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Postmortem examination and causes of death of northern elephant seal (*Mirounga angustirostris*) pups of the San Benito Islands, Baja California, Mexico

ELENA SALOGNI,[1,2] Elephant Seal Research Group, Via Buonarroti 35, 20145 Milan, Italy and Dipartimento di Bioscienze, Università degli Studi di Milano, Via Festa del Perdono 7, 20122 Milan, Italy; SIMONA SANVITO, Elephant Seal Research Group, Via Buonarroti 35, 20145 Milan, Italy and Facultad de Ciencias Marinas, Universidad Autónoma de Baja California, Km 103 Carretera Tijuana-Ensenada, Ensenada 22860, Baja California, Mexico; FILIPPO GALIMBERTI, Elephant Seal Research Group, Via Buonarroti 35, 20145 Milan, Italy.

Early development of an organism may greatly affect its future survival and reproductive success (Lindström 1999). Juvenile mortality is an important aspect of the life history of many species (Stearns 1992), shows variation among the sexes (Van Schaik and De Visser 1990), is affected by reproductive strategies and social behavior (Van Schaik and Kappeler 1997), and has important effects on demography and population dynamics (Eberhardt 1981, Gaillard *et al.* 1998). A peculiar component of juvenile mortality of mammals is preweaning mortality (Caughley 1966), that often changes widely over time and between populations (Gaillard *et al.* 2000, Beauplet *et al.* 2005), is often strongly related to mother's phenotype and care behavior (Lycett *et al.* 1998), and is particularly affected by environmental factors like climate variability (Kerhoas *et al.* 2014). In pinnipeds, preweaning mortality can be affected by various social and environmental factors, including (1) size and density of the social units (McMahon and Bradshaw 2004); (2) disturbance, aggression, and harassment by adults (Kiyota and Okamura 2005); (3) physical characteristics of the breeding habitat (Twiss *et al.* 2000); and (4) weather and sea conditions (Stewart and Yochem 1991). Preweaning mortality varies markedly between different species of pinniped and between populations of the same species (Anderson *et al.* 1979, Harcourt 1992, Reid and Forcada 2005), and this applies also to the two species of elephant seals (genus *Mirounga*). In southern elephant seals (*M. leonina;* SES) preweaning mortality is usually below 5% (Campagna *et al.* 1993, Galimberti and Boitani 1999, Pistorius

[1]Corresponding author (e-mail: fil_esrg@eleseal.org).
[2]Current address: Elephant Seal Research Group, Sea Lion Island, Falkland Islands.

et al. 2001), while in northern elephant seals (*M. angustirostris;* NES) it is usually higher and more variable: in the colonies along the California coast, preweaning mortality is on average about 20% (Le Boeuf and Briggs 1977, Le Boeuf *et al.* 1994) but it can increase up to 80%–90% during El Niño events at some breeding sites (Stewart and Yochem 1991).

Determination of causes of mortality in wild populations is an important but difficult task, because death is often produced by multiple causes that are difficult to assess in the field (Spraker *et al.* 2014). Most studies of preweaning mortality in NES have been carried out at Año Nuevo (AN; Morejohn and Briggs 1973, Le Boeuf and Briggs 1977, Spraker *et al.* 2014) in California, which is a fast increasing colony where the main causes of preweaning mortality seem to be of social origin, including crushing by males and wounds caused by female aggression (Morejohn and Briggs 1973, Le Boeuf and Briggs 1977). Le Boeuf and Briggs (1977) introduced the "trauma starvation syndrome" (TSS), to indicate a set of factors that jointly determine pup mortality, including starvation, wounds produced by alien female aggression, crushing by males (adult harem holders in particular), and general trauma due to male harassment carried out mostly by young males. The starting point of TSS is mother-pup separation, followed by definitive abandonment, such that the pup is not able to suckle and is not protected by the mother, being vulnerable to aggression by alien females and by male harassment. Pup necropsies conducted at AN by Morejohn and Briggs (1973) found internal bleeding and fractures related to crushing, and wounds likely produced by female canine teeth, and suggested the intensity of aggression and pup mortality to be related to harem density. More recently, Spraker *et al.* (2014) identified four main causes of mortality at AN: trauma, starvation, infections, and congenital anomalies, often acting together to produce the actual death. Moreover, they suggested that (1) although trauma is commonly present, it is not always the primary cause of death; (2) drowning can be an important cause of death during high seas and storms; (3) stillbirths are a rather rare phenomenon on AN, probably less frequent than in SES (Baldi *et al.* 1996, Galimberti and Boitani 1999).

