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Stochastic dynamic programming: An approach for modelling the population consequences of disturbance due to lost foraging opportunities

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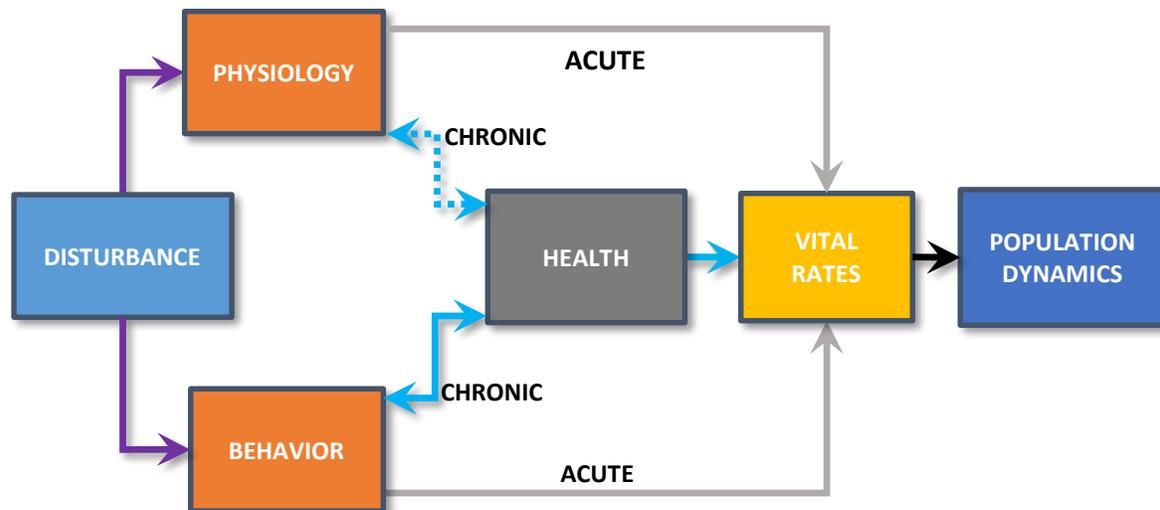
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Since the introduction of the population consequences of disturbance (PCoD) conceptual model, lost energy has become a central component of modelling biologically meaningful disturbance. Long-term datasets on northern elephant seals of Año Nuevo, CA and bottlenose dolphins of Sarasota Bay, FL span several environmental disturbances, allowing us to quantify how behavior, physiology, and vital rates change with natural reductions in prey. While complete PCoD models are possible with large datasets, health metrics in particular can be difficult or impossible to collect for many species. In addition, PCoD models to date have assumed the worst-case scenario, in that animals exposed to a disturbance cannot compensate for lost foraging. Combined with knowledge of energetic requirements of individuals, Stochastic Dynamic Programming (SDP) models examine potential compensatory behavioral mechanisms that individuals can employ in the presence of a disturbance. However, SDP bioenergetic models require data on the energetic landscape, time-activity budgets, movement probabilities between habitats, and metabolic rates on a timescale appropriate for energy acquisition. This approach is currently being implemented for California sea lions and gray whales with the potential to ground-truth SDP models by comparing them with current elephant seal and bottlenose dolphin models.



1. INTRODUCTION

In 2014, a working group sponsored by the Office of Naval Research (ONR) published a new version of the NRC Population Consequences of Acoustic Disturbance, or PCAD, framework (Figure 1 and New *et al.* (2014)). Both frameworks were developed to understand how disturbance of individuals, on both a large and small scale, can lead to population-level effects through a series of transfer functions that quantify the relationships between causes and consequences. In the newer framework, disturbance has the potential to affect both the behavior and physiology of an individual. Those behavioral and physiological changes can lead to acute demographic changes (death or loss of offspring) or reductions in health of an individual. Repeated disturbances that lead to reduced health can eventually adversely impact an animal's reproductive output and survival. Lastly, when enough animals have reduced survival and reproduction, population levels decline.



