconstructed on the altitudinal and geographical (lat-long) information, allowing an accurate and georeferenced topographic representation of the island. The resulting orthomosaic has a spatial resolution defined by a Ground Sample Distance (GSD) of approximately 4.18 cm per pixel, derived from a pixel size of approximately 0.0417845 meters in both the X and Y directions. This GSD was determined based on the pixel size of the orthomosaic, measured as

0.0418meters in both X and Y directions The absolute values of these dimensions were used to calculate the GSD. Each pixel covered an area of approximately 17.46 cm², calculated by the product of the pixel dimensions. This resolution was adequate for identifying and analyzing fine-scale features within the study area, such as burrow entrances.

Using the QGIS software (version 3.34.11), an 11 x 11 m grid was overlaid on the orthomosaic to facilitate systematic analysis of the area. Burrows were manually identified and counted, with each entrance marked as a point feature in a separate vector layer.

For orthomosaic analysis, modelling approaches to estimate detection errors are mandatory, since it is impossible to avoid miscounts such as omissions and double counts (Brack et al., 2025). To estimate detection error between the orthomosaic survey and the actual number of burrows in the colony, 20 circular plots with a 4.37 m radius and an area of 60 m^2) were chosen at random. In each plot all the burrows were counted, and simultaneously, aerial photographs of these same plots were taken with the drone flying at 100 m altitude. Two different people counted either the burrows from the aerial photographs or the plots on-field without exchanging information; comparisons were made between both counts to determine the detection error in the orthomosaic counts (Figure 5).

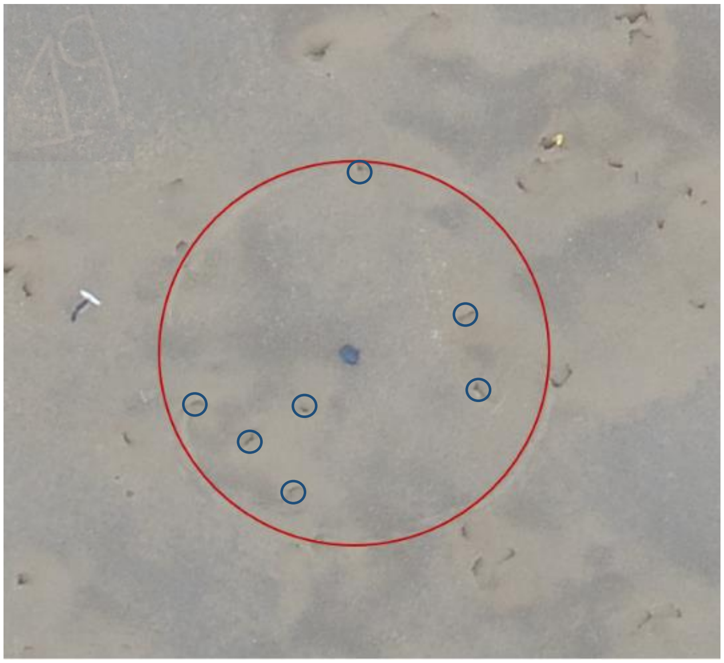

Figure 5 Error calibration plot #19 as photographed by the drone. The red circle represents the plot; blue circles represent each burrow counted on-field and detected by the drone image.

2.2.3.2. Breeding and non-breeding individuals estimates

To estimate the population of breeding and non-breeding BVSH on Isla Natividad, density-specific occupancy rates were applied to the total burrow count to estimate breeding individuals (see 2.2.2.1 and 2.2.2.2). Borescope surveys identified the proportion of non-breeding individuals within a subset of burrows, which was applied to estimate the total non-breeding individuals. These estimates were combined to derive the total population size, accounting for both breeding and non-breeding individuals across the study area.

2.2.4. Apparent Survival and Recapture Probability

Due to the low recapture rate of the chicks, these were not included in the demographic parameter models. For estimating adult survival, an open-population Cormack-Jolly-Seber (CJS) model within a Bayesian framework was implemented. CJS models are commonly used to estimate demographic parameters such as apparent survival (φ) and recapture probability (p) based on the capture history of marked individuals (Cormack, 1964; Glennie et al., 2019; Seber, 1965).

To produce reliable inferences of BVSH demographic parameters, it was necessary to assess how the capture-recapture data fit into the selected models. A Goodness-of-Fit (GOF) analysis was used to address biologically significant sources of deviation between the data and the model, ensuring that the inferences were robust and reliable while accounting for natural variability, biases, and external variations (Gimenez et al., 2018).

Five CJS-derived models were fitted to the Capture-Mark-Recapture (CMR) data. The first four models were applied with different time structures to assess adult survival rates (φ) and recapture probabilities (p): the first model assumed both φ and p are constant, the second model allowed φ to vary over time while keeping p constant, the third model assumed a constant φ with a time-varying p, and the fourth model allowed both φ and p to vary over time. However, since the population trend of the BVSH is reported as “stable” by the IUCN, due to the flexibility of inclusion of informative prior information into the Bayesian MCMC model, the five models were rerun, including the mean survival probability of 90% reported for Procellariiformes for comparison with the models without an informative prior. Additionally, two models incorporating sex as a covariate were included to determine whether apparent survival differed between sexes; one model included constant parameters, while the second included time variation for p. The best model was selected using the lowest WAIC value.

After running the candidate models, these were filtered based on the scale ratio between the mixed chains and each individual chain ($\check{R} \leq 1.01$), a threshold indicating good MCMC convergence. Furthermore, the effective sample size was examined as a diagnostic tool to assess the precision of the estimates (Gelman & Rubin, 1992; Vehtari et al., 2021). The best-fitting model for the general population was selected using the Watanabe-Akaike Information Criterion (WAIC), one of the most widely used model selection criteria in Bayesian analysis. WAIC evaluates model fit by utilizing the posterior likelihood distribution, a key component of Baye's theorem, to compare models and select the one that best represents the data (Du et al., 2023; Watanabe, 2010).

