

Relating behaviour and life functions
to populations level effects in marine
mammals: An empirical and
modeling effort to develop the PCAD
model

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Relating Behavior and Life Functions to Populations Level Effects in Marine Mammals: An empirical and modeling effort to develop the PCAD model

Final Report Contract JIP 22 07-23

Project 1: Relating Behavior and Life Functions to Populations Level Effects in Marine Mammals: an Empirical and Modeling Effort to Develop the PCAD Model

Project Objectives

The goals of the demographic analysis section of the JIP project are to:

1. Create Bayesian models to estimate survival and reproductive rates for two species with different breeding strategies: capital breeders (fasting females that provide high levels of nutrients to their offspring in a short period of time) and income breeders (females that continue to forage while lactating).
 - a. Combine a modeling effort with empirical data and an experiment from two well-studied marine mammals: the northern elephant seal, *Mirounga angustirostris*, and the Antarctic fur seal, *Arctocephalus gazella*.
2. Investigate potential fluctuations in those demographic rates in response to environmental variability and human manipulation. Human manipulation, in the form of deploying various location tags and TDRs, serves as a proxy for many types of human interaction that could potentially reduce fitness.
3. The primary deliverables will be in the form of reports that summarize data analysis and findings of this effort. A key goal is to publish as much of this as possible in peer-reviewed scientific journals. There will be a series of publications that address whether

or not the transfer functions described in the PCAD model exist and whether and how they can be used to define biological significance.

Tasks completed:

1. A conceptual bioenergetics based model was presented and published at the 2nd International conference on “The Effects of Noise on Aquatic Life” held in Cork Ireland.
2. As part of the development of a bioenergetics model for Antarctic fur seals, Birgette McDonald completed the first study of maternal investment as a function of age and or mass for an income breeder, the Antarctic fur seal. Prior to this research the only investigation of maternal investment as a function of age and or size was completed on capital breeders. This work was carried out as part of her dissertation research and resulted in three publications (McDonald 2009, 2012ab).
3. A Bayesian demographic (population model) was developed and applied to first the Antarctic fur seal data set and is now being applied to the northern elephant seal data set. However, this still provides valuable information for how a targeted impact to a distinct demographic class can have population-level effects
 - a. Analysis of the Antarctic fur seal demographic model revealed that, although adult survival and reproductive rates are correlated with environmental variables which could be used as proxies for disturbance, leopard seal predation on young of the year is a significant driver of the fur seal population at Cape Shirreff. A paper documenting these results is in press at Journal of Animal Ecology. These results suggest that further use of the Antarctic fur seal data for the JIP effort is not warranted as the effect of predation swamps out other population-level effectors.
4. The response of northern elephant seal females to disturbance has been

examined with respect to short term behavioral changes (i.e. trip duration, mass gain, dive behavior, swimming mechanics and stress response) and long term demographic parameters (reproductive output i.e. weaning mass, natality, pup and female survival).

- a. The biomechanical and energetic response of elephant seals to disturbance as indicated by a reduction in their ability to forage has been directly measured. Experimental manipulations of animals were carried out where foraging ability was reduced by the addition of drag devices/blocks. Animals were used as their own controls and measurements included changes in stroke rate, swim velocity, dive behavior and patterns, and energy consumption over a trip. The data are still being analyzed and will form the dissertation of doctoral candidate Jen Maresh who will finish next academic year. Her analysis is ongoing but clearly shows that elephant seals work to maintain a given energetic expenditure. That is they continue to work at a given rate independent of how the environment is changing around them. This result is critically important to understanding how elephant seals and probably other marine mammals respond to disturbance. These data suggest that elephant seals have a limited ability to respond to changes in prey availability by increasing foraging effort and thus their response to disturbance is likely to be linear. The good news is that this response will be easier to model, but it means that these animals have limited options to respond to disturbance.
- b. As a proxy for disturbance, we also studied the effects of increased distance to prime foraging habitat (i.e. longer transit times / reduced time in foraging habitat) by instrumenting seals from a distant colony in Mexico. While many of the seals traveled all the way to the north pacific, a larger proportion of the population foraged in local waters

while maintaining adequate feeding rates, indicating behavioral plasticity may mitigate the effects of disturbance. A further analysis of the foraging patterns of elephant seals relative to the oceanographic features of the

North Pacific Ocean was also completed with these data. The results were published in *Endangered Species Research* (Simmons et al 2011). A final effort was a completely new analysis of the diving and movement patterns of northern elephant seals. This analysis utilized the over 300 records now available for female Northern elephant seals, this is the largest data set yet obtained for any large marine vertebrate (see Robinson et al 2012, *PLoS One*). The continued collection and analysis of these data was made possible by the JIP contract.

