

Contribution to the Theme Section 'Tracking fitness in marine vertebrates'

# Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals

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**ABSTRACT:** Environmental changes (a type of disturbance) are altering the habitat of southern elephant seals *Mirounga leonina*, an apex marine predator in the Southern Ocean. As a result, individuals may shift their behaviour, spending more time in transit and less time foraging. The effects of these sublethal changes in behaviour can accumulate, indirectly impacting lifetime fitness through changes in individual survival and reproduction. If a sufficient proportion of the population is affected, the probability of population persistence will be altered. We used data from long-term telemetry studies of female elephant seals at Macquarie Island, Australia, to model the effect of behaviour on the seals' health (i.e. all internal factors that affect homeostasis). Through simulation, we investigated the effect of increasing periods of behavioural shifts, quantifying how the exclusion of maternal southern elephant seals from foraging habitat may affect their health, offspring survival, individual fitness and population growth rate. A long period of altered behaviour (>50% of an average foraging trip at sea) in 1 yr resulted in a small (0.4%) decline in population size the following year. However, a persistent disruption (e.g. 30 yr), caused for example by the long-term effects of climate change, could result in a 0.3% decline in individual fitness and a 10% decline in population size. Our approach to estimating the long-term population effects of short-term changes in individual behaviour can be generalised to include physiological effects and other causes of behavioural and physiological disruption, such as anthropogenic disturbance, for any species.

**KEY WORDS:** Kalman filter · *Mirounga leonina* · Population consequences of disturbance · State-space model · Telemetry data

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## INTRODUCTION

Human activities and changing environmental conditions can have numerous sublethal effects on wild animals that, in the aggregate, may threaten

their regional or global persistence. When environmental changes and anthropogenic actions lead directly to the death of an animal or its offspring, the potential effects on a species' population dynamics are relatively clear. However, sublethal, short-term

changes in behaviour or physiology, such as shifts in habitat use (e.g. Hazen et al. 2012) or increased levels of stress (e.g. Pereira et al. 2006), could lead to changes in life history traits (e.g. Weimerskirch et al. 2012) and long-term population-level effects (e.g. Kight et al. 2012) that are more difficult to characterize, but equally important. Population growth rate is often used to determine whether a given phenomenon or event (e.g. climate change, offshore drilling, habitat restoration) has affected a species of concern (e.g. Kight et al. 2012). As Lande (1982) and Caswell (2001) have shown, it can also be used to estimate individual fitness. Here, we follow Begon et al. (2006, p. 4) in defining fitness as

... a relative not an absolute term. The fittest individuals leave the greatest number of descendants relative to the number of descendants left by other individuals in the population.

However, we extend the definition by considering the fitness of an individual in relation to the fitness of other individuals in the current and historical population, so that it can be used to assess the effects of disturbances, such as climate change, which may influence the fitness of all the individuals in the current population.

Southern elephant seals *Mirounga leonina* are top marine predators that breed in colonies on remote offshore islands in the Southern Ocean. Climate change has the potential to reduce individual fitness and the probability of population persistence through mechanisms such as changing sea-ice conditions (e.g. Bailleul et al. 2007). Furthermore, interannual variations in foraging success and reproductive output have been related to environmental changes in the congeneric northern elephant seal *M. angustirostris* (e.g. Crocker et al. 2006). Long-term data on southern elephant seals allow us to model the rela-

tionships between environmental change, individual behaviour and population growth rate. The seals' large size makes them relatively easy to capture, mark, and equip with telemetry devices when on land (e.g. McMahon et al. 2008), and they haul out at their natal breeding colonies twice per year (Hindell & Burton 1988), allowing recovery of instruments.

While on land, the seals' body composition (lipid, protein, water) can be estimated (Costa et al. 1986, Field et al. 2007). This enables estimation of the fitness consequences of environmental change. Female elephant seals are capital breeders and therefore rely entirely on lipids accumulated at sea for their own survival and the provisioning of offspring during long periods of fasting on land. Maternal mass, which is determined by a female's ability to acquire resources during her foraging trips, directly affects pup mass at weaning (Arnbom et al. 1993). Pup weaning mass then influences the pup's subsequent survival (McMahon et al. 2000, 2003). Therefore, any change in a female's behaviour affecting her ability to gain lipid mass at sea, such as decreased foraging or increased movement, will ultimately affect her fitness. Accordingly, the links between environmental change (i.e. disturbance), individual behaviour, fitness, and population dynamics can be quantified using lipid stores as a measure of individual health (Fig. 1). Maternal lipid mass is the specific measure of health that we use in our elephant seal model, but we define health broadly to include all aspects of individual fitness, such as condition and other internal factors affecting homeostasis (e.g. nutritional, metabolic, and immunological status).

