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The Context of Disturbance

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INTERNATIONAL WHALING COMMISSION

The Context of Disturbance

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INTRODUCTION

The popularity of whale and dolphin watching has grown rapidly, with most coastal cetacean populations now exposed to some form of whalewatching (O'Connor *et al*. 2009). While whalewatching was initially welcomed as a more 'benign' alternative to whaling, concerns soon arose that with the rise in high intensity watching, whales and dolphins were being negatively affected (Higham *et al*. 2014).

Many studies have identified short-term behavioural responses in dolphin (*Tursiops spp.*) populations to boat approaches (e.g., Williams *et al*. 2002; Lusseau 2003; Christiansen 2010). However, the identification of long-term fitness effects has been more difficult, in part because of the challenges of assessing marine mammal fitness. Despite this, it has been possible to link disturbance to fitness consequences for at least one dolphin population (Lusseau *et al*. 2006; Currey *et al*. 2009).

A recently developed modelling approach, the population consequences of disturbance (PCoD) framework (New *et al*. 2014), can help assess this question more widely. The framework was developed to link short-term changes in individual behaviour and physiology to long-term effects on population dynamics. The PCoD framework distinguishes disturbances that have an acute, immediate effect on vital rates (e.g., collision with a vessel) from chronic disturbances (e.g., whalewatching) that alter vital rates by affecting an individual's health, defined as all internal factors that affect homeostasis (New *et al*. 2014). This approach provides us with the capacity to ask whether the effects of disturbance are generalizable, i.e. whether measureable short-term disturbance will always have fitness effects, or whether there are specific characteristics of a population that makes the individuals therein vulnerable or robust to disturbance effects.

Fitness effects have been clearly identified in populations that share certain characteristics, i.e. they are closed, small and food limited (e.g., Doubtful Sound, NZ). From a theoretical perspective, it is conceivable, indeed likely, that open, large populations, or those that are free from resource limitation, may be less sensitive to tourism effects. These populations would suffer lower individual level disturbance, and prey availability may offset any disruption to foraging behaviour. To address this question we extend New *et al*.'s (2013) model to four well studied dolphin populations to explore the effect of disturbance in the context of food limitation, closed populations and population size.

METHODS

The four populations considered in this study were Doubtful Sound, NZ (closed population food limited), Sarasota Bay, FL USA (closed population, no food limitation), Durban Bay, SA (open population, no food limitation) and Jervis Bay, AUS (open population, food limited). The populations also vary in size, with the smallest, Doubtful Sound, being only 61 individuals (Henderson 2013), while the largest, Durban Bay, has over 300 individuals (Natoli *et al*. 2008).

These populations were modelled using a structure adapted from New *et al*. (2013). In that paper the authors construct a model for bottlenose dolphin behaviour in which an individual's behaviour (travelling, foraging, resting and socializing) is dependent upon their internal motivation (fear, hunger, condition, social desire). This allows for the intrinsic state of the individual (e.g., fear) to impact their condition when such changes may not be apparent from their behaviour. The model works by simulating each individual in the population and tracking its daily movement, group membership, behaviour and motivational states over the course of a year. New *et al.* (2013) initially built the model for the population of bottlenose dolphins in the Moray Firth, Scotland. As a result, they used a spatial map of the Firth to direct the movement of the dolphins and determine where certain behaviours (e.g., foraging) could take place, based on environmental features. The probability of disturbance was also tied to the individual's location within the Firth.

Constructing similar spatial maps for the four populations in this study was not feasible, from both a computational and knowledge perspective. The size of the relevant habitats would make it computationally impractical to calculate the geodesic distances on a scale that would be biologically meaningful (1 km^2). Furthermore, there are gaps in the knowledge regarding the habitat over which the individuals range, making it difficult to define the environmental features that may be driving behaviour. As a result, New *et al.*'s (2013) model was simplified.

