Short Note

Allonursing in Guadalupe Fur Seals (*Arctocephalus philippii townsendi*) as a Response to Pup Mortality Caused by a Tropical Depression

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Catastrophic events, such as hurricanes, earthquakes, and tsunamis, are significant forces of nature that might shape the responses of individuals subject to such harsh environmental pressures. Hurricanes can change the shape of coastal areas that are exposed to storm surge (Needham et al., 2015); the frequency and height of oceanic waves that strike the coast with long, high, and massive waves, and the heavy rains and strong winds associated with cyclones also affect the coastline through erosion (Birchler et al., 2014). Thus, these forces might modify the pinniped terrestrial habitat or render it useless temporarily. The Southern Oscillation-El Niño event is one of the most emblematic examples of how climate events can impact survival rates and feeding patterns of pinniped species (Le Boeuf & Reiter, 1991; Trillmich et al., 1991); however, little has been mentioned or documented on how these atmospheric-oceanic nonglobal scale events can impact survival rates and how it disrupts the recognition between mothers and their offspring in a pinniped that is recovering from past human exploitation (Le Boeuf & Reiter, 1991; Gallo-Reynoso et al., 2005). Due to over-exploitation, the Guadalupe fur seal (GFS; Arctocephalus philippii townsendi) shows low genetic variability (Bernardi et al., 1998; Weber et al., 2004). Herein, we report the response of the female GFS to such a short-duration catastrophic event in 1992 when tropical depression "Darby" struck the island from 6 to 10 July 1992 (Lawrence & Rappaport, 1994), just after the median pupping peak on 2 to 3 July (Gallo-Reynoso, 1994). Even though the data are old, it is still important to know how these events can change the viability of an endangered population. Therefore, we approach the impact

effects of this tropical depression by analyzing two different questions: (1) How was the population affected by the tropical depression? and (2) What is the behavioral response of mothers when their pups were affected by the tropical depression?

There is no available historical information for hurricane strength, track, and effects on Isla Guadalupe, nor are there historical censuses of the GFS population at this island that describe how tropical depressions, tropical storms, or hurricanes might have affected the species (Fleischer, 1987; Pierson, 1987). Gallo-Reynoso (1994) conducted censuses and behavioral observations from 1991 to 1993 and mentioned the effects of tropical depression Darby on the GFS population by describing the mortality of offspring and the effect on the breeding population during an initial recovery phase of the species from past exploitation.

The El Niño event of 1992 triggered a higher sea level (30 cm above average) along the California coast (Fahrbach et al., 1991), which was corroborated at Isla Guadalupe (Gallo-Reynoso, 1994). This elevated sea level was similar to the El Niño event of 1983 that affected Galapagos Island during the Galapagos fur seals' (*Arctocephalus galapagoensis*) breeding season, which caused drastic changes in female attention behavior to their pups and population age structure due to the lengthening of female foraging trips (Trillmich & Limberger, 1985; Trillmich & Dellinger, 1991).

This event triggered some behavioral reactions of the GFS not yet observed before, such as alloparental care, which is the care directed by an individual (an alloparent) toward dependent young that are not their offspring (Wilson, 1975). It also may include protecting, feeding, transporting, and interacting with nonfilial offspring (Riedman, 1982; Beaulieu et al., 2009; Stead et al., 2019), although it may be called adoptive suckling or fostering (Stirling, 1975) or fostering behavior (Gemmell, 2003). Fostering behavior, a form of alloparental care, happens when female pinnipeds nurse nonfilial offspring (Lunn, 1992). Alloparental care does not exclude related young such as siblings or grandchildren (Wisenden, 1999). Alloparenting can be energetically costly and might enhance the survival of a nongenetically related individual; increased costs of alloparenting include milk production, inability to care for other descendants, weight loss, and exposure to predators (Stead et al., 2019). Thus, an alloparent's lifelong reproductive success may be reduced (Stead et al., 2019). Therefore, alloparenting should be strongly selected against (Gemmell, 2003; Stead et al., 2019) because it contradicts Darwinian Theory (Clutton-Brock et al., 1989; Kouba et al., 2016). In contrast, investing in relatives will produce direct or indirect fitness if a population has a shared genetic pool as in the GFS (Bernardi et al., 1998; Weber et al., 2004).

