

State-dependent behavioural theory for assessing the fitness consequences of anthropogenic disturbance on capital and income breeders

Elizabeth A. McHuron^{*1}, Daniel P. Costa¹, Lisa Schwarz² and Marc Mangel^{3,4}

¹Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95064, USA; ²Institute of Marine Sciences, University of California, Santa Cruz, CA 95064, USA; ³Department of Applied Mathematics and Statistics, University of California, Santa Cruz, CA 95064, USA; and ⁴Department of Biology, University of Bergen, Bergen 9020, Norway

Summary

1. Anthropogenic disturbance is of increasing concern for wildlife populations, necessitating the development of models that link behavioural changes at the individual level with biologically meaningful changes at the population level.

2. We developed a general framework for estimating the fitness consequences of disturbance that affects foraging behaviour using state-dependent behavioural theory implemented by Stochastic Dynamic Programming (SDP). We illustrate this framework using generalized examples of pinnipeds, a group of marine carnivores that include both capital- and income-breeding species. We examined how disturbance affected pup recruitment separately for each reproductive strategy, and the impact of foraging decisions and parameter values on model results.

3. The effect of disturbance on pup recruitment was greater for income than capital breeders for all disturbance scenarios. Disturbance had negligible effects on pup recruitment when it occurred within less frequented foraging patches, but moderate to large effects when it occurred within an important foraging patch. Model results were sensitive to values of patch productivity (the energy gained from successful foraging), the probability of disturbance and individual behavioural choices in the face of disturbance.

4. State-dependent behavioural theory implemented by SDP is a powerful tool for investigating when behavioural changes in response to disturbance may be meaningful at the population level. This approach allows us to incorporate many factors that are known to influence the behavioural and physiological responses of animals to anthropogenic disturbance, and places disturbance within the context of a temporally and spatially variable environment. The general framework we have developed can be used to estimate the consequences of anthropogenic disturbance across a broad range of species.

Key-words: mammal, pinniped, Population Consequences of Disturbance, Stochastic Dynamic Programming

Introduction

A major challenge in conservation and resource management is in understanding when measurable short-term responses to anthropogenic disturbance result in biologically meaningful changes in populations (Gill, Norris & Sutherland 2001). Quantifying these impacts is critical given increasing overlap between human activities and wildlife in both terrestrial and marine environments. Behaviour is often the first response to disturbance (Hoffman & Parsons 1991), although there may be deleterious physiological changes in response to stressors that do not elicit behavioural changes (Weimerskirch *et al.* 2002). Avoidance or a switch in behavioural states are common responses to disturbance (Carney & Sydeman 1999; Fortin & Andruskiw 2003; Williams, Trites & Bain 2006b), leading to

changes in time-activity and energy budgets (Williams, Lusseau & Hammond 2006a). In these situations, disturbance clearly has an effect on the individual's behaviour, but the question remains as to the broader implications of these behavioural shifts. Assessing the Population Consequences of Disturbance (PCoD) therefore requires models that link changes in an individual's behaviour or physiology as a result of disturbance with health, vital rates and ultimately population dynamics (Fig. 1; New *et al.* 2014; King *et al.* 2015; Fleishman *et al.* 2016b).

There are a variety of approaches that have been used to quantify the transfer functions that estimate the population consequences of anthropogenic disturbance. Matrix models provide a natural framework (Caswell 2001; Williams *et al.* 2016) because the leading eigenvalue of the matrix, with and without disturbance, allows for the assessment of the impact of disturbance on the population; however, the question remains how one fills in the elements of the matrix. Another approach

*Correspondence author. E-mail: emchuron@ucsc.edu

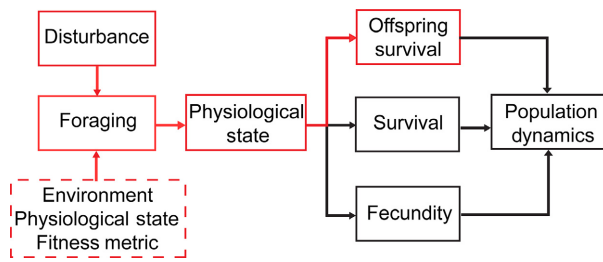


Fig. 1. A conceptual model of the linkages (transfer functions) for how disturbance that affects foraging behaviour translates to a population-level response. Linkages modelled in this paper are shown in red. Our general framework using Stochastic Dynamic Programming also incorporates the influence of environmental conditions (e.g. prey availability and distribution), physiological state (e.g. body condition or mass), and fitness (e.g. decisions based on maximizing reproductive fitness) on foraging behaviour. Figure modified from New *et al.* (2014).

is to use Expert Elicitation, where scientists or other informed individuals provide values based on their own expertise in a structured manner (Martin *et al.* 2012; Fleishman *et al.* 2016a). For example, King *et al.* (2015) used Expert Elicitation to quantify the transfer function between disturbance (exposure to wind farm construction) and vital rates (calf and juvenile survival, and fertility) of harbour porpoises (*Phocoena phocoena*), which was then incorporated into a stochastic population model to estimate the population consequence of disturbance. This approach is problematic when experts themselves disagree (King *et al.* 2015), although the use of models may resolve these differences (Wolf & Mangel 2007; Stier *et al.* 2016). State-dependent behavioural theory, as implemented by Stochastic Dynamic Programming (SDP; Mangel & Clark 1988; Houston & McNamara 1999; Clark & Mangel 2000), is a third tool for scientists who provide advice to managers. In particular, SDP originates from the basic tenet that behaviour is an evolutionary trait and allows for different behavioural responses to disturbance conditioned on the environment, and an animal's physiological state and reproductive fitness.

SDP models have been used to study the effects of natural environmental disturbance across a wide range of taxonomic groups from insects to mammals (Bull, Metcalfe & Mangel 1996; Tenhumberg, Tyre & Roitberg 2000; Denis *et al.* 2012; Satterthwaite & Mangel 2012). The development and use of SDP models involves four main steps: (i) characterization of physiological state variables and how those change in response to environment and behaviour; (ii) linking state variables to a measure of Darwinian fitness; (iii) derivation of backward iteration equations to predict the behaviour of individuals based on state and time; and (iv) Monte Carlo forward simulation to predict the distribution of behaviours. These models are built on the assumption that potential environments are in the evolutionary history of the organism; clearly anthropogenic disturbance is not. The ability to incorporate an individual's state is critical because the response of an individual to disturbance is affected by its physiological and behavioural state (Williams, Trites & Bain 2006b; Stankowich 2008; Goldbogen *et al.* 2013; Naguib *et al.* 2013). Furthermore, changes in behaviour are

difficult to translate to population-level changes without the incorporation of a state variable (Houston, Prosser & Sans 2012).