c. We have found that the stress hormone cortisol is a robust indicator of energetic stress in elephant seals. Animals with lower energy gains over a foraging trip have elevated cortisol levels. These results validate the use of cortisol as an indicator of stress. A manuscript reporting these results is in preparation.

d. A major component of the JIP project is to assess how a decrement in the foraging ability would affect the behavior of marine mammals at sea and the impact on demographic parameters such as survival or reproduction. We have taken advantage of the 2009-2010 El Niño (ENSO) event to examine the effects of reduced foraging ability on both the at sea behavior and demography of northern elephant seals. During the 2010 ENSO event elephant seals were able to accommodate (maintain their mass gain at sea within the same trip duration) by modifying their foraging behavior. This was in contrast to previous studies of the 1983 and 1998 ENSO events where trip duration increased and mass gain was dramatically lower. These results support the concept that elephant seals, and probably other capital breeding marine mammals, have some ability to accommodate to perturbations in their environment. These results are providing the empirical data to model this response.

e. Using data from individually tracked animals, we were able to show northern elephant seal females who gained fat mass at a lower rate during their post-molt foraging trip were less likely to produce a pup.

Further analysis of tracking and diving data may show the timing of the lower rate (potentially at the beginning of the foraging trip) may be a factor.

- f. In addition, northern elephant seal females with less lipid mass after a post-molt foraging trip, an indication of lower foraging success, wean their pups at a lower mass. Lower wean mass is associated with lower pup survival during the first year which, in turn, reduces overall population growth. Results are similar to what is seen in southern elephant seals.
- g. Lastly, northern elephant seal females most-likely do not survive when their percent lipid mass falls below 27%.
5. JIP support allowed our team to be principal players in the ONR PCAD working group.
- a. D. Costa is a member of the Steering Committee and thus has considerable input into the direction of this working group.
 - b. Working Group objectives:
 - Explore how the conceptual model developed by the NRC committee might be translated into a formal mathematical structure
 - Consider how the above model might be parameterized with existing or emerging data on the responses of large vertebrates to disturbance
 - Define conceptual approaches for investigating transfer functions (e.g., time-energy budgets, trait-mediated responses)
 - Expand work by the NRC to include sensitivity analyses on different transfer functions
 - Outline exploratory models that might be used to model transfer functions, synthesize existing knowledge, examine potential mechanisms, or inform research and management efforts
 - c. The ONR working group chose four model systems, elephant seals, bottlenose dolphins, northern right whales and beaked whales, to explore implementation of the PCAD model.

- d. The northern elephant seal data set, supported by the JIP, has been and continues to be a primary data set being used in the development of the PCAD model.
- e. Lisa Schwarz, a post-doc funded by JIP, has been analyzing southern elephant seal demographic data provided by members of the PCAD working group in tandem with northern elephant seal data. The southern elephant seal analysis provides additional results on the population-level effects of disturbance on a capital breeder. The analysis will also allow us to improve our estimates of tag loss in northern elephant seals, a factor that can greatly bias demographic rate estimates. A paper documenting differences in tag loss has been published in the journal *Ecosphere* (Schwarz et al 2012).
- f. The working group developed a hierarchical Bayesian model to estimate the body condition of elephant seals as a marine predator. Observations of drift dives were used to quantify daily changes in lipid stores as a function of the physiological condition of the seal, its foraging strategy, its behavioral state, and the interaction with environmental covariates. This allowed us to estimate body condition at fine spatial and temporal scales. Though the model is specific to elephant seals, it can readily be applied to other species. This approach allows for fine scale ecological understanding of how animals respond to their environment, providing insight into areas and times where disturbance may have the largest negative effect on condition.
- g. The working group developed a first pass demonstration model of the effects of disturbance from short-term changes in individual behavior or physiology to long-term effects on population dynamics. This model used coastal bottlenose dolphins (*Tursiops* spp.), Bald eagles (*Haliaeetus leucocephalus*), and southern elephant seals (*Mirounga leonina*) as examples. We were able to show that this model is transferable among species, life histories, and data types; we demonstrated that data from long-term studies of known

individuals can be used to fit models of the effect of behavior on health, and to infer how those changes in health affect vital rates. The hypothetical exclusion of animals from foraging habitat can affect body condition (a measure of health), survival of offspring, and population growth rate. The method enables one to effectively model the effects of disturbance without assuming the ecological fallacy of homogenous populations. In addition, the method can help one determine what combination of factors, such as the intensity of disturbance and the type of individual affected, can result in unacceptable levels of change in population dynamics. A manuscript reporting these results is in final form and will be submitted to Science shortly (New et al in ms).

