Chapter 19

A Bioenergetics Approach to Understanding the Population Consequences of Disturbance: Elephant Seals as a Model System

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Abstract Using long-term empirical data, we developed a complete population consequences of acoustic disturbance (PCAD) model and application for northern elephant seals. We assumed that the animals would not successfully forage while in a 100-km-diameter disturbance region within their foraging and transit paths. The decrease in lipid gain due to exposure was then translated to changes in birth rate and pup survival. Given their large foraging range, elephant seals were resilient to such a disturbance, showing no population-level effects. However, similar track analysis showed that given their more coastal nature, California sea lions were within a 25-km-diameter region of disturbance more often.

Keywords Population consequences of acoustic disturbance • Acoustic disturbance • Behavior • Sea lion • Demography

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1 Introduction

Although we have developed sophisticated tools and approaches to determine the range of sounds organisms can hear and their responses to underwater sounds (Costa et al. 2003; Tyack et al. 2011; Reichmuth and Southall 2012), we have a difficult time assessing when and if these responses are biologically "meaningful." In the context of conservation and management, a biologically meaningful response is one that results in a change at the population level. The National Research Council Committee on Population Consequences of Acoustic Disturbance (PCAD) developed a framework that detailed how behavioral responses to sound may affect life functions, how life functions are linked to vital rates, and how changes in vital rates cause population change through a series of transfer functions (National Research Council 2005). Although logistical limitations preclude assessment of these transfer functions for most marine mammals, there are a few species, such as elephant seals (*Mirounga leonina* and *M. angustirostrus*), for which data are available to parameterize these transfer functions. Extensive research on their at-sea movement patterns, reproductive biology, and demography have been carried out (Robinson et al. 2012; Schick et al. 2013). The species also provide a relatively simple system because at-sea disturbance only reduces foraging opportunities, not mating or offspring care, which occur on land. Furthermore, the relationship between maternal mass and pup wean mass and subsequent pup survival is well documented as is the threshold between body condition and natality (Arnbom et al. 1993; McMahon et al. 2005). Therefore, elephant seals provide an unusual opportunity to test the PCAD model in its entirety.

The PCAD model proposed a variety of approaches that could be used to detect a biologically meaningful response, including a bioenergetics model where the costs associated with disturbance are linked to reductions in foraging success (Costa 2012; New et al. 2013, 2014). This approach assumes that changes in behavior compromise the maternal condition by reducing the energy gain (interrupting foraging behavior) and increasing the energy expenditure (cost of avoidance); these costs lead to a compromised adult condition, reduced natality and energy delivery to offspring, higher rates of offspring mortality, and, at the extreme, increased adult mortality. In elephant seals, the maternal condition can be measured directly as mass or lipid content, providing an accurate empirical measurement and a strong foundation for this analytical framework (Crocker et al. 2001). Furthermore, changes in buoyancy over their foraging trip can be used to estimate the daily lipid mass gain while at sea (Schick et al. 2013). Using this approach, New et al. (2014) provided a test of the PCAD model for southern elephant seals by assuming that a female would not be able to forage throughout the period of disturbance. This decrease in foraging resulted in a reduction in the female's lipid mass gain, limiting her ability to invest in her pup. The pup would then be weaned at a smaller size and would thus have lower survival. Last, they ran simulations of various periods of disturbance to estimate the changes in population growth rate in southern elephant seals given estimated reductions in pup survival.

Although the New et al. (2014) study was the first implementation of the PCAD model with robust demographic data, it was limited in that the simulated disturbance only occurred during a predetermined period starting at the end of the foraging trip and did not take into account spatial variation in the disturbance and/or variations in the behavior of individuals. Here we extend the PCAD bioenergetics model developed by New et al. (2014) to (1) estimate changes in reproductive rate with disturbance and (2) incorporate spatial and temporal variability in movement patterns during two phases of the postmolting foraging trip of northern elephant seals. Finally, because elephant seals are highly migratory and forage widely, we compared their potential levels of exposure to the highly coastal income breeding California sea lion *Zalophus californianus*.