Resource limitation often occurs either because of patchy prey dynamics or because prey occurs in locations in which dolphins are unable to remain for extended periods of time due to perceived risk (e.g., predation). This means that the dolphins must constantly move between locations to take part in different behaviours. For example, if the risk of predation is higher in foraging areas then individuals are unlikely to rest in these same locations. As a result, for food limited populations the model was modified so that individuals were required to travel for at least one time step before switching to any other behaviour (foraging, resting and socializing). Individuals in populations that are not limited by prey availability were assumed to be able to engage in any behaviour without travelling first.

Disturbance in New *et al.*'s (2013) model was also spatially explicit, requiring an additional modification. Rather than the probability of disturbance being tied to a specific location, we assigned a general probability of disturbance on a given day. For the closed populations, all individuals were assumed to share the same risk of disturbance, as they would be unable to leave the area in which tour boats were operating. For open populations, it was assumed that only the proportion of the population in the area regularly used by tour boats were at risk of disturbance. Between 10-30% of the population could be disturbed at any one point, and the groups effected by disturbance were randomly chosen. For all other individuals, the risk of disturbance was zero.

Each population was simulated for a time period covering one year, with the season and its resulting effects on the model (New *et al.* 2013) switching half way through the simulation. Population size was specific to each population, and were defined as follows: 61 dolphins in Doubtful Sound (Henderson 2013), 160 dolphins in Sarasota Bay (Wells *et al.* 2015), 108 individuals in Jervis Bay (Moller *et al.* 2002) and 350 in Durban Bay (Natoli *et al.* 2008). For Durban Bay, there were a number of estimates from which to choose, depending on how the population was defined, with at least one including over 900 individuals (Browning *et al.* 2014). We used the estimated from Natoli *et al.* (2008) for three reasons. First was computational efficiency, because it is an individual based model, tracking over 900 individuals proved to be overly time consuming. Second, the more restricted area used by these 350 individuals allowed us to assume that the dolphins were only exposed to disturbance over a portion of their range, thus allowing for the population to be considered "open". Third, if open population effects appear with a conservative abundance estimate, they are even more likely higher levels. For each population, four disturbance regimes were investigated, (1) no disturbance, (2) 10% chance of disturbance, (3) 25% chance of disturbance and (4) 50% chance of disturbance.

RESULTS

Given the four different populations and four disturbance regimes there were a total of 16 scenarios investigated. For each scenario 100 simulations were run in R (R Core Team 2016). The results presented below are based upon the output of all the simulations combined. This allows us to account for the variability inherent in our model given the inclusion of stochasticity (New *et al.* 2013).

In the absence of disturbance the behavioural time budgets were determined by food limitation. The behavioural time budgets of two food limited populations (Doubtful Sound and Jervis Bay) were more similar to one another than those observed in the other two populations (Sarasota Bay and Durban Bay) (Fig. 1). However, the motivational states of all four populations did not greatly differ (Fig. 2). Once disturbance was included in the simulations, the populations began to diverge. Doubtful Sound saw the most extreme response to disturbance, with only a 10% chance of encountering a tour boat on any one day giving rise to a notable shift in the behavioural time budget and individuals being highly motivated by fear (Figs. 3 and 4). Sarasota Bay also saw a large shift in behavioural time budget and motivations with a 10% chance of disturbance, although less time was spent travelling then was predicted for Doubtful Sound (Figs. 3 and 4).

