A Bioenergetics Approach to Understanding the Population Consequences of Disturbance:

Elephant seals as a Model System

Daniel P. Costa, Department of Ecology & Evolutionary Biology, University of California, Santa Cruz

CA 95060, costa@ucsc.edu

Lisa Schwarz, Department of Ecology & Evolutionary Biology, University of California, Santa Cruz, CA

95060, schwarz@biology.ucsc.edu

Patrick Robinson, Department of Ecology & Evolutionary Biology, University of California, Santa Cruz

CA 95060, robinson@biology.ucsc.edu

Rob Schick, Centre for Research into Ecological and Environmental Modelling, University of St

Andrews, St Andrews, Fife, KY16 9LZ, Scotland, UK, rss5@st-andrews.ac.uk

Patricia A. Morris, Department of Ecology & Evolutionary Biology, University of California, Santa Cruz,

CA 95060, pamorris@ucsc.edu

Richard Condit, Center for Tropical Forest Science, Smithsonian Tropical Research Institute,

conditr@gmail.com

Daniel E. Crocker, Department of Biology Sonoma State University, Rohnert Park, CA

crocker@sonoma.edu

A. Marm Kilpatrick, Department of Ecology & Evolutionary Biology, University of California, Santa

Cruz CA 95060, akilpatr@ucsc.edu

Corresponding author

Daniel P. Costa

Department of Ecology & Evolutionary Biology

University of California Santa Cruz

costa@ucsc.edu

Abstract

Using long-term empirical data we developed a complete PCAD model and application for northern elephant seals. We assumed that 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 of coastal California sea lions showed greater levels of sound exposure to a disturbance within a 25 km diameter region.

1   Introduction

While 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 in the population. The NRC Committee on Population Consequences of Acoustic Disturbance, or PCAD, developed a framework, which 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 (NRC, 2005). While logistical limitations preclude assessment of these transfer functions for most marine mammals, there are a few species where data are available to parameterize these transfer functions, such as elephant seals (*Mirounga leonina* and *M. angustirostrus*), since extensive research on their at-sea movement patterns, their 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 and offspring care, which occur on land. Further, the relationship between maternal mass and pup weaning mass and subsequent pup survival is well documented; as is the

threshold between body condition and natality (McMahon et al. 2005; Arnbom et al. 1993). 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; New et al. submitted). This approach assumes that changes in behavior compromise maternal condition by reducing energy gain (interrupting foraging behavior) and increasing energy expenditure (cost of avoidance), which leads to 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, 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). Further, 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 (submitted) 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 females' lipid mass gain, limiting her ability to investment in her pup. The pup would then be weaned at a smaller size and would thus have lower survival. Lastly, they ran simulations of various periods of disturbance to estimate changes in population growth rate in southern elephant seals given estimated reductions in pup survival.

While the New et al 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 pre-determined period starting at the end of the foraging trip, and it did not take into account spatial variation in the disturbance and/or variations in behavior of individuals. Here we extend the PCAD Bioenergetics model developed by New et al (submitted) to 1) estimate changes in reproductive rate with disturbance, and 2) include spatial and temporal variability in disturbance during two phases of the post-molt foraging trip of northern elephant seals. Finally, as elephant seals are highly migratory and forage widely, we compare their potential levels of exposure to the highly coastal 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 (Figure 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 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.

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 a 25 km and 100 km diameter circle and assumed that any individual passing through this region would not successfully forage while exposed to the disturbance (Figure 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 1000 times, we used tracks of 105 females to measure how much time each female spent in the two 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). Since 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 km and 100 km foraging) (Figure 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 one year is a function of wean mass. Using the truncated cones

4

method, lipid mass of adult females was measured before and after the post-molt foraging trip, standardized by correcting for time on land before and after the trip (Crocker et al. 2001). Post-weaning pup mass was also collected and back-calculated to mass on day of weaning (unpublished analysis). Since females that do not pup usually have shorter or longer foraging trips compared to females that pup, reproductive rate was measured as a linear 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). Using mark-recapture data of pups with measured wean mass ($n = 1334$), 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, non-informative priors (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 one disturbance area. They spent a mean of 6.4 days in the disturbance zone, with one female spending up to 87 days in a disturbance area. While 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 one female spending 83 days.

