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A state-dependent model for assessing the population consequences of disturbance on income-breeding mammals

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ABSTRACT

Human activities continue to expand in marine and terrestrial environments, leading to increased interactions with wildlife that can have negative impacts on population dynamics. Approaches for quantifying how these interactions translate to population-level effects are therefore crucial for effective management practices and balancing human-wildlife tradeoffs. We developed a method using state-dependent behavioral theory implemented via Stochastic Dynamic Programming (SDP) for predicting the population consequences of disturbance on the physiology and reproductive behavior of an income-breeding mammal, using California sea lions (*Zalophus californianus*) as a motivating species. Emergent properties of the model included reproductive characteristics associated with long-lived species, such as variation in the age at first reproduction, early termination of pregnancy, and skipped breeding. In undisturbed model simulations, reproductive rates and the average wean date were consistent with empirically-derived estimates from sea lions and other marine mammals, highlighting the utility of this model for quantifying fecundity estimates of data-deficient species and addressing fundamental ecological processes. In disturbed model simulations, exposure to prolonged, repetitive disturbances negatively impacted population growth; in addition, short, infrequent disturbances had the potential for adverse effects depending on the behavioral response of sea lions and the probability of being disturbed. The adverse effect of disturbance on population dynamics was due to a combination of reduced pup recruitment (survival to age one) resulting from a lower wean mass and increased abortion rates that led to skipped reproductive years, both of which have been documented for marine mammal populations experiencing natural fluctuations in prey availability. The derivation of state- and time-dependent reproductive decisions using an SDP model is an effective approach that links behavioral and energetic effects at the individual level to changes at the population level, and one that serves a dual purpose in the ability to quantify basic biological parameters and address ecological questions irrespective of disturbance.

1. Introduction

Wildlife populations face increasing pressure from human activities that can result in direct mortality or indirect effects, including behavioral changes or disruption of life histories (Knowlton and Kraus, 2001; Shannon et al., 2016; Smith et al., 2015; Stankowich, 2008). A growing human footprint in the marine environment has led to increased interactions between humans and marine mammals, resulting in concern about the impact of these activities on populations that already face a myriad of other threats (Davidson et al., 2012). Exposure to disturbance from naval exercises and vessel traffic associated with ecotourism results in short-term disruptions of natural behavior (Castellote et al., 2012; DeRuiter et al., 2013; Goldbogen et al., 2013; Melcón et al., 2012; Pirotta et al., 2015; Williams et al., 2006), but these disruptions do not necessarily translate to biologically meaningful effects on population dynamics (Gill et al., 2001). Despite the growing need to understand the consequences of disturbance on marine mammal populations, there have been comparatively few studies that have attempted to quantify the potential long-term effects of disturbance for this taxonomic group (Christiansen and Lusseau, 2015; King et al., 2015; New et al., 2014, 2013; Villegas-Amtmann et al., 2017, 2015).

Early efforts towards understanding the population-level effects of acoustic disturbance led to the development of the Population Consequences of Acoustic Disturbance (PCAD) framework by a US National Research Council committee in 2005 (Wartzok et al., 2005).

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Further development of these ideas led to the Population Consequences of Disturbance (PCoD) framework, which conceptualizes how disturbance translates from the individual to the population level through a series of transfer functions that link a behavioral or physiological response by an individual (often modeled as a change in energy) with changes in health, vital rates, and population dynamics (New et al., 2014). Applications of the PCoD framework have been limited (Costa et al., 2016; Nabe-Nielsen et al., 2018; New et al., 2014) due to the combination of a lack of basic life history data for many species and the challenges of quantifying some of these transfer functions for species that are long-lived and often wide-ranging and elusive.

McHuron et al., (2017a) proposed that state-dependent behavioral theory implemented via Stochastic Dynamic Programming (SDP; Mangel and Clark, 1988; Houston and McNamara, 1999; Clark and Mangel, 2000) is a viable method for quantifying the functions that link behavior with vital rates, thereby enabling implementation of the PCoD framework. SDP models have been applied across a broad range of taxonomic groups for quantifying the effects of natural environmental disturbance (Bull et al., 1996; Denis et al., 2012; Satterthwaite and Mangel, 2012; Tenhumberg et al., 2000), but until recently had not been applied in the context of anthropogenic disturbance (McHuron et al., 2017a; Pirotta et al., 2018). This approach originates from the tenant that behavior is an evolutionary trait and allows for different behavioral responses to disturbance conditioned on the environment and an individual's physiological state.