*Figure 1. The population consequences of disturbance framework showing the links between disturbance to population-level effects (modified from New *et al.* (2014)). Purple arrows indicate the transfer functions addressed in many of the articles in this Proceedings. Black arrow indicates a well-studied transfer function. Blue arrows are the focus of the ONR sponsored working group, with the dashed line indicating a field recently under development.*

Quantifying the transfer functions can be challenging, and the level of effort in defining the functions has varied. For example, much of the research presented in these Proceedings focuses on addressing the transfer functions between disturbance and behavior or physiology. Those complex relationships depend on the location of the disturbance, the species affected, and the behavior of the animals. On the other hand, the well-defined link between demography and population-level effects is guided by general principles relating to all species. The transfer functions that address the consequences of disturbance through chronic, subtle changes in health were, until recently, virtually unexplored for marine mammals. Therefore, the PCoD working group (renamed Population Consequences of Disturbance since the framework applies to all forms of disturbance) decided to focus on quantifying those transfer functions for four case studies representing a range of life history strategies and data availabilities. The primary objectives of this document are to describe the current work to define the transfer functions for

two data-rich case studies, the northern elephant seal (*Mirounga angustirostris*) and Sarasota Bay bottlenose dolphin (*Tursiops truncatus*), and describe the utility of Stochastic Dynamic Programming (SDP) within the PCoD framework (McHuron *et al.*, In review).

2. CASE STUDIES

The two case studies represent very different life history patterns. Elephant seals are capital breeders, meaning reproduction is decoupled from foraging; thus, a female must acquire and store enough energy during the foraging period to successfully rear a pup while she is fasting. In contrast, bottlenose dolphins are income breeders, meaning they primarily support lactation using energy they can consume during lactation.

For both case studies, long-term, comprehensive data are available from mark-recapture efforts, assessments of health, and behavioral observations. Researchers at University of California, Santa Cruz capture and flipper tag elephant seals twice a year at Año Nuevo State beach when they haul out to breed and molt. Consistent and large-scale satellite tagging and recovery provide detailed information on foraging movements, energy acquisition, and reproductive success of individuals. The Sarasota Dolphin Research Program annually captures bottlenose dolphins in Sarasota Bay to assess their health. In addition, their consistent mark-resight efforts span almost 25 years. Most importantly, the data for both case studies span several environmental disturbances (El Niño for elephant seals and red tide for bottlenose dolphins), allowing us to quantify how behavior, physiology, and vital rates change with natural reductions in prey. Such naturally-occurring prey loss can serve as a proxy for anthropogenic disturbance that reduces foraging.

A. HEALTH TO VITAL RATES

We have been able to quantify the link between health and vital rates for both species. For northern elephant seals, the amount of fat a female can accrue during the post-molt trip has a direct link with her ability to produce a pup (Figure 2a). In addition, pup condition at weaning is linked with the amount of energy its mother has when she arrives on the beach (Figure 2b). The pup's survival is, in turn, related to its condition at weaning (Figure 2c).

In Sarasota Bay, bottlenose dolphin survival and the probability a mother will separate from her calf are a function of aldosterone levels (Figure 3). Researchers in the ONR-sponsored stress physiology group are also finding aldosterone to be a strong indicator of stress in other bottlenose dolphin populations, as well as in other species (Houser *et al.*, 2011; Ensminger *et al.*, 2014; Atkinson *et al.*, 2015; Champagne *et al.*, 2015). However, the mechanism behind this relationship is not yet understood.

In addition to the case studies, separate research has shown a bioenergetics approach can be useful for species that cannot be handled. The process involves quantifying the energy needed for an animal to survive and a species to persist based on metabolic rates and reproductive energy costs (fetal growth and lactation in mammals) (New *et al.*, 2013b; Villegas-Amtmann *et al.*, 2015). When animals no longer have the needed energy, either through lost foraging or increased maintenance needs, a reproductive opportunity is lost, or the animal dies.