2.2.5. Mate and Nest Fidelity

To determine mate fidelity in the BVSH colony, the calculation of the divorce probability within the CMR study area was estimated. Divorce is defined as the separation of a pair, followed by a reproductive attempt with another individual by at least one member of the former pair, while both individuals remain alive. Divorce probability is obtained by dividing the total number of divorces by the total number of pairs per year in which both previous partners survived from one year to the next, without considering reproductive success (Bried et al., 2003). This approach is particularly useful in studies where reproductive success is not monitored (Black, 1996; Bried et al., 2003). The same methodology was applied to assess nest fidelity, where the complementary value is the probability of nest change. Nest change probability is calculated as the number of observed nest changes divided by the theoretical number of changes if all adults were to change nests each year that the colony was monitored, without considering the reproductive outcome of the previous year (Bried et al., 2003).

Chapter 3. Results

3.1. Population Size

3.1.1. Drone imagery

Based on the orthomosaic, the colony was represented by 13,722 quadrats of 121 m^2 each containing at least one burrow (Figure 6). The area occupied by the colony was estimated at 166.04 ha: 485 quadrats (5.9 ha) with high density, 1,608 quadrats (19.5 ha) with medium density, and 11,629 quadrats (140.7 ha) with low density. In addition, 15,937 quadrats (192.83 ha) contained no burrows (Figure 7).

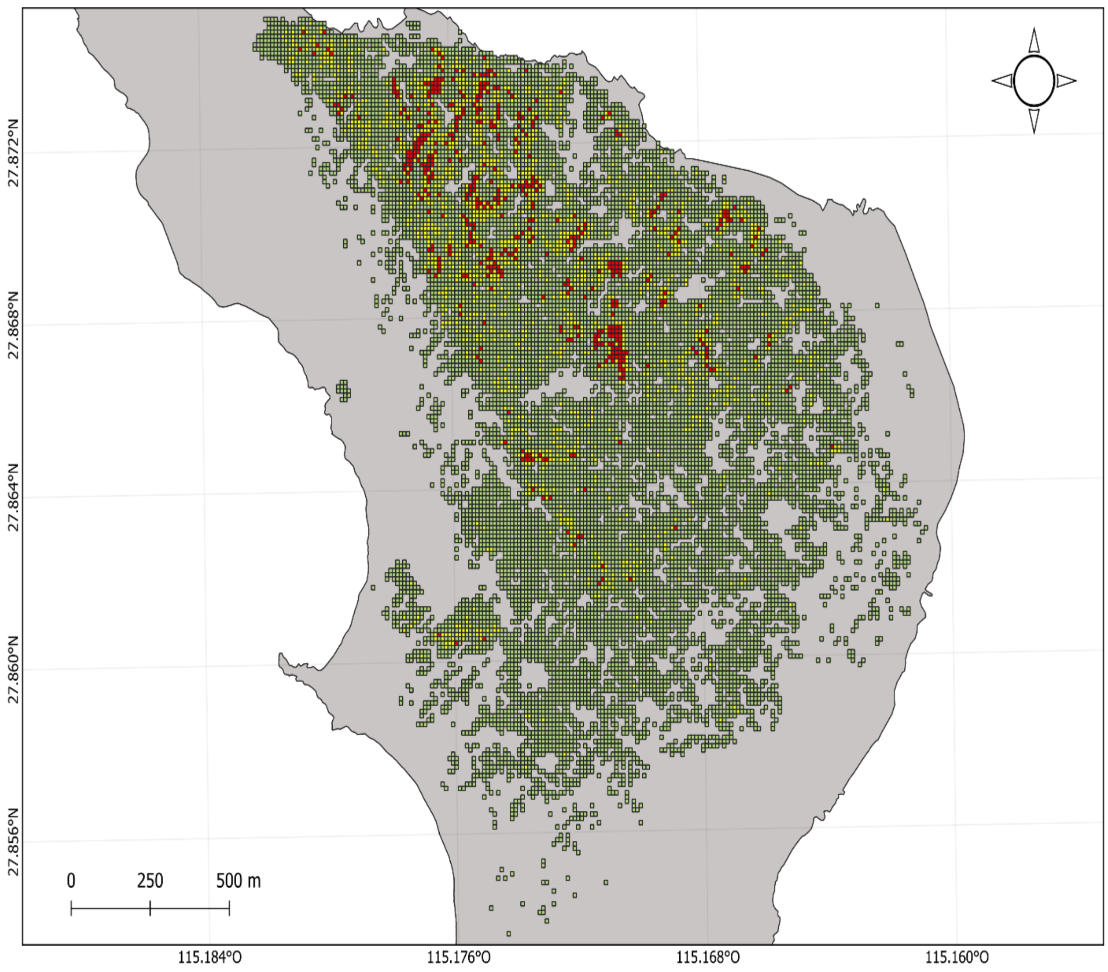

Figure 6 Spatial distribution of burrow density in the BVSH colony. Burrow density is categorized as high (>18 per quadrat, red), medium (12–18, yellow), low (<12, green), and no burrows detected (gray).

