The significance of non-human culture for the conservation of cetaceans and other vertebrates

Submitted by Philippa Louise Brakes, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Biological Sciences, 1st June 2022.

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

Signature: P. Brakes

ABSTRACT

The central proposition of this thesis is that non-human cultural transmission can interface with population dynamics to generate patterns and processes which can cause population level effects and thus inform conservation science, policy and practice. Culture can provide insights for both how conservation is conducted and what managers should be aiming to conserve (the ‘unit to conserve’). In this research, available evidence was gathered and a wide collaboration with experts in this field was established. This enabled the development of a conceptual framework to help guide researchers and practitioners towards ‘future-proofing’ populations by conserving both cultural variation and the capacity for innovation and social learning to maximize the resilience of vulnerable populations.

To illuminate some of the underlying processes, theoretical models were then constructed to investigate the dual dynamics of cultural transmission and population dynamics. Here it is shown that social learning can generate transient dynamics which may inform the timing of some conservation interventions. It is also demonstrated that under certain parameter regimes social learning can bring about cultural bistability, cultural hysteresis, or cultural exclusion. Further, it is shown how in a density dependent system, cultural transmission could generate chaos. These findings are considered within the context of conservation and policy. It is concluded that given the complexity of the coupled processes of population dynamics and cultural transmission - and the practical challenges associated with collecting fine scale data on how culture may influence vital rates - that conservation policy makers and practitioners should aim to conserve cultural diversity, within and between populations, as an essential source of adaptive behaviour.

ACKNOWLEDGEMENTS

This work would not have taken flight if it wasn’t for the hearts, minds and shoulders of many. I am indebted to the many wise field researchers, theoreticians, conservation biologists, policy makers and NGOs that I’ve had the good fortune to collaborate with during this research. There are simply too many to name individually, but my sincerest thanks to the members of the CMS Expert Group on Animal Culture. In particular, thanks to Heidrun Frisch-Nwakanma, Melanie Virtue, Giuseppe Notarbartolo di Sciara, Fernado Spina, Mark Simmonds, Christian Rutz, Andy Whiten, Ellen Garland and Emma Carroll.

Thanks also go to friends and colleagues at WDC, without whom none of this work would have come to fruition and in particular the vision of Chris Butler-Stroud, Ali Wood, Nicola Hodgins, Sarah Dolman, Erich Hoyt, Vanessa Tossenberger and Mike Bossley.

And of course, a big debt of thanks to my supervisors, Sasha Dall and Stuart Townley for your wisdom, patience and good humour, in what have been some challenging pandemic years.

My thanks also go to all those who have spent tireless hours in the field gathering data on non-human culture, but especially to Luke Rendell and Hal Whitehead, for generally being so gracious and inspiring.

Last, but most importantly, to my family. Thank you for always making me chuckle and being kind. Thanks especially are in memory of Mum, for all the wisdom of a matriarch that she encapsulated.

But most of all, thanks to the Captain. This thesis is dedicated to you.

CONTENTS

ABSTRACT

Acknowledgements……………………………………………………….3

Contents………………………………………………………………….4

List of Tables…………………………………………………………….8

List of Figures…………………………………………………………...9

Author Declaration……………………………………………………….11

CHAPTER 1

General Introduction…………………………………………………….12

Sociality, conservation and marine mammals………………………..13

From individuals to populations………………………………………..14

Social learning, culture and population dynamics……………………15

Social learning and vital rates…………………………………………17

Resilience, density dependence and other demographic processes………………………………………………………………….18

Aims and structure of the thesis………………………………………20

CHAPTER 2

Conservation and culture: science, policy and practice………………23

Animal cultures matter for conservation………………………………..25

  Consequences of social knowledge…………………………….26

  Cetaceans, and beyond………………………………………….28

  Moving forward……………………………………………………31

Supplementary materials……………………………………….32

CHAPTER 3

A conceptual framework for integrating animal culture into conservation……………………………………………………………33

A deepening understanding of animal culture suggests lessons for conservation……………………………………………………………35

Abstract…………………………………………………………36

Introduction……………………………………………………. 37

Social learning and culture……………………………………...38

Conservation through the lens of social learning……………..44

a) Influence of social learning on survival…………….45
b) Influence of social learning on reproduction………46
c) Influence of social learning and culture on units to conserve……………………………………………47

Ecological studies through the lens of social learning and animal culture

a) Foraging……………………………………………50
b) Migration…………………………………………...51
c) Communication……………………………………52