We used SDP to develop a general framework for linking behavioural changes as a result of disturbance with reproductive fitness. Specifically, we assessed the consequences of disturbance on offspring recruitment of pinnipeds, a diverse group of semi-aquatic marine carnivores encompassing true seals, sea lions, fur seals and walrus. Pinnipeds are important predators in marine ecosystems in which anthropogenic disturbance is a concern, and they provide good model systems because species within this group encompass the two main reproductive strategies (capital and income breeding) exhibited by a variety of taxonomic groups (Costa 1991; Boyd, Lockyer & Marsh 1999). Reproductive strategies are particularly relevant to disturbance because they involve the transfer of resources from adult females to dependent offspring. Capital breeders solely rely on energy from body stores accumulated before the birth of offspring, and income breeders use energy acquired on foraging trips throughout lactation to support offspring. In this paper, we keep the dichotomy of pure income and capital breeders, recognizing that in nature there is a gradient between these two strategies (Costa 1991; Boness & Bowen 1996). We developed separate SDP models for each reproductive strategy, and discuss how the effects of disturbance are affected by reproductive strategy, animal behaviour and sensitivity to parameter values. We also provide examples and discussion for how this general framework could be adapted for species-specific models.

Materials and methods

All pinnipeds share an annual reproductive cycle that includes: (i) the birth of the offspring at time t_B ; (ii) weaning of offspring at time t_W ; (iii) fertilization at time t_F ; and (iv) delayed implantation at time t_I . The timing and order of these features varies with reproductive strategy and species (Boyd, Lockyer & Marsh 1999), making it difficult to develop a model that is generally illustrative of the ideas, yet applies to a specific species in detail. For illustrative purposes, we considered a single annual reproductive cycle. The relevant time interval for the capital breeder was from the time of weaning in 1 year to the time of birth in the next year; for the income breeder it was from the birth of offspring in 1 year to the time of weaning in the next. To limit notation, we used the same symbols to characterize these intervals and parameters for both reproductive strategies (Table 1). Parameter values were based on general characteristics of pinnipeds (physiology) or arbitrarily chosen (environment, disturbance), since they were not meant to represent any species in particular.

PHYSIOLOGICAL DYNAMICS

We characterized females by a single physiological state, mass in kg $X(t)$ at time t within the feeding period of total time T . We bounded a female's state by a maximum value x_{\max} and a critical value x_c in the sense that a female died if she fell below the critical mass. Regardless of whether females ever reach x_{\max} , an upper bound on mass was necessary to operationalize the model. The income breeder also had a target

Table 1. Description of parameter or variable, interpretation and baseline value used in the Stochastic Dynamic Programming equations.

Parameter/variable	Interpretation	Nominal value
Temporal		
T	Length of foraging interval (days)	300
t	Time within foraging interval	$t = 1, \dots, T = 300$
Physiological		
$X(t)$	Female's mass at time t	Eqns 2–5
x	Specific value of the mass	
x_{\max}	Maximum value of mass	100 kg
x_c	Critical (starvation) value of mass	40 kg
x_{tar}	Target value of mass	75 kg
$M(t)$	Milk deliveries through time t	Eqns 4 and 5
m	Specific value of milk delivery	
m_{\max}	Maximum value of milk delivery	35 kg
$\text{FMR}(x)$	Field Metabolic Rate at mass x	Eqn 1
FMR_{tar}	Field Metabolic Rate at target mass	
Environmental		
λ_i	Probability of finding prey in patch i	0.2, 0.4, 0.5
p_i	Profitability of prey patch i	1:1
Y_i	Value (kg) of prey in patch i	$\frac{p_i \text{FMR}_{\text{tar}}}{\lambda_i}$
β_i	Rate of mortality in patch i	0.0003 day ⁻¹
$p_{d(i)}$	Probability of disturbance in patch i	0.5
ρ	Reduction in λ_i when a female forages in a disturbed patch	0.2
c_s	Increase in β_i when moving to an undisturbed patch	0.2
c_e	Increase in cost when moving to an undisturbed patch	0.3
Fitness function		
Capital breeder		
$\phi_{\text{cap}}(x)$	Probability of pup recruitment given $X(T) = x$	Eqn 6
x_{50}	Female's mass that gives a 50% chance of pup recruitment	60 kg
$F_{\text{cap}}(x, t)$	Maximum expected value of $\phi_{\text{cap}}(X(T))$ given $X(T) = x$	Eqn 7
$V_{\lambda}(x, t)$	Fitness value of visiting patch i when $X(T) = x$	Eqn 11
Income breeder		
$\phi_{\text{inc}}(m)$	Probability of pup recruitment given $M(T) = m$	Eqn 7
m_{50}	Milk delivery that gives a 50% chance of pup recruitment	14 kg
$F_{\text{inc}}(x, m, t)$	Maximum expected value of $\phi_{\text{inc}}(M, T)$ given $X(T) = x, M(T) = m$	Eqn 8
$V_{\lambda}(x, m, t)$	Fitness value of visiting patch i when $X(T) = x, M(T) = m$	Eqn 14
Forward simulation		
$X_k(t)$	Mass of the k^{th} female at time t	$k = 1, \dots, K = 300$
$M_k(t)$	Milk delivery to the k^{th} pup up to time t (income breeder)	Simulation output
E_k	Exploratory index: random variable from beta distribution	$\mu = 0.75, \sigma = 0.025$
\tilde{U}	Random variable uniformly distributed on [0,1]	
\tilde{Z}	Normally distributed random variable	$\mu = 0, \sigma = 1$
$p_r(k)$	Probability that k^{th} pup recruits without disturbance	Simulation output
$p_r^d(k)$	Probability that k^{th} pup recruits with disturbance	Simulation output
\bar{p}_r	Population average of $p_r(k)$	Standard computation
\bar{p}_r^d	Population average of $p_r^d(k)$	Standard computation
V_r	Population variance of \bar{p}_r	Standard computation
V_r^d	Population variance of \bar{p}_r^d	Standard computation
V_p	Pooled variance	Average of variances
d	Cohen's d metric for assessing effect of disturbance	Eqn 15

mass x_{tar} that set her feeding behaviour as described below, and an additional state, $M(t)$, which is the cumulative milk delivered up to time t (ranging from 0 to a maximum value m_{\max}). Pup recruitment was calculated based on the female mass at birth (capital) or total milk delivered at weaning (income; Fig. 2).