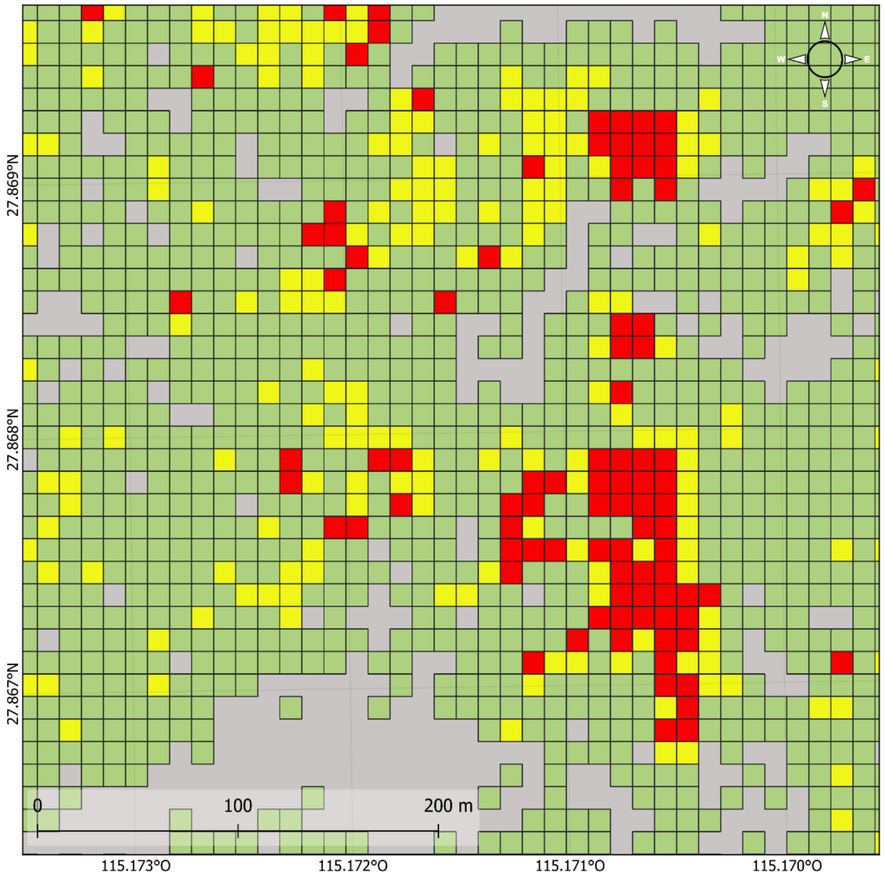

Figure 7 Fine-scale burrow density map of the BVSH colony. Burrow density is categorized as high (>18 per quadrat, red), medium (12–18, yellow), low (<12, green), and no burrows detected (gray).

3.1.1.1. Burrow counts by aerial survey

Comparing aerial and on-field counts leads to a detection error estimate of +2.76%, the aerial counts overestimated 2.76 burrows for every 100 counted. Within the 166 ha of the BVSH colony, 83,052 burrows were counted manually. After applying the detection error correction, the adjusted estimate was 80,760 burrows, distributed across the habitat density categories as follows: 47,738 burrows in low-density areas, 20,029 in medium-density areas, and 12,992 in high-density areas. On average, low-density areas contained 4.22 burrows per quadrant, 0.035 burrows/m², medium-density areas had 13.97 burrows per quadrat, 0.115 burrows/m², while high-density areas reached an average of 21.58 burrows per quadrat, 0.179 burrows/m².

3.1.1.2. Occupancy estimates

Estimating the actual occupancy of BVSH burrows using a borescope was not possible, as this method may miss occupants in deeper or structurally complex burrows, leading to a systematic underestimation of occupancy. To obtain a more accurate estimate, the barricade method was applied, and the error relative to the borescope-derived occupancy values was quantified.

For 2025, 1,529 burrows were surveyed using the barricade method across 25 quadrants. Of these, 7 quadrants were classified as low-density, containing 304 burrows (SD = 32.61), with an average density of 0.08 burrows/m² (0.001 SD), and a mean apparent occupancy of 92.43% (4.99% SD). Six quadrants were classified as medium-density, with 314 burrows (SD = 2.94), averaging 0.13 burrows/m² (0.01 SD) and 95.61% (4.96%) apparent occupancy. The last 12 quadrants were high-density, comprising 911 burrows (SD = 10.75), with an average density of 0.19 burrows/m² (0.03 SD) and 94.37% (3.48% SD) apparent occupancy.

3.1.1.3. Population size estimates

After estimating the occupancy percentage for each burrow density category and adjusting the burrow counts using aerial surveys, the breeding population of BVSH on Isla Natividad in 2025 was estimated at 75,538 ± 2,289 pairs. The proportion of non-breeding individuals was estimated at 7.25%, based on adults observed inside burrows without an egg or chick detected by the borescope. This allowed refining the population estimate, yielding a total of approximately 140,121 ± 4,578 individuals within the colony on Isla Natividad.

3.2. Capture-Mark-Recapture

Over the eight years of sampling, 535 organisms were ringed, 432 first captured as adults and 103 as chicks (Figure 8). BVSH does not show sexual dimorphism; molecular analyses were done to determine sex. Of the 118 organisms tested, 60 were females and 58 males. During the study period, 117 adults were recaptured at least once. In addition, only three chicks—two ringed in 2018 and one in 2019—were recaptured in 2022, all without an associated nest.

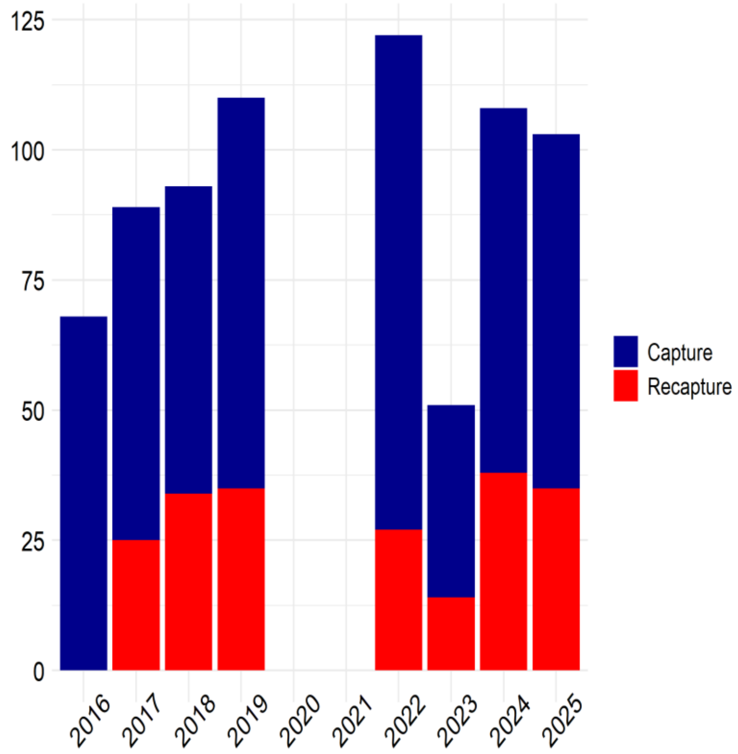

Figure 8 Total number of BVSH captured and recaptured per year between 2016 and 2025. In 2020 and 2021 access to the colony was restricted due to Covid.

3.3. Apparent survival and recapture probability

Before testing and modeling, chicks were excluded from the database due to their low recapture rate, along with individuals ringed outside the CMR area. Therefore, 379 BVSH adults were included in the CJS models.

3.3.1. Goodness Of Fit Test

The GOF test revealed significant heterogeneity in the CMR data ($\chi^2 = 67.48$, df = 21, $p = 8.9 \times 10^{-7}$). To explain the sources of this heterogeneity, four component tests were applied: test 3.SR (transience effect), test 2. CT (trap-dependence), and tests 2.CL and 3.SM (overdispersion). See Table 2 for tests results.

