







NOTE

Abduction and sexual coercion of Guadalupe fur seal pups

Guillermo Vallarino-Orozco¹  | Ingrid Monserrath Burgoin-Diaz¹  |
Fernando R. Elorriaga-Verplancken¹  | Tenaya Norris²  |
Andrew W. Trites³  | Claudia J. Hernández-Camacho¹ 

¹Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, La Paz, Baja California Sur, Mexico

²The Marine Mammal Center, Sausalito, California

³Marine Mammal Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada

Correspondence

Claudia J. Hernández-Camacho, Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, Playa Palo de Santa Rita, C. P. 23096, La Paz, Baja California Sur, Mexico.

Email: cjhernandez78@gmail.com

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Abducting and sexually coercing pups are hypothesized to be a means for immature male otariids to learn how to secure, control, and mate with females—and increase their future reproductive success (Campagna et al., 1988a,b). However, the impact of unintentional pup deaths and the disruption of mother-pup bonds due to the behavior of juvenile and subadult males on population growth is unclear, especially for species such as Guadalupe fur seals (*Arctocephalus townsendi*), which are recovering from the catastrophic effects of sealing that occurred over a century ago (Hubbs, 1956).

To date, Guadalupe fur seals have successfully reestablished only one of their former breeding colonies, Guadalupe Island (Figure 1; Hubbs, 1956). However, they are also giving birth in small numbers (~60 pups) at a second historic breeding site, San Benito Archipelago (~260 km southeast of Guadalupe Island), where large numbers of juvenile and subadult males (~6,000 individuals) occur (Serrano-Rodríguez, 2023). Although pups, juveniles, and subadult males have been counted at San Benito since the late 1990s, the proportion of pups (<1%) is markedly lower than at Guadalupe Island (23%) (Hernández-Camacho & Trites, 2018; Serrano-Rodríguez, 2023). In total, ~16,000 pups were born each year between 2019 and 2022 of which 99% were born on Guadalupe Island. The total population of all ages for this period was estimated to be ~70,000 individuals (Juárez-Ruiz et al., 2022; Serrano-Rodríguez, 2023). The slow rate of recolonization of the San Benito colony as a breeding site has been associated with the warming of the Pacific Ocean caused by El Niño events and the Northeast Pacific marine heatwave ("The Blob") that affected the entire food web (Elorriaga-Verplancken et al., 2016; Gálvez et al., 2023). However, harassment and abductions of pups by juvenile and subadult males may be another significant factor hindering the recovery of this reestablished colony.

We sought to document the reproductive activity, such as births and the establishment and defense of territories, of Guadalupe fur seals at San Benito Archipelago to understand how sites dominated by sexually immature animals transform into breeding colonies (rookeries). Our observations of reproductive behavior took place July 18–29, 2022, at the San Benito Archipelago, coinciding with the typical birthing period for pups on Guadalupe Island (Gallo-Reynoso, 1994). We conducted our behavioral observations at two sites on San Benito West Island (Figure 1). The first site (A) was the most populated reproductive area of the entire West Island (consisting of 274 individuals that were mostly juveniles representing 4.9% of the total San Benito Archipelago population) and had the greatest number of newborns (eight individuals all born within a single reproductive territory that accounted for 13.6% of the total number of pups born on the San Benito Archipelago). The second site (B) had two territories with six pups among a total of 57 mature and immature fur seals. All three reproductive territories consisted of a subadult or territorial male, some mature females, and pups.

We recorded reproductive behaviors at both sites (A and B) from 09:00 to 17:00 local time, as part of a broader study, and noted the first instances of aggressive behaviors towards pups on our initial day of study. However, we

