

# The resilience of animal behavior to disturbance<sup>1</sup>

David Lusseau<sup>1\*</sup>, Rob Williams<sup>2</sup>, Lars Bejder<sup>3</sup>, Karen A. Stockin<sup>4</sup>, David Bain<sup>5</sup>, Marie Auger-Méthé<sup>1</sup>, Fredrik Christiansen<sup>6</sup>, Emmanuelle Martinez<sup>4</sup>, Per Berggren<sup>6</sup>

<sup>1</sup>Dalhousie University, Department of Biology, 1355 Oxford Street, Halifax, B3H 4J1, Canada; <sup>2</sup>University of British Columbia, Marine Mammal Research Unit, Vancouver, Canada; <sup>3</sup>Murdoch University, Cetacean Research Unit, Perth, Australia; <sup>4</sup>Massey University, Coastal Marine Research Group, Auckland, New Zealand; <sup>5</sup>Global Research and Rescue, Seattle, WA; <sup>6</sup>Stockholm University, Department of Zoology, SE-106 91 Stockholm, Sweden

\*present address (corresponding author): University of Aberdeen, Institute of Biological and Environmental Sciences, Zoology Building, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

---

## ABSTRACT

The concept of resilience is now widely used to understand the vulnerability of complex systems to disturbances. It is emerging that more diverse systems are more resilient to disturbances. Here we develop a conceptual understanding of the resilience of behavioral systems and assess how this measure is related to the diversity of behavioral sequences modeled using Markov chains. We show that the resilience of behavior is related to its unpredictability, a diversity measure, using simulations and empirical data collected at ten study sites over 30 years. The more predictable behavior is, the less resilient it becomes. Such influences on behavioral resilience cannot be related to the effect size of disturbances in inter-population comparisons. However, we show that such measures are meaningfully related to the influence of disturbances when comparing the same population exposed to different ecological conditions. We show that behavior predictability can be driven by ecological conditions. For example, an increase in food availability can increase the duration of foraging bouts, hence constraining the dynamics of the population's behavior. Such constraints increase behavioral predictability and in turn weaken its resilience to disturbance. This empirically-driven theoretical study offers a framework to manage exposure of animal populations to disturbance.

**Keywords:** Behaviour (Short-term change, Long-term change); Management (Conservation, Whalewatching)

---

---

<sup>1</sup> Submitted to *American Naturalist*. Do not cite without author's permission

## INTRODUCTION

There is now a large body of evidence confirming that complex adaptive systems can have several stable solutions (Levin et al. 1998; Higgins et al. 2002; Marcos et al. 2003; Folke et al. 2004; Frank et al. 2005; Kinzig et al. 2006; Daskalov et al. 2007; Liu et al. 2007). The likelihood that such systems shift from one state to another depends on properties of the stable state they occupy and the forces applied to these systems to push them away from this initial equilibrium (Figure 1). Such shifts have particularly been documented in marine ecosystems as a consequence of anthropogenic impacts (Hare and Mantua 2000; Scheffer and Carpenter 2003; Frank et al. 2005; Daskalov et al. 2007; Österblom et al. 2007). In such systems, biodiversity is linked to system functioning and health (Naeem et al. 1994; Tilman and Downing 1994; Tilman et al. 1996; Tilman 1999; Loreau et al. 2001; Hooper et al. 2005; Worm et al. 2006; Ives and Carpenter 2007). Systems that are more diverse tend to be more stable and more resilient to perturbations (Hooper et al. 2005; Ives and Carpenter 2007). These concepts of resilience and stability tend to also be linked to diversity in other studied systems such as socioeconomic or technological systems (Levin et al. 1998; Albert et al. 2000; Albert et al. 2004; Kinzig et al. 2006). Understanding the factors driving the resilience of a system provides us with means to predict the influences of perturbations or disturbances on those systems and the likelihood that those will result in state alterations. The term resilience defines two concepts that have recently been shown to be related (van Nes and Scheffer 2007). Firstly, “ecological resilience” represents the maximum perturbation a system can accommodate without shifting into another state (Holling 1973). It represents the width of the basin of attraction surrounding a stable state (Holling 1973); the greater the basin, the harder it is to “push” the system out of a stable state and therefore the system is more resilient in that state. Secondly, “engineering resilience” represents the rate at which the system recovers from a small perturbation (Pimm 1984), a more resilient system recovering faster. In a conceptual representation of system dynamics (Figure 1), ecological resilience would correspond to the breadth of the basin of attraction while engineering resilience would relate to the steepness of the sides of the basin. The steeper the sides are, the faster the system can “roll back” to the stable state. Engineering resilience can be calculated empirically and theoretically using a variety of techniques (Neubert and Caswell 1997; Ives et al. 2003; Hill et al. 2004; Wootton 2004; van Nes and Scheffer 2007). While conceptual work is available on ecological resilience, it has proven extremely challenging to develop techniques to quantify it (van Nes and Scheffer 2007). Recent work by van Nes and Scheffer (2007) show that both these concepts are linked, offering a way to assess resilience using the time it takes systems to recover from a small perturbation. In addition, recovery rates appear to slow down as the system approaches conditions leading to a shift in stable solution (van Nes and Scheffer 2007); in other words as it approaches the hill between two basins (Figure 1). Monitoring recovery rates from small perturbations across a range of conditions can therefore help in understanding how disturbances affect the resilience of a system (Figure 1).

Animal behavior can be understood as a complex adaptive system (Granovetter 1978; Simpson et al. 1999; Nolfi 2004; Sumpter 2006). Behavior is a dynamic phenomena resulting from the integration of several non-linear interactions within individuals and between individuals and their environment (including conspecifics). Like other complex systems, behavioral systems can have alternative stable states influenced by both intrinsic (e.g., homeostasis) and extrinsic (e.g., changes in ecological conditions) factors (Levin et al. 1998; Lusseau 2004; Walker and Meyers 2004). Animal behavior is increasingly used as a tool to understand the influence of

human disturbance on the lives of animals (Blumstein and Fernández-Juricic 2004). Having an understanding of the principles governing the resilience of behavioral systems would provide important theoretical ground to conservation behavior, something that some authors argue this field is lacking (Caro 2007). Some studies have already shown that human disturbances can shift the behavioral regime of targeted populations. Boat interactions affect the behavior of cetaceans (Baker and Herman 1989; Corkeron 1995; Bejder et al. 1999; Lusseau 2003a; Bejder et al. 2006; Williams et al. 2006; Stensland and Berggren 2007). After twenty years of studies, we now understand that this disturbance result from avoidance tactics that disrupt the behavior of targeted individuals, animals forgoing their current activities to move away from boats. These disruptions can lead to reduced fitness and habitat abandonment, which can impact the viability of the targeted populations (Lusseau 2004; Lusseau 2005a; Bejder et al. 2006; Lusseau et al. 2006b; Williams et al. 2006; Stensland and Berggren 2007). These energetic alterations can be driven by shifts in behavioral regimes. For example, bottlenose dolphins (*Tursiops* sp.) in Milford Sound, Fiordland, can respond to boat disturbances using short-term evasive tactics, i.e. moving away from the boat interaction. However, if there is on average less than 70 minutes between two boat interactions in the fiord, dolphins will shift to long-term avoidance tactics, i.e. avoiding the fiord altogether during high boat interaction periods (Lusseau 2004; Lusseau 2005a). The stable states of the behavioral system here are multidimensional, integrating space use and activity budget. It is complicated to manage complex systems that have alternative stable states because they are affected by a wide variety of intrinsic and extrinsic factors (Yodzis 2001; Corkeron 2004; Frank et al. 2005). More importantly, while such system can be pushed into an alternative state by varying conditions, it may take more than reverting to original conditions to shift the system back into its original state (Scheffer et al. 2001). Therefore, management practices need to ensure that the ecological resilience of systems that we use is either maintained or improved in order to minimize the likelihood of unwanted state shifts.

A recent review of resilience studies in ecosystems show the lack of empirical foundations for the mechanisms underlying the observed relationships between resilience and responses to perturbations (Ives and Carpenter 2007). We assess here the mechanism through which ecological conditions can affect the resilience of behavioral systems resulting in differences in the effect disturbances will have on these systems. Firstly, we assess whether the resilience of dolphin behavioral sequences is affected by its diversity, using a measure of engineering resilience. Analyses of animal behavioral sequences collected in the field as a Markov process have proven a useful tool in conservation biology to assess the influence of disturbances on animal behavior (Lusseau 2003a). We compare the resilience of behavior in nine populations of dolphins at ten different sites and assess whether behavioral systems that are more diverse are also more resilient. The rate of convergence to the stationary distribution of a Markov process provides a measure of the time it takes this process to recover from a small perturbation (Hill et al. 2004; Wootton 2004). This rate of convergence can be measured in several ways, one of which is the damping ratio of the transition probability matrix defining the Markov process which provides a minimum estimate of the convergence rate (Hill et al. 2004). Finally using two case studies, we determine whether varying ecological conditions can affect the resilience of the behavioral system studied and in turn influence the way in which disturbances, in this case boat interactions, affect dolphin behavior.