Table 2 Results of GOF tests for heterogeneity: transience, trap dependence, and overdispersion.

Effect test	**χ^2**	**DF**	**P value**
Global heterogeneity	67.476	21	**8.9×10^{-7}**
Transience	42.863	6	**1.2×10^{-7}**
Trap dependence	15.198	5	**0.010**
Overdispersion	0.760	4	0.944
	8.655	6	0.194

3.3.2. Model Selection

With the results of GOF tests, two initial Cormack-Jolly-Seber (CJS) models were developed to account for trap-dependence and transience effects. To evaluate the structure of survival (φ) and recapture probability (p), another 12 candidate models were constructed, incorporating covariate combinations. The model with the lowest WAIC and the strongest support from the data incorporated a transience effect on survival and a constant recapture probability (φ(trans), p), with WAIC = 662.97(Table 3). Over 50 models that included time or sex effects on either parameter showed notably higher WAIC values, indicating poorer fit. For all model combinations, incorporating priors resulted in considerably poorer fit. These results suggest that accounting for transience is essential to adequately model the demographic structure in this BVSH population.

In the best fitting model (φ(trans), p), apparent survival (φ) varies according to whether individuals were newly marked (first-time captured) or previously marked, while recapture probability (p) remains constant throughout the study period. Apparent survival for transients (φ_0) was estimated at 0.442 (95% CI: 0.368–0.523), while survival for residents (φ_1) was notably higher at 0.749 (95% CI: 0.687–0.810), showing a significant difference of 30.7% in the apparent survival between newly ringed and previously ringed BVSH. Recapture probability was estimated at 0.463 (95% CI: 0.393–0.534) for the eight years of study (Figure 9).

For each parameter estimated, the selected model showed good chain convergence ($\hat{R}$ = 1) with high effective sample sizes. Trace plots demonstrated stable mixing across chains, while posterior distributions summarized parameter estimates and their associated uncertainty (Figure 10).

Table 3 Ranking of candidate CJS models by WAIC values from lowest to highest. ΔWAIC represents the difference in WAIC relative to the best-supported model.

#	MODEL	WAIC	Δ WAIC	PRIOR USE
1	φ (trans), p	662.97	0.00	NO
2	φ (t), p(t)	714.62	51.64	NO
3	φ, p(t)	720.68	57.71	NO
4	φ (sex), p(t)	727.36	64.39	NO
5	φ (t), p	749.98	87.01	NO
6	φ, p	756.78	93.81	NO
7	φ (sex), p	757.88	94.91	NO
8	φ, p(trap)	758.21	95.23	NO
9	φ, p(t)	855.25	192.28	YES
10	φ, p	891.99	229.01	YES
11	φ, p(trap)	892.19	229.22	YES
12	φ (trans), p	949.89	286.92	YES
13	φ (t), p(t)	953.65	290.68	YES
14	φ (t), p	1008.99	346.01	YES

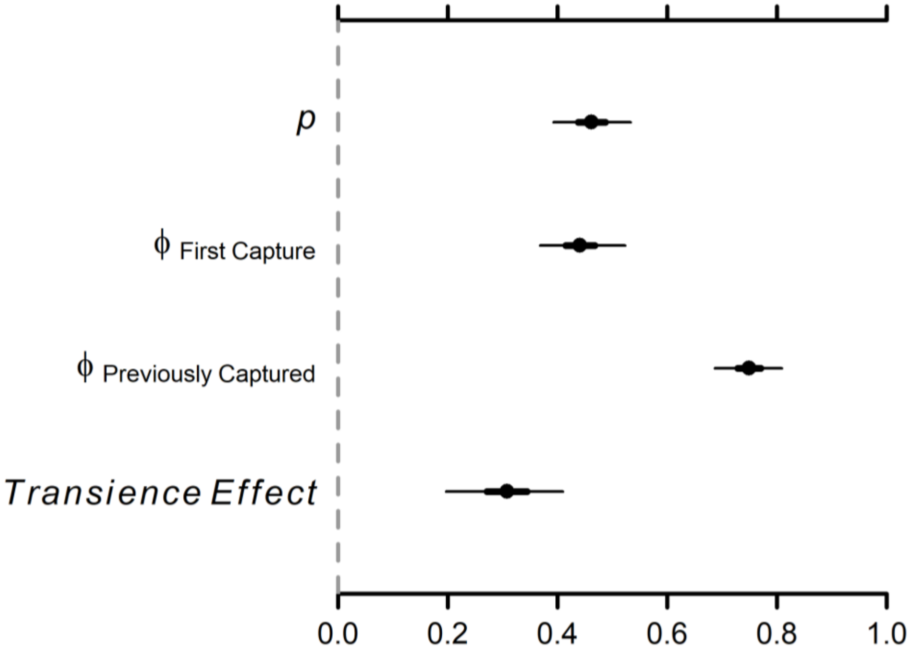

Figure 9 Posterior estimates of apparent survival probability for transients and previously marked individuals, and recapture probability (p) for the BVSH.

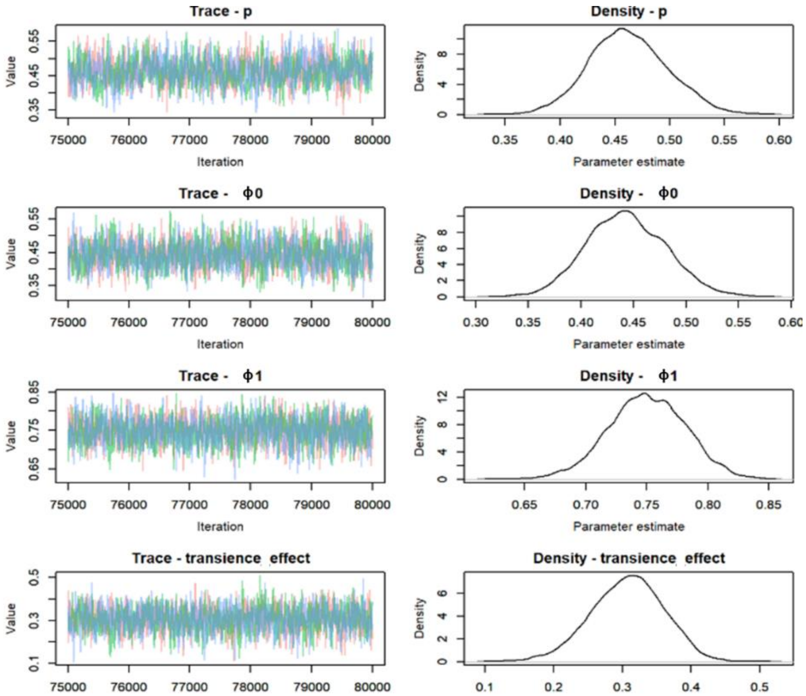

Figure 10 MCMC trace plots (left) and posterior density distributions (right) for key parameters in the CJS model: detection probability (*p*), survival probability of newly marked individuals (φ 0), survival probability of previously marked individuals (φ 1), and the transience effect.