2 Materials and Methods

We simulated the population impact of a disturbance within the foraging range of northern elephant seals by first estimating the proportion of the population that would be exposed to a disturbance and then examined what proportion of their foraging trip would be affected if the disturbance occurred within both a densely populated foraging and transiting region (Fig. 19.1). We used a worst-case scenario in which any exposure resulted in zero foraging success over the period and region of exposure. Using data from individuals whose fat gain had been modeled over their entire foraging trip (Schick et al. 2013), we then subtracted the lipid mass they would have gained over those days from their total gain over the trip. We then

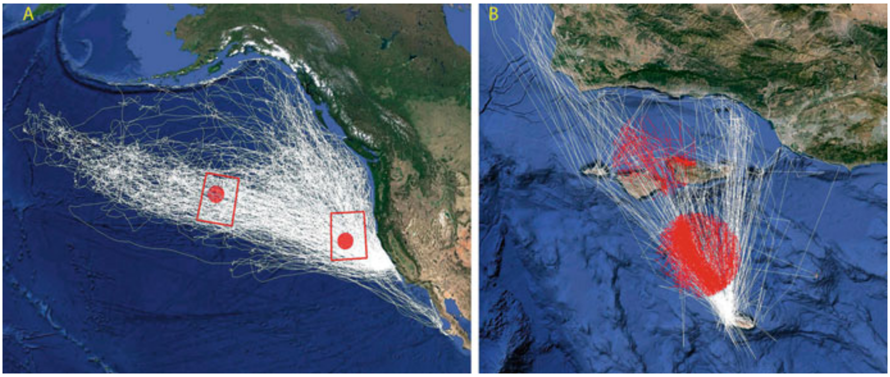

Fig. 19.1 (**a**) Migration tracks of 105 northern elephant seal females. *Red boxes*, areas where the 100-km-diameter circle were randomly sampled. *Left box* and *circle* is in the primary foraging region and *right box* and *circle* is in the transit region. (**b**) Tracks of 39 California sea lion females on their foraging trips from their breeding colony on San Nicolas Island. *Red circle* shows all of the tracks that passed through a 25-km disturbance region during transit and *red* area just above the islands shows the tracks that passed through a 25-km disturbance zone while animals were foraging (imagery from Google Earth)

estimated how that reduced body condition would affect reproductive rate, pup wean mass, and subsequent pup survival. For comparative purposes, we ran a similar simulation with California sea lion females that were tagged on San Nicolas Island, CA, to examine the risk to acoustic exposure only.

2.1 Disturbance

To estimate what proportion of northern elephant seals would be affected by a continuous disturbance that is limited to a specific geographic region, we chose 25-km- and 100-km-diameter circles and assumed that any individual passing through this region would not successfully forage while exposed to the disturbance (Fig. 19.1). These circles were randomly placed within the transit corridor and within a region that had the highest density of foraging female elephant seals. Iterating the random placement of the disturbance 1,000 times, we used the tracks of 105 female elephant seals to measure how much time each female spent in the 2 disturbance regions. Similarly for California sea lions, we used 39 tracks of adult females that were tracked on San Nicolas Island (Costa et al. 2010). Because the sizes of the disturbance were large in comparison to the home range of the individuals, we did not perform multiple iterations of disturbance. Instead, we chose a disturbance with its center either near the center of the colony (100 km transiting) or near the center of the transit or foraging area (25 and 100 km foraging; Fig. 19.1).

2.2 Life History Data and Analysis

We used lipid mass as the metric of maternal body condition that affects reproductive rate and pup wean mass. In turn, pup survival to 1 year is a function of wean mass. Using the truncated cones method, the lipid mass of adult females was measured before and after the postmolt foraging trip, standardized by correcting for time on land before and after the trip (Crocker et al. 2001). Postweaning pup mass was also collected and back calculated to mass on the day of weaning (L. Schwarz, unpublished analysis). Because females that do not pup usually have shorter or longer foraging trips compared with females that pup (Robinson et al. 2012), the reproductive rate was measured as a logistic function of lipid mass gain rate ($n = 115$). For a small subset of females ($n = 11$), both maternal lipid mass and pup wean mass were collected. We used a linear regression to estimate wean mass as a function of maternal lipid mass (Arnbom et al. 1993; Crocker et al. 2001). Using mark-recapture data of pups with a measured wean mass ($n = 1{,}334$), pup survival was estimated as a quadratic function of wean mass, also accounting for tag loss as a function of wean mass (Schwarz et al. 2012). Bayesian posterior parameter estimates for all functions were calculated using a Metropolis-within-Gibbs sampler with vague, noninformative prior estimates (Schwarz 2008). For a subset of elephant seals ($n = 26$), we modeled the lipid composition of seals throughout their migrations using empirical body composition measurements combined with drift rate (buoyancy) data on a daily scale (Schick et al. 2013). We used the 100-km disturbance simulations to subtract any lipid gain they may have accrued while in the disturbance area from their final lipid mass. We then used results from the above analyses to estimate subsequent changes in reproductive rate, pup wean mass, and pup survival.