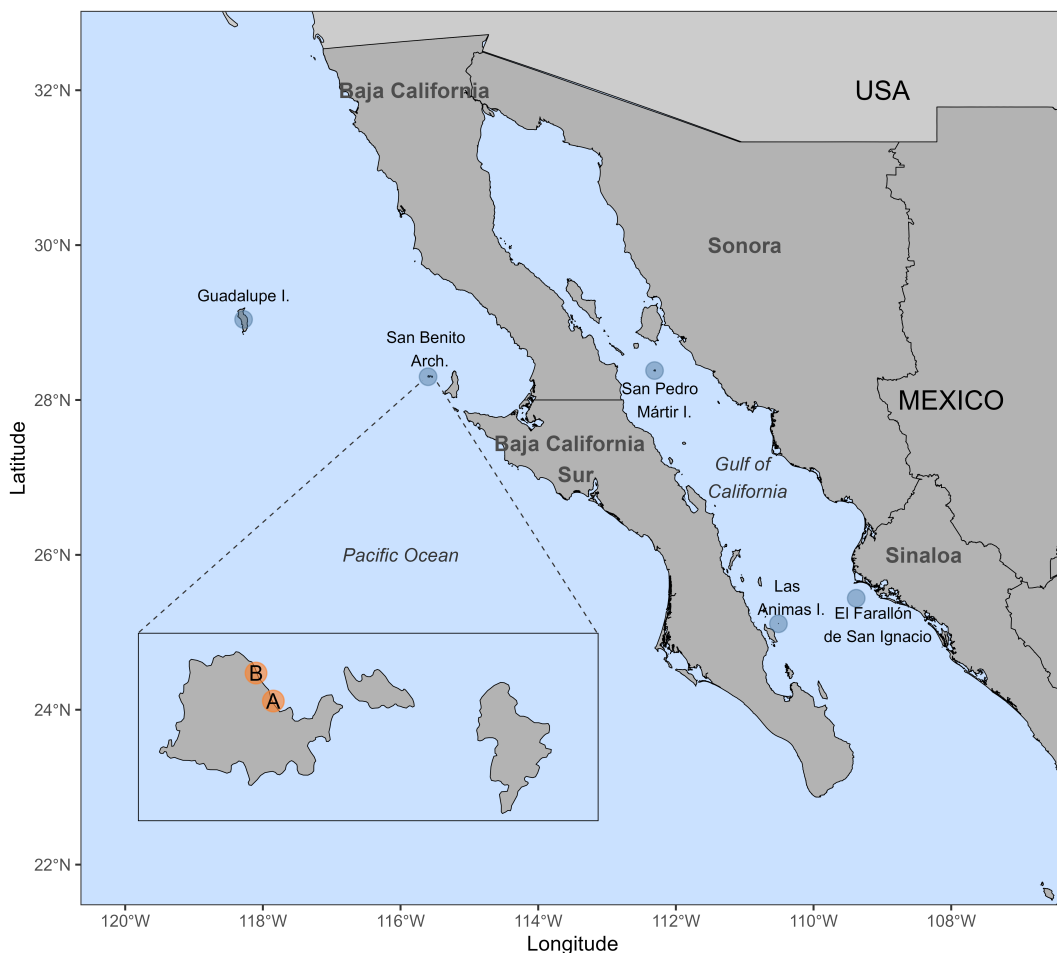


FIGURE 1 The study area showing the Guadalupe fur seal breeding colony (Guadalupe Island) and three sites where little breeding occurs (San Benito Archipelago, Las Animas, and Farallón de San Ignacio Islands) in Mexico. Since 2011, Guadalupe fur seals also have been observed resting in San Pedro Mártir (Gálvez et al., 2022). Study sites A and B were located on the West Island of the San Benito Archipelago.

did not begin to thoroughly document this behavior until the fifth day when an adult male abandoned its territory on Site A. This territorial male never returned and was replaced by subadult males that allowed and contributed to more frequent harassments of pups. Over the next 43 hr of sampling, we recorded 167 aggressive events towards pups (~ 4 events/hr), and nine successful abductions by five juvenile and four subadult males.

We differentiated between juvenile and subadult males based on their size and behavior. Subadults are larger (152 ± 5.6 cm) than juveniles (132 cm), and smaller than adult males (219 ± 18.8 cm; Gallo-Reynoso & Figueroa-Carranza, 1996). We also relied on neck thickness and the presence and size of testicles to confirm that it was a subadult male, and not a juvenile or adult female (148.2 ± 8 cm; Gallo-Reynoso & Figueroa-Carranza, 1996). Almost all aggressive events we observed during this time were perpetrated by juveniles (149 events; 89.2% of the total events), while subadult males accounted for 18 events (10.8%). In contrast, only one harassment event was recorded at Site B, in the territory defended by a subadult male.

