THE RAREST ALCID: STATUS AND HISTORY OF THE GUADALUPE MURRELET *SYNTHLIBORAMPHUS HYPOLEUCUS* AT ISLA GUADALUPE, MEXICO (1892–2007)

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ABSTRACT

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The Guadalupe Murrelet (GUMU) *Synthliboramphus hypoleucus* is the rarest alcid in the world (< 5 000 pairs), with regular breeding documented only at Islas Guadalupe (hereafter, "Guadalupe") and San Benito off the west-central coast of Baja California, Mexico. GUMU were discovered at Guadalupe in 1892, but by then feral cats *Felis catus* had already devastated the population and limited most nesting to predator-free islets just offshore. Despite its status as the only major GUMU breeding island, the population at Guadalupe was never adequately surveyed during the 20th century. In March–April 2007, we used survey techniques developed specifically for *Synthliboramphus* murrelets to assess the status and distribution of GUMU at Guadalupe. We counted 1 511 GUMU during spotlight surveys in waters around the island. GUMU were abundant near the islets, but they were also relatively numerous near suitable breeding habitats off the north and south coasts of Guadalupe proper. Searches on four islets yielded 93 nests, most at Islotes Zapato (66; 71%) and Morro Prieto (21; 23%), where scores of abandoned eggs indicated intense competition for nests. We found seven nests on Guadalupe proper, the first proof of breeding there since 1950, but we also found 68 carcasses that confirmed significant predation by cats and raptors. A spotlight survey correction factor yielded 2 418 breeding pairs (95% confidence interval = 1 662–4 367) at Guadalupe and its islets, which accounted for ~90% of the world breeding population (1 822–4 789 pairs). About 1 150–1 750 pairs were estimated on Islotes Zapato and Morro Prieto in 1968, but comparable data were lacking to assess historical or recent changes in population size. Basic studies of GUMU biology have only recently been initiated and should be a continuing priority. Recent conservation actions have benefited the native biota of Guadalupe, but further measures, such as localized rodent control and robust biosecurity on the islets, should be considered to mitigate serious threats to the vulnerable GUMU population and other seabirds.

Key words: Isla Guadalupe, Islote Morro Prieto, Islote Zapato, Baja California, Guadalupe Murrelet, spotlight surveys, *Synthliboramphus hypoleucus*

INTRODUCTION

The Guadalupe Murrelet (GUMU; Fig. 1) *Synthliboramphus hypoleucus* and its more widespread congener, the Scripps's Murrelet (SCMU) *S. scrippsi*, are the newest species in the marine bird family Alcidae (Chesser *et al*. 2012). Until 2012, GUMU and SCMU were considered subspecies (*S. h. hypoleucus* and *S. h. scrippsi*, respectively) of the former Xantus's Murrelet (XAMU) *S. hypoleucus*, but genetic analyses revealed strong differentiation that warranted splitting XAMU into two species (Birt *et al*. 2012). Specific recognition rendered GUMU to be the alcid species having the smallest and most restricted breeding population (< 5 000 pairs; this study). Regular breeding has been documented only at Isla Guadalupe (hereafter, "Guadalupe") and Islas San Benito off the west-central coast of Baja California, Mexico (Green & Arnold 1939, Jehl & Bond 1975, Drost & Lewis 1995, Keitt 2005, Wolf *et al*. 2005; Fig. 2). This small, restricted population (~90% breed at Guadalupe) makes GUMU among the most vulnerable seabirds. They are classified as Endangered in Mexico (SEMARNAT 2010), State Threatened in California (Burkett *et al*. 2003), and Endangered on the IUCN Red List of Threatened Species (BirdLife International 2018).

Since the early 1800s, introduced mammals have devastated the native flora and fauna at Guadalupe (Thayer & Bangs 1908, Jehl & Everett 1985, Oberbauer 2005). While some non-native mammals have been removed (e.g., domestic goats *Capra hirca*; Aguirre-Muñoz *et al*. 2018), several remain (most notably feral cats *Felis catus*) that pose serious threats to GUMU and other vulnerable seabirds. Cats were primarily responsible for the extinction of

several Guadalupe endemic bird taxa (including the Guadalupe Storm Petrel *Hydrobates macrodactyla*; Howell & Cade 1954, Jehl & Everett 1985, Barton *et al*. 2004) and have limited most breeding GUMU and other seabirds (including the endemic Townsend's *Hydrobates socorroensis* and Ainley's *H. cheimomnestes* storm petrels) to predator-free offshore rocks and islets. In fact, GUMU were once considered possibly extirpated on Guadalupe proper (Jehl & Bond 1975), although it is more likely that undetected breeding persisted in steep cliffs and shoreline boulder fields throughout the 20th century.

Despite its status as the most important GUMU breeding island, the Guadalupe population was never adequately surveyed during the 20th century, mainly due to its remote location and the murrelet's discreet breeding habits and habitats. Like other *Synthliboramphus* murrelets, GUMU are inconspicuous at their breeding colonies, nesting in concealed sites (i.e., crevices and shrubs; Fig. 3), often in inaccessible habitats where they are active only at night (Sealy 1976, Murray *et al*. 1983, Whitworth *et al*. 2013). As a result, almost all information regarding GUMU at Guadalupe has been based on casual observations and museum specimens obtained by naturalists and researchers at Islotes Morro Prieto and Zapato, where nests were relatively accessible (Figs. 2 and 4). In 2000, a nocturnal spotlight survey was developed to detect and count *Synthliboramphus* murrelets in at-sea congregations near nesting areas (Whitworth & Carter 2014). These spotlight surveys have since been proven effective for monitoring population trends and estimating breeding population size at many murrelet islands (Whitworth & Carter 2018; Whitworth *et al*. 2014, 2018a, 2018b, 2020).

During 2002–2008, nocturnal spotlight surveys, night-lighting captures, and nest searches were used to assess the distribution and status of *Synthliboramphus* murrelets at nine islands off the Pacific coast of Baja California. Previous papers presented the first proof

Fig. 1. Guadalupe Murrelet *Synthliboramphus hypoleucus* captured at sea in Melopomene Cove, Isla Guadalupe on 03 April 2007.

Fig. 3. Guadalupe Murrelet *Synthliboramphus hypoleucus* in a crevice nest on Islote Zapato, Isla Guadalupe on 31 March 2007.

Fig. 2. Breeding range of the Guadalupe Murrelet *Synthliboramphus hypoleucus* on islands off the west coast of Baja California, Mexico, and southern California, USA. Islands where breeding is suspected but not confirmed are indicated by a superscript (s). Inset shows Isla Guadalupe, islets, and locations mentioned in the text.