Furthermore, alloparental care directed to nonkin offers no or minimal fitness benefits (Packer et al., 1992). However, according to Armitage (1987), apparent altruism is exerted to gain time, expertise, and maturity, thus increasing the probability of survival. Roulin (2002) stated that alloparental care has some benefits, such as continuing in a specific hormonal state until implantation of the fertilized blastocyst (Riedman, 1982; Solomon & French, 1997), and included gaining experience to help achieve probable long-term reproductive success. Even with the cost associated with the latter, alloparents can accrue some inclusive and direct fitness benefits (Stead et al., 2019).

In mammals, alloparental care is generally observed intra-specifically (Stead et al., 2019). For pinnipeds, expression of alloparental care will depend on the reproductive colony and the high or low density of individuals in the colony (Riedman & Le Boeuf, 1982). Alloparenting has been reported in otariids such as Antarctic fur seals (Arctocephalus gazella; Lunn, 1992; Gemmell, 2003), New Zealand fur seals (Arctocephalus tropicalis; Georges et al., 1999), and Steller sea lions (Eumetopias jubatus; Maniscalco et al., 2007). It is more common in phocid seals such as southern and northern elephant seals (Carrick et al., 1962; Riedman & Le Boeuf, 1982), Weddell seals (Leptonychotes weddelli; Stirling, 1975), and grey seals (Halichoerus grypus; Smith, 1968). Several cetacean species have been shown to engage in alloparental care. This has been observed in Indo-Pacific bottlenose dolphin

(*Tursiops aduncus*; Sakai et al., 2016), sperm whales (*Physeter macrocephalus*), and beluga whales (*Delphinapterus leucas*), which allonurse (i.e., nurse calves not their own; Best et al., 1984; Leung et al., 2010). These cetaceans live in different social groups, including labile fission-fusion societies, stable matrilineal units, and combinations of these structures (Rendell & Gero, 2014). Alloparental care is also found in birds such as Adélie penguins (*Pygoscelis adeliae*; Beaulieu et al., 2009) and Tengmalm's owl (*Aegolius funereus*; Kouba et al., 2016).

Alloparenting may end up in adoption (Riedman, 1982), defined as protecting and feeding the young of a filial or nonfilial offspring (Stead et al., 2019). These affiliative interactions between alloparents and nonfilial offspring can be maintained throughout life (Stead et al., 2019) and might lead to lifelong fitness for both parties (Maestripieri, 1994). Although relatively rare, adoption has been reported in California sea lions (*Zalophus californianus*; Flatz & Gerber, 2010). This altruistic behavior might be favored because it enhances the inclusive fitness of the individual caring for the offspring (Stead et al., 2019).

Did female GFSs provide alloparental care toward unknown pups after tropical depression Darby? Herein, we present the observations related to this catastrophic event on the GFS population at Isla Guadalupe and evidence of alloparenting behavior toward orphaned pups by adult female GFSs for whom kin relations were unknown.

The study site was located on the southeastern coast of Isla Guadalupe at 28° 54' 32.23" N and 118° 14' 25.08" W (Figure 1). This location was chosen because of its low fur seal density ($\bar{x} = 1.8$ \pm 0.6 individuals/100 m²; range: 1.1 to 2.2 individuals/100 m²; n = 3 breeding seasons). The area covers a stretch of shoreline approximately 500 m long by ~ 10 to 40 m wide (total area $\sim 5,000 \text{ m}^2$). The site presents a diversity of pinniped habitats, including coves with cobblestone beaches, large tidal pools, cliff face areas, lava dikes, and a wide lava platform $(\pm 3 \text{ m})$ above sea level with large and shallow tidal pools. The study area includes sections with a very narrow stretch of coastline; the distance between the cliff face and the water's edge averages 8 to 10 m (\pm 4 m). Despite the rough coastline, the area affords good access and visibility from above the cliffs to conduct observations. Water depths range from 10 to 15 m and increase rapidly with distance from shore; at 50 m from shore, it drops to 30 to 70 m. The central part of the observation area has a lava reef at 2 m depth, ranging from 8 to 15 m beyond the reef. Two submerged rocks provide aggregation points for rafting seals. The tides were semidiurnal with a range of \pm 30 cm (Gallo-Reynoso, 1994).



Figure 1. The study area at Isla Guadalupe is shown in the small rectangle in the southeastern part of the island. The coastline and male territories of Guadalupe fur seals (*Arctocephalus philippi townsendi*) are shown in the area.