This measure of health allowed us to estimate the accumulated sublethal effects of environmental change on individual fitness and population growth rate of southern elephant seals. The relationships

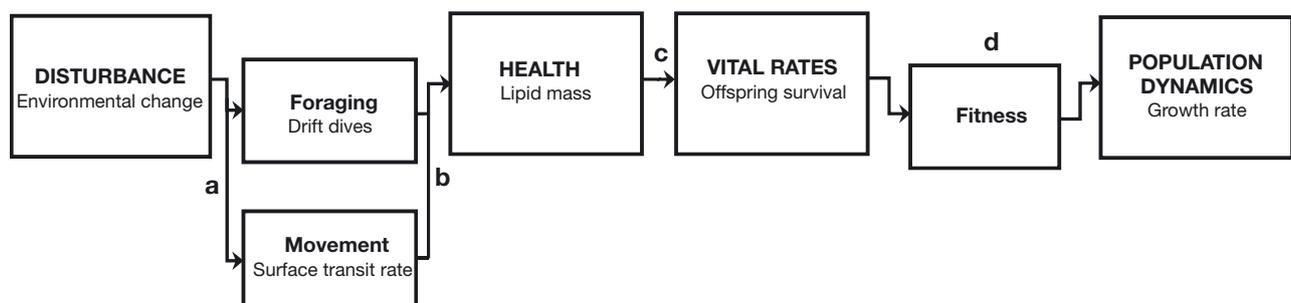


Fig. 1. *Mirounga leonina*. Relationships among disturbance (e.g. environmental change), behaviour, health, vital rates, fitness, and population growth rate. Core elements that would be considered for all species are completely capitalized, whereas the remaining boxes are specific to the elephant seal model. The lower case letters refer to how the links between the boxes were addressed: (a) disturbance scenarios, (b) state-space model, (c) published literature and (d) Leslie matrix. Monte Carlo simulations were used to evaluate the potential effects of the disturbance scenarios

between a species' vital rates and population growth are well-documented (e.g. Caswell 2001), and the links between health and vital rates of southern elephant seals have been quantified (Arnbom et al. 1993, McMahon et al. 2000, 2003). Therefore, we focus here on identifying the functional relationship between behaviour and health. We developed a model to estimate female lipid mass at sea and used this model to investigate the potential effects of decreased foraging time and increased movement on a female's health when she returns to the colony to pup. We show how these predictions can be used to estimate the long-term effects of environmental change on individual fitness and population dynamics of southern elephant seals and present a generalization of the approach that is applicable to other systems and other forms of disturbance, including anthropogenic disturbance.

## MATERIALS AND METHODS

### Data

We used data from 23 female southern elephant seals fitted with telemetry devices before leaving their breeding colony at Macquarie Island, Australia. The Macquarie Island colony is a closed population (i.e. no permanent emigration or immigration), many of whose members are permanently marked and of known age. From the 23 individuals we had information on 30 post-moult foraging trips that took place from 2000 to 2005; 2 individuals had telemetry devices attached in 3 different years (thus, we had information on 3 trips for each of these individuals), and 3 individuals had devices attached in 2 separate years. The devices attached to the seals recorded location and attributes of dives, such as depth and velocity, during the animals' trips to sea (e.g. Hindell et al. 2003, Thums et al. 2008). In this present study we were most interested in the geolocation of individuals, which we transformed into a measure of surface transit rate by calculating the distance travelled between locations per unit time and the seals' drift dives. Drift dives, in which seals use their buoyancy to change depth without active propulsion, were identified, counted, and the rate of vertical movement through the water column during this period was calculated (e.g. Crocker et al. 1997).

Rate of drift is determined largely by an elephant seal's lipid to lean mass ratio (Biuw et al. 2003) and can therefore be used to estimate a female's lipid

mass while at sea (Schick et al. 2013a) if there is information on her lean mass. The body composition (lipid and lean mass) of tagged females was measured before and after a foraging trip, and their pups were captured, marked, and weighed shortly after birth and at regular intervals. Therefore, we were able to infer how much of the female's lean mass upon her arrival at the colony was due to the foetus and to estimate the amount of energy a female transferred to her pup during lactation (Costa et al. 1986, Hindell & Slip 1997). For more details on the data used in this analysis, see Hindell & Slip (1997), McMahon et al. (2000, 2003), Hindell et al. (2003), Thums et al. (2008).