Initial efforts to model the effects of disturbance on marine mammals using SDP models focused on the impact of disturbance on expected reproductive success within a single year and did not explicitly model transitions between reproductive states. Individuals either remained in a fixed reproductive state throughout that time period (McHuron et al., 2017a) or transitioned between two reproductive states (pregnant or not pregnant) based on a simple threshold value (Pirotta et al., 2018). The incorporation of reproductive transitions into SDP models is an important next step that will facilitate species-specific applications, particularly for income-breeding species that have the potential for simultaneous gestation and lactation, necessitating an approach that can capture transitions among reproductive states (i.e. early weaning and abortion) in a way that is more akin to how these transitions likely occur in nature. Income breeding is a reproductive strategy used by many mammalian (and non-mammalian) species (Bonnet et al., 1998; Costa, 1991; Jönsson, 1997; Oftedal, 1997; Schulz and Bowen, 2004) that may increase the susceptibility of individuals and populations to energetic disruptions (Costa et al., 2016; McHuron et al., 2017a). This reproductive strategy complicates PCoD models because, as females rely on energy gained throughout lactation to support offspring growth, the timing of disturbance becomes a more complicated subject and requires an approach that goes beyond bioenergetic models (Costa et al., 2016; Villegas-Amtmann et al., 2017, 2015). SDP models represent a natural framework in which to address these issues, however, as will be seen below, modeling the transitions among multiple reproductive states is not a trivial addition.

We present an SDP model expanding on McHuron et al., (2017a) that includes many of the biologically relevant extensions that would be desired to model the population consequences of disturbance for an income-breeding marine mammal. We illustrate these extensions using California sea lions (*Zalophus californianus*) as a case study because their physiology, behavior, and demographics have been well-studied compared with many other marine mammals. In addition to describing the derivation of the SDP equations, we simulated a variety of hypothetical disturbance scenarios to examine how variability in (1) an individual's response to exposure, (2) the timing of exposure within the year, (3) the duration of exposure, and (4) the repetitiveness of the exposure affected pup recruitment and population growth rates. We focus on highlighting the utility of this approach in implementing the PCoD framework and how it can be used to identify and prioritize research needs, but also discuss its application in addressing key ecological questions and processes irrespective of disturbance.

2. Methods

SDP models involve two primary components, a backward iteration where optimal behavioral decisions are identified assuming individuals act to maximize some metric of Darwinian fitness, and an individual-based forward simulation where the state dynamics and behavioral decisions of a population are simulated. Anthropogenic disturbance can be introduced in the forward simulation under the assumption that it is not in the evolutionary history of the organism, and thus does not influence the behavioral decisions generated in the backward iteration (Clark and Mangel, 2000; Mangel and Clark, 1988; McHuron et al., 2017a). The backward iteration consists of (1) identification of a time horizon, (2) characterization of physiological state variables and how they change in response to the environment and behavior, (3) definition of a function that links the state variables(s) to a measure of Darwinian fitness (referred to as the terminal fitness function), and (4) derivation of the SDP equations that predict the behavior of individuals based on state and time. The sections below follow this progression. A conceptual diagram of the backward iteration and forward simulation as described below is shown in Fig. 1.

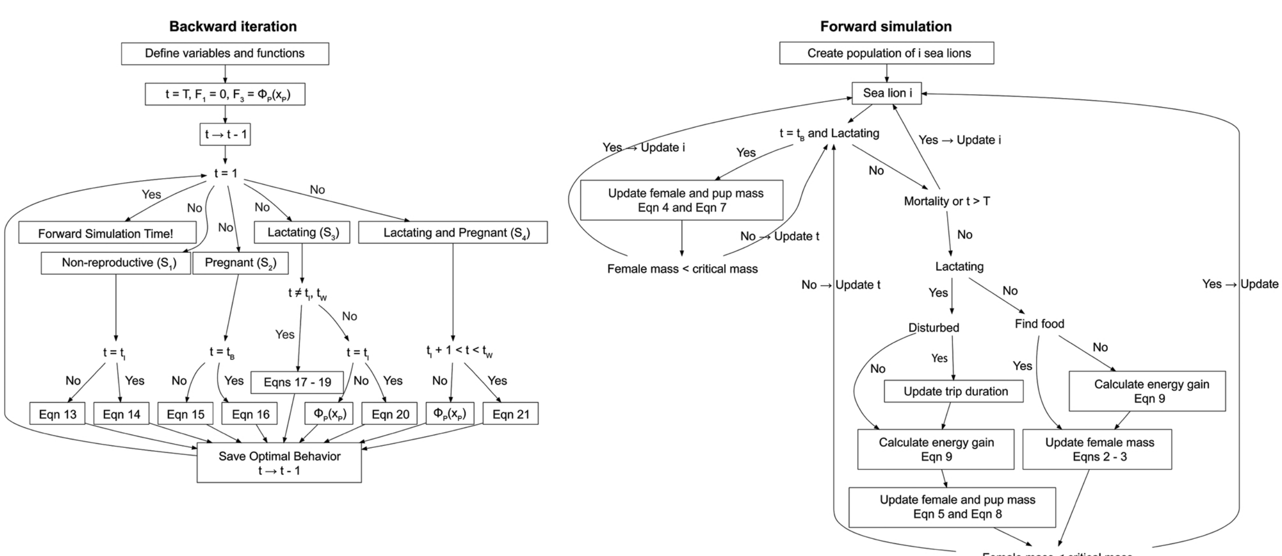

Fig. 1. Conceptual diagram of the model consisting of a backward iteration (left) and a forward simulation (right) as described in the text.