The model accounting for a possible trap effect on the data was ranked 8 by WAIC (758.206). The model estimated an apparent survival of 0.650 (95% CI: 0.597–0.703), and a recapture probability of 0.382 (95% CI: 0.321–0.450). However, the estimated effect of trap-dependence was highly uncertain, with a mean of 0.114 and an uninformative 95% credible interval spanning from −61.99 to 62.10 (Fig 11).

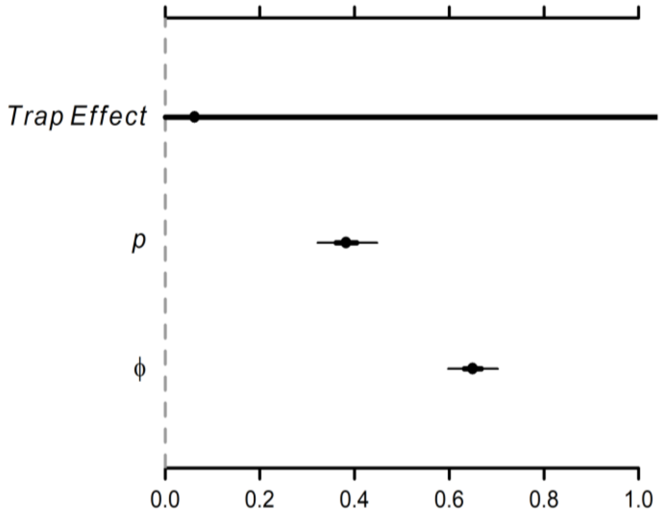

Figure 11 Posterior estimates of candidate model for apparent survival and recapture probability (p) and effect of trapping for the BVSH.

In the models where survival varied over time (ϕ_t) and an informative prior of 0.90 was applied, posterior estimates of survival consistently approached 0.90 across years (Figure 12). Although this alignment suggests agreement between the prior and the observed data, these models exhibited substantially higher WAIC values compared to those without informative priors. Therefore, for this work, the main inferences were based on the models without informative priors, as they provided a more data-driven representation of survival dynamics in the BVSH population.

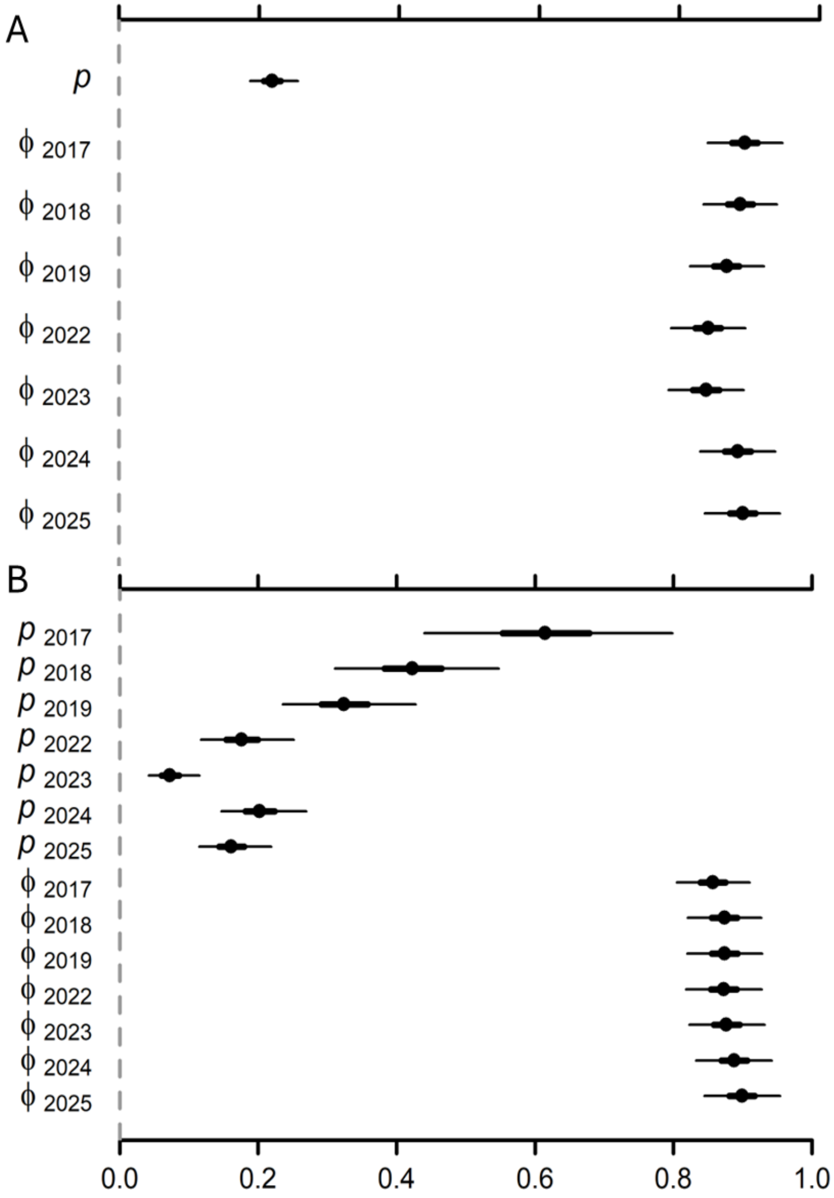

Figure 12 Posterior estimates of the candidate model for apparent survival and recapture probability including prior information for the BVSH. A) model with constant recapture probability B) model with time-varying recapture probability.