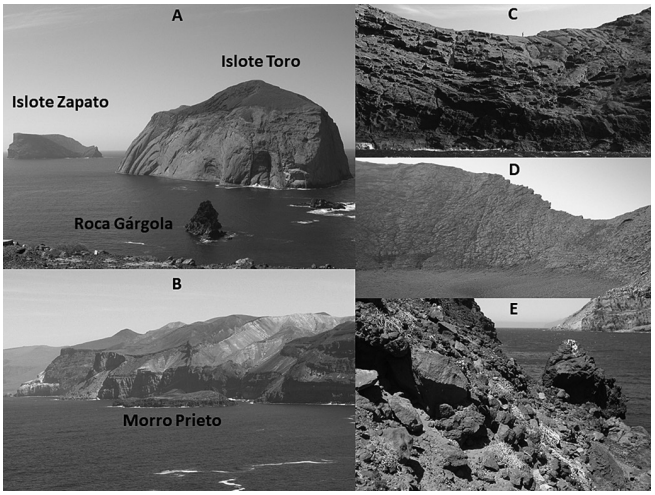

Fig. 4. Guadalupe Murrelet *Synthliboramphus hypoleucus* breeding islets: (A) Islotes Zapato, Toro, and Roca Gárgola; (B) Morro Prieto; (C) crevice habitat on the north shore of Islote Zapato; (D) the inner caldera of Islote Zapato; and (E) crevice habitat on Islote Morro Prieto.

of Craveri's Murrelet *S. craveri* (CRMU) breeding outside the Gulf of California (Whitworth *et al.* 2018a) and examined the status of SCMU at six breeding islands in the region (Whitworth *et al*. 2020). In this study, the third paper of this series, we (1) present the results of 2007 surveys at Guadalupe; (2) briefly summarize the history of GUMU at Guadalupe based on a review of published literature, unpublished data, and museum records (VertNet Portal; http://www.vertnet.org); and (3) review the limited information available for GUMU at five other known, suspected, or historical breeding islands.

STUDY AREA

Isla Guadalupe (29°00′N, 118°16′W) is a large oceanic island (244 km^2; maximum elevation 1 298 m) of volcanic origin that lies in the eastern Pacific Ocean about 250 km off the west-central coast of Baja California, Mexico (Fig. 2). Several islets and large rocks lie off the main island (Figs. 2 and 4), most notably Islotes Zapato (0.37 km^2), Toro (0.38 km^2), Morro Prieto (0.08 km^2), Enmedio (0.01 km^2), and Roca Vapor (< 0.01 km^2). Islotes Zapato, Toro, and Morro Prieto are also known as Islotes Afuera, Adentro, and Negro, respectively. For brevity, we will refer to islands and islets omitting "Isla", "Islas", and "Islote" from their name. The coastline of Guadalupe proper consists mostly of rocky bluffs and cliffs that are particularly high and steep on the north and northwest coasts (Fig. 5). Historically, the island harbored at least 10 distinct vegetation communities before they were devastated due to grazing by introduced goats (Moran 1996, Oberbauer 2005). The dominant vegetation type on southern Guadalupe and the islets is maritime succulent scrub (Rebman *et al*. 2002) or mesa/islet scrub (Oberbauer 2005). This habitat harbors several endemic plants (e.g., Guadalupe cistanthe *Cistanthe guadalupensis* and Zapato Buckwheat *Eriogonum zapatoense*). The few developed areas on Guadalupe proper include a small naval base at Punta Sur, a fishing village (Campo Oeste) on the west-central coast, several abandoned fishing camps, an airstrip, and a research station near the grove of endemic Guadalupe cypress *Cupressus guadalupensis* on the north-central plateau. Since 2005, the island and its islets have been included within the Guadalupe Island Biosphere Reserve.

METHODS

Research permits were issued to EP by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT; SGPA/DGVS/22940, SGPA/DGVS/00318/07, SGPA/DGVS/02719/07, SGPA/DGVS/03217/08). Capture and handling procedures followed the ethical standards and policies applicable in Mexico as presented in the *Guidelines to the Use of Wild Birds in Research* (Fair *et al*. 2010)

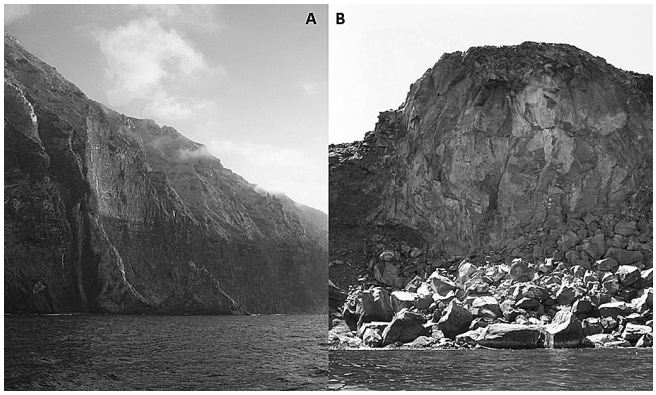

Fig. 5. Coastal habitats on Isla Guadalupe proper where Guadalupe Murrelets *Synthliboramphus hypoleucus* are known or suspected to breed: (A) cliffs on the north coast; and (B) boulder field at the base of a low cliff near Punta Doble.

Spotlight surveys

We used spotlight surveys to assess the number and distribution of GUMU in nocturnal congregations around Guadalupe and its islets. A three-person survey crew (i.e., boat driver, spotlight observer, and data recorder) traveling in an inflatable vessel followed a GPS transect as the observer counted all birds visible in the spotlight beam. Detailed survey methods are described in Whitworth & Carter (2014). Spotlight surveys were conducted over three nights on combined transects that totaled 98.4 km (Table 1). Transects were located 200–400 m from shore depending on navigation hazards (i.e., offshore rocks, reefs, and kelp beds) except at Melpomene Cove, where the transect cut across the cove mouth and extended up to 600 m from shore. Surveys were conducted (1) from Punta Norte west to Roca Elefante and south to Punta Sur on 29–30 March; (2) from Punta Norte south to Morro Sur and west to Punta Sur on 30–31 March; and (3) around Toro, Zapato, and Enmedio on 31 March–01 April (Table 1). Surveys were conducted in good conditions (i.e., winds < 20 km/h, swells < 1 m, partly cloudy skies) just before the full moon on 02 April. Optimal spotlight survey periods with respect to moon phases have not been determined (Whitworth & Carter 2014), but we generally avoid counting on nights around the full moon because moonlight reflected off the water makes it difficult to count murrelets. Unfortunately, we were constrained by the tight schedule during our region-wide surveys at Baja California islands and had to conduct surveys whenever ocean conditions allowed.