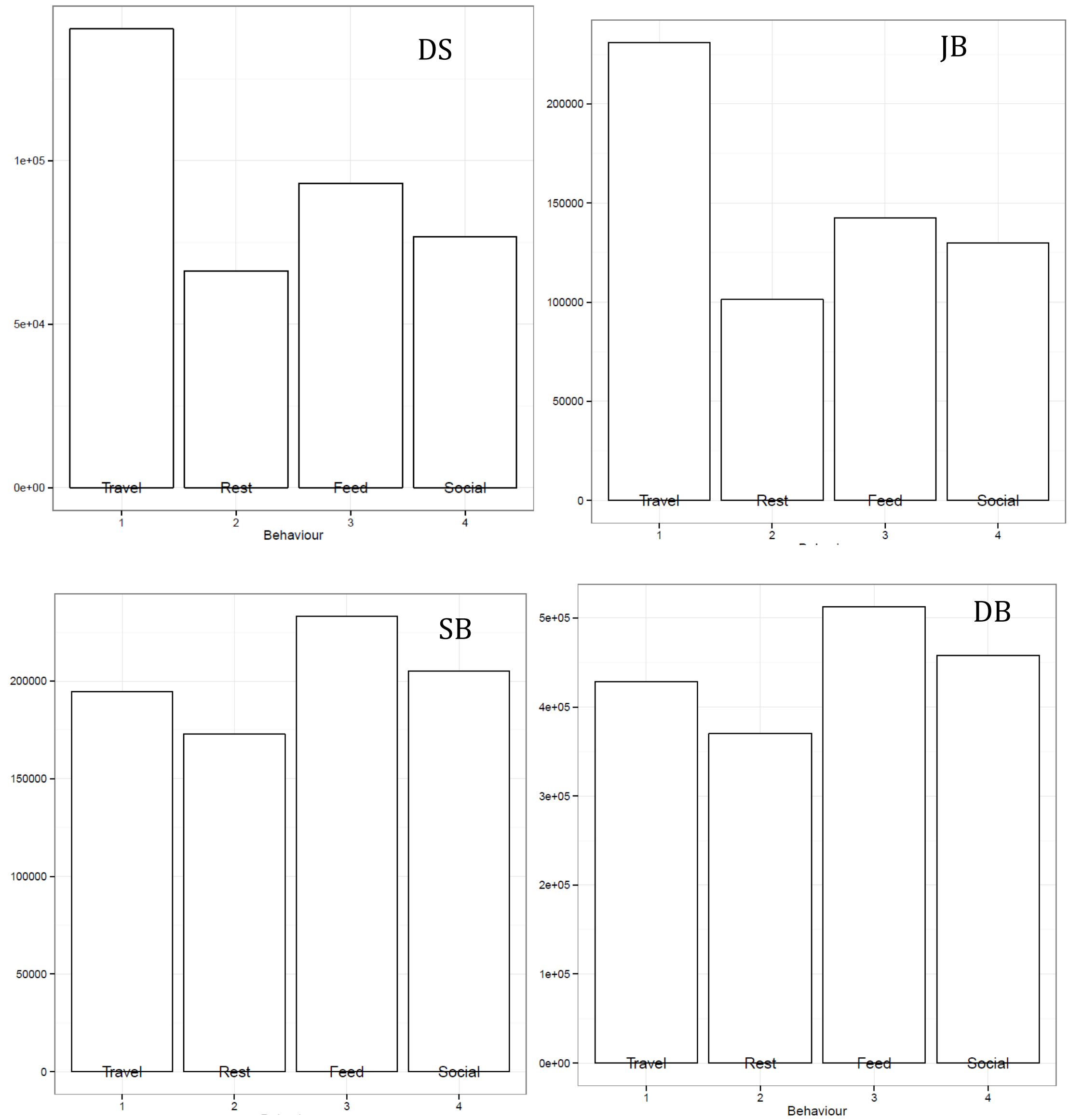

Fig. 1: The behavioural time budgets of the dolphin populations in Doubtful Sound (DS), Jervis Bay (JB), Sarasota Bay (SB) and Durban Bay (DB) in the absence of absences of disturbance.

In contrast, to see the same shift in behaviour and motivational states in Jervis Bay, a 25% chance of disturbance was required (Figs. 3 and 4). Durban Bay was even more extreme, requiring a 50% chance of disturbance to see the same effect observed at the other populations where the probability of disturbance was lower (Fig. 3 and 4). The higher frequency of travel in the Doubtful Sound and Jervis Bay populations are due to food limitation, which requires a group to travel between behaviours, such as foraging and resting.