### Model

Drift dives are thought to be associated with digestive processes (Crocker et al. 1997) and can be used as a measure of foraging success (Biuw et al. 2007). Furthermore, a seal's mass at the end of a foraging trip is affected by its surface transit rate, defined as the linear distance (km) traversed by an animal per day (Le Boeuf et al. 2000). We therefore built a model estimating the daily lipid mass (from time  $t_0$  to  $T_j$ ) of a female elephant seal,  $i$ , as a function of her transit rate ( $S_{i,t}$ ), number of drift dives ( $V_{i,t}$ ), and lipid ( $L_{i,t}$ ) to lean ( $R_{i,t}$ ) mass ratio each day:

$$L_{i,t} = L_{i,t-1} + \alpha_0 + \alpha_1 S_{i,t} + \alpha_2 V_{i,t} + \alpha_3 \frac{L_{i,t-1}}{R_{i,t-1}} + \varepsilon_{i,t} \quad (1)$$

$$\varepsilon_{i,t} \sim N(0, \sigma_{L,i}^2)$$

where  $\alpha_0$  is the change in lipid mass when all other covariates are equal to zero, the remaining  $\alpha$ s measure the effect of the covariates on lipid mass, and  $\varepsilon_{i,t}$  is the process variability with variance  $\sigma_{L,i}^2$ . The inclusion of the lipid to lean mass ratio recognizes that females can regulate their lipid mass: highly buoyant animals, which are in good health, may not seek to gain more lipids (Fedak et al. 1994).

We built a state-space model (e.g. Buckland et al. 2004) to estimate the daily changes in a female elephant seal's lipid mass while at sea. Therefore, in addition to the process model (Eq. 1), we developed an observation model that linked drift rate data collected by telemetry devices to the seal's lipid mass while at sea. The rate at which a female moves through the water column during a drift dive is related to her buoyancy (Biuw et al. 2003). We modelled the relationship between drift rate ( $D_{i,t}$ ) and buoyancy (denoted by  $L_{i,t}/R_{i,t}$ ) as:

$$D_{i,t} = \delta_0 + \delta_1 \frac{L_{i,t}}{R_{i,t}} + \omega_{i,t}$$

$$\omega_{i,t} \sim N(0, \sigma_{D,i}^2)$$
(2)

where the  $\delta$ s relate the lipid to lean mass ratio to drift rate and  $\omega_{i,t}$  is the observation error with variance,  $\sigma_{D,i}^2$ . This variance could be estimated because multiple measurements of drift rate were recorded on most days. We estimated the  $\delta$ s separately for negative and positive values of  $D_{i,t}$  to account for the non-linear relationship between drift rate and buoyancy around zero (Biuw et al. 2003). Although the linear assumption is a simplification of the relationship proposed by Biuw et al. (2003), our model has been shown to be effective in capturing the behaviour of the system while maintaining modelling efficiency and parsimony (Schick et al. 2013a). It is not possible to estimate both lipid and lean mass in the same model. Therefore, we used direct measurements of lean mass from the start and end of an individual's foraging trip ( $R_{i,0}$  and  $R_{i,T}$ , respectively) to calculate the total lean mass gain ( $\Delta R_i$ ) over the course of a foraging trip. We then investigated 5 different functional forms of how lean mass was accumulated over time and used Akaike's information criterion (AIC) to identify the most parsimonious model (Table 1, Fig. 2). These forms were chosen on the basis of different biologically realistic scenarios of the growth of the foetus and whether females replace lean mass lost while on land as soon as possible or at a constant rate.

The wean mass of pup  $p$  ( $W_p$ ) can be predicted from its mother's total mass ( $M_i$ , where  $M_i = L_{i,T} + R_{i,T}$ ) (Arnbom et al. 1993) as:

$$W_p = \beta_0 + \beta_1 M_i$$
(3)

where the  $\beta$ s relate total maternal mass to pup wean mass. This relationship accounts for 55% of the vari-