Studies at Anacapa Island, California have demonstrated a strong relationship between murrelet nesting and the number of birds attending an at-sea congregation (Whitworth & Carter 2018). We estimated the size of the GUMU breeding population using a spotlight survey correction factor that quantified this relationship between the number of SCMU counted in the congregation and the number of nests on the adjacent coastline at Santa Barbara Island, California (Whitworth *et al*. 2018a, 2020). We applied this correction factor (1.60 nests murrelet^{-1}; 95% confidence interval [CI] = 1.10–2.89) to the combined survey count at Guadalupe. All murrelets counted were assumed to be GUMU, which was the only species present during at-sea captures. A replicate survey at the south end of Guadalupe on 03 April was excluded from analyses because (1) GUMU were likely disturbed by captures conducted prior to the survey; and (2) poor conditions (i.e., winds > 25 km/h and swells > 1.5 m) reduced visibility and prevented completion of the survey.

Nest searches

We used hand-held flashlights to search for nests concealed in rock crevices and dense shrubs on four islets/rocks and 15 shoreline locations (i.e., nine boulder fields and six caves) on Guadalupe between Punta Sur and Punta Doble (Table 2; Fig. 6). A site was considered a nest if (1) incubating adults and/or whole, broken, or hatched eggs were found in a suitable crevice or bush; or (2) eggs/eggshells were found near a suitable site where it could be reasonably assumed the eggs were laid. We also recorded all carcasses and eggs/eggshells found "exposed" in open locations that

were not associated with an obvious nest. We searched the south and southeast sides of the island on 29–30 March (two to three crew for 8.75 h), Zapato on 31 March (two crew for 2.4 h) and 02 April (three crew for 2.5 h), Morro Prieto on 31 March (five crew for 1.33 h), Roca Vapor on 31 March (two crew for 0.33 h), and Enmedio on 02 April (two crew for 0.6 h). All areas that were searched were accessed via an inflatable boat. Searches on Guadalupe proper were limited to areas that appeared to harbor potential murrelet breeding habitat. Limited time prevented complete searches on islets and offshore rocks. Steep cliffs prevented searches on Toro (Fig. 4).

At-sea captures

We used the "night-lighting" technique (Whitworth *et al*. 1997) to capture GUMU congregating in Melpomene Cove on 01–02 April (21h45-03h30) and 02–03 April (21h45-23h45 and 02h30-03h17).

TABLE 1
Summary of Guadalupe Murrelets *Synthliboramphus hypoleucus* counted during nocturnal spotlight surveys conducted at Isla Guadalupe, Baja California, Mexico during 29 March–01 April 2007

Night/Time	Area	Murrelets (%)[a]
29–30 March	Punta Norte–Roca Elefante (12.5 km)	139 (9%)
23h25–03h35	Roca Elefante–Punta del Vapor (8.2 km)	19 (1%)
	Punta del Vapor–Punta Oeste (13.0 km)	57 (4%)
	Punta Oeste–Punta Sur (13.4 km)	306 (20%)
	Total (47.1 km)	521 (34%)
30–31 March	Punta Norte–Punta Gorda (12.6 km)	37 (2%)
23h21–02h52	Punta Gorda–Punta Pilar (16.1 km)	19 (1%)
	Punta Pilar–Campo Arroyitos (8.4 km)	15 (1%)
	Campo Arroyitos–Punta Sur (4.7 km)	178 (12%)
	Total (41.8 km)	249 (16%)
31 March–01 April	Islotes Toro–Zapato–Enmedio (9.5 km)	741[b] (49%)
23h08–00h35		
Total	Isla Guadalupe (98.4 km)	1 511

[a] Percent of total count.
[b] Does not include two chicks observed at-sea in separate family groups.

TABLE 2
Summary of Guadalupe Murrelet *Synthliboramphus hypoleucus* nests and other evidence of breeding or predation found at Isla Guadalupe, Baja California, Mexico during 29 March–02 April 2007

	Nest Contents[a]					Exposed eggs and carcasses[a]			
Area/Islet	**AD**	**WE**	**HE**	**BE**	**Total**	**WE**	**HE**	**BE**	**CA**
Melpomene Cove	–	–	–	2[b]	2	–	–	–	21
Morro Sur	1	–	1	3	5	1	–	–	38
Punta Doble	–	–	–	–	–	–	–	–	9
Main Island	1	–	1	5	7	1	–	–	68
Zapato	34[c]	23	6[d]	3	66(5)[e]	13	3	2	2[f]
Morro Prieto	3[g]	8	4	6	21(1)	3	–	–	–
Enmedio	–	2	–	–	2(1)	34	> 9	1	–
Roca Vapor	–	3	–	1	4(2)	–	–	–	–
Islets	37	36	10	10	93(9)	50	> 12	3	2

[a] Data indicates the number of incubating adults (AD), whole eggs (WE), hatched eggs (HE), broken eggs (BE) and carcasses (CA).
[b] One nest also contained an adult carcass and hatched egg.
[c] Includes two nests with adult carcasses.
[d] Includes one nest with a chick carcass.
[e] Numbers in parentheses indicate nests with greater than two eggs.
[f] Includes one chick carcass.
[g] Includes one nest with brooded chicks.

The three-person capture crew (i.e., boat driver, net handler, and spotlighter) in an inflatable vessel used a high-intensity spotlight to locate GUMU and a long-handled dipnet to capture targeted birds. Captured murrelets were taken to the research vessel *Alguita* where (1) species was confirmed based on facial patterns (Jehl & Bond 1975); (2) breeding status was determined based on brood patch development (Sealy 1976); and (3) blood samples were collected to examine taxonomic relationships among *Synthliboramphus* taxa in the region (Birt *et al*. 2012). Murrelets were held 10–15 min for processing.

RESULTS

Spotlight surveys

The combined spotlight count totaled 1511 GUMU (Table 1), including 521 birds off the north and west coasts between Punta Norte and Punta Sur, 249 birds off the east and south coasts between Punta Norte and Punta Sur, and 741 birds off the southern islets (Figs. 7 and 8). The total does not include two chicks in separate family groups observed off Zapato. Applying the spotlight survey correction factor to the combined survey count yielded 2418 breeding pairs (95% CI = 1662–4367) at Guadalupe.