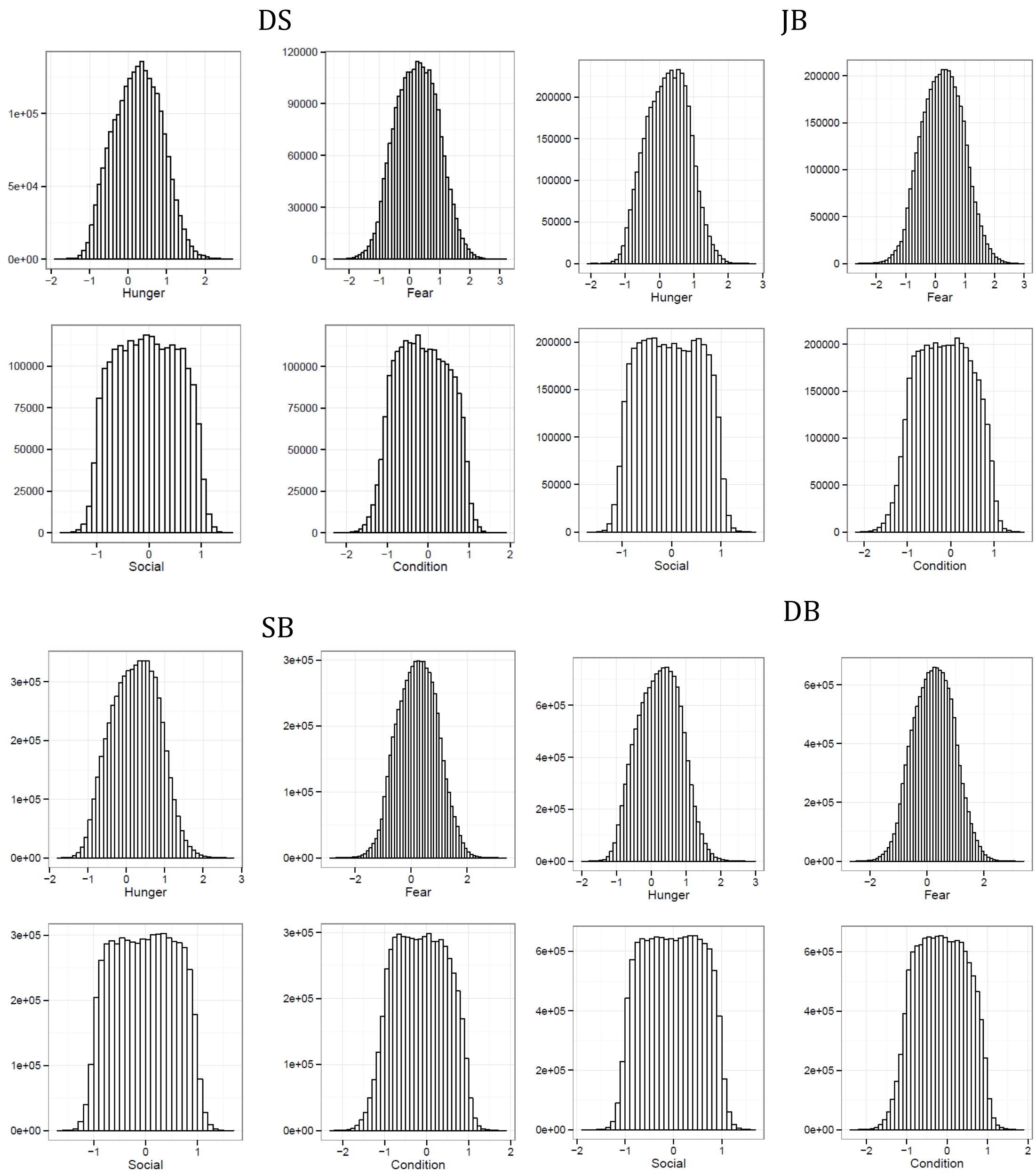

Fig. 2: The motivations states of the dolphin populations in Doubtful Sound (DS), Jervis Bay (JB), Sarasota Bay (SB) and Durban Bay (DB) in the absence of absences of disturbance. A negative value means a lack of motivation (e.g., not hungry), while a positive value indicates the strength of the motivation (e.g., fearful).