- h. In addition to this effort there were two important ancillary publications, which are relevant to the JIP effort. First we participated in a workshop to examine the physiology associated with decompression sickness in diving mammals. Decompression sickness has been suggested as a possible cause of whale strandings associated with seismic surveys and naval activities. This paper reviews what we know and don't know about decompression sickness in marine mammals (see Hooker et al Proc Royal Soc B 2011). Second in an effort lead by Lesley New we developed a bioenergetics model of beaked whales and how they would respond to disturbance. This paper is in review (New et al PLoS One).

6. While this contract is now complete we are continuing to work on the various papers that have resulted from the support. However, we have 1 in press and 11 published in peer reviewed journal articles including papers in Proceedings of the Royal Society, Journal of Experimental Biology and Physiological and Biochemical Zoology.

Future Directions

Using existing data from northern and southern elephant seals, the PCAD working group has examined the linkage between foraging behavior and

reproductive success

and survival and has developed a first generation model. This model assumes a disturbance results in a reduction in foraging effort that is then modeled to determine if and how much that reduction in foraging changes female condition. A change in female body condition is then related to pup mass at weaning and subsequent pup survival. Such information can then be used to predict the potential of a given disturbance to cause a population-level change.

As a first generation model, the elephant seal system requires further refinement to provide realistic outcomes. In particular, the current model assumes that animals have no ability to compensate for lost foraging opportunities. We know that this is not true and that animals can compensate by modifying their dive behavior, foraging intensity, or time at sea. We would like to continue this effort to examine the resilience or ability of a capital breeder to respond to foraging perturbations. Further, the demographic data for the existing ONR-PCAD model were derived exclusively from southern elephant seals, as those data were readily available. Since that time, data on northern elephant seals have been prepared for similar analyses. The northern elephant seal demographic data allow for an examination of the threshold when females skip a reproductive event. Further, this work will be extended by a collaboration where blood samples collected from female northern elephant seals with known at-sea behavior, mass gain and reproductive histories will be analyzed for stress hormones (corticosterone).

The PCAD working group also began investigating the disturbance pathway from individuals to populations in several bottlenose dolphin systems, focusing on the importance of group behavior on individual

decisions. However, the group has yet to link behaviors to individual condition and condition to vital rates. We wish to extend the demographic model developed under the current support for fur seals and elephant seals to bottlenose dolphins. As we have found that we will not be able to use Antarctic fur seals as a model of an income breeder, we would like to extend these analyses to bottlenose dolphin by creating the quantifiable models needed to link behavior to condition and condition to vital rates. The first step of this process will be to prepare and organize data from the Sarasota Bay bottlenose dolphin data set collected by Dr. Randy Wells. We plan to add Leslie New as a post doc supported by this effort to adapt behavioral models she has developed for Moray Firth, Scotland and Doubtful Sound, New Zealand to account for the influence of group behavior on individuals. We will also work with Rob Schick who has developed models linking behavior with condition (or health) for right whales that may be modified for bottlenose dolphin analyses. Lastly, we will develop a life table for bottlenose dolphins, allowing us to complete the same analysis that has been carried out with elephant seals (a capital breeder) on bottlenose dolphins (an income breeder). By modeling the responses of both elephant seals and dolphins, we will greatly broaden the scope of this analysis to include different life history strategies.

Project 2: Use of Electronic Tag Data and associated Analytical Tools to Identify and Predict Habitat Utilization of Marine Mammals in a Risk Assessment Framework

Project Objectives

- a) Use existing TOPP data, augmented by new data as they are collected, to develop the analytical approaches to create habitat maps from tagging data. Develop approaches to identify habitat characteristics that can be used to predict marine mammal habitats and distributions.

- . b) Develop predictive animal movement and distribution models to generate probability maps of dynamic habitat utilization patterns based on different oceanographic climate scenarios;

Tasks completed:

1) High-resolution species-specific spatial-temporal habitat utilization maps have been created for all TOPP species.

a. Habitat utilization maps have been developed for all of the TOPP species, which include northern elephant seals, blue and humpback whales and California sea lions. These habitat maps provide a kernel density plot of each species averaged over the entire data set as well as seasonal occupancy (Autumn, Spring, Summer, Winter). These habitat types have been examined with respect to oceanographic characteristics such as SST, SSH, SSH gradient and satellite remotely sensed Chlorophyll. Three regions have been identified as important biological hotspots, the North Pacific Transition Zone, the California Current and the White Shark Café. This analysis was incorporated into a paper published in Nature in 2011 (Block et al 2011). The detailed maps by species and season are available in Autumn-Lynn Harrison's dissertation.