GUMU congregations were strongly associated with known breeding areas near islets and shoreline areas of Guadalupe proper (Figs. 7 and 8). Over 75% (1134 of 1511) of all GUMU counted were located within ~1 km of Zapato, Toro, Enmedio, Morro Prieto, Roca Vapor, and boulder fields at Melpomene Cove and Morro Sur. Another 183 GUMU (12%) were located near potential breeding habitats on cliffs and offshore rocks (e.g., Rocas Elefante and Vela) along the north coast of Guadalupe proper (Fig. 7). The remaining 194 GUMU (13%) were sparsely distributed, most notably along the west coast between Puntas Oeste and Vapor, and along the east coast near Puntas Doble and Pilar. GUMU were absent from areas with little obvious breeding habitat, especially stretches of the east coast characterized by accessible low bluffs (Fig. 7).

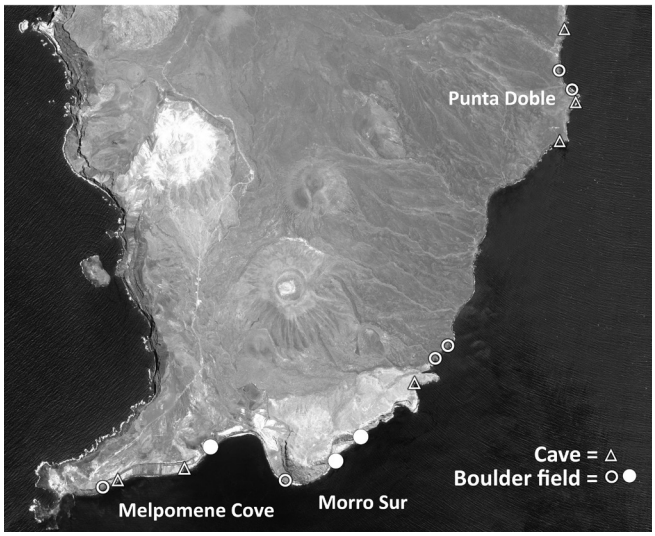

Fig. 6. Boulder fields and caves on the shoreline of Isla Guadalupe proper where Guadalupe Murrelet *Synthliboramphus hypoleucus* nest searches were conducted during 29–30 March 2007. White filled shapes indicate areas where nests were found.

Nest searches

Isla Guadalupe Proper

We found seven nests during searches on the island (Table 2). All nests were located in boulder field crevices at the base of low cliffs in Melpomene Cove and Morro Sur (Fig. 6). One nest contained an incubating adult and the remaining six contained broken or hatched eggs, although one nest with fresh broken eggs also contained an intact carcass and an old, hatched eggshell. We found 68 exposed carcasses (Table 2), most in boulder fields at Morro Sur (38; 56%) and Melpomene Cove (21; 31%), but also nine (13%) in a cave

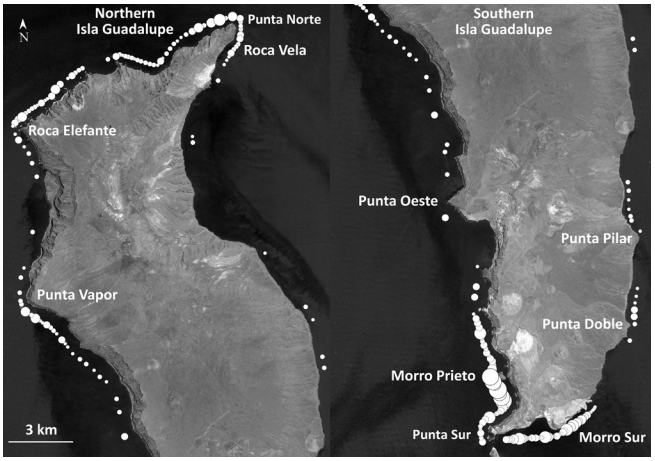

Fig. 7. Distribution of Guadalupe Murrelets *Synthliboramphus hypoleucus* off the northern (left) and southern (right) coast of Isla Guadalupe during spotlight surveys on the nights of 29–30 March and 30–31 March 2007. The number of murrelets is scaled to the size of the circle (smallest = 1; largest = 37).

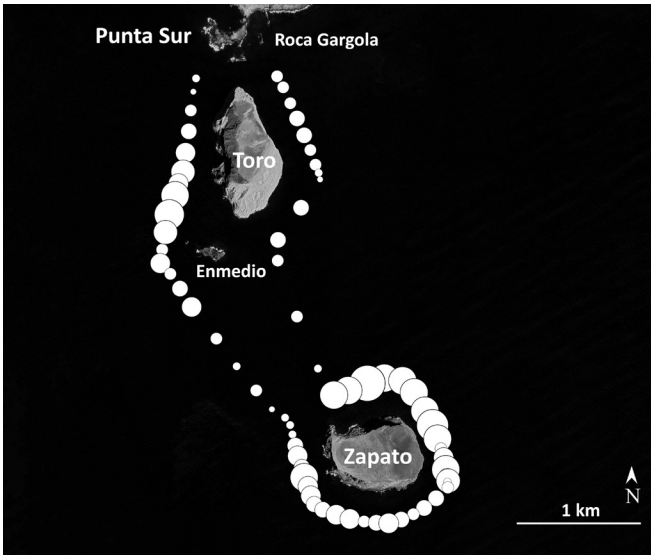

Fig. 8. Distribution of Guadalupe Murrelets *Synthliboramphus hypoleucus* during spotlight surveys around Islotes Toro, Zapato, and Enmedio at Isla Guadalupe on the night of 31 March–01 April 2007. The number of murrelets is scaled to the size of the circle (smallest = one; largest = 48).

near Punta Doble. In contrast, only one exposed egg was found—a whole egg in a boulder field at Morro Sur.

Islets and offshore rocks

We found 93 nests on islets and offshore rocks (Table 2). Most nests on Zapato (n = 66) contained adults (34; 52%) or whole eggs (23; 35%), with fewer hatched (6; 9%) or broken eggs (3; 5%). Nests on Morro Prieto (n = 21) contained mostly whole (8; 38%), broken (6; 29%), or hatched (4; 19%) eggs, and fewer adults (3; 14%). Both nests on Enmedio contained whole eggs, while four nests at Roca Vapor contained whole (3; 75%) or broken (1; 25%) eggs. We recorded more than two eggs in five nests on Zapato, two nests on Roca Vapor, and one nest each on Morro Prieto and Enmedio. As many as seven eggs were found in one nest.