3 Results

3.1 Movements Through Disturbance

For the 100-km disturbance in the high-density foraging zone, 73% of the 105 sampled individuals passed through at least 1 disturbance area. They spent a mean of 6.4 days in the disturbance zone, with 1 female spending up to 87 days in a disturbance area. Although a greater number of individuals passed through the disturbance zone when it was placed within the transit corridor, the duration of exposure was less. All individuals passed through the disturbance in the transit corridor, spending a mean of 3.6 days, with 1 female spending 83 days.

Of the subset of 26 females whose daily lipid gain was estimated, 5 were never exposed and 21 would have experienced some decrement in body condition ranging from no effect to a loss of up to 60% of 1 individual's normal lipid stores (Fig. 19.2).

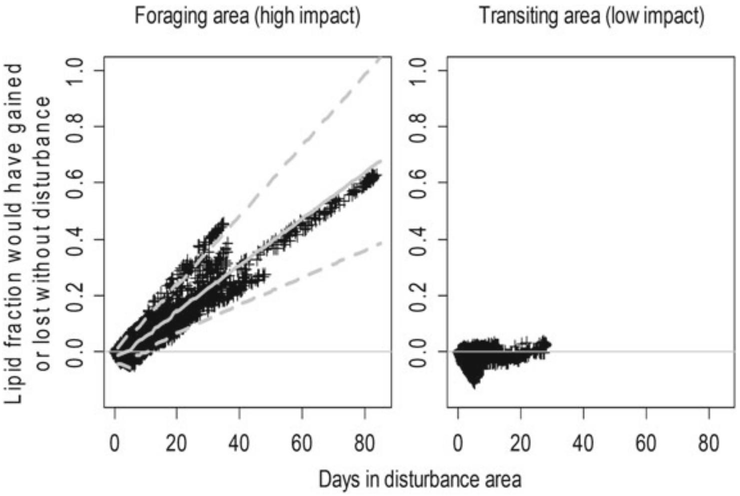

Fig. 19.2 Relative proportion of lipid that would have been gained while the animal was in the disturbance region for elephant seals found in the high-density foraging region and the transit region. We assumed that this lipid would not be gained because animals would not be foraging while in the disturbance region

Animals exposed during the transit phase of their migration experienced little or no loss in body condition (Fig. 19.2). Although the overall mean final lipid mass at the end of the foraging trip, when females come on shore, was similar regardless of the level of disturbance (none: 169.3 kg; transit: 169.3 kg; forage: 167.5 kg), the minimum estimated final fat mass was lowest in the foraging area (none: 142.6 kg; transit: 138.6 kg; forage: 87.9 kg).

3.2 *Relating Disturbance to Reproduction and Pup Survival*

Given the relationship between fecundity and female condition (Fig. 19.3), we were able to convert the projected loss of body condition to a potential reduction in reproductive output. The reproductive rate for these 26 healthy elephant seals when disturbance was not present would be 0.995 (0.975–1.0; mean [95% posterior interval]). Although the high rate was estimated from their fat mass gain, empirical pupping data matched the estimates; all 26 females pupped at the end of the foraging trip in which they were tracked. The normal reproductive rate was in comparison to the estimate of 0.994 (0.971–1.0) for the same animals exposed to disturbance in the foraging area, whereas those animals exposed during transit had no change in reproductive rate. Similarly, given the known relationship between maternal mass and weaning mass, these 26 females' pups would normally weigh 139 kg (97–186 kg) at weaning, and for those that were exposed in the foraging region, they would weigh 138 kg (95–185 kg), with an undetectable change in the wean mass for those exposed during transit. Finally, given the known relationship between weaning mass and survival to the first year of life, pup survival from weaning to 1 year old was the same regardless of exposure (no disturbance: 0.961 [0.847–0.997]; transiting: 0.961 [0.847–0.997]; foraging: 0.960 [0.836–0.998]). Overall, these changes in female fecundity and pup survival would have no effect on the population status of northern elephant seals.