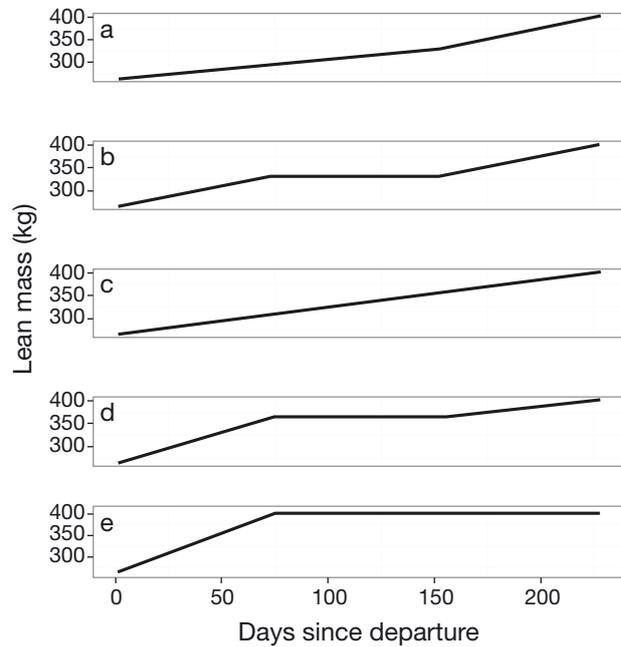


Fig. 2. *Mirounga leonina*. The 5 potential functional forms for the change in lean mass of a single female southern elephant seal (ID b900) during a post-moult foraging trip from Macquarie Island, Australia. From the top, and moving down, the plots represent (a) a linear increase in maternal mass with a linear increase in lean mass due to the foetus in the last third of the foraging trip, (b) half the linear gain in lean mass in the first third of the trip and half in the final third, (c) a linear increase in total lean mass over the course of the foraging trip, (d) total maternal mass gained in the first third of the foraging trip and foetal lean mass gained in the final third, and (e) total lean mass gained in the first third of the foraging trip

ation in weaning mass at South Georgia (Arnbom et al. 1993). Pup survival ( $\phi_p$ ) is defined as the survival over the period from weaning to when the animal returns to the haul out the following year, and is related to wean mass (McMahon et al. 2003) by:

$$\text{logit}(\phi_p) = \gamma_0 + \gamma_1 W_p + \gamma_2 W_p^2$$
(4)

Table 1. *Mirounga leonina*. Model selection results for 5 alternative descriptions of the gain in lean mass ( $R$ ) over time ( $t$ ) in female southern elephant seals, where  $T$  represents the final day of a foraging trip. These models contain no free parameters to be estimated, so there is no effect of changing number of parameters on the Akaike's information criterion (AIC)

Model	$\Delta$ AIC
Linear increase in maternal lean mass from $t_0$ to $T$ , with a linear increase in lean mass due to the growth of the foetus in the last third of the foraging trip ( $t_2 \cdot (T/3)$ to $T$ ).	0
Half the linear gain in lean mass is from $t_0$ to $t_{T/3}$ , with the remainder gained between $t_2 \cdot (T/3)$ to $T$ . Lean mass is constant between $t_{T/3}$ and $t_2 \cdot (T/3)$ .	284.7
Linear increase in total lean mass from $t_0$ to $T$ .	321.89
All maternal lean mass is gained from $t_0$ to $t_{T/3}$ , with a linear increase in lean mass due to the growth of the foetus in the last third of the foraging trip ( $t_2 \cdot (T/3)$ to $T$ ).	413.82
Total lean mass is gained from $t_0$ to $t_{T/3}$ , after which lean mass remains constant.	480.04

where the  $\gamma$ s relate wean mass to pup survival. This relationship accounts for 99% of the observed variation in pup survival at Macquarie Island (McMahon et al. 2003).

In our model, the effect of decreasing lipid mass on an individual female's fitness will manifest as a change in her pup's survival. The consequences of these fitness effects for population dynamics will depend on the proportion of the breeding population affected and the number of years over which the environmental change persists. We inferred the population-level impact by calculating the growth rate of a population entirely composed of females identical to those in our sample (Lande 1982). Values for the underlying demographic rates of an undisturbed southern elephant seal population at Macquarie Island were adapted from the literature (e.g. McMahon et al. 2003), and we assumed this population was in a steady state (McMahon et al. 2005) (Table 2). Treating all demographic rates except for pup survival as fixed values, we placed them into a Leslie matrix, calculating the dominant eigenvalue to estimate the effect of the predicted changes in pup survival on population growth rate (Caswell 2001, McMahon et al. 2005).

### Model fitting and simulation

We used a Kalman filter (Kalman 1960) implemented in R (R Core Team 2013) to fit the state-space model (Eqs. 1 & 2) to the empirical data described above via maximum likelihood estimation, following the format of Harvey (1989) and Besbeas et al. (2002).

We used Monte Carlo simulation, based on the estimated parameters and their variance-covariance matrix, to investigate the potential effects of scenarios in which an environmental change (i.e. disturbance) substantially altered the habitat of southern

Table 2. *Mirounga leonina*. The parameter values for the Leslie matrix used to estimate the population growth rate of female southern elephant seals at Macquarie Island, Australia. The age classes are pups <1 yr, juveniles (1 to 4 yr) and adults (5 to 10+ yr, where 10+ is an absorbing state). These values result in a population in a steady state, but this will change depending on the estimated value for pup survival ( $\phi_p$ ) under different scenarios of disturbance

