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Factors affecting pup survival in the South American fur seal

The South American fur seal, *Arctocephalus australis*, presents a case of evolutionarily selected behaviors that conflict with present habitat limitations to effect an exaggerated infant mortality rate (averaging 36.4% over 5 years) in breeding colonies (Harcourt, 1992b). As has been demonstrated for a number of other pinnipeds, many factors determine the rate of pup survival, including rookery density, maternal aggression, maternal age, predation pressures (including hunting), timing of births, and male breeding behaviors.

South American fur seals breed in colonies on remote coasts or guano islands off South America (Gentry & Kooyman, 1986). Though the population is increasing, they remain restricted to a small range due to human interference (Majluf, 1992). As a result, rookery densities are rising. Maternal aggression rates typically rise with colony density as well as the amount of animal movement within colonies (Harcourt 1992a). As in a number of colonially breeding pinnipeds, including elephant seals (Christenson & Le Boeuf 1978, Reiter et al. 1981), South American fur seal mothers increase aggression levels towards conspecifics when their pups are young, initiating nearly three times more threats to other females postpartum than prepartum (Harcourt 1992a). Maternal aggression directed towards other females has a spacing effect which might originally have served to protect pups from other females but, in densely populated conditions, merely results in crowding of one animal against another. Crowding increases incidences of maternal aggression and mother-pup separation, which in turn may lead to orphaning and subsequent pup death. A pup separated from its mother and deprived of her protection is more likely to be bitten, shaken, or trampled by other females (Le Boeuf & Briggs, 1977), and usually dies of starvation or trauma. On a high density beach, pup mortality was highly correlated to the number of females on the beach as well as levels of aggression (Harcourt 1992a).

Breeding colony aggressions and mother-pup separations are exacerbated by thermoregulatory movement. As the densely-pelaged seals breed in equatorial heat, animals hauled out for any length of time must take regular trips to the ocean to cool down. The disruptive movements of females and/or their pups through a densely populated rookery directly increase intra-female aggression and the likelihood of orphaning. In fact, female aggression rates directly correlate with mean temperature (Harcourt 1992b).

Unlike phocids, which remain with their pups until weaning, otariids return to sea periodically to forage for food during breeding. Fur seal mothers typically stay with their pups for 6-9 days after birth, leave to forage for 1-7 days, and return to nurse for 1- to 3-day periods (Gentry and Kooyman, 1986). Females do not usually defend their pups from predators, typically southern sea lions (*Otaria byronia*). In fact, sea lion attacks tend to cause all females to stampede off the rookery. Chaotic fleeing, which often results in sea lions capturing pups, also increases chances of mother-pup separation. The high risk of serious maternal injury in encounters with predators, and the fact that interfemale threats are likely to be resolved with minimal physical harm, might account for selective aggression. In addition, the necessity of leaving pups vulnerable to

predation during long maternal feeding bouts renders any potential increase in pup survival due to maternal predator defense minimal (Harcourt 1992a).

Maternal age also affects pup survivorship, as significantly more primiparous females lose pups shortly after birthing (Majluf 1992, Reiter 1984). However, maternal size and age past primiparity do not correlate with pup mortality (Majluf, 1992), nor does birth weight correlate with maternal size, as in elephant seals (Majluf 1992, Reiter 1984).

The seals' degree of breeding synchrony affects colony density and thus pup mortality. In one study, over 90% of pups were born within 40 days (Majluf, 1992). Females giving birth close to the peak of pupping are nearly 24% more likely to lose their pups within 120 days than females pupping early and late in the season. The day of peak pup death is consistently 6-9 days later than the day of peak pup births (Majluf 1992). This may be due to heightened levels of maternal aggression in crowded conditions, which in turn lead to more pup injury and orphaning (Le Boeuf & Briggs, 1977) (Reiter, 1984). Yet reproductive synchrony continues to prevail, as off-schedule breeders are more likely to birth on schedule in succeeding years (Majluf 1992).

Evolutionary pressures have selected for the establishment of breeding synchrony. South American fur seal breeding coincides with the annual population swell of their primary food source, the anchoveta (*Engraulis ringens*). Synchrony might originally have evolved to allow breeding females with elevated energetic demands to take advantage of increased food availability. However, near the tropics, food sources are relatively constant throughout the year, and small differences in access around the peak of births do not compensate for present-day costs of breeding synchrony (Majluf, 1992).

Some advantages of synchrony on pup survival include the effects of paternal selection and male protection. Bulls most likely to father robust pups are themselves strong and aggressive. Females indirectly select good fathers by beaching on prime breeding territories that the strongest bulls dominate. Bulls compete for good breeding territories in order to attract the most females. Females breeding in dense areas are more likely to have access to premium paternal genes. In one study, predation rates were lower at high-density beaches because males expelled most attacking sea lions. Breeding in a superiorly situated, though dense, colony also affords more safety from predators. Superior territory criteria may include a high degree of insulation from predators; a beach sheltered by a buffer zone of other males' areas experiences fewer sea lion attacks, as front line males are likely to catch interloping predators. Females giving birth on an aggressive bull's territory suffer fewer predator disturbances, as he is more effective at expelling sea lions. The study concluded, however, that gains made in avoiding predation were offset by the higher levels of female aggression found at the high density beach (Harcourt, 1992b). Additional advantages of breeding in crowded colonies include reduced harassment of center-situated females by subordinate males and improved predator detection (Majluf, 1992).

The evident disadvantages of colonial, synchronous breeding and corresponding hazards of high rookery densities and infant mortality rates are likely side-effects of modern human incursion on South American fur seal breeding habitat and intense poaching outside protected areas. Unable to expand, existing colonies have reached a critical density at which evolutionarily effective strategies such as interfemale aggression and defense, mate choice, group predator defense, and

high levels of prey availability are offset by the extreme levels of female aggression found in densely populated breeding colonies.

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