Of the nine successful abductions of pups we observed (5.4% of all negative interactions with pups), two involved attempted copulations by two subadult males (involving pelvic movements without penetration). These two perpetrators often submerged their captured pups in tide pools for a few minutes at a time while attempting to copulate with them. All the abducted pups showed signs of physical exhaustion, although none were killed or appeared to suffer serious injuries. However, the lack of visible injuries does not preclude the possibility that some later died from starvation due to separation from their mothers or fatal internal injuries. Pups that escaped their abductors spent the remainder of the day resting or nursing if their mothers were in the territory. In contrast, pups that were not assaulted by juveniles or subadults appeared to be more active throughout the day (e.g., playing in tidal pools).

All the invading juvenile and subadult males at Site A infiltrated the periphery of the territory by exploiting the territorial subadult male's blind spot, keeping out of his field of vision (Figure 2). It appeared from a qualitative assessment of call types, that some of the young males tried to attract the attention of pups by mimicking the characteristic vocalizations of mothers calling for their pups after returning from feeding trips. Unfortunately, vocalizations were not recorded to confirm the similarity between calls heard.

Once the perpetrator seemed to successfully lure a pup closer, he would rush forward and attempt to grab the fleeing pup by the back of the neck or body. Once caught, the pup would be carried or dragged out of the reproductive territory and kept for 10–30 min, with the longest abduction lasting >12 hr. When their abduction attempts failed, the mostly juvenile perpetrators would linger in the territory for hours, resting and mimicking female-like behaviors such as open-mouth sniffing. Eventually, another opportunity to harass or abduct a pup would arise.



FIGURE 2 A subadult male Guadalupe fur seal entering the periphery of the territory of a sleeping adult male at site A during the reproductive season in the San Benito Archipelago to harass and abduct a pup.

Harassment, abduction, and sexual coercion of pups has been reported in other pinniped species, primarily otariids (Table 1). While isolated cases of pup harassment have been reported in the Guadalupe fur seal on Guadalupe Island (Gallo-Reynoso, 1994), such incidents appear to be more prevalent at the San Benito Archipelago where the frequency of harassment events averaged 20.7 ± 7.59 times per pup during 43 hr of observation, which was also much higher than reported for other species of otariids. For example, South American sea lion (*Otaria byronia*) pups were harassed 0.18 ± 0.09 times on average per breeding season (calculated from Campagna et al., 1988b). Similarly,

TABLE 1 Pinniped species that have been reported to sexually coerce pups (modified from Ryazanov, 2021).

Species	Age group of perpetrators	Sites	Targets of coercion	Source
South American sea lion (<i>Otaria byronia</i>)	Juvenile, subadult and adult male	Argentina, Peru, Uruguay, Chile, Falkland (Malvinas) Islands	Conspecific pups, South American fur seal pups	Campagna (2018), Campagna et al. (1992, 1988a,b), Cassini (1998), Drago et al. (2011), Le Boeuf and Campagna (1994), Harcourt (1992)
Australian sea lion (<i>Neophoca cinerea</i>)	Subadult and adult male	Dangerous Reef	Conspecific pups	Higgins and Tedman (1990), Marlow (1975), Ryazanov (2021)
New Zealand sea lion (<i>Phocarctos hookeri</i>)	Adult male	Enderby Island	Conspecific pups	Marlow (1975)
Northern fur seal (<i>Callorhinus ursinus</i>)	Subadult	St. Paul Island, Commander Islands, Kuril Islands, Tuleny Island	Conspecific pups	Kiyota and Okamura (2005), Ryazanov (2021)
	Subadult		Steller sea lion pups	Ryazanov (2021)
Guadalupe fur seal (<i>Arctocephalus townsendi</i>)	Subadult	San Miguel Island	California sea lion pup (<i>Zalophus californianus</i>)	Stewart et al. (1987)
		Guadalupe Island	Conspecific pups	Gallo-Reynoso (1994)
Antarctic fur seal (<i>A. gazella</i>)	Subadult	Macquarie Island	Conspecific pups	Robinson et al. (1999)
	Adult	Marion Island	Adult king penguin (<i>Aptenodytes patagonicus</i>)	de Bruyn et al. (2008), Haddad et al. (2015)
South American fur seal (<i>A. australis</i>)	Subadult	Isla de Lobos (Uruguay)	Conspecific pups	Ryazanov (2021)
Northern (<i>Mirounga angustirostris</i>) and southern (<i>M. leonina</i>) elephant seal	Adult and subadult	Año Nuevo Island, Protection Island	Conspecific pups and juveniles, harbor seal pups (<i>Phoca vitulina</i>)	Hayward (2003), Le Boeuf and Campagna (1994), Rose et al. (1991)
Gray seal (<i>Halichoerus grypus</i>)				Campagna (2002)
Hawaiian monk seal (<i>Monachus schauinslandi</i>)	Adult	Northwestern Hawaiian Islands	Conspecific pups	Campagna (2002), Hiruki et al. (1993)