The energy requirements of a female were calculated at each time step using the equation from Williams & Maresh (2015) for field metabolic rate (FMR) in kJ day⁻¹ as a function of body mass

$$\text{FMR}_{\text{kJ}}(x) = 3511x^{0.45} \quad \text{eqn 1}$$

For the capital breeder, we assumed that FMR also included the cost of gestation. We converted $\text{FMR}_{\text{kJ}}(x)$ and foraging gains to mass (kg day⁻¹) assuming that mass gain or loss occurred solely

through changes in blubber, an energy storage tissue used by pinnipeds during fasting (Markussen, Ryg & Oritsland 1992). The energy content of blubber was assumed to be 33 kJ g⁻¹ based on measurements from two Arctic pinnipeds (Kuhnleini & Soueida 1992). A female at x_{tar} would need to catabolize 0.75 kg of blubber per day (1% of body mass) to meet her daily energy requirements, which is similar to estimates of daily mass loss (0.64–3.6 kg day⁻¹, 1.2–3.2% body mass day⁻¹) for pinnipeds during fasting (Fedak & Anderson 1982; Costa & Trillmich 1988; Markussen, Ryg & Oritsland 1992; Rea, Rosen & Trites 2007).

Capital and income breeders used only one patch per day in the absence of disturbance. When the capital breeder did not find prey on any given day the state dynamics were

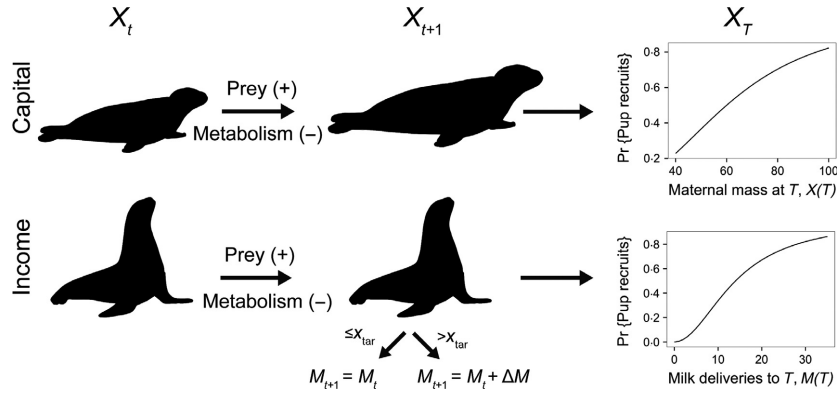


Fig. 2. Schematic illustrations of the physiological dynamics for capital and income breeders. The capital breeder accumulates mass (X) from the time of weaning (t) to the time of birth (T), whereas the income breeder transfers milk to a pup from birth to weaning after raising her own mass to the target level (x_{tar}). If a female is below x_{tar} and encounters prey that is insufficient to raise her mass above x_{tar} , she keeps all of the energy for herself and delivers no milk. If the prey brings her above x_{tar} , then any excess after accounting for metabolism is delivered as milk. We determined pup recruitment based on $X(T)$ for the capital breeder and $M(T)$ for the income breeder.

$$X(t+1) = x - FMR(x) \quad \text{eqn 2}$$

and when she did find prey in patch i with energy content Y_i (in kg) the state dynamics were

$$X(t+1) = x - FMR(x) + Y_i \quad \text{eqn 3}$$

When the income breeder did not find prey, Eqn 2 applied to her as well and no milk was delivered, so that $M(t+1) = M(t)$. If she did find prey but the energy was not enough to account for her energetic needs and raise her current mass to x_{tar} , she kept all of the energy for herself. In this case

$$\begin{aligned} X(t+1) &= x - FMR(x) + Y_i \\ M(t+1) &= M(t) \end{aligned} \quad \text{eqn 4}$$

Alternatively, if there was excess energy it was supplied to the offspring as milk. That is, given the current mass and energetic needs, the amount of prey needed to reach x_{tar} was $x_{tar} - x + FMR(x)$ since she had to cover current metabolic costs and then raise her mass to the target level. Since the excess prey that can be converted to milk was $Y_i - [x_{tar} - x + FMR(x)]$, the dynamics in this case were

$$\begin{aligned} X(t+1) &= x_{tar} \\ M(t+1) &= M(t) + Y_i - [x_{tar} - x + FMR(x)] \end{aligned} \quad \text{eqn 5}$$

THE ENVIRONMENT

The foraging environment consisted of three patches that were equidistant from the rookery. Patch i was characterized by the long-term probability of finding prey on any given day λ_i , the long-term average value of prey Y_i , and the risk of mortality β_i in the sense that the probability of surviving a foraging day was $e^{-\beta_i}$. All patches had the same risk of mortality, but we retained this variable as a general feature in the model because the assumption of equal predation risk may not hold in nature. To focus on how disturbance affected the ability to forage, we assumed that the quality of prey in a patch was constant over the feeding interval. For a patch to be profitable, it must contain sufficient energy for both female maintenance and pup growth (Costa 2012). To capture this idea we set $Y_i = \frac{p_i FMR_{tar}}{\lambda_i}$ where p_i is the productivity of the patch. Because we chose one value for p_i , the expected mean daily return from foraging was identical among patches, but the predictability of

successful foraging varied greatly among patches (e.g. for the values in Table 1, only 1 in 5 visits to Patch 1 likely resulted in success in comparison with 3 out of 5 visits to Patch 3).