Age class (yr)	Survival	Fecundity
<1 (pup)	0.8	0
1–4	0.8	0
5–10+	0.841	0.4

elephant seals (e.g. Hazen et al. 2012). We assumed these alterations affected seal behaviour by decreasing the number of drift dives (i.e. foraging success index) and increasing the rate of surface transit. These changes imply that, although foraging may take place, the seals are less successful and that individuals are actively seeking better foraging areas. We assumed the 30 foraging trips used for parameter derivation were a random sample of the population and that environmental change affected all individuals equally. Disturbance is assumed to affect the elephant seals' behaviour by reducing the number of drift dives ( $V_{i,t}$ ) in which they engage and increasing their transit rate ( $S_{i,t}$ ). Therefore, in our disturbance scenarios we reduced  $V_{i,t}$  to zero and increased  $S_{i,t}$  to the individual's observed maximum for each day of disturbance. Starting on the last day of a foraging trip, we linearly increased the number of days on which this behavioural shift occurred, running simulations of disturbances with durations from one day to the entire length of the seal's foraging trip ( $T_i$ ). This enabled us to examine the effects of different durations of disturbance on the population growth rate. We assumed that  $T_i$  did not change, as number of days of disturbance increased and lean tissue continued to accumulate at the same rate regardless of the changes in behaviour. Therefore, since a foetus' mass contributes to a female's lean mass and the daily cost of producing a foetus is small (Brody 1945), behavioural change will not affect foetal growth.

## RESULTS

Model selection led us to assume that a pregnant elephant seal's lean mass increased linearly over time but had a steeper slope in the last third of the foraging trip, due to the foetus' growing mass (Table 1). Our model parameter and daily lipid mass estimates for female southern elephant seals were biologically realistic (Table 3; Fig. 3 & Fig. S1 in the Supplement at [www.int-res.com/articles/suppl/m496p099\\_supp.pdf](http://www.int-res.com/articles/suppl/m496p099_supp.pdf)). Our predictions of females' final lipid mass upon return to the breeding colony corresponded with direct observations, with only 9 of the observations failing to capture the observed final lipid mass at the 95% confidence interval for the predicted value (Fig. 4). In addition, the maximum daily gain or loss at sea was never greater than the estimated maximum daily loss from observed weight change when seals were on land. As we increased the number of days on which behaviour changed, each seal's final lipid mass upon return to the colony

Table 3. *Mirounga leonina*. Parameter estimates, with 95% confidence intervals (CI), for the process model describing the daily lipid mass of a female elephant seal at sea (Eq. 1,  $\alpha$  parameters) and the observation model linking drift rate data to female lipid mass (Eq. 2,  $\delta$  parameters). The plus sign (+) on the  $\delta$  parameters indicates the observation model parameter estimates for positive values of drift rate

Parameter	Estimate	95% CI
$\alpha_0$	2.44	2.36, 2.51
$\alpha_1$	-0.005	-0.007, -0.003
$\alpha_2$	0.017	0.001, 0.032
$\alpha_3$	-5.07	-5.18, -4.96
$\beta_0$	-0.97	-1.03, -0.91
$\beta_0^+$	-0.35	-0.38, -0.32
$\delta_1$	2.17	2.02, 2.30
$\delta_0^+$	1.19	1.11, 1.27

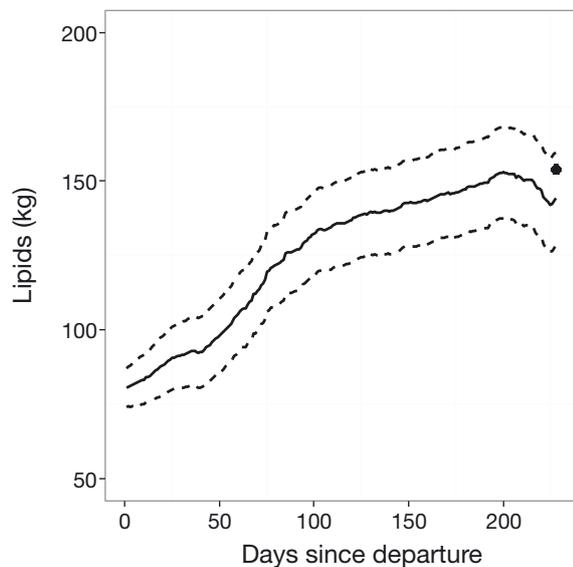


Fig. 3. *Mirounga leonina*. Changes over time in the estimated lipid mass of a single female southern elephant seal (ID b900) during a post-moult foraging trip from Macquarie Island, Australia (solid line) with 95% confidence intervals (dashed lines). Black dot indicates the measured final lipid mass of the seal upon return to Macquarie Island

decreased. The mean final lipid mass of females also declined steadily as the number of days of disturbance increased (Fig. 5a). As lipid mass decreased, pup weaning mass (Fig. 5b) and pup survival (Fig. 5c) were also predicted to decrease. For example, a disturbance with a duration of 50% (111 d) of the length of an average trip resulted in a decrease in average total maternal mass of 9.8% (95% CI: 4.7%, 14.6%) and a change in pup survival of -1.7% (95% CI: -5.6%, 2.3%). The predicted decrease in pup survival would result in a 0.4% (95% CI: -0.7%,