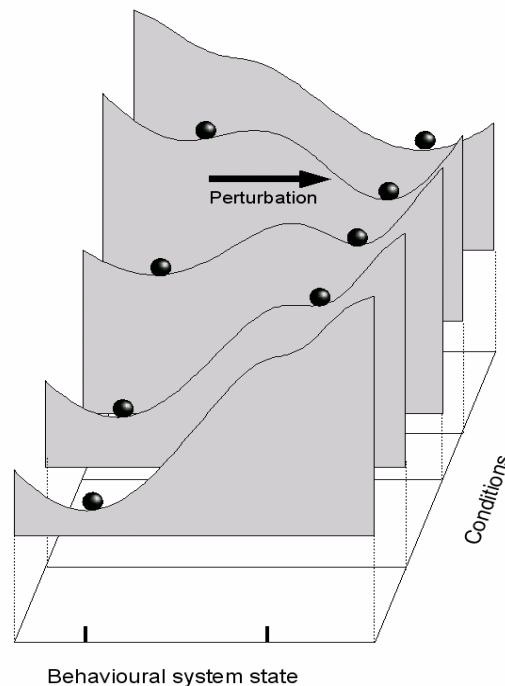


Figure 1: Diagram showing how extrinsic conditions (*e.g.*, food availability) can influence the resilience of a behavioral system that has several stable states (two in this diagram). Stable states are represented by basins of attractions in which the system (represented by the black ball) rests. The system shifts its state when it rolls from one basin to another. Such movement is going to be impaired/aided by the shape of the basin. The resilience of the system in a given state is represented by the width of the basin (ecological resilience, see text) and the steepness of the basin (engineering resilience, see text). External conditions can change the resilience of the different states meaning that in some instances, as the resilience becomes small, a small perturbation can shift the system from one state to another. Figure adapted from the concept presented in Scheffer and Carpenter (2003).

## MATERIALS AND METHODS

### Sampling behavioral state

Several studies have now defined the behavioral state repertoire of dolphins and analyzed the temporal sequence of those states as a Markov process (Lusseau 2003a; Lusseau 2004; Bejder 2005; Williams et al. 2006; Stockin et al. 2008; Bain et al. submitted; Christiansen et al. submitted). We collated information about state transition probability at these ten sites spanning six species, three continents, and cumulatively represented 31 years of field sampling (Figure 2). At all sites we used scan sampling of focal schools to define the predominant behavioral state of focal schools of dolphins at a constant sampling interval (Altmann 1974; Mann 2000; Lusseau 2003a). The sampling interval was 15 minutes at most locations except for four sites (Figure 2). We defined behavioral states to be mutually exclusive and cumulatively inclusive (as a whole

they described the entire behavioral budget of the dolphins at that given site). We refer readers to the articles cited above for further details on each of the study site.

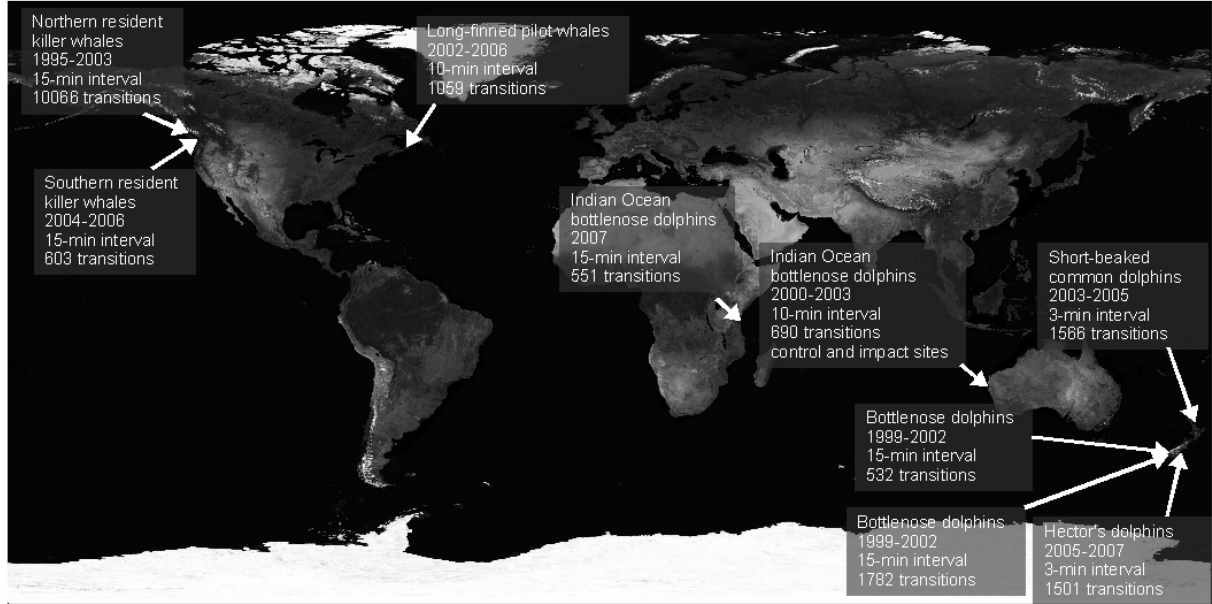


Figure 2: Location of study sites and sampling details. World map provided by NASA- Visible Earth (<http://visibleearth.nasa.gov/>)

We estimated transition probabilities as first-order time discrete Markov chains using these observed samples of state sequences. We constructed two chains for each site. If no boat interaction occurred between two state samples, we tallied the transition between these two samples in a control table. If a boat interaction occurred between two samples, we tallied the transition in an impact table. We discarded transitions between a sample succeeding an interaction and the following sample. In other words, if a boat interaction occurred between sample 1 and 2, we did not consider the transition between samples 2 and 3. If sample 2 was affected by boat interaction, then the transition between 2 and 3 could be considered neither impact nor control. We obtained square matrices of size  $s$ , where  $s$  was the number of states in the behavioral budget at a site, transition probabilities being:

$$p_{ij} = \frac{a_{ij}}{\sum_{j=1}^s a_{ij}}, \quad \sum_{j=1}^s p_{ij} = 1 \quad (1)$$

Where  $i$  was the preceding behavior,  $j$  was the succeeding behavior ( $i$  and  $j$  range from 1 to  $s$ ),  $a_{ij}$  is the number of transitions observed from behavior  $i$  to  $j$ , and  $p_{ij}$  is the transition probability from  $i$  to  $j$  in the Markov chain. All subsequent analyses were carried out on the control chains, unless stated otherwise. Given the pilot whale sampling scheme transitions were dominated by control conditions but a small minority of transitions may be impact conditions (Auger-Méthé and Whitehead 2007). We could not distinguish between those in the dataset.

## Quantifying resilience and diversity

The engineering resilience of transition probability matrices was estimated using the convergence rate of the Markov chains; that is the log of its damping ratio (Hill et al. 2004; Wootton 2004):

$$\ln \rho = \ln\left(\frac{\lambda_1}{|\lambda_2|}\right) \quad (2)$$

Where  $\lambda_1$  is the dominant eigenvalue and  $\lambda_2$  the second eigenvalue. Given this definition, resilience estimates can vary from zero to infinite. This damping ratio estimates how long it takes the chain to converge on the behavioral budget, the equilibrium, from its initial conditions. We used the entropy of the matrices to quantify their diversity (Hill et al. 2004) for two reasons. Firstly, this measure is directly related to other diversity measures used in ecosystem studies (*e.g.*, Shannon's diversity index) and therefore can be intuitively linked to the concept of system diversity. Secondly, it relates to the predictability of the Markov chain. A matrix with high entropy will be more unpredictable, that is the state in which it will be at the next step cannot be determined easily. The concept of flexibility is at the core of the concept of resilience, the more flexible a system the less likely it is to be shifted by a perturbation (Levin et al. 1998). This translates in behavioral system into the concept of predictability where a more unpredictable system is less likely to be shifted by perturbations, which is what the entropy measure allows us to test. The entropy of the transition matrices was defined as (Hill et al. 2004):

$$H(P) = -\sum_{j=1}^s w_j \sum_{i=1}^s p_{ij} \ln p_{ij} \quad (3)$$

Where  $\mathbf{P}$  is the transition matrix of size  $s$ ,  $\mathbf{w}$  is the dominant eigenvector of the matrix normalized to sum to 1 (it estimates the proportion of time spent in each state, *i.e.* the behavioral budget), and  $p_{ij}$  is the transition probability from state  $i$  to state  $j$ . Since the size of behavioral state repertoire was not the same in all populations (those were composed of four or five states in the nine populations) we normalized the entropies (Hill et al. 2004):

$$H_{norm}(P) = \frac{H(P)}{\ln\left(\frac{1}{s}\right)} \quad (4)$$

$H_{norm}$  varies from 0 when the state of the chain at the next time step is always known (transition is deterministic) to 1 when transition are completely unpredictable. We bootstrapped 1000 times the transition matrices, given the sample size and the number of samples for each transition for each study, to obtain confidence intervals around resilience and entropy estimates.