The Mexican NES colonies, concentrated in the northern part of Baja California, are much less studied than the Californian colonies, and have a different demography (stable or decreasing *vs.* increasing; Stewart *et al.* 1994; FG, personal observation). Moreover, they also show a greater variation in factors that may affect preweaning mortality, including harem size and density, and topography and substrate of the breeding areas. The San Benito Islands colony is particularly interesting, not only because it had a crucial role in NES demography history and recovery (Bartholomew and Hubbs 1952, 1960) but also because it is the southernmost breeding colony of the species (Stewart *et al.* 1994), and presents a hotter local climate, compared to California colonies, that may produce a significant thermal stress for the seals, and pups in particular (White and Odell 1971).

We studied NES at the San Benito Islands (SB) during the 2006–2007 breeding season (December–February). We marked pups with numbered plastic tags (Jumbo Rototags, Dalton Supplies, http://www.dalton.co.uk) placed in the interdigital webbing of the hind flippers, and with hair bleach marks. We carried out daily surveys of the breeding beaches to identify pups and recover the dead ones. We did regular observations of marked mother-pup pairs to determine separation, abandonment, aggression by females, and crushing events. Dead pups were also marked with a numbered metal tag attached to the rear right flipper with a cable tie. We carried out full necropsies of 21 pups shortly after death (9 within 24 h, 12 between 24 and 48 h). For the necropsy, dead pups were moved to a flat, shaded area, away from harems, as soon as they were recovered. The necropsy protocol followed Le Boeuf *et al.* (1972) and Dierauf (1994). The postmortem examination included (1) external examination of the carcass to collect information about identity of the pup, phenotypic characteristics (sex, age, size class, and body fatness), general conditions, and level of decomposition; (2) examination of fur and skin conditions (including skin hydration), presence of excoriations, wounds, edema, scars, and others anomalies; (3) check of the presence of the umbilical cord, rigor mortis, obstructions or anomalies of body orifices, and teeth emergence; (4) collection of morphometric data, including standard body length (straight length measured from the tip of the nose to the tail), and girth (measured around the body at the point of connection of the front flippers), with three replicates; (5) detailed examination of skull and skeleton to determine the presence of fractures; (6) detailed examination of internal organs to determine the presence of trauma, bleeding and congenital anomalies. We placed great care in the examination of the respiratory system, to check for drowning, and of the stomach content, to check for the presence of milk and extraneous objects. We calculated confidence interval of percentages using the Wilson score method (Newcombe 1998).

Of the 21 pups examined (Table 1), 12 were females and 9 were males, 11 aged 1 wk (81.8% with umbilical cord, 95% confidence interval (CI) = 52.3%–94.9%), 9 aged 2 wk, and 1 aged 3 wk. Mean standard body length was 131.1 cm (standard deviation (SD) = 7.5 cm, n = 20; age 1: mean = 127.6 cm, SD = 7.4 cm, n = 10; age 2: mean = 135.3 cm, SD = 5.9 cm, n = 9) and mean girth was 70.3 cm (SD = 3.8 cm, n = 17; age 1: mean = 69.9 cm, SD = 3.7 cm, n = 9; age 2: mean = 71.0 cm, SD = 4.3 cm, n = 7). Eleven pups showed onset of rigor mortis, two in the whole body, and nine in only the fore part. Wounds were identified in 66.7% of the pups (95% CI = 45.4%–82.8%) and, based on the size and shape of these wounds, the main cause of them was probably female aggressions. Of the wounded pups, six had wounds on the head, six on the head and body, and two only on the body. Four of the 21 pups had a damaged skull, with depression and fractures produced by blunt force trauma in two cases and by penetrating trauma, likely due to bites of adult females, in the other two cases. We found no sign of crushing of internal organs, because there was no internal bleeding or organ damage in any of the examined pups, with the only exception of a pup that had a small amount of blood in the abdomen but no organ damage. Twelve of the dead pups were previously marked, and 66.7% (95% CI = 39.1%–86.2%) of them were registered as surely abandoned. All the orphan pups had wounds, and 75% (95% CI = 40.9%–92.9%) of them showed clear abrasions on the bottom side of front flippers that are produced by intensive movements on hard substrate. These abrasions were more frequent in orphans (75%, n = 8 *vs.* 8%, n = 13, Fisher's exact test: P = 0.0032). Moreover lean and emaciated pups had higher percentage of excoriations (55.6%, n = 9) than normal (25%, n = 8) or fat pups (0%, n = 4, Cochran-Armitage test for trend: P = 0.0393). In the stomach we found gastric juices, milk, fur, algae, sand, and stones (diameter up to 15 mm).