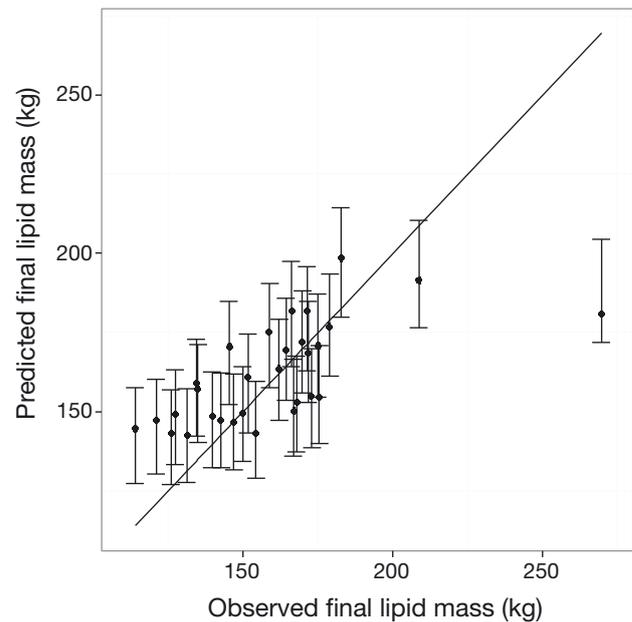


Fig. 4. *Mirounga leonina*. The observed versus predicted values of final lipid mass of female southern elephant seals from Macquarie Island, Australia, at the end of post-moult foraging trips. Bars are 95% confidence intervals on the predicted values

-0.08%) decline in abundance in the year following the disturbance. If this disturbance continued over 30 yr, and the population did not adapt, individual fitness would be reduced by 0.3% (95% CI: -0.5%, -0.06%) on average compared to historical levels, and the population size would decline by approximately 10%.

## DISCUSSION

Individual female southern elephant seals have high fidelity to particular foraging zones (Authier et al. 2012). Accordingly, changes to the species' habitat could affect individuals' ability to obtain resources. Such changes have been hypothesised to cause observed decreases in population size (e.g. McMahon et al. 2003). Our model provides a quantitative, mechanistic description of this relationship, explicitly linking the short-term effects of environmental change (i.e. disturbance) on individual behaviour to population dynamics. When an average of 50% of each female's foraging trip was disrupted in any one year, the model predicted a small decrease in fitness and population size. Given elephant seals' life history strategy and their dependence on accumulated lipid stores, a decline in population size of this magnitude