All nests on Morro Prieto, Roca Vapor, and Enmedio were in crevices. In contrast, shrubs accounted for 26 nests on Zapato (39%; n = 66), compared to 27 nests in crevices (41%) and 13 nests with no data (20%). GUMU used at least five different shrub species on Zapato, including California boxthorn *Lycium californicum* (10 nests), the endemic Zapato buckwheat (5), cliff spurge *Euphorbia misera* (3), Guadalupe hazardia *Hazardia cana* (1), and dwarf saltbush *Atriplex barclayana* (1). Shrub species were not identified at six nests.

Only two exposed GUMU carcasses were recorded on the islets, one adult and one chick carcass found separately on Zapato (Table 2). Both carcasses were intact and did not appear to have been depredated. However, three carcasses (two adults and one chick) were found in three separate nests; again, none appeared to have been depredated. At least 44 exposed eggs were found on Enmedio and 18 on Zapato, compared to only three on Morro Prieto and none on Roca Vapor.

At-sea captures

We captured 50 GUMU over two nights (8.55 h), including 30 in 5.2 h on 01–02 April and 20 in 7.1 h on 02–03 April. No other murrelet species were seen or heard during captures. Only eight GUMU (16%) displayed brood patches. All developed brood patches were completely defeathered and vascularized (score = 3; Sealy 1976), indicating very recent egg-laying or current incubation.

DISCUSSION

Status at Isla Guadalupe

These were the first surveys conducted to examine the status and distribution of GUMU over the entire island and its islets. These surveys yielded (1) the first standardized population estimate for GUMU at its major breeding location; (2) the first nests found on the main island since 1950; (3) the first nest with an incubating adult ever found there; (4) the first nests recorded at Enmedio and Roca Vapor; (5) indirect evidence of breeding on the steep north coast of Guadalupe proper; and (6) continued evidence of chronic overcrowding and intense competition for nests on Zapato, Enmedio, and Morro Prieto (see *Hatching Success*, below). While the overall population was small in absolute terms, spotlight surveys found that GUMU were locally abundant around the islets and relatively numerous at several locations around the island, an unexpected and encouraging result after nearly 150 years of impacts from cats. These results bode well for a rapid increase in GUMU nesting on the main island after a proposed cat eradication program is completed (see *Conservation of the Guadalupe Murrelet*, below).

Ideally, the population estimate would have been based on a larger sample of spotlight surveys conducted throughout the breeding season, but logistical, financial, and time constraints permitted only one complete survey in 2007. We recommend adopting the 95% CI as the best estimate for population size because the wide range (1 662–4 367 pairs) likely accounted for uncertainties regarding whether the single survey was a representative count when, in fact, the number of murrelets attending congregations can vary considerably over time (Whitworth & Carter 2014). We had no reason to suspect that the combined spotlight count in 2007 was an outlier; thus, we assumed that the survey was representative and that the range of the 95% CI derived from this count included the actual population size.

As at other Baja California islands in 2002–2008 (Whitworth *et al*. 2018a, 2020), we were not concerned that the correction factor used at Guadalupe was developed at an island where only SCMU have been known to breed since 1977 (Winnett *et al*. 1979). We observed two or three murrelet species congregating together at several islands (Whitworth *et al*. 2018a, 2018b, 2020) and did not notice any obvious differences in behavior or attendance patterns among the closely related taxa to indicate that the correction factor was not valid for GUMU and CRMU, nor did we have concerns that large numbers of "non-breeding" GUMU (i.e., birds without brood patches) attending the at-sea congregation would bias the population estimate. The concept underlying the correction factor assumed that the total number of murrelets (regardless of their breeding status) attending the at-sea congregation was related to the number of nests at the adjacent colony. Large proportions of non-breeding murrelets have consistently been documented in the congregations at all *Synthliboramphus* murrelet breeding islands surveyed to date, regardless of species (e.g., Whitworth *et al.* 1997, 2018a, 2018b, 2020; Matsui *et al*. 2020). Thus, the presence of a large proportion of non-breeding birds at Guadalupe was not problematic because a large proportion of non-breeding birds were also present at Santa Barbara Island where the correction factor was developed. Determining a correction factor specifically for GUMU was not possible because there were no shoreline areas at Guadalupe where all (or even most) of the nests could be safely counted by researchers.

The only previous population estimates for Guadalupe were provided by the Pacific Ocean Biological Survey Program (POBSP) during surveys at Zapato and Morro Prieto in 1967–1968. Two estimates were given for Zapato: 2 000 birds (presumably 1 000 pairs; DeLong & Crossin 1968) and 4 000 adults (1 000 non-breeding = 1 500 pairs; Crossin 1968) in June 1968. A note by L.N. Huber on an egg record (Western Foundation of Vertebrate Zoology [WFVZ] #192756) indicated that GUMU were "An abundant nesting bird…" on Zapato. Thus, the islet clearly harbored a large proportion of the GUMU population at Guadalupe in 1968 and 2007. Estimates for Morro Prieto were variously reported as 150 pairs in April 1967 (DeLong 1967), 300–400 birds (150–200 pairs; DeLong & Crossin 1968), and 800 adults (300 non-breeding = 250 pairs; Crossin 1968) in June 1968. Crossin (1968) also estimated "1 000+ egg sets" on Zapato and "200 egg sets" on Morro Prieto in June 1968, although the meaning of "egg sets" was not explained.

Combining the Zapato and Morro Prieto estimates yielded 1 150–1 750 pairs in 1968. No details were provided regarding the methods used to estimate population size, but we suspect they were the authors' general impressions during their studies at the islets. Direct comparison between the 1968 and 2007 population estimates was not possible because different methods were used, and the 1968 estimates included only Zapato and Morro Prieto. Spotlight surveys and nest monitoring were recently conducted by the Grupo de Ecología y Conservación de Islas (GECI; Méndez-Rosas *et al*., unpubl. data), but results are not yet available to determine if any obvious changes in population size may have occurred since 2007.