Of the subset of 26 females whose daily lipid gain was estimated, five were never exposed and 21 would have experienced some decrement in body condition ranging, from no effect to one individual that would have lost 60% of her normal lipid stores (Figure 2). Animals exposed during the transit phase of their migration experienced little or no loss in body condition (Figure 2). While the overall mean final lipid mass was similar regardless of 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 (Figure 3), we were able to convert the projected loss of body condition to any reduction in reproductive output. The normal reproductive rate for these 26 elephant seals would be 0.995 (0.975 – 1.0; mean (95% posterior interval)), compared to 0.994 (0.971 – 1.0) for animals exposed in the foraging area and no change for animals exposed during transit. Similarly, given the known relationship between maternal mass and weaning mass, these 26 females' pups would normally weigh 139 kg (97 – 186), and for those that were exposed in the foraging region they would be 138 kg (95 - 185), with an undetectable change in 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 one 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.

3.3 Comparison to California sea lions.

Of the 39 California sea lions followed, all individuals passed through the 100 km transit disturbance zone, while all but one individual passed through the 100 km foraging disturbance area. Fewer individuals were found within the 25 km disturbance areas (97% transiting and 64% foraging). Individuals spent a mean of 26.2 ± 11.7 (stdev) 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 a mean of 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 to elephant seals (Figure 4).

4   Discussion and conclusions

We anticipated that given the widely foraging nature of northern elephant seals, 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, as we assumed a complete cessation of foraging behavior, which is not likely to occur as animals are likely to 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 of 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). While 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, as these females represent a small proportion of the population, the population-level effect of the disturbance is low. While 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 greater potential to be impacted by a disturbance within their home range.

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 will 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, and interactions with other females, and the quality of the harem master. Further, survival to year one is affected by processes other than weaning mass. Some

7

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 reduce the linkage 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.

Acknowledgements

References

Arnbom T, Fedak MA, Boyd IL, McConnell BJ (1993) Variation in weaning mass of pups in relation to maternal mass, postweaning fast duration, and weaned pup behaviour in southern elephant seals (Mirounga leonina) at south Georgia. Can J Zool 71 (9):1772-1781

Costa DP (2012) A Bioenergetics Approach to Developing the PCAD Model. In: Popper AN, Hawkins A (eds) The Effects of Noise on Aquatic Life. Advances in Experimental Medicine and Biology Springer Science+Business Media, pp pages 423-426. in. doi:10.1007/978-1-4419-7311-5_96

Costa DP, Crocker DE, Gedamke J, Webb PM, Houser DS, Blackwell SB, Waples D, Hayes SA, Le Boeuf BJ (2003) The effect of a low-frequency sound source (acoustic thermometry of the ocean climate) on the diving behavior of juvenile northern elephant seals, Mirounga angustirostris. Journal of the Acoustical Society of America 113 (2):1155-1165

Costa DP, Robinson PW, Arnould JP, Harrison AL, Simmons SE, Hassrick JL, Hoskins AJ, Kirkman SP, Oosthuizen H, Villegas-Amtmann S, Crocker DE (2010) Accuracy of ARGOS locations of Pinnipeds at-sea estimated using Fastloc GPS. PLoS ONE 5 (1):e8677. doi:10.1371/journal.pone.0008677

Crocker DE, Williams JD, Costa DR, Le Boeuf BJ (2001) Maternal traits and reproductive effort in
  northern elephant seals. Ecology (Washington D C) 82 (12):3541-3555

McMahon CR, Hindell MA, Burton HR, Bester MN (2005) Comparison of southern elephant seal
  populations, and observations of a population on a demographic knife-edge. 288:273-283

New L, F., Clark J, S. , Costa D, P. , Fleishman E, Hindell MA, Klanjšček T, Lusseau D, Kraus S,
  McMahon CR, Robinson PW, Schick RS, Schwarz LK, Simmons SE, Thomas L, Tyack P,
  Harwood J (submitted) Using short-term measures of behaviour to estimate long-term fitness of
  southern elephant seals. Marine Ecology Progress Series

New LF, Moretti DJ, Hooker SK, Costa DP, Simmons SE (2013) Using Energetic Models to Investigate
  the Survival and Reproduction of Beaked Whales (family *Ziphiidae*). PLoS ONE
  8 (7):e68725. doi:10.1371/journal.pone.0068725

Reichmuth C, Southall BL (2012) Underwater hearing in California sea lions (Zalophus californianus):
  Expansion and interpretation of existing data. Mar Mammal Sci 28 (2):358-363.
  doi:10.1111/j.1748-7692.2011.00473.x

Robinson PW, Costa DP, Crocker DE, Gallo-Reynoso JP, Champagne CD, Fowler MA, Goetsch C,
  Goetz KT, Hassrick JL, Huckstadt LA, Kuhn CE, Maresh JL, Maxwell SM, McDonald BI,
  Peterson SH, Simmons SE, Teutschel NM, Villegas-Amtmann S, Yoda K (2012) Foraging
  behavior and success of a mesopelagic predator in the northeast Pacific Ocean: insights from a
  data-rich species, the northern elephant seal. PLoS One 7 (5):e36728.
  doi:10.1371/journal.pone.0036728