We identified various causes of death, described below.

TSS—This cause of death included orphan, emaciated pups with many excoriations and wounds that were previously observed in agony, alone and away from harems. For example, pup #122, found dead on 8 February 2007, was an orphan since 31 January and three females attacked and wounded it on the head and back on 1 February, producing extensive bleeding and damage of its left eye. During the necropsy, we found a large number of wounds (on the head, between the eyes, over the nose, on the shoulders and on the rear flippers), extensive excoriations of the front flippers, a

Table 1. Summary of the phenotypic characteristics of pups subject to postmortem examination.

ID	Sex	Age	Cord	SBL	GC	Blubber	Orphan	Abrasions	Wounds	Fractures	Cause
#001	M	1	X	127.67	V	5					Drowning
#002	F	2		136.50	G		X	X	X		TSS
#003	M	3		129.33	P		X	X	X		TSS
#013	F	1		121.17	P				X		TSS
#016	M	1	X	132.00	G						Stillbirth
#033	F	1	X	128.25	G	11					Drowning
#043	F	1	X	121.67	G	10			X		Unknown
#050	F	2		137.00	G	10				X	Crushing
#058	F	1	X		V	9					Heat stress
#060	F	1	X	129.50	G	14	X	X	X		TSS
#064	F	2		140.50	G	17	X		X		Drowning
#071	M	2		123.50	P	15	X	X	X		TSS
#072	F	2		128.50	P	8	X		X	X	Trauma
#099	F	2		138.83	P	8	X	X	X		TSS
#107	F	1		116.50	E	2					Starvation
#113	M	1	X	122.00	V	13					Drowning
#122	M	2		132.83	P	9	X	X	X	X	TSS
#130	M	2		141.00	E	7		X	X		TSS
#133	F	1	X	138.00	V	15			X	X	Trauma
#138	M	2		139.00	P	12			X		Drowning
#142	M	1	X	138.83	G	13					Drowning

Note: Sex: F = female, M = male; Age: age in weeks from birth; Cord: umbilical cord, X = present; SBL: standard body length, in cm; GC: general condition, V = very good conditions, G = good conditions, P = poor conditions, E = emaciated; Blubber: blubber thickness, in mm; Orphan: X = surely abandoned pup; Abrasions: X = presence of excoriations of the front flippers; Wounds: X = presence of wounds on the head and/or the body; Fractures: X = presence of skull or bones fractures; Cause: established cause of death.

hole over the left eye corresponding to a skull fracture, and a fracture of the jaw. We found no internal bleeding or organ damage, and we found no milk in the stomach.

Starvation—This cause of death included pups that were orphan and emaciated, but had no wounds or fractures. For example, pup #107 was in very poor body conditions, but had no wounds and no sign of external or internal trauma. Behavioral observations showed that it had problems in suckling, it was recorded many times as separated from the mother, and had no milk in the stomach during the necropsy.

Crushing—This cause of death included pups in good body conditions with no significant wounds but with fractures in the skull, sometimes with abundant nose bleeding, and/or in the body. For example, pup #050, aged 2 wk, had no external wounds but was observed to have nose bleeding just before death, and during the necropsy showed a depressed skull fracture. We found abundant milk in its stomach and esophagus.

Trauma—This cause of death included pups with deep wounds, likely produced by adult aggressions. For example, pup #133, aged 1 wk, was a female in very good body conditions. It had a fresh wound on the head corresponding to a hole in the skull, likely due to an adult female bite, four fresh smaller wounds on the head, an old 4-cm-long wound over the nose, and another old one on the rear left flipper. It had no excoriations of the front flippers and during the necropsy we found no internal bleeding or organ damage.

Drowning—This cause of death included pups found dead after storms and high seas. For example, pup #001 was found dead on 17 December 2006 between kelp washed up on shore, near the water line, and far from all harems. It was a male of 1 wk of age in very good body conditions, and was last seen alive and healthy on 17 December in the morning. It had aerated lungs, no external wounds or excoriations, and no bone fractures. During the necropsy we found sand, algae, and gastric juices in the stomach and little stones and sand in the esophagus and in the trachea.

Stillbirth—This included pups that were delivered already dead. For example, pup #016 was a stillbirth recorded on 29 December 2006. The mother was first observed at 0810 with the rear flippers of the pup protruding. At 0944 the pup was still with the head inside the body of the mother. The pup was checked just after delivery, and it was already dead. During the necropsy we found no fractures or wounds, and no damage or anomalies of internal organs. The stomach was empty and lungs were not aerated.