the average northern fur seal pup (*Callorhinus ursinus*) at St. Paul Island, Alaska, was reportedly harassed 3.8 times per breeding season (Kiyota & Okamura, 2005).

Although our 43 hr of observations on the San Benito Archipelago falls far short of an entire breeding season as observed for northern fur seals and South American sea lions, the frequency of harassments we observed of Guadalupe fur seal pups is an order of magnitude higher than those observed elsewhere. Part of the high discrepancy in pup harassment rates between species is likely due to differences in the numbers of pups and juveniles present and the lack of adult territorial males. Whereas the northern fur seal and South American sea lion breeding colonies had territorial bulls with more than 400 pups in each study area, the San Benito Archipelago colony we studied only had ~100 pups among an overall population composed of ~90% juveniles with greater numbers of younger mature males defending breeding territories. As such, there was a greater likelihood of Guadalupe fur seal pups being more exposed to harassment by immature males from the margins of the breeding territories at San Benito Archipelago than at Guadalupe Island.

In general, the events we observed with Guadalupe fur seals at the San Benito Archipelago followed a similar pattern to that reported in northern fur seals, South American sea lions, New Zealand sea lions (*Phocarctos hookeri*), and Australian sea lions (*Neophoca cinerea*)—whereby invasive males enter the periphery of reproductive territories via the blind spots of territorial males (Campagna et al., 1988b; Kiyota & Okamura, 2005; Marlow, 1975). These invaders also appear to imitate female-pup calls to attract and seize pups that approach, then abduct them from the safety of the reproductive territories for minutes or hours (Campagna et al., 1988b).

Harassment of pups by subadult and juvenile males may reflect their sexual inexperience, physical immaturity, and high sexual motivation (Campagna et al., 1988b; de Bruyn et al., 2008; Rose et al., 1991). The intense sexual drive of males has led juveniles of some species to copulate with stones and logs (e.g., northern fur seals; Ryazanov, 2021) or with other males (e.g., New Zealand sea lion and harbor seals, *Phoca vitulina*; Marlow, 1975; Thompson, 1988). Instances of young adult male Subantarctic fur seals (*Arctocephalus tropicalis*) sexually coercing adult king penguins have also been recorded (de Bruyn et al., 2008; Haddad et al., 2015).

During our study at San Benito Archipelago, we observed juvenile Guadalupe fur seals performing pelvic movements with other subadult and adult males, including those defending reproductive territories. The combination of a sexually stimulating environment, high sexual motivation, and the inability to control adult females may drive some immature males to harass, abduct and attempt to copulate with pups that they can easily control (Campagna et al., 1988a,b; Le Boeuf & Campagna, 1994; Tinbergen, 1952).

Sexual coercion of pups may ultimately enhance the future reproductive success of young male otariids who engage in this behavior. Such behavior may provide them with territorial-like experiences in copulating and controlling the movements of subordinates (Campagna et al., 1988a,b; de Bruyn et al., 2008). Males that abduct pups learn to briefly fight with other males and engage in territorial defensive behaviors that have little risk of causing themselves physical harm. There is also little likelihood of being attacked or harmed by territorial males that only need to vocalize and approach to drive immature males from their territories. Thus, the seemingly aberrant sexual behaviors we observed may be part of an evolutionary strategy of pinniped polygynous breeding systems, enabling males to gain early breeding-type experiences that improve reproductive success when they eventually need to engage in territorial behavior to access and mate with adult females (Campagna et al., 1988b; Cassini, 1998; Kiyota & Okamura, 2005). It is also possible that sexual coercion of pups occurs more frequently at newly established reproductive colonies where the number of territorial males protecting adult females and pups from harassment by immature males is lower than in well-established reproductive colonies (Campagna et al., 1992; Drago et al., 2011), as seen at the San Benito Archipelago Guadalupe fur seal colony.