GFSs were counted daily at the study site during the breeding seasons of 1991 (29 d), 1992 (35 d), and 1993 (37 d) (Figure 2), as well as in winter, spring, and fall (Gallo-Reynoso, 1994). Censuses were conducted in daylight between 0700 and 1900 h by walking along the cliff border from south to north (average height of 5 m). Males and females were individually identified by their size, natural marks (e.g., scars, cuts in their flippers, coloration), or individual vocalization characteristics. Pups were manually captured and marked when most females in a territory were foraging at sea, allowing us to confirm female-pup pairs when females returned to nurse their pups. Therefore, the pup marking procedure did not cause noticeable perturbation to the colony. A total of 50 pups were marked during the 1992 breeding season. There were 79 females in the study site; 15 of these were captured with a hoop net, measured, restrained, weighed, and marked (Gallo-Reynoso & Figueroa-Carranza, 1996). Pups and females were marked with white cream bleach (Wellite, Wella Corp., Englewood, NJ, USA) to facilitate their identification for at least the nursing period of 9 mo (Gallo-Reynoso & Figueroa-Carranza, 1996). Most females were marked by noting their natural marks on an identification card, such as scars, bites, missing body parts, coloration, vibrissae color, and so on (Figueroa-Carranza, 1994).

GFSs present in male territories were assigned to the following age/sex classes: adult males (territorial bulls and other males with a silver mane and a thick neck), adult females, subadult males, juveniles, and pups (with black natal coat changing to dark brown across the reproductive season and to a silver coat when weaning). Identified females were classified according to Gallo-Reynoso (1994) and Gallo-Reynoso & Figueroa-Carranza (1996) into three categories: (1) *multiparous females* were those that presented cream-white vibrissae, including animals more than 6 y old, of about 1.52 m (\pm 59 cm; range: 1.38 to 1.65 m; n = 10) in length, with a mass of 52 kg (\pm 4.9 kg; range: 41 to 55 kg; n = 4), with



Figure 2. Population of Guadalupe fur seal pups from 1991 to 1993 at Corralitos, Isla Guadalupe, México: (A) newborn pups at the rookery in 3-y period. Note that after tropical depression "Darby" struck the island in early July 1992, pup mortality increased, followed by an increase of newborn pups, and then decreased again due to the death of starving pups that were separated from their mothers by the storm; and (B) the number of dead pups on the rookery after the tropical depression struck the island in 1992 compared with pup mortality in the previous and following years. (Modified from Gallo-Reynoso, 1994)

a pup; (2) *primiparous females* were those with white and black vibrissae, 1.39 m in length, with a mass of 41 kg, also with a pup; and (3) *nulliparous females* (juvenile), 1.32 m in length, at a mass of 37 kg (n = 1), with completely black whiskers, aged 3 to 4 y, without a pup (Gallo-Reynoso & Figueroa-Carranza, 1996).

During the breeding season, births peaked between 22 June and 4 August, with a median date of 3 July (combined data from 1991, 1992, and 1993; Figure 2). The last pup was born on 4 August 1993. This extended the parturition period for more than 13 d compared to another report in which the population peaked on 21 June (Fleischer, 1987).

Pups in the study area were captured, weighed, and measured a week after birth so as not to disrupt the bond between mother and pup. Afterwards, they were weighed and measured weekly or, when possible, they were captured in different climatic seasons to assess their growth rate until weaning (Gallo-Reynoso & Figueroa-Carranza, 2010). While pups were restrained in a net, they were also bleach-marked to identify them and to know who their mothers were. In 1992, the sea took away many marked pups (including those of females instrumented with time-depth recorders; Gallo-Reynoso et al., 2008). As a result, additional unmarked orphan pups that drifted to the study area were caught (n = 8), and their body condition was assessed (size and body mass measurements). They were also marked similarly; these individuals are included in the total number of pups measured.

Was the GFS population affected by the tropical depression? Darby struck the island from 6 to 10 July 1992 (Lawrence & Rappaport, 1994), just after the median pupping peak on 2 to 3 July

(Gallo-Reynoso, 1994; Figure 2). We observed that long oceanic waves with crests as high as ~ 10 m (height compared to known depth rocks and known altitude cliffs) arrived during high tide and penetrated the GFS territories (Figure 3). These waves washed away almost all pups born (47 out of 50 marked pups) before the storm. Still, 15 of those pups managed to return to shore and survived.