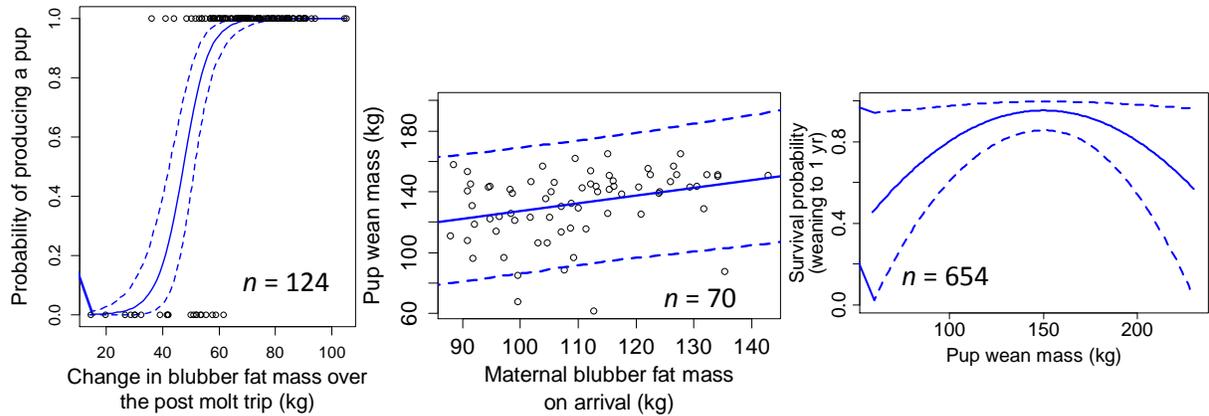


Figure 2. Transfer functions linking female condition to reproductive success in the northern elephant seal. (a) the probability of producing a pup vs. the amount of blubber fat mass a female can gain during her post-molt foraging trip. (b) pup wean mass vs. the amount of blubber fat mass a female has upon arrival on the beach. (c) Pup survival probability vs. pup wean mass.

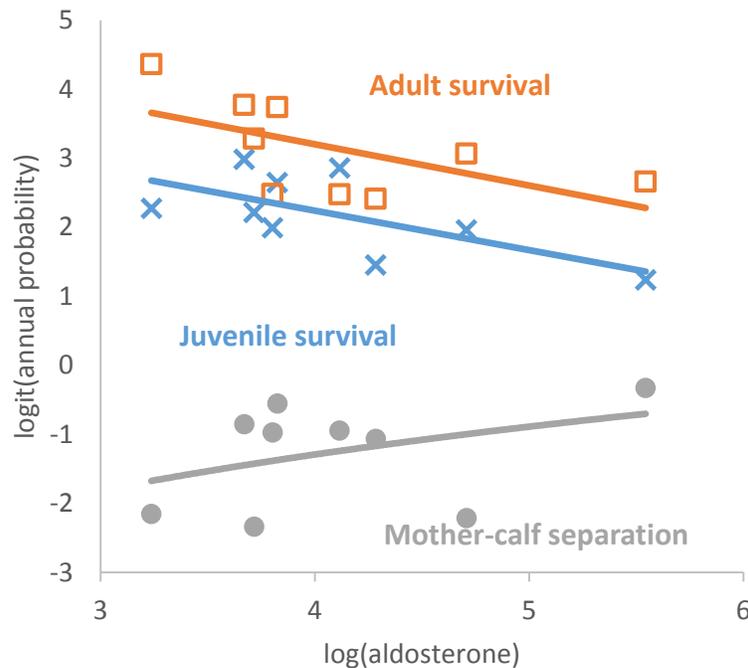


Figure 3. Probability of survival for adults (8+ years old; orange) and juveniles (2 – 8 years old; blue) and probability of mother-calf separation (gray) as a function of measured aldosterone levels.