SDP EQUATIONS AND FORWARD SIMULATIONS

Step 1. Fitness Function and End Conditions for the Dynamic Programming Equations

The capital breeder

The probability of recruitment to the population by a pup whose mother has terminal reserves $X(T) = x$ was denoted by $\phi_{cap}(x)$. We chose a fitness function that depended upon a single parameter and had a sigmoidal shape

$$\phi_{cap}(x) = \frac{x^3}{x^3 + x_{50}^3} \quad \text{eqn 6}$$

where x_{50} is the value of female mass that gives a 50% chance of the pup recruiting the next year (Fig. 2). We defined fitness $F_{cap}(x, t)$ as the maximum (taken over behavioural decisions by the female) expected (taken over stochastic events of survival and finding prey) value of pup recruitment given that $X(t) = x$

$$F_{cap}(x, t) = \max E\{\phi_{cap}(X(T)|X(t)) = x\} \quad \text{eqn 7}$$

The income breeder

The probability of recruitment to the population by a pup with terminal milk delivery $M(T) = m$ was denoted by $\phi_{inc}(m)$. We again used a sigmoidal relationship to describe the relationship between milk delivery and pup recruitment

$$\phi_{inc}(m) = \frac{m^2}{m^2 + m_{50}^2} \quad \text{eqn 8}$$

where m_{50} is the value at which $\phi_{inc}(m) = 0.5$ (Fig. 2). We defined fitness $F_{inc}(x, m, t)$ as the maximum (taken over behavioural decisions by the female) expected (taken over stochastic events of survival and finding prey) value of pup recruitment given that $X(t) = x$, $M(t) = m$

$$F_{\text{inc}}(x, m, t) = \max E\{\phi_{\text{inc}}(M(T)|X(t) = x, M(t) = m)\} \quad \text{eqn 9}$$

Step 2. Dynamic Programming Equations

The capital breeder

If $V_i(x, t)$ denotes the fitness value of visiting patch i when $X(t) = x$, then in light of the definition in Eqn 7

$$F_{\text{cap}}(x, t) = \max_i \{V_i(x, t)\} \quad \text{eqn 10}$$

We constructed $V_i(x, t)$ for the capital breeder as follows:

1. If the female did not die while foraging and did not find prey, which happened with probability $e^{-\beta_i} (1 - \lambda_i)$, then her state at the start of the next time period was $x - \text{FMR}(x)$ and her future fitness $F_{\text{cap}}(x - \text{FMR}(x), t + 1)$.
2. If the female did not die while foraging and found prey, which happened with probability $e^{-\beta_i} \lambda_i$, then her state at the start of the next time period was $x - \text{FMR}(x) + Y_i$ and her future fitness $F_{\text{cap}}(x - \text{FMR}(x) + Y_i, t + 1)$.

Thus

$$V_i(x, t) = e^{-\beta_i} [\lambda_i F_{\text{cap}}(x - \text{FMR}(x) + Y_i, t + 1) + (1 - \lambda_i) F_{\text{cap}}(x - \text{FMR}(x), t + 1)] \quad \text{eqn 11}$$

We solved Eqns 6, 10 and 11 backwards in time starting at $t = T$. Doing so generated the optimal patch to visit $i^*(x, t)$ for every value of female mass at time t and the optimal alternative patch $j^*(x, t)$ if she arrived at the best patch and was disturbed.

The income breeder

The logic of the derivation of the dynamic programming equation for the income breeder is similar to that for the capital breeder. In principle, even if the female died, the pup could recruit to the population if it had sufficient resources, so we set

$$F_{\text{inc}}(x_c, m, t) = \phi_{\text{inc}}(m) \quad \text{eqn 12}$$

If $V_i(x, m, t)$ denotes the fitness value of visiting patch i when $X(t) = x$, $M(t) = m$, then in light of the definition in Eqn 9

$$F_{\text{inc}}(x, m, t) = \max_i \{V_i(x, m, t)\} \quad \text{eqn 13}$$

We constructed $V_i(x, m, t)$ for the income breeder as follows:

1. If the female died while foraging, which happened with probability $1 - e^{-\beta_i}$, pup recruitment was calculated based on the milk already delivered.
2. If the female did not die while foraging and did not find prey, which happened with probability $e^{-\beta_i} (1 - \lambda_i)$, then her state at the start of the next time period was $x - \text{FMR}(x)$, her milk delivery remained unchanged, and her future fitness was $F_{\text{inc}}(x - \text{FMR}(x), m, t + 1)$.
3. If the female did not die while foraging and found prey, which happened with probability $e^{-\beta_i} \lambda_i$, then we must consider two cases. If $Y_i < x_{\text{tar}} - x + \text{FMR}(x)$ then the prey was insufficient to bring her to x_{tar} and no milk was delivered. Her state at the start of the next time period was $x - \text{FMR}(x) + Y_i$ and milk delivery remained unchanged. In this situation, future fitness was $F_{\text{inc}}(x - \text{FMR}(x) + Y_i, m, t + 1)$. Alternatively, if $Y_i > x_{\text{tar}} - x + \text{FMR}(x)$ then her state at the next time period was x_{tar} , milk was $m + (Y_i - [x_{\text{tar}} - x + \text{FMR}(x)])$, and future fitness was $F_{\text{inc}}(x_{\text{tar}}, m + (Y_i - [x_{\text{tar}} - x + \text{FMR}(x)]), t + 1)$. If we let $H(z)$ denote the indicator function that is 1 if $z \geq 0$ and 0 otherwise, we have

$$\begin{aligned} V_i(x, m, t) = & (1 - e^{-\beta_i}) \phi(m) + e^{-\beta_i} (1 - \lambda_i) \\ & F_{\text{inc}}(x - \text{FMR}(x), m, t + 1) + \\ & e^{-\beta_i} \lambda_i H(Y_i - [x_{\text{tar}} - x + \text{FMR}(x)]) \\ & F_{\text{inc}}(x_{\text{tar}}, m + Y_i - [x_{\text{tar}} - x + \text{FMR}(x)], t + 1) \\ & e^{-\beta_i} \lambda_i (1 - H(Y_i - [x_{\text{tar}} - x + \text{FMR}(x)])) \\ & F_{\text{inc}}(x - \text{FMR}(x) + Y_i, m, t + 1) \end{aligned} \quad \text{eqn 14}$$

As above, we solved Eqns 8 and 12–14 backwards in time starting at $t = T$ to generate the optimal $i^*(x, m, t)$ and optimal alternative patch $j^*(x, m, t)$ if she arrived at the optimal patch and was disturbed.