. 2) Using environmental characteristics of the specific habitats of the TOPP species we have developed predictions of how climate change will affect the distribution of TOPP species. This analysis was published in Nature Climate Change (Hazen et al 2012).

. 3) Developed guidelines and tools for the use of tracking data to create and assess habitat utilization patterns of marine vertebrates.

a. Using the TOPP data set we have assessed the minimum number of animals that would need to be tracked to reliably assess the distribution of a pelagic or coastal marine mammal population. For many species a sample size of between 40-50 individuals provides a robust estimate of home range, including core areas.

These results are available in the Dissertation of Autumn-Lynn Harrison.

- b. Analytical methods have been developed to assess what animals are doing, where and when they are doing it. This included an assessment of how 2D surface tracks can be used to detect regions where foraging occurs. We used diving behavior data obtained from northern elephant seals as a model to determine if and how well tracking data can be used

to effectively predict foraging success at the level of the entire trip and/or within a trip. We found that transit rate, a simple easily defined metric, is a robust and reliable indicator of foraging success in at least elephant seals and probably other marine vertebrates. This is an important result as for many species the only data available are surface movement patterns. Thus we provide validation that foraging behavior can be inferred from surface movement patterns alone and were published in the *Journal of Animal Ecology* (see Robinson et al 2010)

- a. Integrating and comparing the conceptual basis for understanding patterns of migration across taxa and systems (marine vs. terrestrial) is challenging. Systematically distinguishing migratory behavior from other types of movement requires theoretical approaches that are broadly applicable across taxa. We found that the migratory patterns of species as ecologically dissimilar as moose and Pacific blue fin tuna are well-fit by theoretical models based upon random walk theory, suggesting that a unified approach to quantifying and predicting migration across a range of taxa and biomes may be possible. The analytical approach to merge these divergent data sets was published in *Methods in Ecology and Evolution* (Winship et al 2012) and detailed figures are available in the Dissertation of Autumn-Lynn Harrison.

- 4) Further developed and refined algorithms for the use of State Space

Models (SSM) to filter and derive behavioral information from animal movements (surface tracks).

- . a) Existing behavioral switching SSM model runs in WinBUGS, which is slow and difficult to use. Following the fundamental approach of a SSM we have developed an algorithm and software that runs in Matlab. This is more accessible and more transparent than what was previously available. More importantly this program can handle large multidimensional environmental datasets, something that was not possible in SSM programs running in WinBugs. This model and approach was published in Ecological Modeling (Breed et al 2012).
- . b) The fractal landscape analytical tool currently written in Matlab was translated to the R programming language. R is an open access statistical programming language that is widely used in the diving behavior community. This will make the analytical technique available to a larger user community.

5) Discovered a fundamental flaw in a commonly used programming approach to duty cycle Argos tags.

c) This approach where the number of transmissions per day is limited produces reasonable looking tracks but these tracks do not accurately

reflect the behavior patterns of animals monitored over short distances or time frames. Further these tracks cannot be analyzed using powerful time series analysis such as State Space models. We found that when movement scale is small, regular observations are critical to recover hidden behavioral state and produce good location estimates. Small movement scales also greatly magnify the effect of programming errors. In addition, we found tracks with more frequently collected locations (increasing N) can make up for low accuracy of individual locations. This suggests that frequently collected Argos is as good as less frequently collected GPS locations. From these results and our experience tracking animals more

generally, we produced a set of guidelines for programming, and deploying electronic tracking tags to maximize the utility of the data they produce. This analysis was published in *Ecosphere* (Breed et al 2011).

- . 6) We published a current of tracking of large marine vertebrates. This review provided an overview of what we have learned and how animal tracking is being used for conservation and management. In addition there are sections on animal navigation and a summary of the methods used for the analysis of tracking data. This paper was published in the *Annual Reviews of Ecology Evolution and Systematics* (Costa et al 2012).
- . 7) A missing element in studies that utilize ARGOS tracking data is validation of the quality of the positions provided by ARGOS. Surprisingly there have been few if any studies where the accuracy of ARGOS positions was determined. The most frequently used study was positional data acquired from a grey seal swimming and diving in a tanks at the Sea Mammal Research Unit. To remedy this situation we compared the accuracy of ARGOS locations to those acquired with Fastloc GPS on a variety of different marine mammals, including Calif. sea lions, Northern elephant seals, and Galapagos sea lions. Australian and South Africa fur seals. The results of this study were published in *PLoS One* (Costa et al 2010).

In the process of addressing the above objectives we have published 34 peer reviewed journal articles two papers in press and six in manuscript including papers in *Nature*, *Proceedings of the Royal Society* and the *Journal of Animal Ecology*. This effort also supported four doctoral dissertations.

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