Heat stress—This cause of death included pups in good general condition and with no wounds, but with poor skin hydration, found far from the water, usually belonging to terrestrial harems. For example, pup #058 died during a very hot day, with no wind, in which seals showed clear signs of thermal stress (very high sand flipping rate) and it was in a flat, not shaded area, away from the water line. It was never seen separated from the mother, it suckled normally, and during the necropsy we found no wounds, either external or internal.

The most important causes of death (Fig. 1) were TSS (38.1%; 95% CI = 20.8%–59.1%) and drowning (28.6%; 95% CI = 13.8%–50.0%). On the other hand, trauma (9.5%; 95% CI = 2.7%–28.9%), stillbirth (4.8%; 95% CI = 0.8%–22.7%), crushing (4.8%; 95% CI = 0.8%–22.7%) and heat stress (4.8%; 95% CI = 0.8%–22.7%) were rare. The majority of pups that died of TSS were orphans (75%; CI = 40.9%–92.9%).

Causes of pup death observed at SB largely agree with the ones found previously (Morejohn and Briggs 1973, Le Boeuf and Briggs 1977), and TSS was the main cause as it was at AN (Le Boeuf *et al.* 1972, Spraker *et al.* 2014). This indicates the pres-

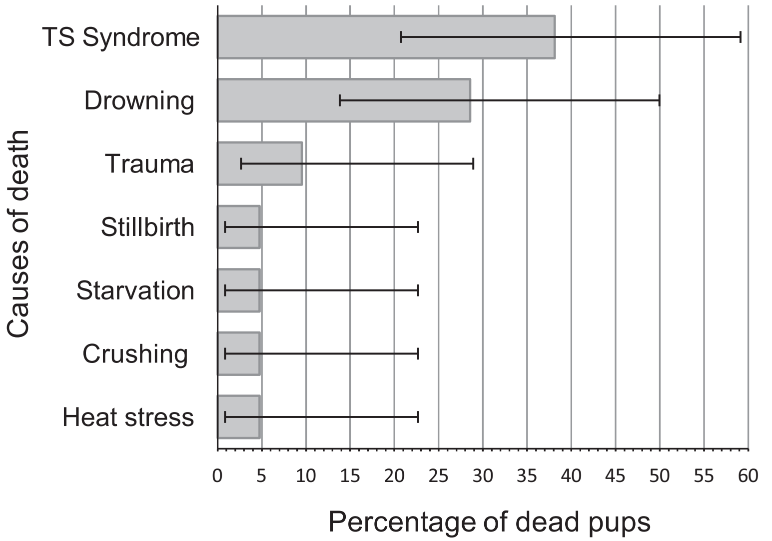

Figure 1. Causes of death of 21 preweaned pups, from necropsies performed in the San Benito Islands in the 2006–2007 breeding season. Each bar is the percentage of the cause of death, and lines are 95% confidence intervals (Wilson score method).