Step 3. Forward Simulations

We used forward Monte Carlo simulations (Mangel & Clark 1988; Clark & Mangel 2000) to predict the fitness consequences of disturbance for a simulated population of $K = 300$ individuals. For both capital and income breeders, $X_k(t)$ denoted the mass of the k^{th} female at time t and for the income breeder, $M_k(t)$ denoted the milk delivery to the pup through time t , with $M_k(0) = 0$. All individuals started at the target mass $X_k(0) = x_{\text{tar}}$, which eliminated one source of variation when assessing the consequences of disturbance. At the beginning of each time step, a female visited the optimal foraging patch derived using the SDP equations.

We incorporated an aspect of individual behaviour in the form of a personality trait into our model to allow females to respond to disturbance in different ways. We chose this as an example because personality traits influence foraging behaviour (Patrick & Weimerskirch 2014; Mella *et al.* 2015), thus may influence the behavioural reactions of an individual to disturbance (Martin & Réale 2008). When a female arrived at the optimal patch and discovered it was disturbed she could: (i) continue foraging in the disturbed patch at a reduced probability of finding prey (p); or (ii) move to the optimal alternative patch at an increased energy cost (c_e) and mortality risk (c_c). If she moved to the optimal alternative patch and discovered it was disturbed, she could choose to stay or move to the final patch that had no disturbance (by assumption). This decision was determined by a female's exploratory behaviour ($0 \leq E \leq 1$; Table 1); we assumed that individuals with high exploratory behaviour were more likely to leave a patch when disturbed based on the findings of van Overveld & Matthysen (2010) that fast-exploring birds were more likely to switch foraging areas when faced with an abrupt change in prey availability. See Appendix S1, Supporting Information for pseudocode for implementing the forward Monte Carlo simulation.

ASSESSING THE CONSEQUENCES OF DISTURBANCE

We chose seven disturbance scenarios that encompassed all potential disturbance combinations, ranging from no disturbance to disturbance in a maximum of two patches. We explored three values for the probability of disturbance ($p_d = 0.1, 0.3$ and 0.5); based on this preliminary analysis we chose $p_d = 0.5$ for the base case since it resulted in the widest range of disturbance effects for both reproductive strategies. Because significance tests are not appropriate for simulation models (White *et al.* 2014), we used Cohen's d (Cohen 1992) to assess the magnitude of differences in pup recruitment between the simulations relative to their standard deviation. Cohen's d is the difference between the means scaled by the pooled standard deviation

$$d = \frac{\bar{p}_r - \bar{p}_r^d}{\sqrt{V_p}} \quad \text{eqn 15}$$

where \bar{p}_r and \bar{p}_r^d are the mean pup recruitment without and with disturbance, respectively, and V_p is the pooled variance, which in this case

was simply the average of the two variances because we simulated the same number of individuals in the absence and presence of disturbance. The resulting value is a measure of the reduction in pup recruitment due to the presence of disturbance in multiples of the common standard deviation. Values of $d = 0.2, 0.5$ and 0.8 correspond with small, intermediate and large effect sizes respectively (Cohen 1977, 1992). For each simulation of 300 individuals, we obtained the average probability of recruitment of offspring and Cohen's d , and then averaged them across the 100 simulations.

SENSITIVITY ANALYSIS

We used a sensitivity analysis to examine how changes in parameter values influenced the effect of disturbance on pup recruitment and the resulting values of Cohen's d . We allowed the following variables to vary from the baseline values: p_i , x_{50} or m_{50} , c_c , c_s , ρ , p_d and the mean distribution of exploratory behaviour (E). Each of these parameters was varied by ± 10 , ± 20 or $\pm 40\%$ from the baseline value, while holding all other variables constant. For each percentage change in parameter, we calculated the pup recruitment under no disturbance and disturbance from one of the seven scenarios (see Results), and the resulting value of Cohen's d . We assessed the sensitivity of the model to each parameter by comparing Cohen's d between the baseline and altered values.

Results

In the absence of disturbance, females primarily foraged in Patch 3 at intermediate and high states, but Patch 1 was important at lower states. Mean pup recruitment was similar for the two reproductive strategies, with a value of 0.75 for the capital and 0.76 for the income breeder. For all disturbance scenarios, the effect of disturbance on pup recruitment was greater on the income compared with the capital breeder (Fig. 3). Under disturbed conditions, pup recruitment values ranged from 0.52 to 0.75 for the capital breeder and 0.50 to 0.76 for the income breeder. This resulted in values of Cohen's d from <0.01 to 0.79 for the capital breeder and 0.03–1.09 for the income breeder.

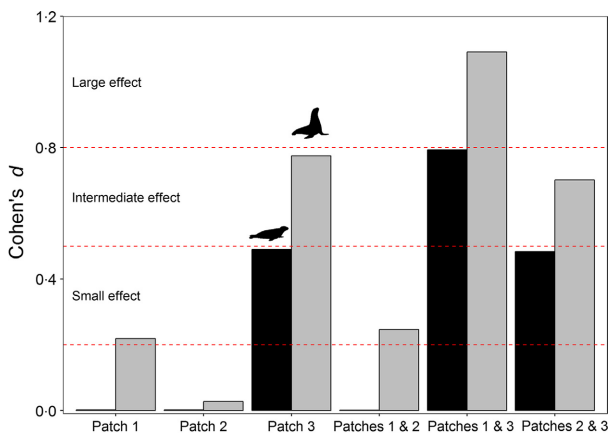


Fig. 3. The effect of disturbance on pup recruitment (assessed using Cohen's d) of a capital (black) and income breeder (grey) when probability of disturbance in patch/s (p_d) = 0.5. Results are shown for seven scenarios where disturbance occurs in a maximum of two patches. The dashed lines indicate the value of Cohen's d corresponding to small (0.2), intermediate (0.5), and large effects (>0.8) on pup recruitment.

The effect of disturbance on pup recruitment was not the same across all scenarios, but exhibited a similar pattern for both reproductive strategies (Fig. 3). The magnitude of the effect was insignificant-to-small when it occurred in Patch 1, Patch 2, or Patches 1 and 2. It increased to an intermediate or large effect when it occurred in Patch 3, either alone or in combination with disturbance in either of the other two patches.