Hatching success, predation, and breeding phenology

Hatching success

Synthliboramphus murrelet chicks depart nests with their parents just two to three nights after hatching (Sealy 1976, Murray *et al.* 1983); thus, hatching success is the only practical measure of murrelet breeding success. Unfortunately, GUMU hatching success at Guadalupe was not measured until 2014 (Méndez-Rosas *et al*., unpubl. data). While we discovered far more abandoned and broken eggs compared to hatched eggshells (Table 2), our surveys were conducted too early in the breeding season (before most nests had the opportunity to hatch; see *Breeding Phenology*, below) to make any reliable assessments of hatching success. Historical assessments of hatching success were limited to a few vague and sometimes contradictory accounts. For example, in June 1968, Crossin (1968: 5) reported "Many chicks… scampering about the islets" and "Large numbers of hatched egg shells lying about" that suggested a "recent high hatching rate", but later stated that "Old, infertile or addled partially incubated eggs are found in practically every good Xantus' nest site. Perhaps a high population makes for lessened hatching success."

Many abandoned eggs were also reported by other visitors to the islets. In July 1937, Green & Arnold (1939: 29) described "a surprising number of discarded murrelet eggs" on Zapato totaling "over 100 in an area of about 2 500 square yards" likely resulting from the "overcrowded condition of the nesting ground." Keitt (2005) also reported several hundred exposed eggs on Morro Prieto in 2003. Given the lack of terrestrial predators on the islets, one plausible explanation for abandoned eggs was disturbance caused by competition for nests. Nests with more than two eggs have been attributed to pairs competing for a site (Drost & Lewis 1995) and usually resulted in abandonment by both pairs (DW, unpubl. data). We discovered nine nests with more than two eggs, while Green & Arnold (1939: 29) reported "As many as seven old eggs…in one crevice, while groups of two and three were common" and DeLong (1967: 10) noted "Nests were found with one, two, and three eggs."

Predation

Abandoned eggs also might have resulted from avian predation of incubating adults, but the only direct evidence we found of raptor predation was > 20 storm petrel (*Hydrobates* spp.) wing-sets on Roca Vapor. None of the five GUMU carcasses on Zapato appeared to have been depredated and no owls were noted at Zapato or Morro Prieto in 2007, even though Crossin (1968: 7) noted "owls were feeding primarily upon on baby Xantus' Murrelets" on Zapato in 1968. He did not specify the owl species but did note that chick carcasses lined a burrow, which suggested the involvement of Burrowing Owls *Athene cunicularia*, the only owl species commonly recorded at Guadalupe (DeLong 1967, Barton *et al*. 2004, Quintana-Barrios *et al.* 2006). Furthermore, DeLong (1967: 10) noted that a Burrowing Owl on Morro Prieto had "done considerable damage to breeding storm petrels" but found no evidence that they had preyed on any of the other breeding birds. Barn Owls *Tyto alba* are voracious predators of murrelets at Santa Barbara and other islands (Murray *et al*. 1983, Thomsen *et al*. 2018), but the only evidence that they occur at Guadalupe is a single feather found on the island interior (Sweet *et al.* 2001).

Some GUMU breeding on the islets may have been preyed on at sea or captured at the islet and taken elsewhere to be eaten. We found three headless carcasses at a shoreline "plucking site" in Melpomene Cove and nine in a cave near Punta Doble; these were likely caught by raptors, most likely Peregrine Falcons *Falco peregrinus* (Barton *et al*. 2004, Quintana-Barrios *et al*. 2006). Other reports of carcasses from Guadalupe proper included (1) nine carcasses "in caves along cliffs on the east side of the island" in 1977 (Jehl & Everett 1985); (2) two pairs of wings "on the mesa at the south end of the island" in March 1988 (Oberbauer *et al.* 1989: 89); (3) an adult found at Punta Sur on 19 March 1993 (Quintana-Barrios *et al.* 2006); (4) "several cat-killed" carcasses at "the south end of the main island" in 2001–2003 (Keitt 2005: 110); and (5) an adult found at Punta Sur on 25 April 2011 (Universidad Nacional Autónoma de México Museo de las Ciencias #24336).

While our results indicated that some eggs do occasionally hatch on Guadalupe proper, it is safe to assume that hatching success there has been consistently low due to cat predation since at least 1875 (Bryant 1887, Thayer & Bangs 1908, Keitt 2005). We saw a few cats and found widespread evidence (e.g., skeletons, skulls, tracks, and feces) at the south end of the island. Hatching success may be higher on cliffs at the north end of the island, but nests have never been found there. Rats are not present at Guadalupe, but the introduced house mouse *Mus musculus* is a potential egg predator, although we saw no sign of them in shoreline areas or evidence that broken eggs were preyed upon by mice. More frequent standardized shoreline searches are needed to better assess predation by cats, owls, and mice; we suspect such searches would detect many carcasses preyed on by cats and raptors.

Breeding phenology

We obtained little information on breeding phenology in 2007, other than observations of five chicks in three family groups on 31 March–01 April (the earliest that chicks have ever been reported at Guadalupe), and this indicated some egg-laying occurred in mid-February (~40 d before hatch; Murray *et al*. 1983). However, 38 nests with incubating adults also indicated that the breeding season was far from over. We could not estimate laying dates at nests with unattended eggs; these eggs could have been (1) freshly laid eggs prior to incubation (begins two days after clutch completion; Murray *et al.* 1983); (2) viable eggs occasionally "neglected" during incubation (Murray *et al.* 1980); or (3) abandoned eggs. Furthermore, previous data (see below) indicate that GUMU without brood patches (84%) in our capture sample may have included many birds that had not yet attempted to breed in 2007.

Breeding phenology has not been studied at Guadalupe, but previous research has demonstrated great variability in egg-laying and hatching dates within and between years. Unfortunately, the available information is probably biased, as most visits occurred in

April and June. Chicks were reported as early as 27 April in 1967 (DeLong 1967: 10), but incubating adults were reported as late as 13 July in 1937 (San Diego Natural History Museum [SDNHM] #17668; Green & Arnold 1939). In 1968, Crossin (1968: 5) reported chicks during the same period (21–23 June) that "One female laid an egg… in my hand". C.L. Hubbs reported apparently "fresh" eggs as early as 05 March and as late as 29–30 August (Jehl & Everett 1985), although the criteria used to assess egg "freshness" was not specified. Jehl & Everett (1985: 327) concluded that "the peak of the breeding season is late April–June", but added that "the breeding season may be protracted" as a result of nest site limitations that acted as "a strong selective agent for an expanded breeding season". Clearly, standardized studies are needed to better determine GUMU breeding phenology at Guadalupe.