DISCUSSION

New *et al.*'s (2013) model had previously been extended to the population of bottlenose dolphins in Doubtful Sound (Pirotta *et al.* 2014), supporting the applicability of the model to populations other than that of the Moray Firth. The disturbance scenarios investigated in the Doubtful Sound study were more complex than those explored here and very specific to the tourism currently occurring the area (Pirotta *et al.* 2014). Given that our goal was not to determine the effects of specific disturbances, but rather explore the role that population characteristics may have in regulating the effects of disturbance, we chose to generalize our model structure and disturbance scenarios. This enabled us to investigate the effects of disturbance on a range of populations whose characteristics included food limitation, closed populations and population size.

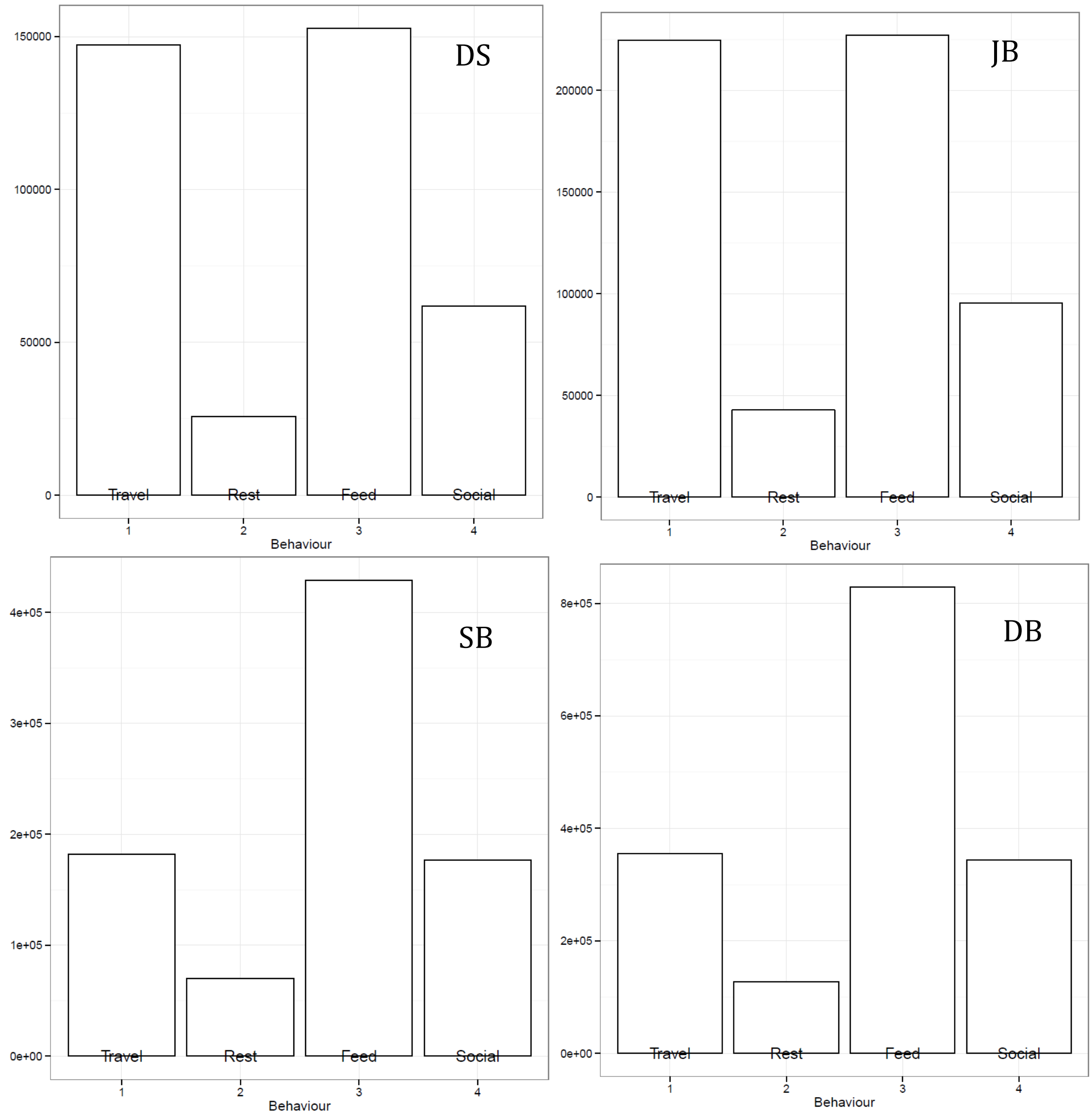

Fig. 3: The behavioural time budgets of the dolphin populations under different scenarios of disturbance. The populations in Doubtful Sound (DS) and Sarasota Bay (SB) had a 10% chance of experiencing a disturbance from a tour boat on any given day, while Jervis Bay (JB) had a 25% chance of an encounter and in Durban Bay each individual had a 50% chance of being disturbed by a whalewatching vessel.

Our results highlight the importance of context when assessing the effect of disturbance on inshore dolphin populations. The two closed populations, Doubtful Sound and Sarasota Bay, proved to be the most sensitive to disturbance, with only a 10% change of encountering a tour boat having a notable effect on the dolphins' behavioural time budget and motivations (Figs. 3 and 4). In contrast, the open populations, Jervis Bay and Durban Bay, required much higher probabilities of disturbance, 25% and 50% respectively, in order to see the same shift in behavioural time budgets and motivations that was observed in the closed populations at only a 10% change of encountering a tour boat (Figs. 3 and 4). The only effect food limitation appeared to have on the dolphin populations was in the behavioural time budgets.