### The influence of sampling

While most sites used a similar 15-min. sampling rate, four sites used different rates (common dolphins (*Delphinus* sp.): 3 minutes, Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in Shark Bay: 10 minutes, long-finned pilot whales (*Globicephala melas*): 10 minutes, Hector's dolphins (*Cephalorhynchus hectori hectori*): 3 minutes, Figure 2). We therefore calculated the relationship between resilience and entropy in two ways. We first used all the original datasets and we subsequently used re-sampled, with a 15-min. sampling rate, datasets for those sites that had different sampling rate. Sample size prevented us from re-sampling the original datasets directly. We therefore created samples for each of the three sites using the transition matrices to

inform a hidden Markov model. For each study, we created a sequence of 100,000 states using a hidden Markov model informed by the transition probability matrix in Matlab. The first 50,000 states were discarded to escape initial conditions (burn-in) and the transition probability matrix was reconstructed using the sequence of the last 50,000 states. We then constructed two matrices using this sequence. The first transition matrix had the same sampling rate as the original one had and the second one was constructed by re-sampling the sequence using a 15-min sampling interval. We then calculated the resilience and entropy of both matrices to first assess how the matrix with the original sampling rate differed from the observed matrix and second to infer what the resilience and entropy values would have been for these sites if sampling had occurred at a 15-min. rate. We repeated this process 1000 times, bootstrapping the observed transition matrix at each iteration to estimate the uncertainty in resilience and entropy estimates due to sample size.

We also assess the robustness of these two values to sample misclassification; that is the influence from a sample was wrongly assigned to a given state. We randomly reassigned  $p$  samples ( $p$  ranging from 0 to 20%) in the Doubtful Sound Markov chain and assessed the proportion of departure in resilience and entropy values.

### **Relationships between resilience and diversity in simulated matrices**

We assessed whether the observed relationship between entropy and resilience may have occurred by chance using three sets of simulations. These simulations aimed at defining which feature of behavioral Markov chains may influence the relationship between entropy and resilience. First, we designed random matrices with elements drawn from a uniform random distribution [0;1]. Second, we designed random transition probability matrices, i.e. matrices with similarly drawn random elements but with the sum of the rows being one. Lastly, we designed random transition probability matrices for which the maximum value of each row was on the diagonal. For each of these three cases, at each iteration we drew ten 5x5 square random matrices and calculated the Pearson's  $r$  correlation coefficient between their resilience and their entropy. We iterated this process 1000 times to obtain the confidence intervals around these correlation coefficients. We used this matrix size and number configuration to compare directly results to our observed dataset, using larger matrices, and more of them, yielded similar results.

### **Elasticity of resilience and entropy measures**

Prospective perturbation analyses can help understanding the functional relationships between elements of a transition matrix and a feature of the matrix as a whole. For example such analyses can be used in population ecology to understand how, and which, vital rates influence population growth rate (Caswell 2000). We therefore used perturbation analyses to determine the contribution of different behavioral states to resilience and entropy. Hence, we were interested in the sensitivity of these two measures to small perturbations in transition probabilities. We calculated the sensitivity of resilience and entropy estimates to small changes in the transition matrices via simulations. We measured proportional changes in resilience and entropy in relation to proportional changes in transition probabilities by calculating the elasticity of those measures. We systematically perturbed each of the transition probability by 0.1% and then calculate the proportion by which each of the two measures changed after this perturbation (Caswell 2001) hence inferring the sensitivity of these measures to each transition probability. From these

sensitivity matrices, we derived the elasticity of resilience and entropy to each state by calculating the proportional changes attributed to each state. In the case of entropy:

$$E_i = \sum_j \frac{p_{ij}}{H} \frac{\partial H}{\partial p_{ij}} \quad (5)$$

Where  $\frac{\partial H}{\partial p_{ij}}$  is the sensitivity of the entropy  $H$  to the transition probability  $p_{ij}$  and  $\frac{p_{ij}}{H} \frac{\partial H}{\partial p_{ij}}$  is the

elasticity matrix. The same applies to the resilience measure. From these estimates we can then define whether the predominance of a state in the population's behavioral budget relates to its contribution to the resilience and entropy of behavioral sequences. That is we can estimate whether changes to predominant behavioral states are more likely to perturb the resilience or the entropy of the behavioral system.

### **The influence of varying conditions on killer whales**

Interactions between boats and dolphins influence the dolphin's behavioral transition probability and consequently can influence the behavioral budget of the affected population (Lusseau 2003a; Lusseau 2004; Williams et al. 2006; Stockin et al. 2008; Bain et al. submitted; Christiansen et al. submitted). Such consequences can lead to impacts on the biology of the targeted populations (Lusseau 2005a; Bejder et al. 2006; Lusseau et al. 2006b). Here we are trying to understand whether variation in ecological conditions to which the population is exposed can affect its resilience to disturbance, which would mean a change in the magnitude of the effect of disturbances on the behavioral budget of the population.

Previous work at the Robson Bight-Michael Bigg Ecological Reserve (Figure 2) shows that the behavior of northern resident killer whales (*Orcinus orca*) at that site is influenced by availability of preferred prey, principally the local density of Chinook salmon (*Oncorhynchus tshawytscha*) (Ford et al. 1998; Lusseau et al. 2004; Ford and Ellis 2006). We also showed that boat interactions disrupt the behavior of killer whales at this location (Williams et al. 2006). We estimated the resilience and entropy of the behavioral Markov process for each year from 1995 to 2003 to assess whether varying ecological conditions, Chinook salmon density in the area (estimated using catch per unit effort, CPUE), affected indirectly the magnitude of the impact caused by boat disturbance. This density measure is site-specific and does not quantify the overall salmon abundance over the whole home range of the population, but it also means that it represents the food conditions at the location sampled (Lusseau et al. 2004). We estimated the duration of foraging bouts from the transition probability matrix (Williams et al. 2006):

$$\bar{t}_{ii} = \frac{1}{1 - p_{ii}} \quad (6)$$

The intensity to boat exposure did not change significantly over the nine years (Williams et al. 2006). We assessed the effect of boat interaction disturbances on the behavioral budget of killer whales by comparing the behavioral budget estimated from the control transition matrix and from the impact transition matrix. The budget was estimated by the left eigenvector,  $\mathbf{w}$ , of the dominant eigenvalue of the matrices (Caswell 2001; Lusseau 2003a). The magnitude of the impact was defined as the impact budget's mean deviance from the control budget:



$$d_i = \frac{(w_{impact_i} - w_{control_i})^2}{\frac{(w_{impact_i} + w_{control_i})}{2}} \text{ and } d = \bar{d}_i \quad (7)$$

Where  $d_i$  is the deviance for state  $i$  and  $w_i$  is the element of  $w$  for state  $i$ . We tried a variety of ways to calculate the difference between the two budgets, which all lead to similar conclusions.