History at Isla Guadalupe

Isla Guadalupe proper

By the time naturalists began visiting in 1875, cats were already established (Bryant 1887, Thayer & Bangs 1908) and had likely devastated the GUMU population. Thus, despite frequent ornithological expeditions during the late 19th and early 20th centuries (Jehl & Everett 1985), scant evidence of breeding was found. Prior to 1900, the only evidence of GUMU recorded anywhere at Guadalupe was collected by A.W. Anthony in 1892; an eggshell (US National Museum [USNM] #B25236; Carter *et al.* 2005) from "Walrus Bay" (probably Melpomene Cove) sometime during 16–26 May (J. Unitt, pers. comm.) and an adult (SDNHM #38) from an unspecified location on 18 May. The eggshell was the first direct evidence of breeding at Guadalupe. In a letter dated 23 July 1923 (USNM), Anthony described this "weathered" eggshell and stated that "the nesting grounds of this species has not been discovered or its egg described…I also found dead bodies of *Brachyramphus hypoleucus* [name for XAMU from 1859–1909; Carter *et al*. 2005] in several places on the island and in such numbers as to warrant the belief that they bred in great abundance somewhere in the cliffs but found no burrows that I was sure were theirs."

A downy chick collected (SDNHM #10687) by L.W. Huey on 23 June 1926 was the only evidence of breeding on the island in the early 1900s. It was "picked up from the sand…in the midst of the seal herd" (probably on Playa Elefante; P. Unitt, pers. comm.) after being "rolled on by one of the animals" (L.W. Huey field notes; SDNHM). This unpublished account was also the first and only direct evidence of breeding at the north end of the island. Nesting had been suspected near Playa Elefante in July 1923 when "two pairs of Murrelets were observed flying...toward shore" in the evening which suggested "the birds were still nesting" (L.W. Huey field notes; SDNHM).

Between 1926 and 2007, the only direct evidence of breeding on Guadalupe proper was an egg (University of California, Museum of Vertebrate Zoology [MVZ] #13082) collected by J.R. Hendrickson at Melpomene Cove on 31 January 1950. However, carcasses found during 1977–2011 (see *Predation*, above) indicated that undetected breeding probably occurred despite the presence of cats.

Islote Zapato

GUMU breeding on the island's islets and offshore rocks was not mentioned in any of the early avifaunal accounts from Guadalupe, a rather surprising fact considering that they were presumably abundant and conspicuous on the islets throughout the late 19th and early 20th century. We assume that early naturalists eschewed visiting the islets because boat access was difficult, and they were more focused on study and collection of the quickly disappearing Guadalupe endemics. An egg set (WFVZ #280) and incubating adult (SDNMH #17668) collected on 13 July 1937 were the first documented evidence of GUMU breeding on Zapato and the first published account of GUMU breeding anywhere at Guadalupe (Green & Arnold 1939). Apparently unaware of the eggshell collected in 1892, Green wrote that these eggs were "the only set of the true Xantus Murrelet – those previously taken belonging to a newly described different race" (SCMU), likely referring to eggs collected at Islas San Benito, Los Coronados and other islands (Whitworth *et al.* 2020).

Although breeding on Zapato was known during the mid- to late-1900s (e.g., DeLong 1967, Crossin 1968, Jehl & Everett 1985), the islet apparently received little attention compared to Morro Prieto based on the number of specimens in museum collections (Appendix 1, available on the website). The only evidence of breeding during this period was a chick carcass found on the caldera floor on 13 June 1955 (MVZ #134051) and four egg sets collected on 21 June 1968 (Appendix 1). Keitt (2005) reported 35 nests on Zapato during a brief search on 16 May 2004.

Islote Morro Prieto

The years 1955–1968 were a period of intense ornithological investigation at Guadalupe, with much effort focused on Morro Prieto (Jehl & Everett 1985). Somewhat surprisingly, breeding was not documented there until 1955 when five adults were collected on 12–15 June (Appendix 1). One or two adults were collected each year in 1958, 1963, 1965, and 1966, but an estimate of colony size was not reported. In contrast, a substantial colony was documented during more extensive surveys in 1967–1968, when seven egg sets, 21 adults, and four chicks were collected (Appendix 1). Other unpublished data included 15 adults banded on 27 April 1967 (DeLong 1967) and "about 31 adults" captured on 19 April 1968 (R.W. Schreiber, unpubl. data), of which at least 19 were collected (Appendix 1).

Roca Gárgola

An incubating adult (SDNHM #35260) found on 21 April 1963 was the first breeding record for this islet (Fig. 4). Keitt (2005) reported four nests with abandoned eggs in 2003–2004.

Murrelets captured at sea

A report of two adult murrelets "taken at sea" on 27 June 1906 (Thayer & Bangs 1908: 104) was the first published mention of any *Synthliboramphus* murrelet at Guadalupe, although one was actually a CRMU (Harvard University, Museum of Comparative Zoology #305512; Green & Arnold 1939) while the other has not been located. The first published mention of GUMU at Guadalupe referred to two adults (California Academy of Sciences #28056–57) captured aboard a ship in Melpomene Cove on 19 April 1925 (McClellan 1926). GUMU flying aboard ships at night was apparently a rather common occurrence, as birds captured at sea accounted for nearly half (49 of 106; 46%) of all the museum specimens from Guadalupe (Appendix 1). Thirty-seven (76%) of

these 49 specimens were collected during 1953–1972, the most intense period of ornithological research at Guadalupe. This total does not include 59 GUMU banded at-sea near Zapato on 29 April and 02 May 1967, or two birds banded at Northeast Anchorage on 03 May 1967 (DeLong 1967). Unfortunately, specific capture locations were recorded for only 12 museum specimens, eight at Melpomene Cove/South Anchorage and four at Northeast Anchorage (Appendix 1). Capture locations for other specimens were either not mentioned or were vague (e.g., "off of E shore" or "off S point").

Breeding at other Baja California and California Islands

Islas San Benito, Baja California

These are the only islands where SCMU, GUMU, and CRMU are known to breed sympatrically (Keitt 2005, Wolf *et al.* 2005, Bedolla-Guzmán *et al.* 2019), although SCMU are undoubtedly the more numerous of these species (Whitworth *et al.* 2020). *Synthliboramphus* murrelets were first detected at San Benito in the late 1890s (Carter *et al*. 2005), but GUMU breeding was not suspected until 1968–1971 when considerable numbers were captured aboard ships at night (Jehl & Bond 1975). GUMU nesting was not confirmed until 1999 (Keitt 2005) and again in 2003–2004 (Wolf *et al*. 2005). However, a thorough review of museum egg and bird specimens (possibly including genetic analysis) might discover an earlier GUMU nest. In 2002, the spotlight survey correction factor yielded 214 pairs (95% CI = 147–387) of GUMU (including some SCMU–GUMU hybrids; Jehl & Bond 1975) compared to 336 pairs of SCMU (95% CI = 231–607; Whitworth *et al.* 2020). A population estimate was not provided for CRMU because they were not detected at San Benito in 2002 (Whitworth *et al.* 2018a).