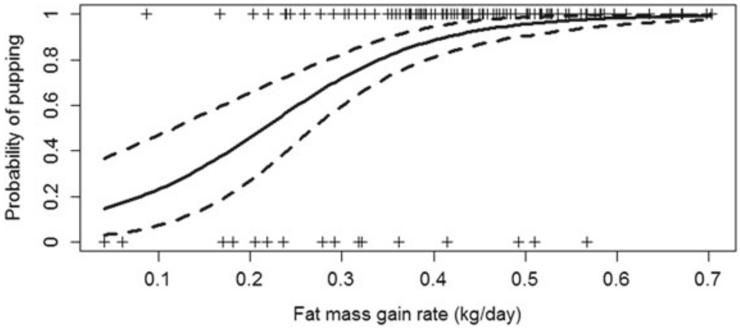

Fig. 19.3 Probability of an elephant seal female giving birth to a pup as a function of her mass gain rate while foraging at sea

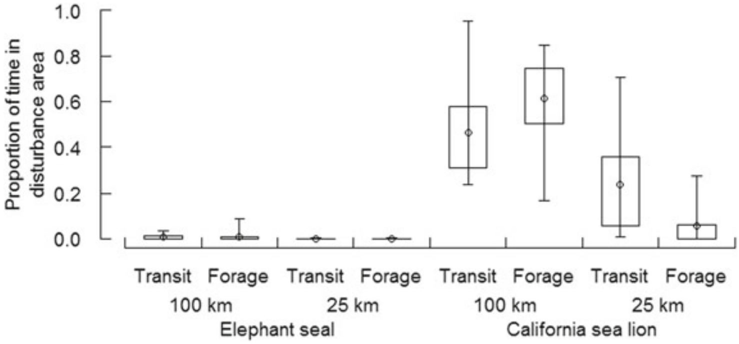

Fig. 19.4 Relative proportion of time that elephant seals and sea lions spent in 100- and 25-km-diameter disturbance areas during transit and foraging phases of their foraging trips

3.3 Comparison to California Sea Lions

Of the 39 California sea lions tracked, all passed through the 100-km transit disturbance zone, and all but one passed through the 100-km foraging disturbance area. Fewer individuals were found within the 25-km disturbance areas (38 transiting and 25 foraging). Individuals spent 26.2 ± 11.7 (mean ± SD) days in the 100-km transit disturbance area and 36.9 ± 15.2 days in the 100-km foraging disturbance area. With a smaller 25-km disturbance area, individuals spent 6.5 ± 16.3 days transiting with disturbance and 3.4 ± 6.2 days foraging with disturbance. Overall, the proportion of time spent within a disturbance area was considerably larger for California sea lions compared with elephant seals (Fig. 19.4).

4 Discussion and Conclusions

We anticipated that given the northern elephant seals' comparatively large foraging range, a large disturbance area (100 km) would be required to have any effect on their foraging success. Regardless, our simulation was a worst-case scenario because we assumed a complete cessation of foraging behavior. This is not likely to occur because animals will probably avoid the area and look for other foraging opportunities. We also did not include any potential compensatory increases in foraging effort that may occur outside the disturbance region (Costa 2012). Such a change in behavior is relatively straightforward for elephant seals that forage along the North Pacific transition zone where resources are widely dispersed over a rather large area (Robinson et al. 2012) and may be applicable to other wide-ranging species. Although this foraging pattern is the most common for northern elephant seals, there are individuals who forage in coastal regions and spend most of their time in a localized region. A disturbance within such a region would have a much greater impact on an individual. This is likely the case for the female who could potentially be exposed to the disturbance for more than 80 days. However, because these females represent a small proportion of the population, the population-level effect of the disturbance is low. Although demographic data were not available for California sea lions, our results show that a coastal species like sea lions with a more limited foraging range would have a greater potential to be impacted by a disturbance within their home range.

The reproductive rates and pup survival rates without disturbance do not represent the overall rates for the population because the 26 females selected for this analysis were not randomly drawn. They were all healthy and did produce pups after their tracked foraging trips. We will continue to refine these estimates by including more females in the analysis. However, even with overall lower demographic rates, they are unlikely to decline much further in the presence of the modeled disturbance compared with what we have reported here. Namely, for this type of disturbance, we would see little-to-no effect on the population status of northern elephant seals.

It is important to note that pup survival relationships have high levels of posterior uncertainty, mostly because factors other than maternal lipid mass and wean mass affect pup survival. For example, the relationship between maternal lipid mass and weaning mass is quite variable. This is not unexpected because weaning mass may also be affected by many random processes on the colony, such as the degree of disturbance on the colony, weather, interactions with other females, and the quality of the harem master. Furthermore, survival to year one is affected by processes other than weaning mass. Some pups may find high-quality prey patches or, conversely, may be weaned during a poor year when resources are less available. All of these features weaken the link between maternal condition and pup survival. However, the quantified uncertainty is a realistic representation of how disturbance that reduces foraging ability will likely impact northern elephant seal populations and other widely foraging species.

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