To assess sex-specific survival, the best-supported model had a WAIC of 727.24 and included time-varying detection probability (p_t) and sex-specific apparent survival ($\varphi_{s\ ex}$). Recapture probabilities varied across years, ranging from 0.129 (95% CI: 0.070–0.208) in 2023 to 0.723 (95% CI: 0.529–0.893) in 2017, reflecting temporal heterogeneity in detection (Figure 13). Apparent survival estimates differed slightly by sex: females showed the highest survival at 0.671 (95% CI: 0.518–0.857), followed by males at 0.609 (95% CI: 0.406–0.865), and individuals of unknown sex at 0.679 (95% CI: 0.576–0.786).

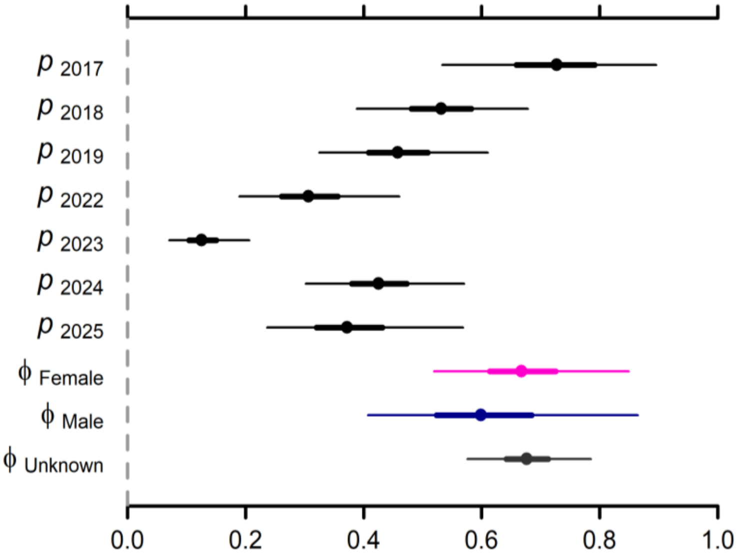

Figure 13 Posterior Estimates of Sex-Specific Apparent Survival and Recapture Probabilities for BVSH (Females: Pink, Males: Blue, Sex unknown: Gray).

3.4. Mate and Nest Fidelity

Over the eight-year study period, 61 BVSH breeding pairs were recorded in the preselected burrows. CMR data showed that 16 individuals changed mates between breeding seasons, corresponding to a mate change probability of 1.87% and a mate fidelity rate of 98.13% among ringed adults. Mate fidelity did not differ significantly between sexes, with rates of 97.78% in males and 98.55% in females. A total of 183 adults were recorded nesting, of which only eight changed burrows, yielding a nest change probability of 0.62% and a nest fidelity rate of 99.38%. Among these, four were males and three females, confirming that nest fidelity exceeded 99% for both sexes. Of the 16 individuals that changed mates, only two also switched burrows, while the other 14 continued breeding in the same burrow. Conversely, of the eight individuals that changed burrows, only two also paired with a new mate.

Chapter 4. Discussion

This study presents the first comprehensive demographic assessment of BVSH on Isla Natividad, integrating multiple parameters: apparent survival, mate and nest fidelity, and updated population size estimates. While aspects of the specie’s biology, diet, distribution, and ecology have been documented (Everett, 1988; Keitt et al., 2000, 2003; Soldatini et al., 2019, 2021), demographic research has previously focused on population size (Albores-Barajas et al., 2018; Keitt et al., 2003; Méndez Sánchez et al., 2022). No prior study has simultaneously examined the demographic processes that shape population dynamics in this species using an integrated approach that combines long-term CMR data, drone-based surveys, and Bayesian modelling. This framework offers a more integrative ecological perspective on the status of the breeding population of BVSH and establishes a valuable baseline for future demographic monitoring and conservation planning.

4.1. Population size

The updated population size estimate of 141,120 birds from this study suggests a larger breeding population of BVSH on Isla Natividad compared to the estimates of 84,802 individuals in 2016 by Albores-Barajas et al. (2018), a significant result given the methodological comparability between both studies. By applying the same integrated drone and ground-based survey methodology used in 2016, this study ensures comparability while also incorporating improvements in image resolution and overall survey design. Notably, the use of a more recent drone model with higher image resolution and the current survey extended across the entire BVSH breeding colony at a consistent altitude of 100 m allowed a more uniform detectability of burrows and coverage of previously unsurvey areas, particularly the northwestern portion of the colony. Although the values reported here are lower than those presented by Mendez-Sánchez et al. (2022), this does not necessarily indicate a population decline, as the methodologies used are not directly comparable; similarly to the earlier estimates by Keitt et al. (2003), which relied on different survey techniques.

Compared to Albores-Barajas et al. (2018), a greater overall number of burrows and a larger total area occupied by the colony were observed, with a notable increase in medium and high-density zones. Despite these higher numbers, the global extent of the breeding area remains consistent with the perimeter described by Keitt et al. (2003). Large patches with no burrows were found inside that perimeter, a pattern also reported by Albores-Barajas et al. (2018), which may have biased earlier estimates from 1997 and 1998, including estimates from 2022. The total area identified as low-density in Albores-Barajas et al. (2018) is consistent with this work; however, the distribution of burrow density appears to have shifted, with denser clusters now located farther from the village.

The spatial redistribution of burrows on Isla Natividad warrants further investigation. Although information on avoidance behavior in Procellariiformes is limited (Soldatini et al., 2015), there is substantial evidence that disturbance and artificial light pollution constitute major threats to this order; specifically for larger petrels and shearwaters such as the BVSH (Dias et al., 2019). These factors may influence nest-site selection in burrow-nesting species. It is therefore plausible that the observed shift in burrow density reflects a behavioral response by BVSH to anthropogenic pressures associated with the nearby continuous development of human settlements and light pollution increase.

In addition to the greater number of burrows observed compared with the 2016 estimate, this study recorded a significantly higher number of occupied burrows. Such variation may be linked to climatic fluctuations associated with the El Niño–Southern Oscillation (ENSO) (Schreiber & Burger, 2002). ENSO drives large-scale changes in sea surface temperature (SST) and weather, raising SSTs in the eastern Pacific. Warmer conditions reduce marine productivity and, in turn, lower prey availability for seabirds, leading to declines in colony attendance and reproductive success. The National Oceanic and Atmospheric Administration (NOAA) monitors these events using the Oceanic Niño Index (ONI), which is based on 3-month running means of SSTs in a central Pacific region and provides records from 1950 to the present (NOAA, 2025). Previous studies, such as Keitt et al. (2003) and Albores-Barajas et al. (2018), conducted fieldwork during El Niño years and reported lower population and occupancy estimates, consistent with these unfavorable conditions. During the 1997–1998 El Niño, ONI values ranged from +0.5 to +2.4, while the 2015–2016 event reached ONI values of +0.5 to +2.6, among the strongest anomalies on record (NOAA, 2025).