Three forms of disruption caused by this tropical depression were identified: (1) the sea level was already \pm 30 cm above the average due to El Niño oceanographic conditions in 1992; (2) the storm surge was 2 m high (compared to the water level increase at initial observations on the lava platform we used to disembark)-together. these two disruptions enabled high surf and tides to flood the territories, creating confusion between individuals and separating pups from their mothers (Figure 3); and (3) oceanic waves rolled over the rookery. Storm surges and waves washed away 94% of the pups from the rookery, causing most adult females, subadults, and juveniles to abandon the area for the sea. The territorial bulls remained on their territories (even floating in the strong waves). Some juveniles and subadult males sought refuge on higher ground or in the vegetated area above the cliffs. Pups remained in the water, trying to haul out for several hours to 3 d. Because of the changing direction of the surface currents, surviving pups floated to the north and the south several times, finally returning to land, although, in many cases, to the wrong area of the rookery. Sometimes, pups landed kilometers from the beach where they were born (as witnessed in in situ observations of marked pups away from their natal rookery).



Figure 3. In these images (blurry old transparency slides), the storm surge hit the rookery in this GFS male's territory. Pups close to the water's edge were vulnerable. Females were constantly calling their pups. Note that the male position is guarding against the waves; several pups were washed away from that territory. All females departed to the sea, and the male stayed on defending its territory during the event.

After Darby passed, it took over a week to calm down the movements of GFS individuals at the study site at Isla Guadalupe. New pups continued to be born; the population increased despite this setback (Gallo-Reynoso, 1994; Figure 2).

Between 5 to 8 d after the tropical depression struck the island, we conducted a general census of the breeding population of GFSs around the island's coasts. The overall mortality of GFS pups calculated for the whole population at Isla Guadalupe was 36% in 1992 due to this single storm (Gallo-Reynoso, 1994); pups were washed away and killed by storm surge and pounding waves (many pups were struck against rocks), drowned, or, once on land, starved. Many pups lost their mothers or returned to land in a different territory. Alive pups were seen swimming in the sea near the eastern coast of the island, trying to reach the coast; other pups were on the beaches used by elephant seals and California sea lions as haulouts on the northeastern side of the island or at an islet to the south of the main island. Many dead pups, partially eaten by sharks, were seen floating in the following days.

At our study site, newborns to month-old pups were washed away by storm surges and waves, causing the death or disappearance of 35 pups (out of 50 marked pups) or 70% mortality (Figure 2). On 19 July, we counted 30 unmarked pups that arrived at the study site after being washed away by waves, plus 15 marked pups that survived and remained in the rookery, totaling 45 pups. These 30 new pups were categorized as orphans. Death due to starvation for orphaned pups began on 21 July. By 9 August, the number of pups on the rookery was 35 alive and 10 dead.

Female foraging trips were modified, and females leaving the island during the storm took 3 to 28 d to return to attend to their pups. Several unattended/orphaned pups died after 30 d of fasting. Two orphaned and starving pups had lower body mass (3.5 and 3.8 kg) than the mean newborn body mass of both sexes of 4.5 kg (female) and 5.5 kg (male) (Gallo-Reynoso & Figueroa-Carranza, 2010); days later, both pups were found dead.

Tropical depression Darby was not the only cause of pup mortality. This depression along with the warm waters of El Niño in 1992 were the cause of death for orphaned and not-orphaned pups due to their mothers shortening their foraging trips by 4.5 d, compared to their foraging trips of 1992 to 1993. Even though there is no significant difference, the trip shortening was probably due to not finding enough resources at sea because of the reduced primary productivity in the California Current due to El Niño event warm surface waters (Heath et al., 1991). Female foraging trips in 1992 had a mean duration of 9.0 ± 6.4 d (n = 24); during 1993, remnants of El Niño conditions were milder, even though female foraging trips were extended, with a mean duration of 13.5 ± 7.0 d (n = 31). The extended foraging trips were probably due to females finding more resources (Figueroa-Carranza, 1994; Gallo-Reynoso, 1994). Their pups were found in a better condition as well, suggesting that pups were better fed and able to fast for more days.

The mean duration of female attendance to pups during 1992 was 5.1 ± 3.5 d (n = 15) and 6.5 ± 3.8 d (n = 26) during 1993. These were somewhat different even though the difference is not significant. Females who lost their pups due to the tropical depression in 1992 had a mean extended stay on land of 3 d (n = 10)—time that was spent searching for them (Figueroa-Carranza, 1994; Gallo-Reynoso, 1994).