We used the scenario with disturbance in Patches 1 and 3 for our sensitivity analysis because it had the greatest effect on pup recruitment and largest values for Cohen's d . Changes from the baseline values of the productivity of a food patch (p_i) and the probability of disturbance (p_d) resulted in the greatest percentage change in Cohen's d , regardless of reproductive strategy (Fig. 4; Appendix S2). As the overall productivity of a food patch increased or decreased, the effect of disturbance decreased, particularly with changes greater than 10% from the baseline values. Changes in the values of the remaining variables generally had a relatively small influence on Cohen's d ($<25\%$ change for most scenarios), particularly ρ , c_s and c_c (income breeder only). Unexpectedly, a 20–40% reduction in the mean value for exploratory behaviour resulted in a 63–138% change in Cohen's d , but only for the income breeder.

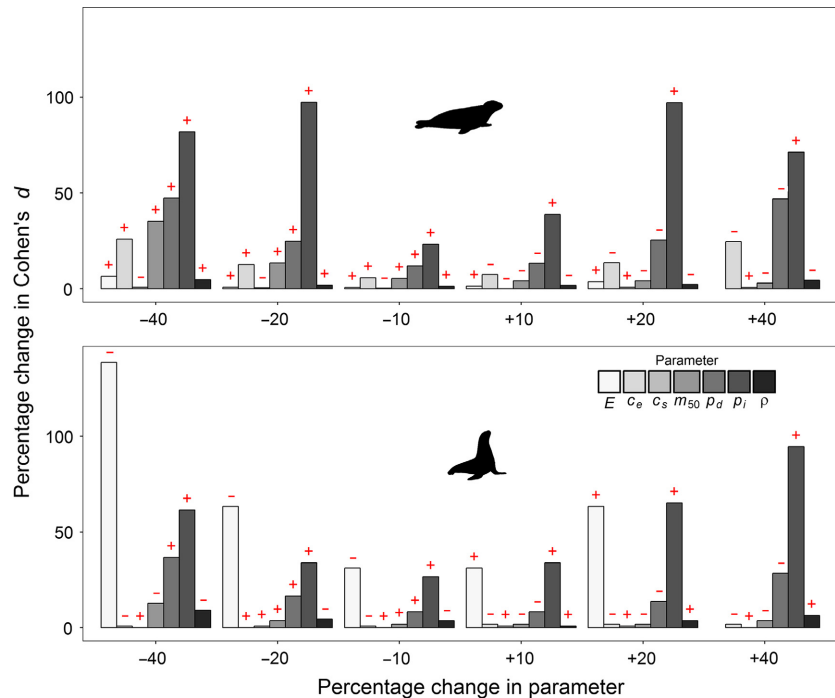
Discussion

We have shown that state-dependent behavioural theory implemented by SDP is a powerful tool for investigating the potential impacts of anthropogenic disturbances on wildlife populations. Because our goal was to develop and illustrate a framework, the current models are very general and for this reason our results do not apply to any particular species of pinniped. To focus on the development of the fundamental methodology, we simplified the model by linking behaviour with pup recruitment across a single reproductive season, and excluded many biologically relevant extensions of the methods. Our goal in doing so was to provide a relatively user-friendly introduction to this approach in the context of anthropogenic disturbance that does not apply to any species but has much in common with many species, thereby facilitating the application of this method to a broad range of species.

To fully operationalize the PCoD framework as described in New *et al.* (2014), one would need to model the effects of disturbance on additional metrics of population dynamics, such as fecundity and adult and juvenile survival (Fig. 1). This and other biologically relevant extensions can be readily included but may require considerable work as the physiology, life history and available data of specific species are considered. In Appendix S3, we discuss potential additions and suggestions for implementation because of the importance of these extensions in using SDP models to estimate the effects of disturbance for a particular species.

Despite their generality, our results do provide insight into the factors that influence the magnitude of the impact of disturbance when using SDP models. Reproductive strategies appear to be important, since we found the effect of disturbance on pup recruitment was higher for the income compared with the capital breeder. This corresponds with the intuition that capital

Fig. 4. The effect of changes in parameter values on the percentage change in Cohen's d for a capital (top) and income breeder (bottom) with simultaneous disturbance in Patches 1 and 3. The direction of change is indicated by the sign above each bar. Parameters were altered by ± 10 , 20, and 40% of baseline values and are as follows: exploratory index (E), the additional cost of moving to a new patch when disturbed (c_e), the additional risk of predation when moving to a new patch when disturbed (c_s), maternal mass (capital) or milk delivery (income) at which pup recruitment is 50% (x_{50} or m_{50}), the probability of disturbance (p_d), the profitability of the patch (p_i), and the reduced probability of finding food when foraging in a disturbed patch (ρ). Results are not shown for a 40% increase in E as this value was outside the range of the distribution.



breeders have a long period of time to accumulate energy for lactation, thus are predicted to be more resilient to negative effects from short-term foraging losses than income breeders that transfer energy to a dependent pup after each foraging trip. These results are consistent with the finding of Costa *et al.* (2016), as well as studies that have found that reproductive success and population dynamics of many income-breeding pinnipeds are strongly influenced by natural variations in prey availability (Trillmich & Limberger 1985; Soto, Trites & Arias-Schreiber 2004). Within a reproductive strategy, patch utilization was an important component of disturbance effects. Thus, the effective use of SDP models in estimating the effects of disturbance requires some prior knowledge of animal movements and foraging areas. These data are useful in the backwards iteration for characterizing the environment (e.g. the number of foraging patches), as well as in the forward iteration for parameterizing the probability that an individual will be disturbed in any given foraging patch.

A potential challenge in implementing SDP models is that they require a variety of parameters related to the environment, physiology, behaviour and disturbance. For many species, some of these parameters may be unknown or have high uncertainty due to the challenge of collecting these types of data on wild populations. For illustrative purposes, we selected values that were not necessarily representative of a single species, but many of the physiological parameters were selected from the pinniped literature. Indeed, our goal here was to develop the modelling framework, rather than focus on parameter selection; however, the selection of appropriate values is paramount when the SDP model is implemented to assess the consequences of disturbance for a particular population. We found that the parameter values that had the most influence on the SDP model results were the profitability of the patch and the probability of disturbance. In contrast,

parameters that were related to the cost associated with being disturbed appeared to have little-to-no effect on model results. This indicates the importance of research efforts focused on quantifying energy requirements, prey fields (abundance, distribution and energy content) and short-term behavioural responses to understand at what level individuals respond to a disturbance (e.g. the sound level that elicits a physiological or behavioural reaction). The incorporation of individual choice into the model affected the results for the income breeder, suggesting that allowing individuals to vary in their response to disturbance is an important part of predicting the effects of disturbance on reproductive success of income-breeding species, at least when that decision affects energy acquisition or expenditure. Although we used a personality trait in this general framework, there are many alternative intrinsic and extrinsic factors that could be used for incorporating individual choice into species-specific applications, such as characteristics of the disturbance itself, or the animal's behavioural, reproductive, informational or physiological state.