### Behavioral regime shift in bottlenose dolphins

Recently the population of bottlenose dolphins living in Doubtful Sound, New Zealand has gone through a rapid shift in population biology parameters (Currey et al. 2008; Currey et al. submitted). While the adult survival rate remained constant from 1990 to 2007 ( $\phi_{adult(1990-2007)} = 0.9368$ ; 95% CI: 0.9163 – 0.9526), the calf survival rate decreased sharply and suddenly between 2001 and 2002 ( $\phi_{calf(1994-2001)} = 0.8621$ ; 95% CI: 0.6851 – 0.9473;  $\phi_{calf(2002-2007)} = 0.3913$ ; 95% CI: 0.2177 – 0.5976) (Currey et al. submitted). One hypothesis for this decline is that the added energetic constraints of boat interactions on females is leading to reduced reproductive success as observed through a decrease in calf survival (Lusseau 2003b; Bejder 2005; Lusseau et al. 2006a; Lusseau et al. 2006b). Boat interactions lead schools of dolphins to spend significantly more time traveling and less time resting (Lusseau 2003a). More importantly they lead to increased traveling bout duration which is energetically costly for individuals that already have other energetic constraints such as pregnancy or lactation (Conradt and Roper 2000; Lusseau 2003a; Lusseau 2004). The 2001/2002 threshold corresponds to an increase in boating activities around the dolphins that may have pushed the population in a new, energetically more expensive, behavioral regime (Lusseau et al. 2006b). In summer 2001 boating activities lead dolphins to have on average 110min. between two boat interactions while this measure decreased to 70min. in summer 2002 (Lusseau 2005b; Lusseau et al. 2006b). This latter inter-interaction time lapse is similar to the ones observed triggering a shift in behavior in Milford Sound as discussed in the introduction (Lusseau 2004). We assessed whether such a shift occurred by comparing the control Markov chains for 2001 and 2002 and the impact boat interactions had on the behavioral budget of these dolphins in both years (using Eq. 7).

## RESULTS

The resilience of the behavioral systems studied was significantly correlated to their diversity, the more unpredictable a system was (the higher its entropy) the more resilient it was (Figure 3). This relationship did not occur by chance. The resilience and entropy of random matrices were not correlated (Pearson's  $r = 0.09$ , 95% bootstrapped confidence interval over 1000 iterations: -0.612 – 0.660). These measures were also not related for random Markov chains ( $r = 0.53$ , 95% CI: -0.100 – 0.880). However, they were in the cases where the random Markov chains had a dominant diagonal ( $r = 0.65$ , 95% CI: 0.138 – 0.923). Hence behavioral sequences, in which behavioral states are performed in bouts, are inherently likely to have their resilience related to their predictability. We found that varying the size of the matrices or the number of matrices used to assess the relationships between resilience and entropy did not change these overall results. Therefore, the diagonal of matrices, which dictates the length of behavioral bout duration, plays a role in defining the relationship between entropy and resilience. Re-sampling chains with varying sampling intervals affected the estimates of resilience and entropy we obtained.

However, the relative relationship between these two measures was not affected by re-sampling (Figure 3a,b). Sample misclassification did not have an important influence on resilience and entropy (Figure 4).

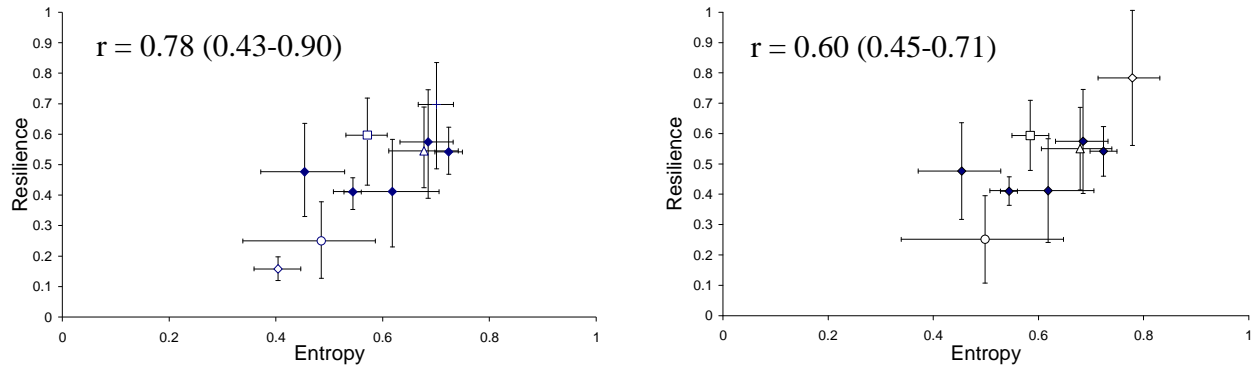


Figure 3: The relationship between resilience and entropy for (a) the original Markov chains and (b) the re-sampled Markov chains so that all chains had the same sampling interval (15 minutes). Re-sampled chains are marked with open symbols. Error bars are bootstrapped 95% confidence intervals. Pearson's  $r$ , with 95% bootstrapped confidence intervals, is presented for each panel for relationship between resilience and entropy.

The behavioral resilience was not related to the observed impacts on behavioral budget (Pearson's  $r = -0.28$ , 95% bootstrapped confidence interval:  $-0.55 - 0.27$ ). That is, more resilient systems, as defined using the damping ratio of the Markov process characterizing them, were not in fact more resilient to disturbances.

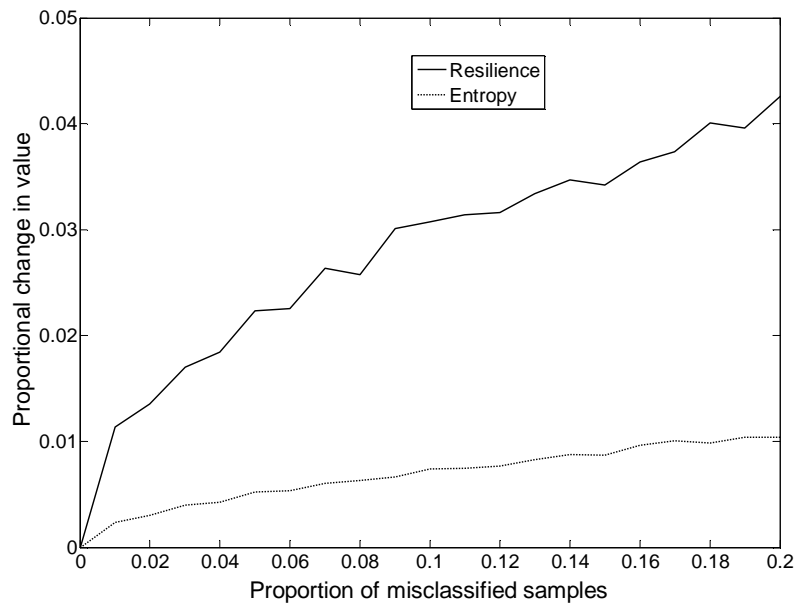


Figure 4: The robustness of resilience and entropy to sample misclassification measured by proportional changes in each of these values for given proportions of samples misclassified.

### **Elasticity of resilience and entropy measures**

The elasticity of entropy seems to be consistently, across studies, related to state rank, with predominant states having more influence on entropy than rarer ones (Figure 5a). The contribution to the elasticity of entropy of each state was significantly related to state rank in seven out of the ten studies (Spearman's rank correlation  $< -0.8$ , p-values  $< 0.05$  estimated using 1000 permutations in each instance). The predominant state had in all studies the most influence on entropy; given repertoire size such result could have occurred by chance with a probability of  $4 \cdot 10^{-7}$ . This trend was not apparent for the elasticity of resilience (Figure 5b). However, resilience and entropy were more influenced by the diagonal of the transition probability matrix, with maximum values of the elasticity matrices being preferably on the diagonal of the elasticity matrix (Figure 6a,b). Therefore, bout duration most influenced resilience and entropy estimates.