B. BEHAVIOR TO HEALTH

Behavior is easier to measure than many other metrics in marine mammal research. However, we have only begun to link behavior with health. Costa *et al.* (2016) estimated the population consequences of disturbance due to lost foraging for northern elephant seals. Female energy reserves can be measured by determining the rate at which they float or sink during a foraging trip (Robinson *et al.*, 2010). Costa *et al.* (2016) modeled disturbance in a portion of the

seals' range and assumed no foraging occurred while an animal was within the area of disturbance, leading to a reduced amount of energy available for reproduction. The method of simulating disturbance and lost energy presents a worst-case scenario and is precautionary since animals could not compensate by either leaving the zone of disturbance or increasing their foraging effort later in the season. Nevertheless, foraging exclusion circles with a diameter of 100 km (considered large for an acoustic disturbance) resulted in little-to-no change in reproduction or pup survival since the foraging habitat is comparatively large. While the results emphasize the importance of foraging range when addressing disturbance, the methods did not consider potential behavioral compensation for lost foraging, which could be important in cases where the proportion of affected foraging range is higher.

For bottlenose dolphins, New *et al.* (2013a) developed a behavioral model with a complex set of decisions for individuals to make based on competing internal states, such as hunger, fear, and a need to socialize. Simulations with disturbance showed that an increase in traffic from 70 to 470 vessels per year would not change the time-activity budget for a population in Moray Firth, Scotland. While "health" was an underlying motivational state, health consequences of behavioral choices were not addressed. In addition, behavioral choice assumptions did not account for maximizing health or demographic fitness.

3. STOCHASTIC DYNAMIC PROGRAMMING

In behavioral ecology, SDP models were first developed in an effort to understand behavioral choices that balance the risk of predation with the need to gain energy to survive and reproduce (Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000). These models have evolution by natural selection as an underlying principle. In general, species exist because their predecessors were successful at eating, surviving, and reproducing. Along with physiological traits, behavioral choices are a consequence of evolutionary adaptation based on tradeoffs. For example, animals that are in a poorer nutritional state are more likely to take risks, since the odds of surviving are lower if they do not. In the basic patch choice model of Mangel and Clark (1988), animals inhabit environments in which patches have different risks and rewards based on the probability of dying in a patch, the energy cost of visiting the patch, the probability of finding food, and the energy gain in the patch.

SDP models rely on several assumptions. First, animals will make decisions based on maximizing their future reproductive fitness. Second, there are limitations as to how an individual can achieve maximum demographic fitness (reproduction). For example, marine mammals are incapable of producing all potential offspring in one year. Therefore, physiological and behavioral limitations must be set. Third, animals have perfect knowledge of their environment. Lastly, while behavioral responses are shaped at an evolutionary time scale, disturbance is a stimulus on a shorter time scale. SDP is a method that allows us to predict how animals will behaviorally compensate to maintain maximum fitness given a novel disturbance that reduces available energy.

The story then becomes a process of following changes in nutritional state due to energy acquisition and allocation. Unless an animal is investing in its last offspring, an animal will allocate gained energy first to itself for maintenance, activities, and growth. Any additional energy can be used for reproduction. As a result, demographic fitness can be reduced by either reducing the amount of energy an animal can acquire or increasing the cost to survive. Noren *et al.* (In review) demonstrate that odontocetes are physiologically adapted to their environment to

the point that increases in the cost of survival, such as increased metabolic rate during faster swimming, are very small when a disturbance creates ephemeral behavioral changes. The higher priority concern then involves loss of energy acquisition, or how disturbance reduces foraging options (Noren *et al.*, In review).

A disturbance can reduce an animal's foraging options, and thus fitness, by either increasing the probability of dying in a patch, increasing the energy cost of visiting a patch, decreasing the probability of finding food, or decreasing the energy gain in the patch. Note that the actual environment does not need to change. Sometimes only the perception or the abilities of the foraging animal will change. For example, a loud noise may make an animal think predation risk has increased, driving the animal out of preferred foraging habitat. Or, the noise may reduce an animal's ability to detect prey or predators.