ence of a high rate of female aggression, which produces pup wounding, separation and abandonment (AN: Le Boeuf *et al.* 1972, Riedman and Le Boeuf 1982; SB, unpublished data). Evidence of aggressions and wounds caused by females was found in other pinnipeds species (Doidge *et al.* 1984, Harcourt 1992). On the contrary, although postmortem examinations performed at Macquarie Island showed that wounds and trauma were frequent also in SES pups (Bryden 1968), this was attributed mostly to young males and crushing, and not to females and their direct aggression on pups. These results are somewhat in contrast to findings from other SES populations. In the Valdés Peninsula (Argentina) pup mortality is low (Campagna *et al.* 1993), female interference is scarce (Baldi *et al.* 1996), and dead pups rarely show signs of direct aggression (FG, personal observation). At Sea Lion Island (Falkland Islands) pup mortality is very low (Galimberti and Boitani 1999), female aggression on pups is very rare (unpublished data), and a negligible percentage of pups died due to either female aggression or male crushing in 20 cohorts (unpublished data). At South Georgia, where female density is higher, female aggression on alien pups and pup abandonment are more frequent, but they are a rare phenomena, and overall pup mortality is only about 5% (McCann 1982). In several pinniped species the frequency of pup deaths related to adult aggression increases with population density (Doidge *et al.* 1984, Harcourt 1992, Reid and Forcada 2005). Differences in pup mortality, female aggression, and TSS rate between NES and SES were often attributed to differences in population and harem density (Le Boeuf *et al.* 1972, Morejohn and Briggs 1973, McCann 1982, Baldi *et al.* 1996, Galimberti and Boitani 1999), and in particular to higher female crowding of the AN harems. However, this is contradicted by the fact that demography, female density and operational sex ratio are similar between the San Benito Oeste NES colony and the Sea Lion Island SES colony, and, notwithstanding this, female interference, pup separation, and abandonment, incidence of TSS, and overall mortality are still much higher in the first colony (unpublished data). The impact of crushing by males on pup mortality is dubious. While at AN postmortem examinations showed internal bleeding, organ damage, and presence of blood within bronchial tubes (Le Boeuf *et al.* 1972, Morejohn and Briggs 1973), none of these lesions were found in our SB study. Although one of the pups that we examined actually died by crushing, we observed a rather large number of episodes in which males crushed and trampled pups, often remaining over them for up to 15 min, without affecting in any way their survival to weaning (unpublished data). At Sea Lion Island, where regular observations of SES behavior was carried out for 20 yr, just one case of death due to crushing was observed, and all other crushed or trampled pups were successfully weaned (unpublished data). In the gray seal (*Halichoerus grypus*) the impact of crushing by males is thought to be dependent on pup condition (Boyd and Campbell 1971), with lean pups being more affected. At SB we observed no relationship of body condition and vulnerability to crushing events: the only pup that died by crushing was in good condition, and emaciated abandoned pups were frequently trampled but none of them was affected. In New Zealand sea lion (*Arctocephalus forsteri*) pups, liver rupture is associated with fights between males that crush pups against rocks when breeding on rocky substrate instead of sandy beaches (Maloney *et al.* 2009). The nature of the substrate, and in particular the presence of rocks under the sand could be the probable cause of death of the only pup dead by crushing at SB. A difference in the nursing substrate may explain some of the variability in the incidence of crushing between the colonies.

An important class of factors that may cause pup mortality, and produce significant variation in mortality across years, are factors related to the state of the sea, including tide level, swell intensity, and incidence of storms (Bowen 1991). These factors can have a direct effect, causing drowning of pups still unable to swim, and an indirect effect, influencing female movements and increasing the risk of mother-pup separations (Bowen 1991, Boness *et al.* 1992, Gazo *et al.* 2000). At SB drowning was the second most important cause of death in preweaned pups, confirming previous results from AN (Le Boeuf and Briggs 1977, Spraker *et al.* 2014) and the Channel Islands (Stewart and Yochem 1991). The impact of drowning in SES is variable. Some articles reported in some years an important effect of winter weather and high tide (Laws 1953), while in other studies there was no evidence that drowning is an important factor of mortality (Galimberti and Boitani 1999, Pistorius *et al.* 2001). The effect of storms on pup mortality depends on the time of the season in which they happen, because their effect is stronger when most pups are young and are therefore more easily washed away, and on the topography of the breeding beaches, that often reduces the capability of seals to move inland (Gazo *et al.* 2000). Therefore, the combination of sea condition, time of the season, and topography of beaches can have significant effects not only on the total mortality, but also on the importance of the different causes of mortality (Stewart and Yochem 1991). Contrary to our expectations, thermal stress was not an important cause of death in our sample of necropsies. On the other hand, previous observations showed that thermal stress can produce mass mortality of pups of terrestrial harems at SB (up to 90%, unpublished data), but this is likely a rare event, that was observed once in a 10 yr study.

Stillbirths represent a minor cause of death in NES, which is in agreement with previous studies on elephant seals (Baldi *et al.* 1996, Galimberti and Boitani 1999, Spraker *et al.* 2014), and other pinnipeds (Castinel *et al.* 2007, Kaplan *et al.* 2008, Seguel *et al.* 2013). In pinnipeds, high rates of stillbirth are associated with elevated levels of environmental contaminants (Gilmartin *et al.* 1976) or bacterial infections (Steiger *et al.* 1989). Moreover, younger females can be more affected by these factors and/or be less able to cope with the energetic requirements to carry their fetus to term (Georges and Guinet 2000). All together, the low rate of stillbirths at SB seems to indicate that the population is rather healthy, and this is in contrast to the observed deceasing trend in population size.

In conclusion, social factors, and in particular female aggression and pup abandonment, are the main determinants of preweaning mortality in NES of the SB colony. In addition, environmental conditions, including topography of the breeding site and presence of heavy seas and storms, may produce local variability in mortality rate, and differences between sites and years.

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