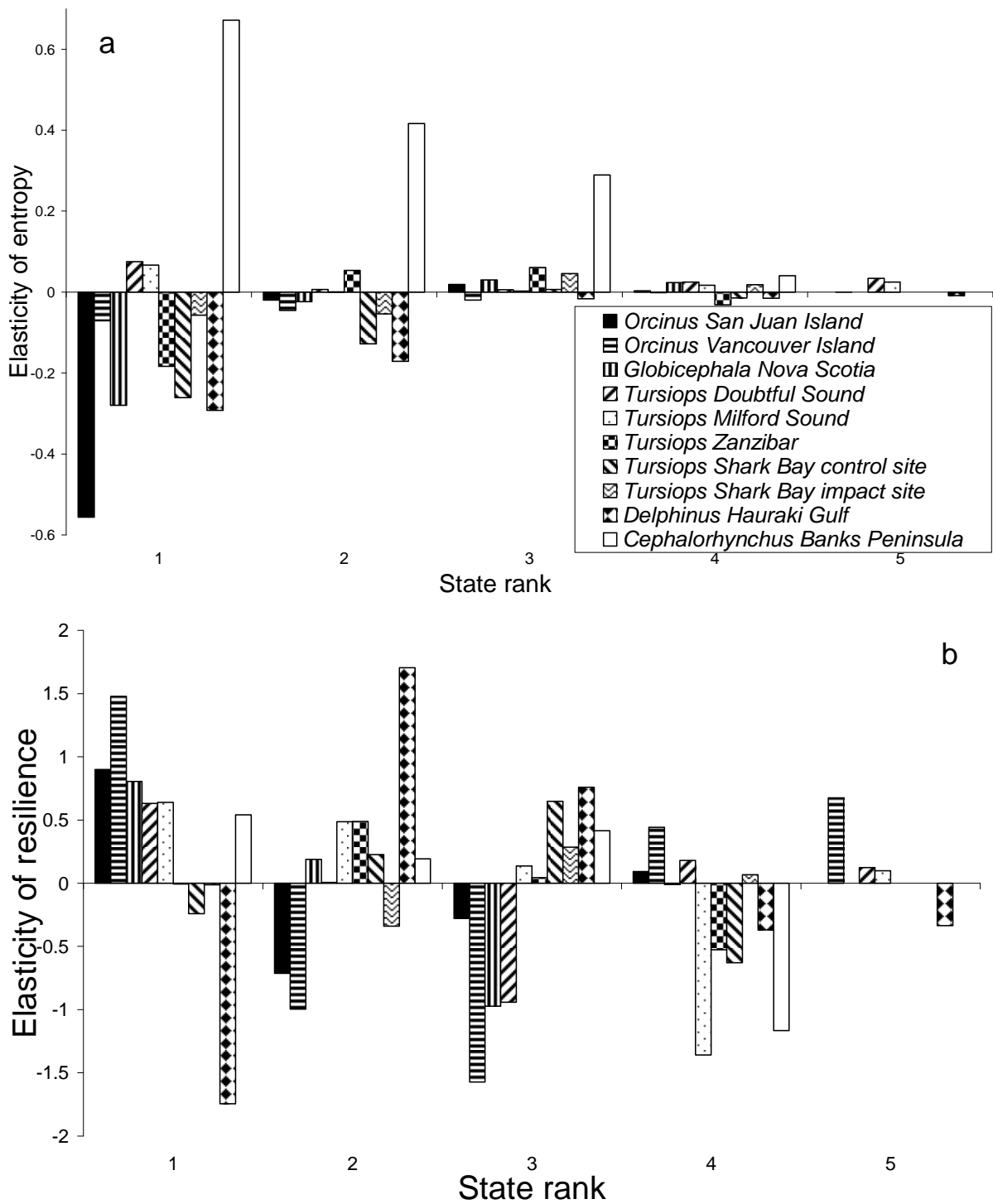


Figure 5: The elasticity of (a) entropy ( $H$ ) and (b) resilience to the transition probability matrices, note the different scales on the axes. The proportional elasticity is presented for each state ranked from the predominant state (rank 1) in the behavioral budget (greatest element of  $\mathbf{w}$ ) to the rarer state (rank 4 or 5 depending on the state repertoire size).

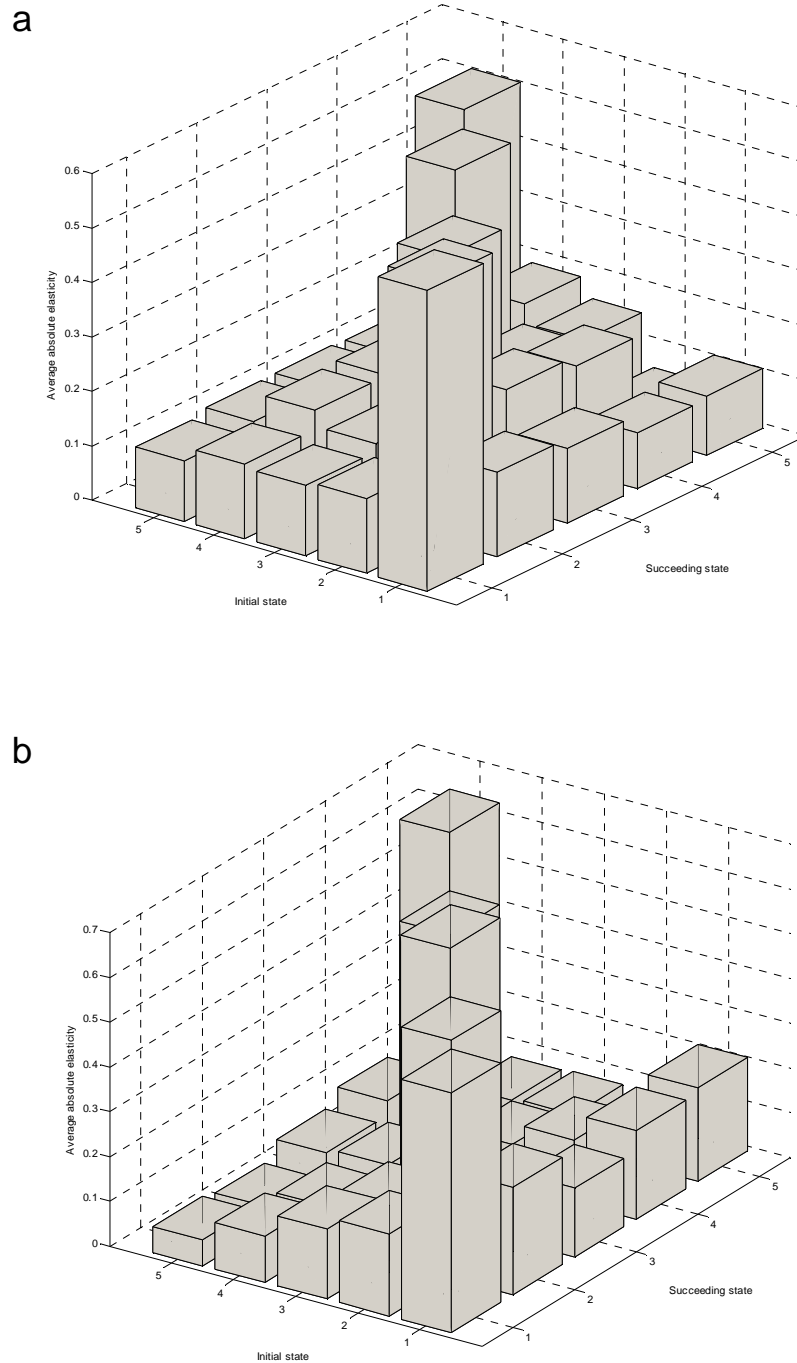
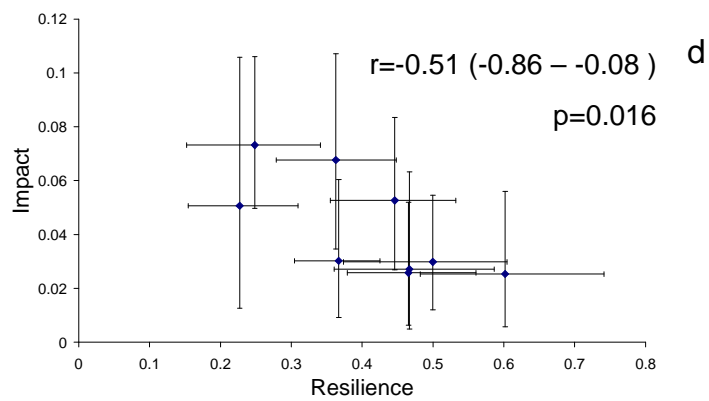
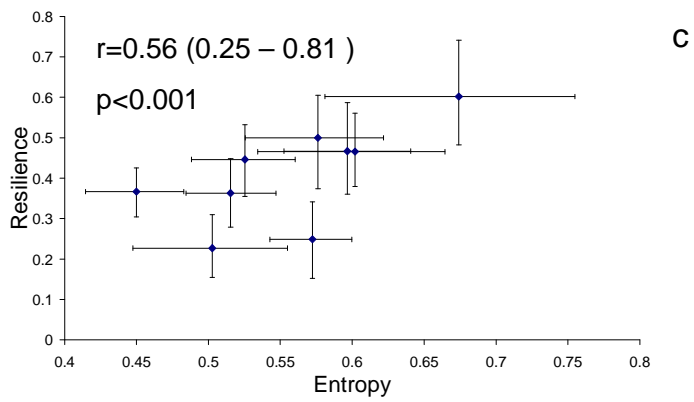
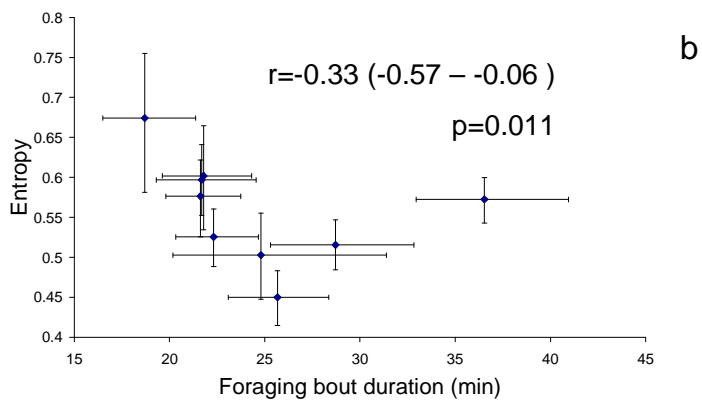
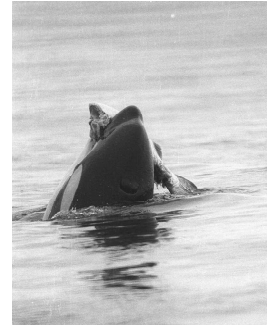
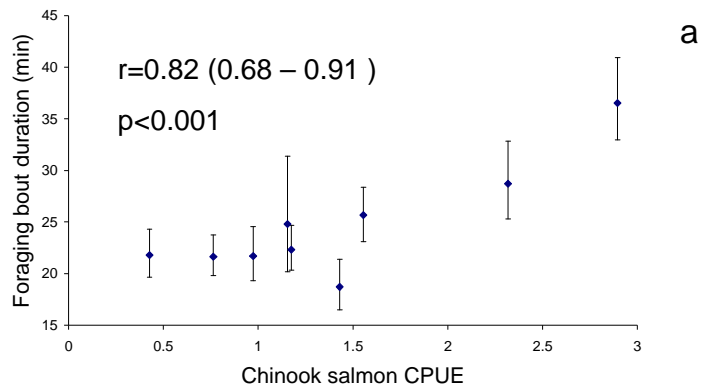