The drone imagery in this study was collected in 2022, during the second consecutive year of La Niña conditions. ONI values for that year ranged between –1.0 and –1.1, confirming strong La Niña conditions that are typically associated with cooler SSTs and enhanced marine productivity in the eastern Pacific (NOAA, 2025). Such conditions likely promoted both greater reproductive effort and possibly burrow construction by BVSH, as improved foraging supports breeding activity (Spear et al., 2001). The burrow occupancy assessment conducted in 2025 coincided with a neutral ENSO phase, when ONI values ranged from –0.6 to –0.1, still slightly cooler than average (NOAA, 2025). Increased productivity under these conditions may explain the high proportion of occupied burrows observed in this study.

This study's drone imagery covered approximately 620 ha of Isla Natividad, representing a significantly larger area than the 2016 aerial survey by Albores-Barajas et al. (2018). The high-resolution orthomosaic provided a comprehensive assessment of burrow distribution across the island. However, direct comparisons of total burrow count between studies are limited due to differences in survey methods and detectability. The broader spatial coverage and finer resolution of this study offer a more representative estimate of burrow abundance for BVSH.

4.2. Apparent survival and recapture probability

This study provides the first estimates of survival and recapture probabilities for the BVSH, using a Bayesian framework. Although maximum likelihood approaches remain the most common in seabird demographic studies (e.g., Clucas et al., 2008 for Sooty Shearwaters; Horswill et al., 2018 for an assessment on multiple seabird species; Genovart and Pradel, 2019 for Scopoli's Shearwaters; Petersen et al., 2020 for Arctic Tern, etc.), Bayesian methods provide enhanced flexibility for modelling uncertainty, incorporating prior information, and handling small sampling sizes (Van De Schoot et al., 2021). Despite their advantages, Bayesian frameworks remain underutilized in seabird demographic studies, primarily due to the programming complexity and steep learning curve associated with packages like NIMBLE. By adopting this approach, this work contributes not only novel demographic estimates for the species but also demonstrates the applicability of Bayesian tools in ecological modelling, particularly for species with limited data.

Within the genus *Puffinus*, demographic studies remain scarce despite the availability of population size estimates for nearly all 21 species. Detailed assessments of demographic parameters, such as survival and recapture probabilities, have been conducted for only six species: Ainley et al. (2001), Cuthbert et al. (2001), Genovart et al. (2016), Oppel et al. (2011), Perrins et al. (1973), Vanderwerf et al. (2015). For several stable populations of Procellariiformes, the survival rates for adults are higher than 90%, but reports for the Yelkouan Shearwater and the Balearic Shearwater have shown lower survival rates ≤80% (Genovart et al., 2016; Oppel et al., 2011), with bycatch being a critical source of mortality for both species. Low adult survival rates can be influenced negatively by several factors such as anthropogenic disturbance, alien species, climate change, contaminants, by-catch, etc. (Croxall et al., 2012; Lavers et al., 2019).

The model here yielded relatively low estimates of apparent survival for the BVSH adult population (74.9%), lower even than those reported for the endangered Balearic Shearwater (Genovart et al., 2016; Oro et al., 2004). Previous studies have suggested that survival probabilities below 90% are generally unsustainable for shearwater populations (Oppel et al., 2011). Therefore, these unexpected low estimates may be biased due to the spatial and temporal limitations of the study. While Procellariiformes are known for strong pair bonds and high nest fidelity (Sacchi et al., 2023), the monitoring plot represents only 0.2% of an estimated 166 ha breeding colony. It is thus highly plausible that some individuals may have relocated to nearby areas within the colony that were unmonitored (Genovart & Pradel, 2019), leading to non-detections and an underestimation of survival.

Although the GOF test indicated statistical signals for both transience ($p = 1.2 \times 10^{-7}$) and trap-dependence ($p = 0.010$), only the model accounting for transience demonstrated improved fit (lowest WAIC) and biologically interpretable parameter estimates. The model, including trap-dependence, performed poorly and yielded an estimated trap effect with wide intervals overlapping zero, suggesting weak support for its inclusion. This contrast highlights the importance of complementing GOF results with model-based inference and ecological reasoning. The statistically significant signal for trap-dependence, but lack of biological interpretability, led to exploring multiple alternative models, including simple CJS formulations without a transience effect. These attempts underscored the value of accounting for transients, as models excluding this effect captured the structure of the data ineffectively.

Including a transience effect in the model significantly improved fit and provided biologically meaningful insights into the BVSH population (Pradel et al., 1997). Higher apparent survival was estimated for previously marked breeding adults, while first-time captures exhibited markedly lower survival, consistent with the presence of transient individuals. Such transients may represent birds that do not permanently belong to the study area but are merely passing through (Genovart & Pradel, 2019). Accounting for both transience and trap-dependence is often necessary in CMR studies of seabirds to accurately describe population dynamics (Clucas et al., 2008). The model estimated that 40.98% of marked individuals during the study period were transient. This proportion was likely influenced by the higher number of birds ringed outside burrows, as the burrows of many individuals remained unidentified. Consequently, although BVSH exhibits very high nest fidelity, not all ringed individuals could be recaptured. Failure to recapture does not necessarily indicate that individuals were transient, but rather that methodological limitations prevented their detection. Differentiating transients from residents is therefore essential, since failing to do so will bias survival estimates downward and misrepresent demographic processes in long-lived seabird populations (Clucas et al., 2008; Pradel et al., 1997).

As noted by Bradley et al. (1989), sex-specific variation in adult survival is generally less pronounced in Procellariiformes compared to other seabird groups. However, demographic patterns can vary considerably across species, and identifying sex-specific differences in survival may have important implications for conservation. Barbraud & Weimerskirch (2012) found significant differences in adult survival between males and females in the Wandering Albatross (*Diomedea exulans*), emphasizing the potential biological relevance of sex as a covariate. Contrary to the present work, survival probabilities estimated for Bulwer's Petrel (*Bulweria bulwerii*) revealed lower survival rates for females (both breeders and non-breeders), likely due to the high energetic costs of egg production and laying, imposing greater physiological demands on females (Cruz-Flores et al., 2021). For the European Storm-Petrel (*Hydrobates pelagicus*) reproduction is particularly demanding for inexperienced individuals, negatively affecting female survival (Sanz-Aguilar et al., 2012).