Schick RS, New LF, Thomas L, Costa DP, Hindell MA, McMahon CR, Robinson PW, Simmons SE,
  Thums M, Harwood J, Clark JS (2013) Estimating resource acquisition and at-sea body condition
  of a marine predator. J Anim Ecol:n/a-n/a. doi:10.1111/1365-2656.12102

Schwarz LK (2008) Methods and models to determine perinatal status of Florida manatee carcasses.
  Marine Mammal Science 24 (4):881-898. doi:10.1111/j.1748-7692.2008.00232.x

Schwarz LK, McMahon CR, Hindell M, Costa D (2012) The implications of assuming independent tag

loss in southern elephant seals. Ecosphere 3 (81). doi:10.1890/ES12-00132.1

Tyack PL, Zimmer WMX, Moretti D, Southall BL, Claridge DE, Durban JW, Clark CW, D'Amico A,

DiMarzio N, Jarvis S, McCarthy E, Morrissey R, Ward J, Boyd IL (2011) Beaked Whales

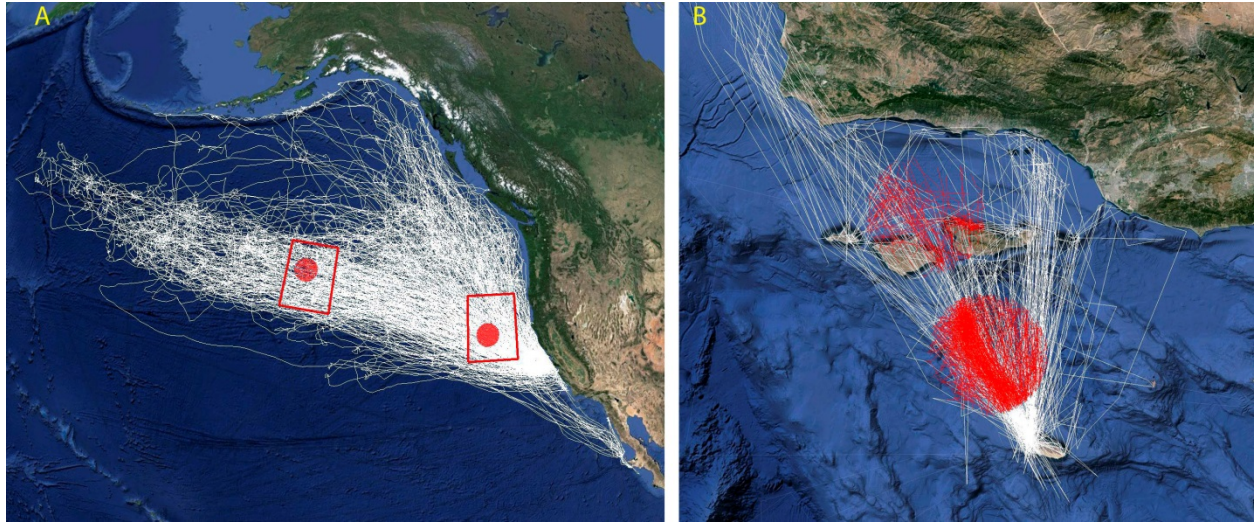Respond to Simulated and Actual Navy Sonar. PLoS ONE 6 (3):e17009