Santa Barbara Island, California

An incubating GUMU recently observed in a crevice on the western cliffs in March 2021 (CIES/NPS, unpubl. data) was the first documented nesting on Santa Barbara Island since 1977 and 1978 (Winnett *et al*. 1979). Only GUMU were observed in the nest in 1977, but a mixed GUMU-intermediate plumage pair (Jehl & Bond 1975) was observed in 1978. A GUMU pair was observed (one was captured) several kilometers off the island on the night of 16 May 2009 (DW, unpubl. data).

San Clemente Island, California

A small GUMU population (five pairs; 95% CI = 3–9) was suspected at San Clemente based on their consistent presence in the predominately SCMU congregation at Seal Cove (Whitworth *et al*. 2018b). Twenty-nine GUMU (31% with brood patches) were captured in 2012–2020, which was 12% (n = 234) of all murrelets banded (DW, unpubl. data). However, GUMU nests have not yet been found. We did not consider the lack of GUMU nests to be definitive evidence against breeding because only nine SCMU nests have ever been found at Seal Cove, a location where terrestrial mammals restrict murrelet breeding to relatively inaccessible habitats (Whitworth *et al*. 2018b). It is possible that Seal Cove is a regular stop for some GUMU dispersing from Guadalupe or San Benito, although such visitation has not been documented at other southern California islands during the breeding season (Whitworth *et al.* 2018b).

Isla San Martín, Baja California

The only evidence of possible breeding was one GUMU (without brood patches) captured at sea with five CRMU and two SCMU in April 2008 (Whitworth *et al*. 2018a, 2020). It is possible that this lone GUMU may have been (1) an adult visiting San Martín prior to or after breeding; (2) a prospecting sub-adult; or (3) simply passing by San Martín from another colony. If GUMU were breeding at San Martín in 2007–2008, the estimated population was small (14 pairs; 95% CI = 10–26; Whitworth *et al.* 2020). More surveys are needed to better determine the breeding status of *Synthliboramphus* murrelets at San Martín.

Isla San Jerónimo, Baja California

Population size was not estimated because GUMU were not observed among the 72 SCMU captured at San Jerónimo in 2007–2008 (Whitworth *et al.* 2020). The only evidence of possible breeding was a photograph of a GUMU–SCMU "pair" taken by a motion-sensor camera on the island in April 2015 (Bedolla-Guzmán *et al*. 2019). GUMU may occasionally breed on San Jerónimo, but more surveys are needed to determine their status.

World breeding population of Guadalupe Murrelets

Combining GUMU population estimates for Guadalupe, San Benito, San Clemente, and San Martín yielded a world population of 2 651 pairs (95% CI = 1 822–4 789), with Guadalupe contributing 91% of this total. GUMU breeding at Santa Barbara, San Clemente, San Martín, and San Jerónimo islands is infrequent or not confirmed, but if breeding occurs, the populations are negligible compared to those at Guadalupe and San Benito.

Conservation of the Guadalupe Murrelet

Extraordinary conservation measures are warranted to preserve and enhance the vulnerable GUMU population at Guadalupe, the primary breeding island of the rarest alcid in the world. Guadalupe has been deservedly recognized as a global priority for continued eradication efforts (Holmes *et al.* 2019). Conservation actions led by GECI have already benefited the native flora and fauna by removing dogs and goats (Aguirre-Muñoz *et al*. 2018). However, further actions are needed to control and eliminate other threats to the breeding seabirds. Since 2010, GECI has been implementing many of the monitoring, restoration, and biosecurity measures recommended below, although many details of the methods used and results are not yet available (GECI, unpublished data).

Cats have long been the major factor limiting seabirds at Guadalupe. Fortunately, planning to eradicate cats is well underway (Luna-Mendoza *et al*. 2011). In the interim, local control measures (e.g., trapping and predator fencing) to benefit the Laysan Albatross *Phoebastria immutabilis* breeding colony have also resulted in improved breeding conditions for GUMU, which are "recovering and steadily" increasing in the albatross breeding area (Hernández-Montoya *et al*. 2014; Méndez-Rosas *et al*., unpubl. data). There are valid concerns about mesopredator release of the house mouse population after cats are eradicated (Luna-Mendoza *et al*. 2011), although the effects of mice (e.g., increased egg predation) would likely be less severe than predation of adult murrelets by cats. Mouse eradication would be difficult and costly over an island as large as Guadalupe, but local mouse control in GUMU breeding

areas could reduce their impacts. Introduction of cats or mice from Guadalupe proper to nearby Morro Prieto (< 100 m), Toro (< 400 m), or Zapato (< 3 200 m) would pose a serious threat to GUMU and other breeding seabirds on those islets. Therefore, robust biosecurity measures (i.e., baited traps and motion-sensitive surveillance cameras) and response plans are needed to detect and remove cats and mice before they become established and damage the sensitive seabird populations.

Development of effective conservation actions to benefit GUMU will require specific knowledge of the factors affecting their breeding success and population trends. Therefore, establishment of an effective population monitoring program should be a priority. Specific monitoring protocols will depend on logistic and funding constraints, but immediate priorities should include (1) annual nest monitoring at Zapato and Morro Prieto to determine timing of breeding, hatching success, nest occupancy, causes of clutch failure, and population trends in standardized plots; (2) intensive spotlight surveys (≥ 8/y) on standardized transects at the south end of Guadalupe proper and the islets to assess seasonal and annual variation in congregation attendance; and (3) spotlight surveys (1–2/y) around Guadalupe proper to better determine the distribution and number of GUMU in areas where breeding may occur but where nest monitoring and frequent spotlight surveys are not practical. The population monitoring protocols used for SCMU at Anacapa Island, California provided excellent data with minimal disturbance (e.g., Whitworth *et al*. 2013, Whitworth & Carter 2018) and could easily be adapted for Guadalupe. Once seasonal and annual variability in spotlight counts has been analyzed, power analyses could determine the most effective spotlight survey schedule for monitoring overall population trends (e.g., Whitworth *et al*. 2018b), which could then be compared with trends in nest monitoring plots (e.g., Whitworth & Carter 2018).

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