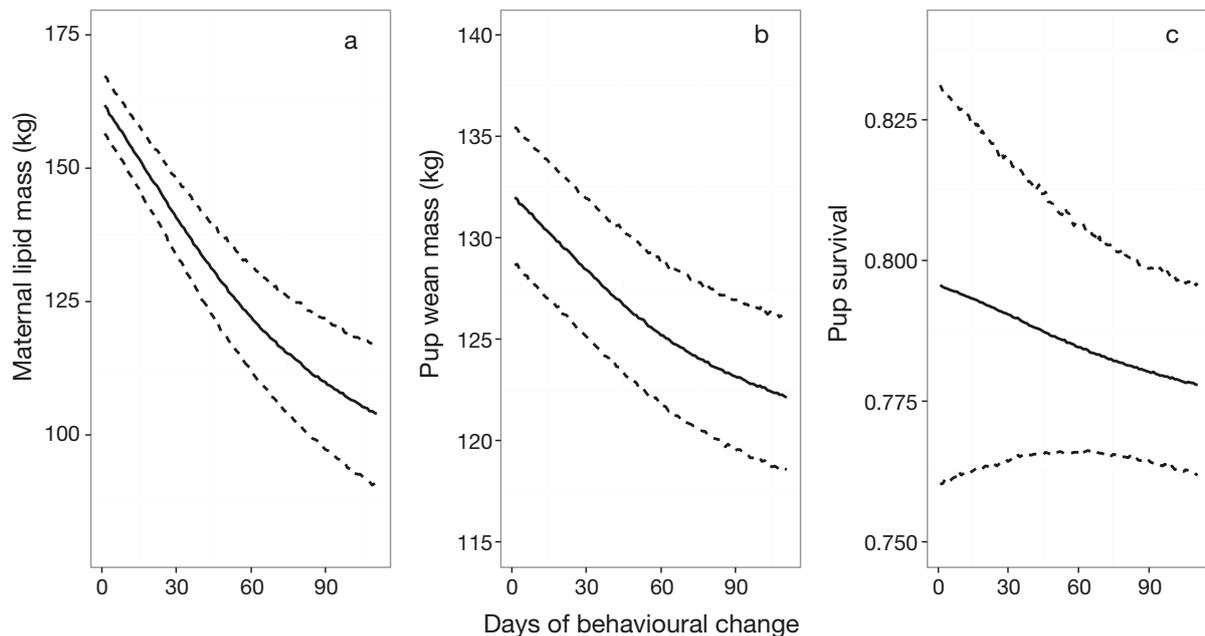


Fig. 5. *Mirounga leonina*. Effect of duration of behavioural change (in days) on (a) estimated average maternal lipid mass of southern elephant seals upon return to land, (b) average pup mass at weaning, and (c) pup survival (solid lines). Dotted lines are 95% confidence intervals

is unlikely to affect the probability of population persistence if the environmental change occurs episodically (e.g. El Niño events; Vergani et al. 2001, Crocker et al. 2006). Elephant seals amortize their foraging behaviour over a single long trip to sea, buffering them from short-term variations in prey availability (Costa 1993), and respond to the average suitability of a foraging region, ‘expecting’ a particular region to be profitable over a period of years (Bradshaw et al. 2004). However, climate change has the potential to cause long-term, spatially extensive environmental changes in the Southern Ocean, changing the profitability of these regions and rendering the females’ response ineffective. Therefore, the aggregate effect of the predicted decrease in population growth rate could be substantial, especially if the population is unable to adapt to the environmental changes. Furthermore, if the effect of a shift in behaviour on lipid reserves has consequences extending beyond the year in which the disturbance occurred, the long-term effects on population dynamics will be greater than we have predicted.

We assumed that individuals did not compensate for lost foraging opportunities (see Costa 2012) and that the effects of environmental change on elephant seal behaviour occurred on consecutive days moving backwards from the end of a foraging trip. The end of an elephant seal’s foraging trip is normally spent in transit, so the effects of a shift in behaviour would not

be as severe during this time. Therefore, shorter periods of behavioural change distributed throughout the foraging trip would have a greater impact on fitness and population growth rate if the disturbance occurred in the regions or periods when the seals’ foraging success is greatest. However, we were not able to simulate more sporadic environmental change because using drift rate data to inform lipid mass during periods without a behavioural shift would force the estimates in that time period to be comparable to those estimated in the complete absence of disturbance, regardless of any change in behaviour in the preceding time step(s).

While our predictions of females’ final lipid mass corresponded closely with direct observations, our model did not fully capture lipid mass gain at the extremes (Fig. 4). There appeared to be a systematic bias, so that the predicted lipid mass was overestimated at low observed mass and underestimated when the observed lipid mass was high. Therefore, our estimate of the effect of disturbance will be underestimated for smaller females and overestimated for larger individuals. The discrepancy between the observed and predicted lipid mass was greatest for larger females (Fig. 4), leading to a possible downwards bias in our assessment of the effect of disturbance on population growth. Furthermore, our model does not account for the effects of lost foraging opportunities and increased transit on lean mass. Had we

been able to do so, the decrease in total maternal mass as a result of a shift in foraging behaviour would have been greater than projected, with consequent effects on pup survival ( $\phi_p$ ). This explains our predicted change in  $\phi_p$ : the decrease in maternal lipid mass, although substantial, is only a small percentage of total mass. Disruption of foraging as a result of disturbance could conceivably increase pup survival, as indicated by the confidence limits, due to the quadratic relationship between  $\phi_p$  and wean mass ( $W_p$ ) (McMahon et al. 2003): our starting estimates for  $W_p$  span the vertex of the curve (Eq. 4). However, the behavioural shift reduces average pup survival below the level necessary to maintain a stable population and individual fitness declines. In light of our assumptions, our estimates for the reduction in individual fitness and population growth form a lower bound on the potential effects of environmental change (i.e. disturbance) on southern elephant seals.

Traditionally, relationships between environmental change, individual fitness and population dynamics have been established with data from long-term monitoring (e.g. Besbeas et al. 2002, Schick et al. 2013b). However, these approaches are only able to detect population-level changes after they have occurred, negating any possibility of proactive conservation action (Taylor & Gerrodette 1993). Rather than managers delaying decisions or taking an ad hoc precautionary approach to conservation while waiting for the analysis of data from extended moni-

toring programs, we have developed a framework that can effectively forecast long-term impacts within the time frame relevant for making management decisions. We have combined long-term monitoring data with information on short-term changes in behaviour to address a fundamental ecological question: how does one determine the population-level consequences of changes in the behaviour of individual animals?