Figure 1. 1A left shows the migration tracks of 105 satellite northern elephant seal females. The red box boxes show the areas where the 100 km diameter circle were randomly sampled. The box and circle to the left is in the primary foraging region and to the right the transit region. Figure 1B at right shows the tracks of 39 California sea lion females on their foraging trips from their breeding colony on San Nicolas Island. The lower red spot shows all of the tracks that passed through a 25 km disturbance region during transit and the upper red area just above the islands shows the tracks that passed through a 25 km disturbance zone while animals were foraging.
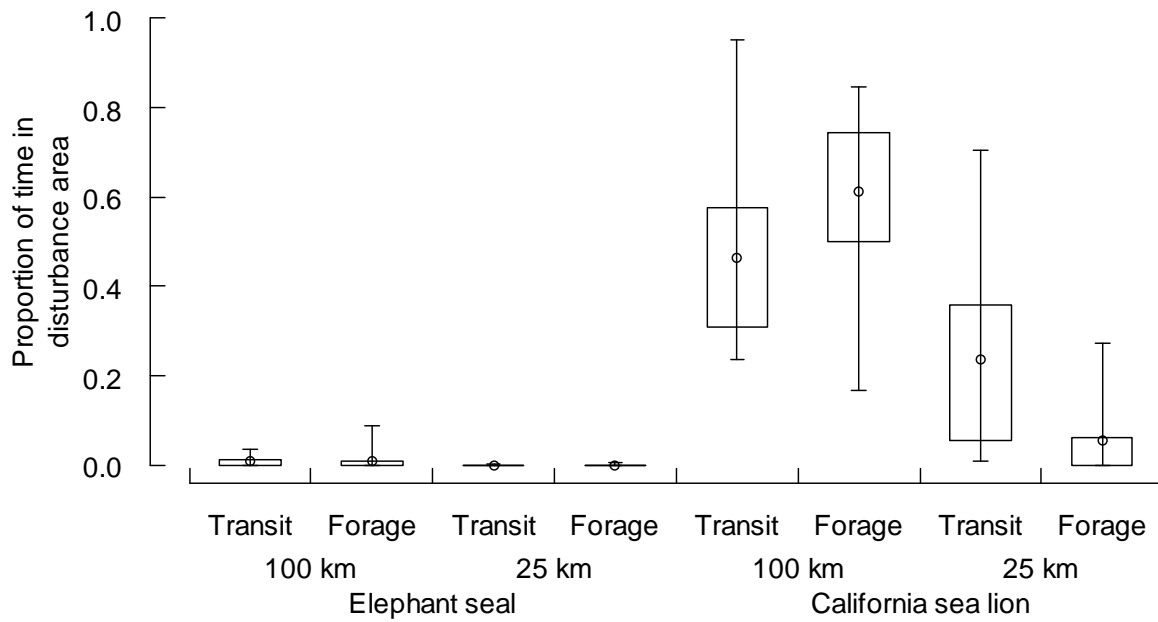