In some cases, the behaviors of immature males toward pups can increase pup mortality and reduce parental reproductive success (Campagna et al., 1988b; Higgins & Tedman, 1990; Marlow, 1975; Ryazanov, 2021). Indeed, harassment is considered one of the main causes of pup deaths among northern fur seals (Kiyota & Okamura, 2005), Antarctic fur seals (Robinson et al., 1999), South American sea lions (Campagna et al., 1992; Drago et al., 2011), and Australian sea lions (Higgins & Tedman, 1990). Death is often attributed to physical trauma caused by handling or

crushing the pup, leading to bruising, internal bleeding, fractures, or cranial damage. Pups may also drown if forcibly taken into the water. Additionally, these events can sometimes result in the separation of mother-pup pairs and suspension of nursing, causing the pup to become lost and unable to return to its mother for two or more days leading it to lose weight or die from starvation (Campagna, 2018; Kiyota & Okamura, 2005). The extended fasting that Guadalupe fur seal pups incur while their mothers are foraging for two weeks or more (Norris & Elorriaga-Verplancken, 2020) may also increase the likelihood of pups dying from the stress of harassment and abduction.

Although we did not observe any dead pups in the San Benito Archipelago colony, 43% of nursing sessions (56 of 129) were interrupted at Site A. Of these interruptions, 54% (30 of 56) were due to juveniles harassing the pups, and 12.5% (7 of 56) were due to harassment by subadult males. Invading immature males also harassed females, but to a lesser extent. In two instances, the persistence of the juvenile and subadult invaders caused the females to go to sea and stop nursing their pups, thereby abandoning the reproductive area. One of the mothers we observed returned after 4 hr, while the other did not return until the following day. The severity of disturbances may affect whether females return to San Benito Archipelago next year or whether they go back to the stability of the rookeries at Guadalupe Island.

We suspect that the harassment and abduction of pups, as well as interruptions of nursing by juvenile and subadult males is negatively affecting the recovery of Guadalupe fur seals at the San Benito Archipelago colony as reported for South American sea lions (Drago et al., 2011). The disruptive actions of immature males may explain why this expansion colony has yet to become a well-established reproductive colony nearly 30 years after being first discovered (Maravilla Chavez & Lowry, 1999). Our hypothesis can be tested by comparing the reproductive behaviors at the San Benito Archipelago with those at the established breeding colonies at Guadalupe Island over entire breeding seasons, while simultaneously assessing diet quality, pup body condition, pup growth rates, immune system status, pup stress hormone levels, and pup mortality rates (Banuet-Martinez et al., 2017; Drago et al., 2011). Comparing these variables between island colonies would offer valuable insights into the factors that ultimately control the establishment of new breeding colonies. Understanding the recovery process of a species that was once on the brink of extinction is needed to set realistic conservation goals and assess current population status and threats.

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AUTHOR CONTRIBUTIONS

Guillermo Vallarino-Orozco: Conceptualization; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Ingrid Monserrath Burgoin-Diaz:** Conceptualization; investigation; methodology; visualization; writing – review and editing. **Fernando Elorriaga-Verplancken:** Funding acquisition; investigation; supervision; writing – review and editing. **Tenaya Norris:** Funding acquisition; writing – review and editing. **Andrew Trites:** Conceptualization; investigation; writing – review and editing. **Claudia Janetl Hernández-Camacho:** Conceptualization; formal analysis; funding acquisition; methodology; project administration; supervision; visualization; writing – original draft; writing – review and editing.

ORCID

Guillermo Vallarino-Orozco  <https://orcid.org/0009-0008-0931-2162>

Ingrid Monserrath Burgoin-Diaz  <https://orcid.org/0009-0009-7270-959X>

Fernando R. Elorriaga-Verplancken  <https://orcid.org/0000-0002-7360-8039>

Tenaya Norris  <https://orcid.org/0000-0003-1682-7881>

Andrew W. Trites  <https://orcid.org/0000-0003-0342-5322>

Claudia J. Hernández-Camacho  <https://orcid.org/0000-0002-6309-9728>

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