Others have attempted to develop a general conceptual framework for addressing this question. For example, a committee of the US National Research Council (NRC 2005) suggested that the population-level effects of sound on marine mammals could be assessed via a series of transfer functions connecting sound exposure to changes in behaviour, life functions, vital rates, and population dynamics. Furthermore, similar mechanisms to those we describe are responsible for the behaviourally mediated indirect cascading effects of predation risk in ecosystems (e.g. Fortin et al. 2005). For example, the behavioural responses of elk *Cervus elaphus* to predation risk affect their foraging behaviour and ultimately impact their reproductive success (Creel et al. 2007) and/or their habitat selection. This can have consequences for not only on the elk population but also on plant population dynamics (Ripple & Beschta 2004).

Our elephant seal model can be generalized to assess the population consequences of both physiological and behavioural changes at the individual

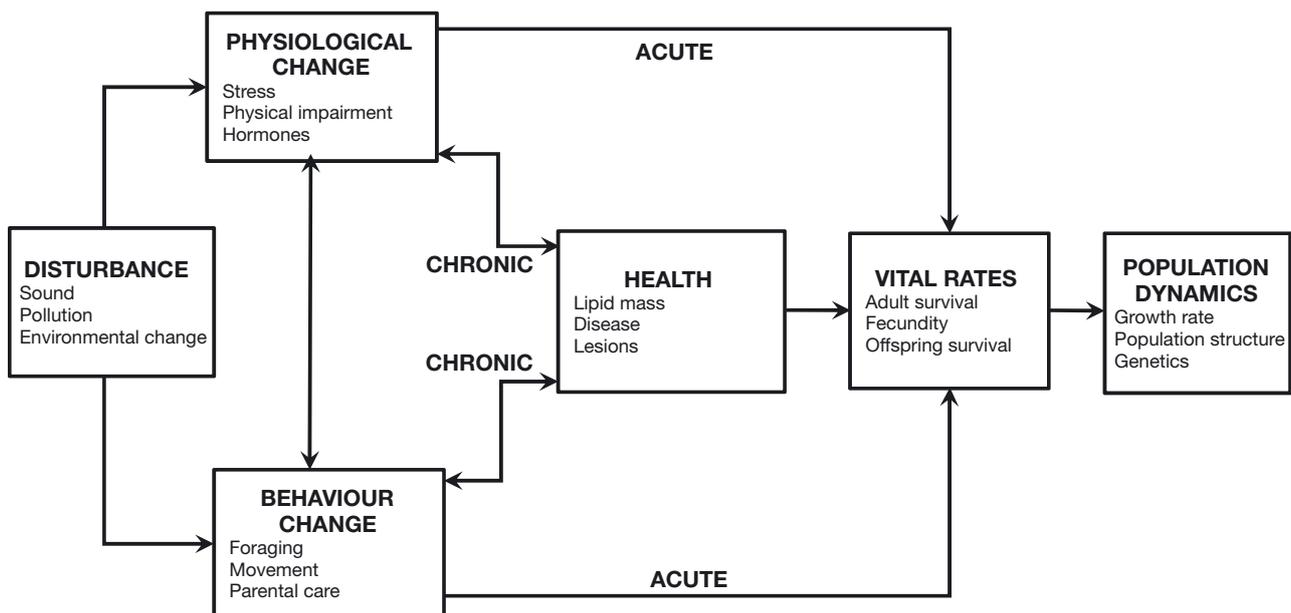


Fig. 6. A conceptual model of the relationships linking disturbance to changes in behaviour and physiology, health, vital rates and population dynamics

level for any species (Fig. 6). Sublethal physiological changes can be measured via hormone levels (e.g. Pereira et al. 2006), body or skin condition (e.g. Schick et al. 2013b), scars, or disfigurement (e.g. Bradford et al. 2009). Moreover, changes in an individual's physiology can affect its behaviour and vice versa (e.g. Hooker et al. 2012). Behavioural and physiological changes can lead directly to changes in vital rates (i.e. an acute effect), such as when changes in habitat use or raised stress levels increase the probability of predation, or mother-offspring separation. Alternatively, behavioural and physiological changes can have indirect and long-term (i.e. chronic) effects on vital rates, such as when changes in activity time budgets or increased susceptibility to disease affect health, which then affects vital rates. Whatever way disturbance affects vital rates, the ultimate effect will be a change in population-level demographic rates. Thus, it is possible to determine the population consequences of disturbance from short-term changes in individual animals.

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