Figure 2. The relative proportion of lipid that would have been gained while the animal was in the disturbance region for elephant seals found in the high-density foraging region and the transit region. We assumed that this lipid would not be gained since animals would not be foraging while in the disturbance region.
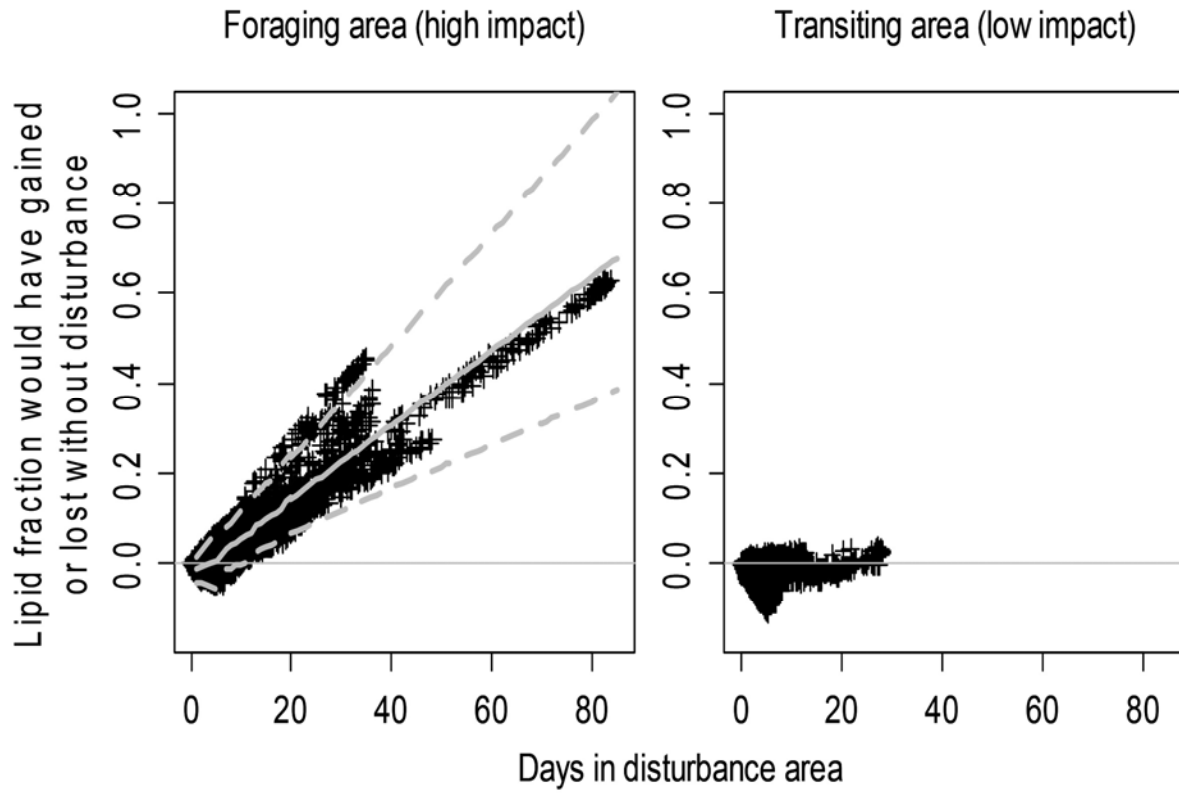
Figure 3. The probability of an elephant seal female giving birth to a pup as a function of her mass gain rate while foraging at sea.
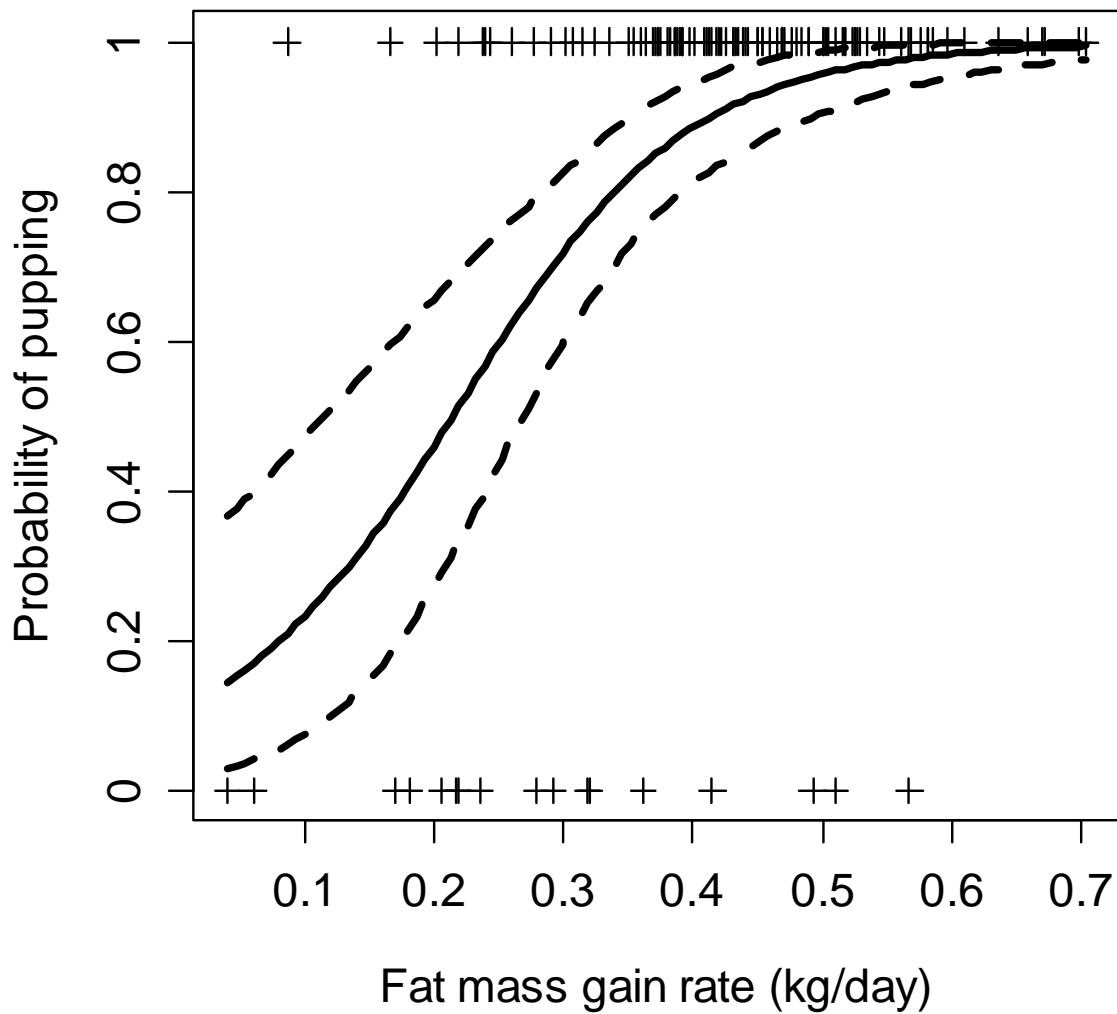
Figure 4.The relative proportion of time that elephant seals and sea lions spent in disturbance areas that had diameters of 100 and 25 km are shown for transit and foraging phases of their foraging trips.