SDP models require several species-specific and environmental inputs. First, we need to pick a time horizon over which an animal can increase its demographic fitness. Examples are the length of pregnancy, the length of lactation, or an animal's entire lifetime. Second, the model requires a metric of fitness, which could be offspring recruitment, successful pregnancy, or lifetime reproductive success. Third is the physiological state and how it links to the metric of fitness. For instance, metabolic needs for survival and reproduction, milk production, and female mass qualify as physiological states. Next, the model needs biologically realistic limitations. For example, a capital breeding marine mammal should not be capable of acquiring all of its annual energetic needs in one foraging day. Lastly, modeling a specific system requires an understanding of the spatial characteristics of prey (energetic landscape) and predators. The last two steps require dialogue between researchers building the SDP models and the biologists who understand the species' system and physiological limitations.

Next, a fitness function needs to be defined, which is essentially estimating the relationship between the physiological state and reproductive success or survival. Empirically determined estimates of such functions are shown in Figures 2 and 3. Therefore, the process of designing an SDP model essentially incorporates the PCoD health-to-vital rates relationship in to the model. Lastly, we start at the end of the time horizon with a successful fitness score, and iterate the energy value and behavioral choices backwards in order to understand the way behavior works in the forward direction.

4. THEORETICAL EXAMPLE

McHuron *et al.* (In review) have made the first effort to use SDP modelling in the context of marine mammals and disturbance by developing a theoretical example. They looked at capital and income breeders living in three different patches, and the only differences between the patches were the types of prey. One patch had high energy but inconsistent prey. A second patch had prey that was moderate in both energy quality and consistency. The third patch consisted of low-energy but consistent prey. The long-term average value of each patch and the probability of mortality from predation were the same for all patches. The fitness metric was successful birth of an offspring for capital breeders and successful weaning of an offspring for income breeders. They then introduced different levels of disturbance in to each patch or combination of patches. Individuals were allowed to forage in a disturbed patch at a reduced probability of finding prey, or move to a new foraging patch at an increased energetic cost.

Overall, disturbance in the patch with the most consistent but lowest quality prey resulted in reduced fitness for income breeders (Figure 4). Also, capital breeders were generally well

buffered from any disturbance. So, a first pass using an SDP model with a theoretical example yields interesting results. For the first time, we have a method to quantify how either incidental or intentional exclusion zones will affect the energetic input of the target species, and we have shown how variation in the characteristics of the excluded area affect the target species.