The SDP framework we described provides the ability to incorporate many of the factors that are known or are likely to influence the behavioural response of animals and fitness implications of anthropogenic disturbance. These factors include the physiological and behavioural state of an individual (Appendix S3; Williams, Trites & Bain 2006b; Stankowich 2008; Goldbogen *et al.* 2013; Naguib *et al.* 2013), as well as environmental factors that affect foraging decisions and energy balance (Costa 2008, 2012). Existing methods for quantifying transfer functions do not explicitly account for the dynamics of the foraging environment, which is a key feature of our model and one that is likely to be important when predicting the PCoD. This allows us to place anthropogenic disturbance within the context of a temporally and spatially variable environment, which mimics natural systems and is particularly

valuable given the rapid climate change faced by both marine and terrestrial species. The use of SDP models requires existing physiological and ecological data, and although all of the model parameters are clearly measurable, this likely limits the use of this approach for data poor species. In situations where these empirical data are lacking, it may be more appropriate to use alternative methods for quantifying parameters and transfer functions, such as Expert Elicitation (King *et al.* 2015). Alternatively, as these two methods can be complementary, it may be beneficial to use the approaches described in King *et al.* (2015) for estimating unknown parameters, and the SDP model for quantifying the transfer functions that link individual behavioural or physiological responses to disturbance with health and vital rates.

Authors' contributions

All authors conceived the ideas and designed methodology; E.M. and M.M. developed and implemented the model and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

We thank C. Law for pinniped artwork, R. Holser for computational assistance and two anonymous reviewers for their helpful suggestions. This work was supported by the Office of Naval Research (ONR) grant N00014-13-1-0134 and contract # JIP 22 07-23 from the E & P Sound and Marine Life Joint Industry Project of the IGOP to D.C. and L.S. M.M. was partially supported by NSF grant DEB 14-51931.

Data accessibility

The values of parameters or variables used in the model are provided in Table 1. A complete description of the backwards model is provided in text, and pseudocode for implementing the forward Monte Carlo simulation is provided in Appendix S1.

References

- Boness, D.J. & Bowen, W.D. (1996) The evolution of in maternal care in pinnipeds. *BioScience*, **9**, 645–654.
- Boyd, I.L., Lockyer, C. & Marsh, H. (1999) Reproduction in marine mammals. *Biology of Marine Mammals* (eds J. Reynolds & S. Rommel), pp. 218–286. Smithsonian Institution Press, Washington, D.C., USA.
- Bull, C.D., Metcalfe, N.B. & Mangel, M. (1996) Seasonal matching of foraging to anticipated energy requirements in anorexic juvenile salmon. *Proceedings of the Royal Society B*, **263**, 13–18.
- Carney, K.M. & Sydeman, W.J. (1999) A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds*, **22**, 68–79.
- Caswell, H. (2001) *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, MA, USA.
- Clark, C.W. & Mangel, M. (2000) *Dynamic State Variable Models in Ecology: Methods and Applications*. Oxford University Press, New York, NY, USA.
- Cohen, J. (1977) *Statistical Power Analysis for the Behavioral Sciences*. Academic Press, New York City, NY, USA.
- Cohen, J. (1992) A power primer. *Quantitative Methods in Psychology*, **112**, 155–159.
- Costa, D.P. (1991) Reproductive and foraging energetics of pinnipeds: implications for life history patterns. *The Behaviour of Pinnipeds* (ed. D. Renouf), pp. 300–344. Springer, The Netherlands.
- Costa, D.P. (2008) A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **17**, S44–S52.
- Costa, D.P. (2012) A bioenergetics approach to developing a population consequences of acoustic disturbance model. *The Effects of Noise on Aquatic Life* (eds A.N. Popper & A. Hawkins), pp. 423–426. Springer, New York, NY, USA.
- Costa, D.P. & Trillmich, F. (1988) Mass changes and metabolism during the perinatal fast: a comparison between Antarctic (*Arctocephalus gazella*) and Galapagos fur seals (*Arctocephalus galapagoensis*). *Physiological Zoology*, **61**, 160–169.
- Costa, D.P., Schwarz, L.K., Robinson, P.W., Schick, R.S., Morris, P.M., Condit, R., Crocker, D.E. & Kilpatrick, A.M. (2016) A bioenergetics approach to understanding the population consequences of disturbance: elephant seals as a model system. *The Effects of Noise on Aquatic Life II* (eds A.N. Popper & A. Hawkins), pp. 161–169. Springer, New York, NY, USA.
- Denis, D., Pierre, J.S., van Baaren, J. & van Alphen, J.J.M. (2012) Physiological adaptations to climate change in pro-ovigenic parasitoids. *Journal of Theoretical Biology*, **309**, 67–77.
- Fedak, M.P. & Anderson, S.S. (1982) The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *Journal of Zoology (London)*, **198**, 473–479.
- Fleishman, E., Burgman, M., Runge, M.C., Schick, R.S. & Kraus, S. (2016a) Expert elicitation of population-level effects of disturbance. *The Effects of Noise on Aquatic Life II* (eds A.N. Popper & A. Hawkins), pp. 295–302. Springer, New York, NY, USA.
- Fleishman, E., Costa, D.P., Harwood, J. *et al.* (2016b) Monitoring population-level responses of marine mammals to human activities. *Marine Mammal Science*, **32**, 1004–1021.
- Fortin, D. & Andruskiw, M. (2003) Behavioral response of free-ranging bison to human disturbance. *Wildlife Society Bulletin*, **31**, 804–813.
- Gill, J., Norris, K. & Sutherland, W.J. (2001) Why behavioural responses may not reflect the population consequences of human disturbance. *Biological Conservation*, **97**, 265–268.
- Goldbogen, J.A., Southall, B.L., Deruiter, S.L. *et al.* (2013) Blue whales respond to simulated mid-frequency military sonar. *Proceedings of the Royal Society B*, **280**, 20130657.
- Hoffman, A.A. & Parsons, P.A. (1991) *Evolutionary Genetics and Environmental Stress*. Oxford University Press, Oxford, UK.
- Houston, A.I. & McNamara, J.M. (1999) *Models of Adaptive Behavior: An Approach Based on State*. Cambridge University Press, Cambridge, UK.
- Houston, A.I., Prosser, E. & Sans, E. (2012) The cost of disturbance: a waste of time and energy? *Oikos*, **121**, 597–604.
- King, S.L., Schick, R.S., Donovan, C., Booth, C.G., Burgman, M., Thomas, L. & Harwood, J. (2015) An interim framework for assessing the population consequences of disturbance. *Methods in Ecology and Evolution*, **6**, 1150–1158.
- Kuhleini, H.V. & Soueida, R. (1992) Use and nutrient composition of traditional Baffin Inuit foods. *Journal of Food Composition and Analysis*, **5**, 112–126.
- Mangel, M. & Clark, C.W. (1988) *Dynamic Modeling in Behavioral Ecology*. Princeton University Press, Princeton, NJ, USA.
- Markussen, N.H., Ryg, M. & Oritsland, N.A. (1992) Metabolic rate and body composition of harbour seals, *Phoca vitulina*, during starvation and refeeding. *Canadian Journal of Zoology*, **70**, 220–224.
- Martin, J.G.A. & Réale, D. (2008) Animal temperament and human disturbance: implications for the response of wildlife to tourism. *Behavioural Processes*, **77**, 66–72.
- Martin, T.G., Burgman, M.A., Fidler, F., Kuhnert, P.M., Low-Choy, S., McBride, M. & Mengersen, K. (2012) Eliciting expert knowledge in conservation science. *Conservation Biology*, **26**, 29–38.
- Mella, V.S.A., Ward, A.J.W., Banks, P.B. & McArthur, C. (2015) Personality affects the foraging response of a mammalian herbivore to plant toxins and predation risk. *Oecologia*, **177**, 293–303.
- Naguib, M., van Oers, K., Braakhuis, A., Griffioen, M., de Goede, P. & Waas, J.R. (2013) Noise annoys: effects of noise on breeding great tits depend on personality but not on noise characteristics. *Animal Behaviour*, **85**, 949–956.
- New, L.F., Clark, J.S., Costa, D.P. *et al.* (2014) Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Marine Ecology Progress Series*, **496**, 99–108.
- van Overveld, T. & Matthysen, E. (2010) Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters*, **6**, 187–190.
- Patrick, S.C. & Weimerskirch, H. (2014) Personality, foraging and fitness consequences in a long lived seabird. *PLoS ONE*, **9**, e87269.
- Rea, L.D., Rosen, D.A.S. & Trites, A.W. (2007) Utilization of stored energy reserves during fasting varies by age and season in Steller sea lions. *Canadian Journal of Zoology*, **85**, 190–200.
- Satterthwaite, W.H. & Mangel, M. (2012) Behavioral models as a common framework to predict impacts of environmental change on seabirds and fur