What is the behavioral response of mothers regarding their pups that were affected by this tropical depression? Female pup recognition in otariids is mainly vocal but has some odor clues (Figueroa-Carranza, 1994; Insley et al., 2003; Southall et al., 2006; Maniscalco et al., 2007). To a human ear, recently arrived pups in some territories had a similar vocalization to that of known pups in the same territory (those of marked pups that we knew had disappeared during the storm). We focused our observations and meticulously observed two marked females who returned from a foraging trip (we knew they had lost their marked pups, but the females did not). Upon arriving, both females started to make the attraction call to their offspring (Southall et al., 2006), and the response came from some marked surviving pups and other unmarked surviving pups. The females were confused and restless for a day or two, but both females ended up allonursing nonrelated pups (unmarked pups) until weaning.

In three instances, unmarked pups from other areas were reunited with their unmarked mothers, who also arrived at the rookery making attraction calls to their missing offspring. The pups responded, resulting in recognition by both individuals. We marked these pups to follow their growth when there was an opportunity. Those alien female–pup pairs remained in the study area for the rest of the year. Furthermore, these three females were found in the study area during the following breeding season (1993).

Other females that were already on a foraging trip during the storm, or that went out to sea when the storm struck the rookeries and unknowingly lost their pups, returned and persisted in doing the attraction call for 2 or 3 d in their territory and then visited other adjacent territories for a couple of days, searching and calling for their pups. After that search, several marked females that did not find their pups went back to sea. When doing the seasonal census of GFSs around the island in July 1992, we observed a marked pup with its marked mother that had survived in a distant territory where we could not follow up on its development until weaning.

A week after the storm, some females were still searching for their pups and were mobbed by raids of hungry, orphaned pups waiting for their mothers. In a particular case, pups that were fasting and waiting for their mothers, upon the arrival of an unknown female who was calling for her pup, responded to her call, moving toward the calling female and cornering her, trying to suckle. The female avoided this situation by biting the pups, opening a way to get out of the situation.

In another case, the male pup of a known female had a dark snout and chin (no yellow color in the snout area and chin as is usual in the species) and was already marked by us. The pup was lost in the storm, and the female allonursed an unmarked female pup with a yellow snout and chin. The pair was observed again in November 1992 while we were measuring and weighing all the marked pups in the study site. Also, in November 1992, we found that other marked females who had lost their pups to the storm and consequently went to sea to forage were observed allonursing unmarked pups. Of 79 females in the study site, seven marked females had allonursed unmarked pups and exhibited long-term alloparenting behavior until weaning in February 1993. Thus, seven GFS females, or 8.9% of females in the study area, allonursed unrelated offspring.

GFS females exhibited an extended allonursing behavior during the year when these atmosphericoceanic nonglobal scale events occurred. In some cases, this allonursing behavior may have resulted in alloparenting, even though there was no way to confirm kin relations between mothers and pups. Why will a female GFS invest resources in the survival of another female's offspring? Allonursing and alloparenting in mammals, such as pinnipeds, should happen only in situations in which the members of the group are related—mainly, if females present a high degree of philopatry. Due to this philopatry, females tend to live in the same rookery in which they were born, which increases the chances of relatedness. Riedman (1982) explains that females in pinniped species will provide allonursing, alloparental care, fostering behavior, or adoption if there is a way to obtain parental experience that might be particularly valuable to those females with the following reproductive traits: (1) a prolonged or energy-intensive period of parental investment, (2) production of single young, and (3) limited lifetime reproductive potential (few offspring). The GFS is a species in which those traits are satisfied.

Also, these behaviors might be observed in species that share a lower degree of genetic variability due to rookery isolation or a recent genetic bottleneck. Perhaps the low genetic variability of the GFS (Bernardi et al., 1998; Weber et al., 2004) answers why these females exhibit allonursing behavior and why they may foster offspring that may or may not be related.

However, the decreasing pup numbers at the study site were mainly due to the storm surge and large waves produced by the tropical depression rather than the shortening of female feeding trips due to the El Niño event that produced low resource availability, as noted in the cited research elsewhere. Finally, as stated by several studies, allonursing in pinnipeds is eventually a consequence of environmental conditions in which mothers and pups are separated, as we report in the present study; the reunion of mother and pup might be hindered because mother-pup recognition may not be well established due to the age (several days) of pups, or it might be caused by maternal inexperience (Bowen, 1991; Boness et al., 1992; Lunn, 1992; Georges et al., 1999).

In the words of Burney J. LeBoeuf, "Alloparental care is making the best of a bad situation: the nursing female recoups her pup loss partially, and the adoptee survives via the largesse of the unrelated mother" (pers. comm. to JPG, July 2024).

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