Figure 6. The elasticity of (a) entropy and (b) resilience to proportional changes in transition probabilities. The figure represents the average absolute elasticity for each transition (5 states) across the ten studies. Note the peak along the first diagonal of the matrix, showing that bout duration disproportionately influences resilience and entropy.

### **The influence of varying conditions on killer whales**

As predicted from foraging theory (Mangel and Clark 1986), the duration of foraging bouts observed off Robson Bight increased with local salmon density (Figure 7a). While untested, given the small number of years studied, there is some indication that this relationship may be non-linear. The increase in foraging bout duration was related to a decrease in the entropy of the Markov chain as expected from the simulation work described above (Figure 7b). As bout duration increased, the chain became more predictable. As expected the relationship between these two variables, while robust, may be more complex as there appears to be outliers. This is expected given that foraging is only one of the states influencing the entropy measures and non-linear interactions could emerge from conditions influencing different states in different manners. The resilience of the chain was related to its entropy, and therefore an increase in predictability lead to a decrease in resilience (Figure 7c). Resilience appear to be linked to the impact of boat interactions on the behavioral budget of the population (Figure 7d), hence a decrease in resilience would lead to an increase in the magnitude of the impact of boat disturbance (leading to a mechanism similar to the one described in Figure 1).

Figure 7 (overleaf): The relationship between ecological constraints on the behavioral system and the effect of disturbance on that system in the case of northern resident killer whales. Prey density is related to foraging bout duration (a); as those bouts lengthen, the entropy of the behavioral system decreases (b), leading to a decrease in resilience (c), and a decrease in resilience is related to an increase in disturbance effect size on the behavioral budget (d). Error bars are 95% bootstrapped confidence intervals. The 95% bootstrapped confidence intervals of Pearson's  $r$  correlation coefficient is also provided along with the likelihood that the relationship is not different from zero (significance at  $p=0.05$ ). Photos are courtesy of Ken C. Balcomb and Rob Williams.



### Behavioral regime shift in bottlenose dolphins

The behavioral budget observed during control conditions varied from 2001 to 2002 (Figure 8a). Dolphins spent significantly more time traveling and less time resting and socializing. The nature of these variations is similar to the observed impact of boat interactions (Lusseau 2003a; Lusseau 2004) on the behavioral budget of these dolphins (comparing control and impact conditions). This energetically more constraining budget was not matched by an apparent increase in energy intake as there was no changes in the amount of time spent diving (foraging most likely to occur during the diving state, Figure 8a, Lusseau 2003a). The duration of traveling bouts significantly increased (by 37%) but the duration of resting bouts did not (Figure 8b). We can conclude from the budget and bout duration results that dolphins engaged less often in resting bouts during control conditions in 2002. The impact of boat disturbance on the dolphin budget did not change significantly from 2001 ( $d_{2001} = 0.056$ , 95% bootstrapped confidence interval: 0.0187 – 0.0991) to 2002 ( $d_{2002} = 0.044$ , 95% CI: 0.007 – 0.114).

As expected (Figure 5) this increase in bout duration of the predominant behavior (traveling) lead to a significant increase in the predictability of the Markov chain ( $H_{2001} = 0.78$ , 95% bootstrapped CI: 0.748-0.813;  $H_{2002} = 0.70$ , 95% bootstrapped CI: 0.654-0.741). This decrease in entropy was however not matched with a decrease in resilience ( $R_{2001} = 0.57$ , 95% bootstrapped CI: 0.464-0.687;  $R_{2002} = 0.62$ , 95% bootstrapped CI: 0.511-0.747).

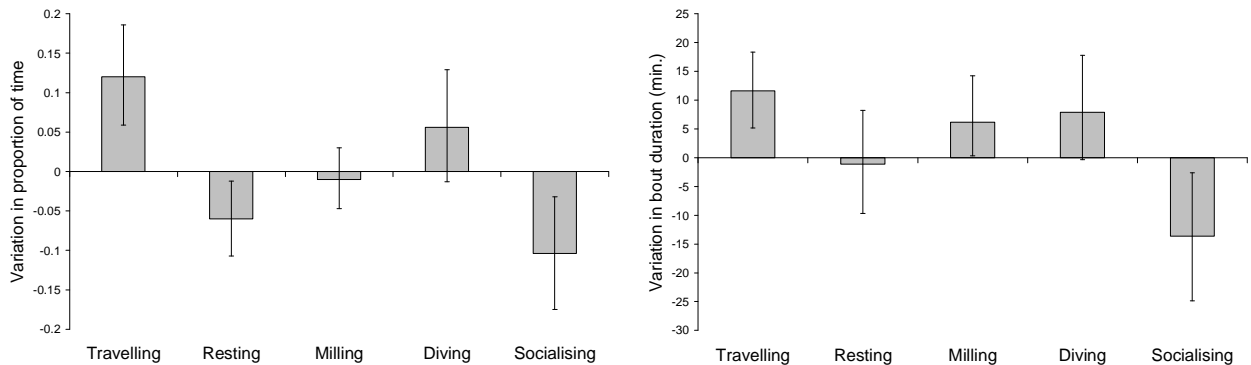


Figure 8: Variation in the Doubtful Sound behavioral system from 2001 to 2002 assessed from the differences in behavioral transitions during control conditions: (a) variation in behavioral budget (proportion of time spent in a given state) and (b) variation in bout duration. Error bars are 95% bootstrapped confidence intervals.

We would have expected to see a slowing down of the recovery rate of the Markov process (resilience) with the increase in boating activity (changing conditions) that occurred from 2001 to 2002 (van Nes and Scheffer 2007). Given that we saw both no change in this measure and significant changes in the behavioral budget leading towards a more predictable regime, we hypothesise that this represents a shift in the stable state of the behavioral system in Doubtful Sound (Figure 1). The 2002 behavioral regime was energetically more expensive which could explain the observed population-level changes.