- seals. *Deep Sea Research Part II: Topical Studies in Oceanography*, **65–70**, 304–315.
- Soto, K.H., Trites, A.W. & Arias-Schreiber, M. (2004) The effects of prey availability on pup mortality and the timing of birth of South American sea lions (*Otaria flavescens*) in Peru. *Journal of Zoology*, **264**, 419–428.
- Stankowich, T. (2008) Ungulate flight responses to human disturbance: a review and meta-analysis. *Biological Conservation*, **141**, 2159–2173.
- Stier, A.C., Samhouri, J.F., Gray, S., Martone, R.G., Mach, M.E., Halpern, B.S., Kappel, C.V., Scarborough, C. & Levin, P.S. (2016) Integrating expert perceptions into food web conservation and management. *Conservation Letters*, doi:10.1111/conl.12245.
- Tenhumberg, B., Tyre, A.J. & Roitberg, B. (2000) Stochastic variation in food availability influences weight and age at maturity. *Journal of Theoretical Biology*, **202**, 257–272.
- Trillmich, F. & Limberger, D. (1985) Drastic effects of El Niño on Galapagos pin-nipeds. *Oecologia*, **67**, 19–22.
- Weimerskirch, H., Shaffer, S.A., Mabile, G., Martin, J., Boutard, O. & Rouanet, J.L. (2002) Heart rate and energy expenditure of incubating wandering albatrosses: basal levels, natural variation, and the effects of human disturbance. *The Journal of Experimental Biology*, **205**, 475–483.
- White, J.W., Rassweiler, A., Samhouri, J.F., Stier, A.C. & White, C. (2014) Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos*, **123**, 385–388.
- Williams, R., Lusseau, D. & Hammond, P.S. (2006a) Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation*, **133**, 301–311.
- Williams, T.M. & Maresh, J.L. (2015) Exercise energetics. *Marine Mammal Physiology: Requisites for Ocean Living* (eds M.A. Castellini & J.-A. Mellish), pp. 47–68. CRC Press, Boca Raton, FL, USA.
- Williams, R., Trites, A.W. & Bain, D.E. (2006b) Behavioural responses of killer whales (*Orcinus orca*) to whale-watching boats: opportunistic observations and experimental approaches. *Journal of Zoology*, **256**, 255–270.
- Williams, R., Thomas, L., Ashe, E., Clark, C.W. & Hammond, P.S. (2016) Gauging allowable harm limits to cumulative, sub-lethal effects of human activities on wildlife: a case-study approach using two whale populations. *Marine Policy*, **70**, 58–64.
- Wolf, N. & Mangel, M. (2007) Strategy, compromise, and cheating in predator–prey games. *Evolutionary Ecology Research*, **9**, 1293–1304.

Received 2 August 2016; accepted 25 October 2016

Handling Editor: Jason Matthiopoulos

Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. Pseudocode for implementing forward Monte Carlo simulations.

Appendix S2. Results of the sensitivity analysis.

Appendix S3. Discussion of potential extensions of the general framework and suggestions for implementation.