This study evaluated sex-specific survival in BVSH by fitting a model that included sex as a covariate. Although results revealed only slight differences between females and males, this analysis provides a first step toward understanding sex-related variation in survival. One hypothesis supported by the findings of Abaunza (2024) suggests that BVSH males may be more likely to interact with fisheries than females, potentially leading to unequal survival rates. Furthermore, previous studies by Soldatini et al. (2019, 2021) have shown that BVSH exhibit sex-specific differences in foraging behavior and body condition during unfavorable warming water events such as El Niño. These patterns support the inclusion of sex as a biologically meaningful factor in demographic models of the species and highlight the importance of accounting for sex-based ecological roles in future demographic studies.

Horswill et al. (2018) showed that survival estimates are greatly improved by extended time series. The dataset used for this work spans eight years, whereas most long-term CMR studies on Procellariiformes use 10 to 25 years of data (Ainley et al., 2001; Clucas et al., 2008; Genovart & Pradel, 2019). Shorter time series may reduce the precision of survival estimates and fail to capture longer-term trends. Nonetheless, this study provides the first demographic survival estimates for BVSH, offering a valuable reference point for future assessments. These estimates can serve as a baseline or threshold against which future monitoring efforts can be compared to more accurately track survival over time.

Given that the BVSH faces ongoing pressure from multiple avian predators, such as *Larus livens, Corvus corax,* and *Tyto alba*, as well as latent risks from bycatch, habitat loss, and light pollution, continued demographic monitoring is essential (Croxall et al., 2012; Dias et al., 2019; Rodríguez et al., 2019). Future studies should assess the relative impact of these threats on survival in the BVSH population at Isla

Natividad. However, bycatch remains particularly challenging to evaluate due to the limited availability of fisheries data. Although the negative impacts of bycatch on seabird populations are well documented globally, there is a notable lack of information regarding seabird bycatch across most fishing gear types used in Mexican waters (Brito, 2011; Brothers et al., 1999; Rodriguez Valencia et al., 2008). Despite these constraints, the survival estimates presented here provide a crucial baseline for understanding adult survival in the species and offer a foundation for future conservation strategies under both current and emerging pressures.

4.3. Nest and Mate Fidelity

In some seabird species, such as terns, increased predation at breeding colonies can lead to reduced site fidelity and greater movement away from nesting areas (Braby et al., 2012; Spendelow et al., 1995). In contrast, Procellariiformes are well known for exhibiting strong fidelity to breeding sites, nesting burrows, and mates (Warham, 1990). Despite ongoing predation pressure in the BVSH colony, findings indicate high fidelity both to mates and to nesting sites. Prior to this study, no formal assessment of mate or nest fidelity had been conducted for the species. However, Keitt et al. (2003) reported a reproductive success rate of only 36% between 1997 and 1998, a relatively low percentage compared to species of similar size (Ainley et al., 2001; Brook, 1990). In Cory's Shearwater (*Calonectris diomedea*), Thibault (1994) observed that low breeding success was associated with a higher likelihood of mate changing, particularly among males at the same nesting site, as well as increased nest changes in subcolonies with high predation rates.

Further evidence from *C. diomedea* suggests that individuals skipping a breeding season are less likely to reuse the same nesting site (Sanz-Aguilar et al., 2011). Skipping, a strategy observed in several Procellariiformes, allows individuals to forgo breeding for one or more years to recover or improve body condition before a future reproductive attempt (Danchin et al., 1998; Soldatini et al., 2016). The data presented here suggests a different pattern in BVSH. Among the 22 identified skippers during the study period, only two changed their nesting burrow. Further analyses are needed to better characterize skipping behavior in BVSH and evaluate potential environmental drivers.

Although there is a lack of direct measurements of reproductive success or fledgling survival for the BVSH, fidelity results may indicate a stable breeding population. The eradication of feral cats in the early 2000s (Keitt et al., 2002), which were previously the main predator on Isla Natividad, likely reduced nest predation pressure and may have contributed to improved breeding outcomes. In this context, the low frequency of mate and nest switching observed could reflect increased breeding success and reduced environmental disturbance. However, without concurrent monitoring of reproductive output, these interpretations remain speculative. Future studies should aim to quantify fledgling survival and breeding success to fully evaluate the demographic stability of the population on Isla Natividad.

Chapter 5. Conclusions

The results suggest a larger and more widely distributed population than previously reported. The enhanced spatial coverage and image resolution provide a more comprehensive assessment of burrow abundance and demographic parameters. Further assessments using similar aerial surveys and CMR methodologies are needed to monitor population trends and evaluate environmental influences, such as food availability, on BVSH population dynamics.

The survival model incorporating transience provided biological insights, although the estimates obtained were lower than those reported for other seabird species. This lower value may reflect bias introduced by the high proportion (41%) of individuals classified as transients. Many of these birds may not be true transients, but rather individuals unlikely to be detected again because their nesting burrows were not identified. Further assessments are needed to determine whether these individuals are actual breeders within the study area or temporary visitors.

Mate and nest fidelity were very high, >98%, consistent with patterns reported for other Procellariiformes, and may serve as indirect indicators of breeding success and population stability following the eradication of feral cats and the absence of strong El Niño events in recent years. Sex-specific survival estimates showed slight differences but highlight the need for more balanced sampling to assess sex-related dynamics in greater detail.

Despite providing valuable baseline insights, this study is limited by its spatial coverage and the relatively short period of monitoring the species. These constraints are typical in studies of burrow-nesting seabirds due to logistical challenges and lead to underestimations of parameters such as survival. Although a considerable number of individuals were sexed, increasing the sample size would allow for more precise estimates of sex-specific survival patterns.

Long-term monitoring of the BVSH in Isla Natividad is recommended to enable future comparisons. Continued efforts should include the assessment of reproductive success and the quantification of anthropogenic impacts and mortality by predation, to support evidence-based strategies for the conservation of this endemic seabird. Given ongoing threats such as avian predation, bycatch, light pollution, and habitat loss, demographic monitoring remains essential.

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