## DISCUSSION

Changes in transition probabilities do not affect the resilience of the behavioral system directly. However, these changes can affect the resilience indirectly by affecting the predictability of the system. As the system becomes more predictable, often because of added constraints in the form of increased bout duration, it becomes less resilient. Indeed, our prospective perturbation analyses confirmed that bout duration is an important driver of behavioral resilience and entropy. This decrease in resilience does affect the impact disturbances will have on the system, showing that this resilience measure is a biologically relevant mean to assess the relative consequences of disturbances on behavioral systems. However, this measure is not absolute and cannot be used to compare directly the resilience of different systems. This could be for two reasons. First, while the stimulus was the same in all studies (boat interactions), the disturbance this stimulus would have created was different for each system. Boat interactions can disrupt the acoustic cues dolphins use for foraging and staying in contact (Erbe 2002). The behavior of boats during the interactions can also physically constrain the movement of these animals (Lusseau 2003b). Therefore, the disruptions incurred on the behavioral budget of the studied populations may be emerging from either disturbance mechanism or a combination of both depending on characteristics of the population ecology. Second, each system is indirectly influenced by a wide variety of extrinsic conditions. The magnitude of the effects of these conditions on the resilience of the system will vary between sites, as we show with the killer whale case study, and hence influence inter-site comparisons of resilience.

When compared within a site, resilience and entropy are useful measures to infer the conditions of a system. They can be used to draw general principles on the way to both maximize the resilience of behavioral systems and minimize the impact of disturbances. The northern resident killer whale example shows that at that site the effects of disturbance and the whale's prey local density are indirectly related. Such relationship should be further investigated to inform the management of human disturbances. Moreover, the understanding we gained in this study on the link between entropy and resilience provides useful guidelines for the application of the precautionary principle in disturbance management. Systems that have behavioral constraints are likely to be more impacted by disturbances because they are less plastic. Examples of such constraints may be spatial and/or temporal heterogeneity in prey availability or in access to conspecifics. The entropy measure is particularly sensitive to influences on the predominant behavioral state in the behavioral repertoire and hence disturbances to those states will have greater impacts on the behavioral budget overall. In Robson Bight, an increase in prey availability increases foraging bout duration constraints on the killer whale population. This may be because the schooling behavior of salmon changes as their abundance increases; salmon moving in fewer, larger schools. These behavioral constraints in turn influence the effect size of disturbance on the whale's behavior. There are some indications that large-scale climatic variations in the Pacific Ocean are a good predictor of salmon abundance for this location with a two-year lag (Mantua et al. 1997; Mote et al. 2003; Lusseau et al. 2004). Hence, it may be useful to make use of this relationship to predict the years during which the killer whale population will be less resilient to disturbance.

In Doubtful Sound, an increase in bout duration has led to a decrease in the plasticity of the dolphin behavior. The increase in time spent traveling may be the result of a decrease in prey density at foraging patches (Lusseau and Wing 2006). However, the lack of variation in diving behavior does not support an influence of food availability. In contrast, such increase can be

likened to the shift in avoidance tactics observed in Milford Sound at the same inter-interaction interval threshold (~70min., Lusseau 2004). Boat interactions only occur in 1/7<sup>th</sup> of the population home range for the bottlenose dolphin population visiting Milford Sound. In contrast, boat interactions are pervasive in Doubtful Sound occurring throughout the population's home range. An increase in time spent traveling may be perceived as a shift in avoidance tactics to maintain control on the impact of interaction disturbances by increasing spatial avoidance when the intensity of boat interactions increased.

Given the resilience estimate in Doubtful Sound, which is a measure of the system's recovery rate, the behavior of a dolphin school is 98% recovered after 110min and 93% recovered after 70min since the chain converges at least as fast as  $\exp(-t/\tau)$  (Hill et al. 2004). If the inter-interaction interval is 70min, a school of dolphins will have on average six interactions per day, while if it is 110min they will have four interactions per day. This means that at the end of the day in the 110min scenario the school will be 92% recovered ( $0.98^4$ ) and in the 70min scenario they will be 65% recovered ( $0.93^6$ ). Therefore, disturbances can have a cumulative effect on these systems in instances where the systems are not given sufficient time to recover after each disturbance. Extrinsic conditions and lack of sufficient recovery can therefore interact to result in shifts in stable state even when the resilience of the state would have been preventing such a shift. This could explain dolphins using larger-scale avoidance tactics to manage the cumulative effects of disturbance as we observed in Milford Sound (Lusseau 2004).

These effects are particularly compounded in group-living species that are not assorted by body size/metabolic regimes (Conradt and Roper 2000). In these instances, conflicts between survival and reproduction can lead to sub-optimal immediate behavioral solutions for some members of the groups (Heithaus and Dill 2002; Lusseau et al. 2003; Bejder 2005). These discrepancies can be exacerbated by disturbance management tactics, leading to behavioral regime shift that brings the population into a sub-optimal biological basin of attraction (such as observed in Doubtful Sound). This study provides a theoretical framework to investigate how such biological shifts can evolve from the way animals behaviorally manage disturbances to which they are exposed.

## ACKNOWLEDGEMENTS

DL was funded by Killam trusts. Data sampling was funded by a variety of agencies. The authors thank the many colleagues and volunteers that have participated to data collection. DL thanks the New Zealand Department of Conservation, Real Journeys Ltd., and the New Zealand Whale and Dolphin Trust for funding the Fiordland study. RW and DL thank the contractors and volunteers who collected the killer whale data, and Linda Phillips, BC Parks, for permission to use the data in these analyses. LB thanks the Western Australian Department of Conservation and Land Management and the Killam trusts. KAS thanks the One World Challenge (America's Cup 2002) and additionally supported by the Institute of Natural Resources (INR) Massey University, Whale and Dolphin Adoption Project (WADAP), Mercury Power New Zealand Ltd., Gulfland Marine Ltd, Gulf Harbour Marina and the Biscay Dolphin Research Programme (BDRP). EM thanks Massey University, the New Zealand Department of Conservation, the New Zealand Federation of Graduate Women, the Helping Hand Fund, the Whale and Dolphin Conservation Society, Forest and Bird, and Project Aware. DB, RW, and DL thank NMFS for funding the southern resident killer whale study. MAM and DL thank Hal Whitehead and Captain Mark's Whale and Seal Cruise. FC and PB thank the Institute of Marine Sciences, University of Dar es

Salaam, for their support and co-operation, the Menai Bay Marine Conservation Area for approving the research, and the Swedish International Development Cooperation Agency (Sida) for funding the Zanzibar study.

# **LITERATURE CITED**

- Albert, R., I. Albert, and G. L. Nakarado. 2004. Structural vulnerability of the North American power grid. *Physical Review E* 69:art. 025103.
- Albert, R., H. Jeong, and A. L. Barabasi. 2000. Error and attack tolerance of complex networks. *Nature* 406:378-382.
- Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49:227-267.
- Auger-Méthé, M., and H. Whitehead. 2007. The use of natural markings in studies of long-finned pilot whales (*Globicephala melas*). *Marine Mammal Science* 23:77-93.
- Bain, D. E., D. Lusseau, R. Williams, and J. C. Smith. submitted. Effects of vessels on activity states of southern resident killer whales (*Orcinus* sp.). *Endangered Species Research*.
- Baker, C. S., and L. M. Herman. 1989. Behavioral responses of summering humpback whales to vessel traffic: experimental and opportunistic observations, Pages 50. Anchorage, Alaska, National Park Service NPS-NR-TRS-89-01.
- Bejder, L. 2005. Linking short and long-term effects of nature-based tourism on cetaceans. PhD thesis, Dalhousie University, Halifax.
- Bejder, L., S. M. Dawson, and J. A. Harraway. 1999. Responses by Hector's dolphins to boats and swimmers in Porpoise Bay, New Zealand. *Marine Mammal Science* 15:738-750.
- Bejder, L., A. Samuels, H. Whitehead, N. Gales, J. Mann, R. C. Connor, M. R. Heithaus et al. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology* 20:1791-1798.
- Blumstein, D. T., and E. Fernández-Juricic. 2004. The emergence of conservation behavior. *Conservation Biology* 18:1175-1177.
- Caro, T. M. 2007. Behavior and conservation: a bridge too far? *Trends in Ecology & Evolution*.
- Caswell, H. 2000. Prospective and retrospective perturbation analyses: Their roles in conservation biology. *Ecology* 81:619-627.
- . 2001, *Matrix population models: construction, analysis, and interpretation*. Sunderland, Sinauer Associates, Inc.
- Christiansen, F., D. Lusseau, E. Stensland, and P. Berggren. submitted. The effects of tourist boats on the behaviour of Indo-Pacific bottlenose dolphins of the South coast of Zanzibar. *Animal Conservation*.