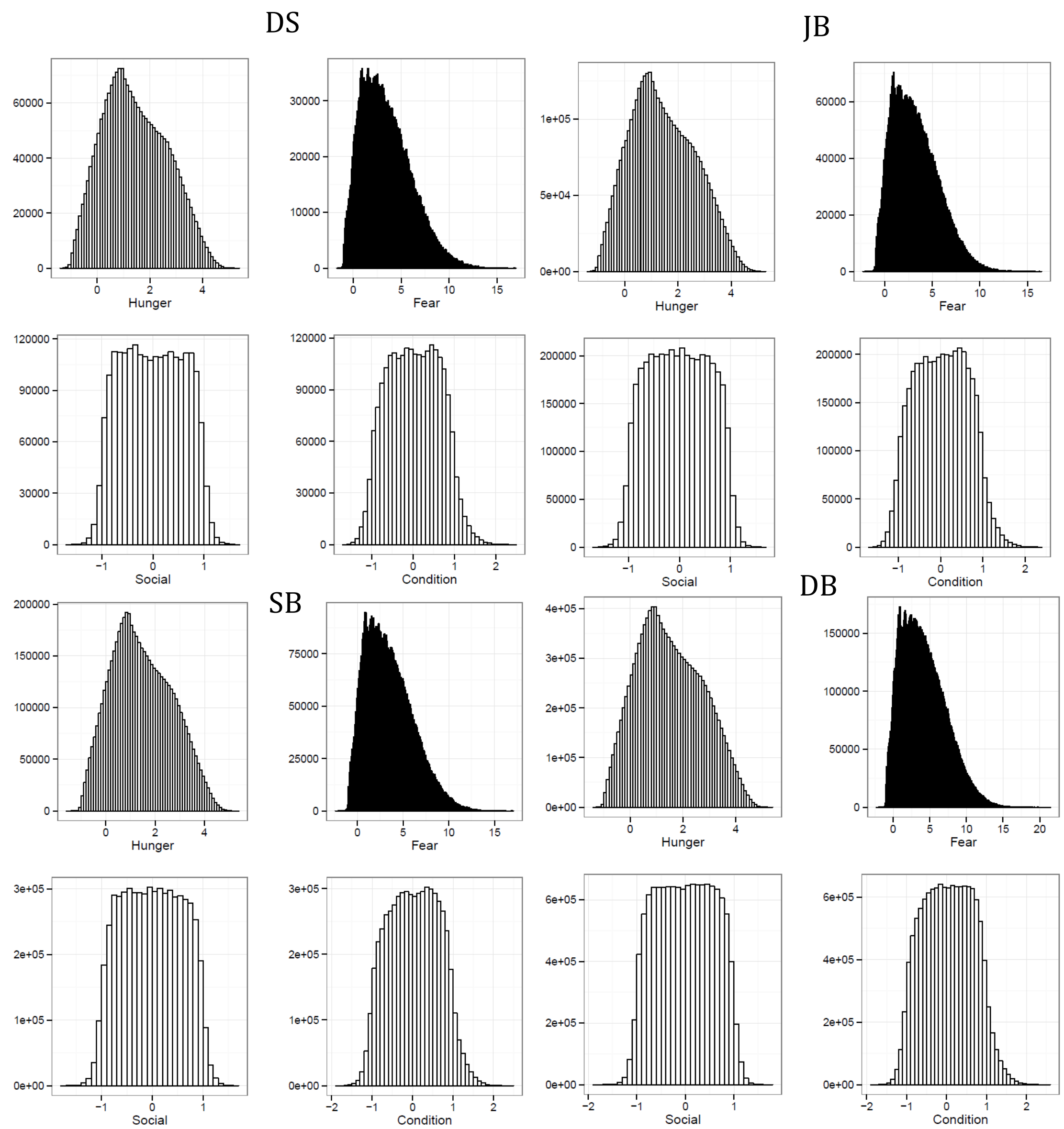

Fig. 4: The motivational states of the dolphin populations under different scenarios of disturbance. The populations in Doubtful Sound (DS) and Sarasota Bay (SB) had a 10% chance of experiencing a disturbance from a tour boat on any given day, while Jervis Bay (JB) had a 25% chance of an encounter and in Durban Bay each individual had a 50% chance of being disturbed by a whalewatching vessel. A negative value means a lack of motivation (e.g., not hungry), while a positive value indicates the strength of the motivation (e.g., fearful).

The difference in the amount of disturbance the open populations can tolerate is likely due to the population size. Durban Bay is a large population at 350 individuals, while Jervis Bay is small at only 108 individuals. Population size does not seem to have played a role in the effects of disturbance on the closed populations, likely because all individuals were considered to be at the same risk regardless of the number of resident individuals. Given that many areas have restrictions on the number of whalewatching vessels and the hours they can operate, this assumption may be too conservative. For example, it may be more reasonable to include a maximum number of encounters that can occur on any one day along with the probability of disturbance to account for the limitations on the tour boat operators.

The most obvious effect of food limitation is in the behavioural time budgets, not the motivational states. This is likely a function of the model structure, which requires populations facing resource restrictions to travel between taking part in different behaviours. As a result, while all populations saw an increase in the time spent forging when exposed to disturbance, those populations that were food limited also saw an equivalent increase in the time spent travelling. It is possible that food limitation played a role in Jervis Bay having a lower threshold of disturbance than Durban Bay. However, the fact that no difference due to food limitation was observable in the closed population lends weight to the belief that the difference in the open populations is due to their size.

Our current model simplifies the dolphins' interactions with their environment. However, it enables us to explore the effect of disturbance in the context of food limitation, closed populations and population size. We found that the characteristics of the populations being disturbed are important with regards to the amount of disturbance that could be tolerated. Closed populations, being unable to avoid the disturbance, were the most sensitive, while open populations were able to withstand a higher probability of disturbance. The population with the most tolerance to disturbance was Durban Bay, a large, open population with no resource limitation. Our results imply that the individual characteristics of a population play an important role in the level of disturbance that can be tolerated and should be accounted for when determining the intensity of the whale-watch operations suitable for a given area.

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