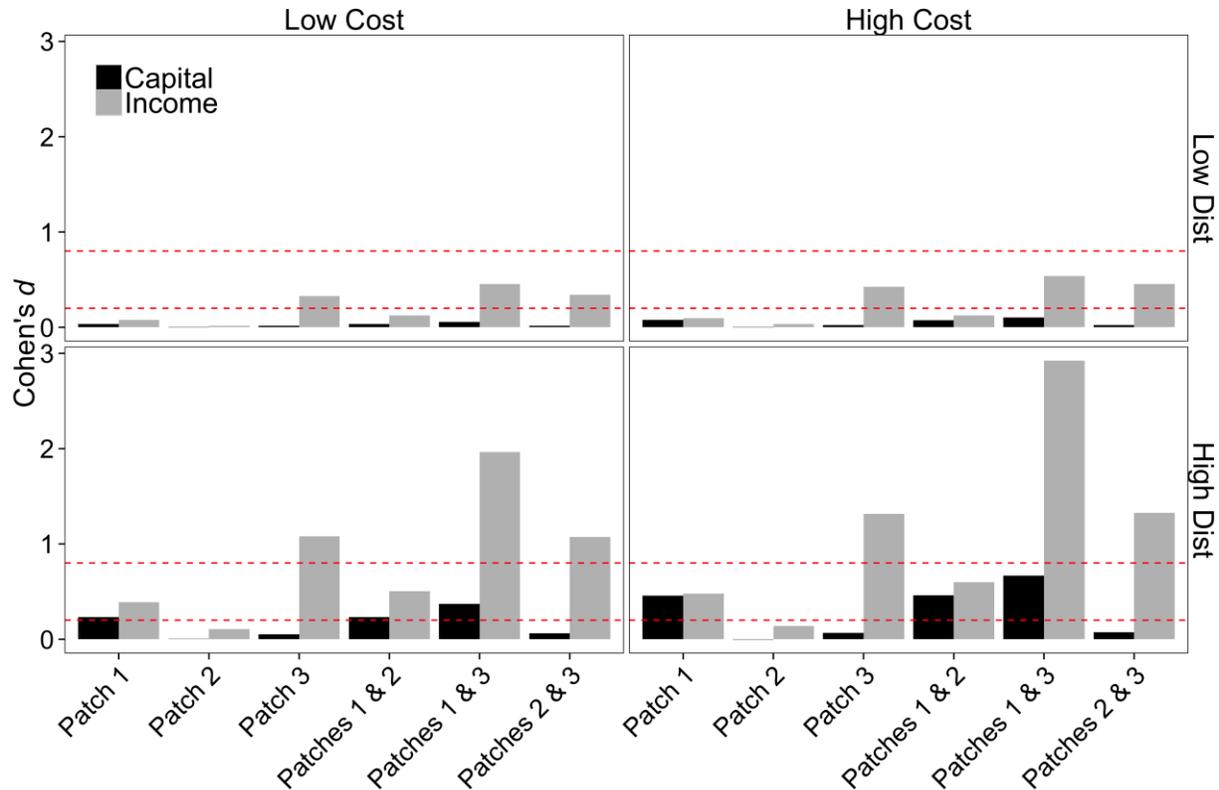


Figure 4. Values for Cohen's d averaged over 100 simulations for a capital (black bars) and income-breeding (gray bars) pinniped. Each subplot represents a different cost (columns) and probability of disturbance (rows). Disturbance scenarios correspond to the foraging patch/s where disturbance was allowed to occur. Patch 1: high energy but inconsistent prey. Patch 2: moderate energy and consistency. Patch 3: low energy, consistent prey. Cost is a multiplier of field metabolic rate (either 20% or 40%), corresponding to the additional cost incurred by a female to move to an alternate patch when disturbed. The probability of being disturbed in a patch was low (0.1) or high (0.5). The interpretation of Cohen's d is that 0.2 is a small effect (dashed line), 0.5 is a modest effect, and values greater than 0.8 represent a large effect (dashed line).

Current studies are extending the SDP method to an income-breeding species, the California sea lion. In addition, an SDP model will be developed for the highly endangered western gray whale stock which exhibits a very limited foraging range off Sakhalin Island. Their foraging area is also a region of intense oil exploration and extraction. Both efforts began with research on the bioenergetics of the stock or species (Villegas-Amtmann *et al.*, 2015; McHuron *et al.*, In prep; Villegas-Amtmann *et al.*, In review).

5. CONCLUSIONS

Although it was not originally developed for this purpose, early results show SDP can be an appropriate and time-tested method to predict behavioral compensation when lost energy is a

consequence of disturbance. SDP fits well within the PCoD framework and folds the link between health and vital rates in to the model. While not discussed here, forward simulations can also include individual stochasticity and complete the PCoD framework through to population-level effects. Because of that, development of SDP models for ONR case studies could be of benefit to further our general understanding of the PCoD framework.

Even simple SDP models provide valuable insight into when and where disturbance can be most problematic. In addition, the models are quite flexible, as they can be adapted for any species and are capable of handling cumulative impacts. However, increased complexity comes at the cost of increased computer processing time and increased data needs.

Even for simple modeling exercises, the SDP framework requires data that previously have not been of high priority for many PCoD models. First, they require an understanding of the energetic landscape in which a species lives and how individuals respond to that landscape in the context of disturbance and potentially predation. Specifically, time-activity budgets, movement probabilities between habitats, habitat quality, and metabolic rates are needed on a timescale appropriate for energy acquisition, ideally on a daily scale. Energetic requirements for capital breeders are also needed on a larger timescale, since energy input is decoupled from energy output during fasting. Lastly, to implement of a full predictive PCoD model, dose-response curves and measures of the probability of exposure are still needed.

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