- Conradt, L., and T. J. Roper. 2000. Activity synchrony and social cohesion: a fission-fusion model. *Proceedings of the Royal Society of London Series B-Biological Sciences* 267:2213-2218.
- Corkeron, P. 2004. Fishery management and culling. *Science* 306:1891-1892.
- Corkeron, P. J. 1995. Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, Queensland: behaviour and responses to whale-watching vessels. *Canadian Journal of Zoology* 73:1290-1299.
- Currey, R. J. C., S. M. Dawson, and E. Slooten. 2008. New abundance estimates suggest Doubtful Sound bottlenose dolphins are declining. *Pacific Conservation Biology*.
- Currey, R. J. C., S. M. Dawson, E. Slooten, D. Lusseau, K. Schneider, P. Haase, O. J. Boisseau et al. submitted. Identifying the demographic source of a population decline: survival rates and risk assessment for bottlenose dolphins in Doubtful Sound. *Biological Conservation*.
- Daskalov, G. M., A. N. Grishin, S. Rodionov, and V. Mihneva. 2007. Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America* 104:10518-10523.
- Erbe, C. 2002. Underwater noise of whale-watching boats and potential effects on killer whales (*Orcinus orca*), based on an acoustic impact model. *Marine Mammal Science* 18:394-418.
- Folke, C., S. R. Carpenter, B. Walker, M. Scheffer, T. Elmqvist, L. Gunderson, and C. S. Holling. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annual Review of Ecology, Evolution, and Systematics* 35:557-581.
- Ford, J. K. B., and G. M. Ellis. 2006. Selective foraging by fish-eating killer whales in British Columbia. *Marine Ecology Progress Series* 316:185-199.
- Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm, and K. C. Balcomb. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76:1456-1471.
- Frank, K. T., B. Petrie, J. S. Choi, and W. C. Leggett. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science* 308:1621-1623.
- Granovetter, M. 1978. Threshold models of a collective behavior. *American Journal of Sociology* 83:1420-1443.
- Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography* 47:103-145.
- Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. *Ecology* 83:480-491.

- Higgins, P. A. T., M. D. Mastrandrea, and S. H. Schneider. 2002. Dynamics of climate and ecosystem coupling: abrupt changes and multiple equilibria. *Philosophical Transactions of the Royal Society B-Biological Sciences* 357:647-655.
- Hill, M. F., J. D. Witman, and H. Caswell. 2004. Markov chain analysis of succession in a rocky subtidal community. *American Naturalist* 164:E46-E61.
- Holling, C. S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1-23.
- Hooper, D. U., F. S. Chapin, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75:3-35.
- Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. *Science* 317:58-62.
- Ives, A. R., B. Dennis, K. L. Cottingham, and S. R. Carpenter. 2003. Estimating community stability and ecological interactions from time-series data. *Ecological Monographs* 73:301-330.
- Kinzig, A. P., P. Ryan, M. Etienne, H. Allison, T. Elmqvist, and B. Walker. 2006. Resilience and regime shifts: assessing cascading effects. *Ecology and Society* 11:20.
- Levin, S. A., S. Barrett, S. Aniyar, W. Baumol, C. Bliss, B. Bolin, P. Dasgupta et al. 1998. Resilience in natural and socioeconomic systems. *Environment and Development Economics* 3:221-262.
- Liu, J., T. Dietz, S. R. Carpenter, M. Alberti, C. Folke, E. Moran, A. N. Pell et al. 2007. Complexity of coupled human and natural systems. *Science* 317:1513-1516.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper et al. 2001. Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science* 294:804-808.
- Lusseau, D. 2003a. Effects of tour boats on the behavior of bottlenose dolphins: Using Markov chains to model anthropogenic impacts. *Conservation Biology* 17:1785-1793.
- . 2003b. Male and female bottlenose dolphins *Tursiops* sp. have different strategies to avoid interactions with tour boats in Doubtful Sound, New Zealand. *Marine Ecology-Progress Series* 257:267-274.
- . 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. *Ecology and Society* 9:2.
- . 2005a. The residency pattern of bottlenose dolphins (*Tursiops* spp.) in Milford Sound, New Zealand, is related to boat traffic. *Marine Ecology Progress Series* 295:265-272.

- . 2005b. The state of the scenic cruise industry in Doubtful Sound in relation to a key natural resource: bottlenose dolphins, Pages 246-262 in S. Boyd, ed. Nature-based Tourism in Peripheral Areas: Development or Disaster? London, Channelview Publications.
- Lusseau, D., S. M. Lusseau, L. Bejder, and R. Williams. 2006a. An individual-based model to infer the impact of whalewatching on cetacean population dynamics. St Kitts, International Whaling Commission SC/58/WW7.
- Lusseau, D., K. Schneider, O. J. Boisseau, P. Haase, E. Slooten, and S. M. Dawson. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations - Can geographic isolation explain this unique trait? Behavioral Ecology and Sociobiology 54:396-405.
- Lusseau, D., E. Slooten, and R. J. C. Currey. 2006b. Unsustainable dolphin-watching tourism in Fiordland, New Zealand. Tourism in Marine Environments 3:173-178.
- Lusseau, D., R. J. Williams, B. Wilson, K. Grellier, T. R. Barton, P. S. Hammond, and P. M. Thompson. 2004. Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. Ecology Letters 7:1068-1076.
- Lusseau, S. M., and S. R. Wing. 2006. Importance of local production versus pelagic subsidies in the diet of an isolated population of bottlenose dolphins *Tursiops* sp. Marine Ecology Progress Series 321:283-293.
- Mangel, M., and C. W. Clark. 1986. Towards a unified foraging theory. Ecology 67:1127-1138.
- Mann, J. 2000. Unraveling the dynamics of social life: long-term studies and observational methods, Pages 45-64 in H. Whitehead, ed. Cetacean Societies. London, University of Chicago Press.
- Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069-1079.
- Marcos, S. H. C., S. R. Lopes, and R. L. Viana. 2003. Boundary crises, fractal basin boundaries, and electric power collapses. Chaos, Solitons & Fractals 15:417-424.
- Mote, P. W., E. Parson, A. F. Hamlet, W. S. Keeton, D. Lettenmaier, N. Mantua, E. L. Miles et al. 2003. Preparing for climatic change: The water, salmon, and forests of the Pacific Northwest. Climatic Change 61:45-88.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining Biodiversity Can Alter the Performance of Ecosystems. Nature 368:734-737.
- Neubert, M. G., and H. Caswell. 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology 78:653-665.

- Nolfi, S. 2004. Behaviour as a complex adaptive system: on the role of self-organization in the development of individual and collective behaviour. *Complexus* 2:195-203.
- Österblom, H., S. Hansson, U. Larsson, O. Hjerne, F. Wulff, R. Elmgren, and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10:in press.
- Pimm, S. L. 1984. The complexity and stability of ecosystems. *Nature* 307:321-326.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* 18:648-656.
- Scheffer, M., S. R. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. *Nature* 413:591-596.
- Simpson, S. J., A. R. McCaffery, and B. F. Hägele. 1999. A behavioural analysis of phase change in the desert locust. *Biological Reviews of the Cambridge Philosophical Society* 74:461-480.
- Stensland, E., and P. Berggren. 2007. Behavioural changes of nursing female Indo-Pacific bottlenose dolphins in response to boat-based tourism. *Marine Ecology Progress Series* 332.
- Stockin, K., D. Lusseau, V. Binedell, and M. Orams. 2008. Tourism affects the behavioural budget of common dolphins in the Hauraki Gulf, New Zealand. *Marine Ecology Progress Series*:in press.
- Sumpter, D. J. T. 2006. The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B-Biological Sciences* 361:5-22.
- Tilman, D. 1999. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* 80:1455-1474.
- Tilman, D., and J. A. Downing. 1994. Biodiversity and Stability in Grasslands. *Nature* 367:363-365.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379:718-720.
- van Nes, E. H., and M. Scheffer. 2007. Slow recovery from perturbations as a generic indicator of a nearby catastrophic shift. *American Naturalist* 169.
- Walker, B., and J. A. Meyers. 2004. Thresholds in ecological and socio-ecological systems: a developing database. *Ecology and Society* 9:art. 3.
- Williams, R., D. Lusseau, and P. S. Hammond. 2006. Estimating relative energetic costs of human disturbance to killer whales (*Orcinus orca*). *Biological Conservation* 133:301-311.

- Wootton, J. T. 2004. Markov chain models predict the consequences of experimental extinctions. *Ecology Letters* 7:653-660.
- Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. C. Jackson et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314:787-790.
- Yodzis, P. 2001. Must top predators be culled for the sake of fisheries. *Trends in Ecology & Evolution* 16:78-84.