Conceptual framework and future directions…………………55

Acknowledgements……………………………………………...57

CHAPTER 4

Content base social learning and population dynamics……………..58

Abstract………………………………………………………………...58

Introduction……………………………………………………………….58

The model……………………………………………………………...60

Directly-biased transmission…………………………………...62

Model exploration for content-biased social learning………………..66

Perturbation of vital rates………………………………………….....70

Exploring dynamics for other species PPMs………………………...72

Exploring optimal thresholds for population growth………………...75

Discussion……………………………………………………………….84

Conclusion………………………………………………………………87

CHAPTER 5

Abstract………………………………………………………………….89

Introduction……………………………………………………………..90

Transmission……………………………………………………...…92

Conservation options…………………………………………………..94

Option 1 – conserve the naive unit…………………………..96

Option 2 – manipulate transmission………………………..100

Transient dynamics…………………………….….103

Option 3 – maintain cultural diversity……………………....109

Conclusion………………………………………………………….…111

CHAPTER 6

Cultural bistability, exclusion and chaos in a

scalar population……………………………………………113

From risky foraging strategies to alternative facts: cultural transmission and population dynamics…………………………………………..114

Abstract…………………………………………………………114

Introduction……………………………………………………..115

Cultural bistability – Cultural exclusion……………………118

Cultural bistability – Cultural hysteresis…………………..122

Cultural transmission as a route out of chaos……………123

Discussion…………………………………………………129

CHAPTER 7

General Discussion and Future Directions………………………136

Overview……………………………………………………..136

Modelling insights…………………………………………...138

Implications for conservation policy and practice………..141

Received wisdom and other considerations……………..144

Future directions……………………………………….………145

Conclusions………………………………………….…………147

APPENDICIES

Appendix 1.1 Extracts from: Marine mammal behaviour: a review of conservation implications………………………………………149

Appendix 4.1 Vital rate perturbation projections for 2-stage mammalian and avian PPMs with social learning…………………………….....163

Appendix 4.2 MATLAB and R code……………………………167

Appendix 6.1 Reduction to a 1-D map…………………………...173

REFERENCES…………………………………………………………..174

List of Tables

Chapter 4

Table 1 – Social learning pathways in coupled PPM model

Table 2 – Two stage PPMs for declining bird and mammal populations

Chapter 5

Table 1 – Conservation options for culturally heterogenous populations

List of Figures

Chapter 2

Figure 1 – Sperm whale acoustic clans in eastern tropical Pacific

Figure 2 – African elephant matriarchs as informed elders

Chapter 3

Figure 1 – Defining conservation units

Figure 2 – Examples linking social learning across behavioural contexts

Figure 3 – Conceptual framework

Chapter 4

Figure 1 – Vulnerability of cultural foraging strategies

Figure 2 – Life-cycle graph for coupled units and PPMs

Figure 3 – Parameter space exploration for content biased transmission

Figure 4 – Schematic for population projection with transmission

Figure 5 – Projection for two initial cultural units

Figure 6 – Simulations with randomly selected initial population structures

Figure 7 – Projections for perturbed declining sperm whale population

Figure 8 – Projections for perturbed declining mammal and avian populations

Figure 9 – Parameter space exploration for horizontal transmission between adults (sperm whale)

Figure 10 – Parameter space exploration for non-vertical social learning juveniles (sperm whale)

Figure 11 – Parameter space exploration for horizontal transmission between adults (other species)

Chapter 5

Figure 1 – Barn swallow perturbation projections for varying transmission rates

Figure 2 – Parameter space exploration with juvenile survival perturbed

Figure 3 – Parameter space exploration with adults survival perturbed

Figure 4 – Parameter space exploration with adult fecundity perturbed

Figure 5 – Parameter space exploration juvenile survival other species

Figure 6 – Transient envelop analysis A

Figure 7 – Transient envelop analysis B

Figure 8 – Transient envelop analysis C

Figure 9 – Transient envelope analysis D

Chapter 6

Figure 1 – Schema for scalar map model

Figure 2 – Depiction of stable and unstable equilibrium properties

Figure 3 – Depiction of cultural hysteresis

Figure 4 – Transition into and our of chaos through cultural transmission

Figure 5 – Steady state equilibrium plots for chaos

Figure 6 – Inter-generational population density

AUTHOR DECLARATION

I had no involvement with collection of any of the field data used in this thesis. The sources of data, including via the compiled PPM database COMADRE, are all recognised and cited.

My supervisors commented on earlier drafts of this work and the additional contributions of all co-authors are clearly stated in the manuscripts reproduced here.

With these exceptions, I declare that the work contain in this thesis is my own and has not been submitted for any other degree or award.

“*The more closely one looks at individual organisms, the more ways in which they appear to differ. The problem of heterogeneity is to figure out how those differences affect population dynamics*” (Caswell et al., 2018).

CHAPTER 1

GENERAL INTRODUCTION

Conserving biodiversity, by maintaining adaptive potential through genetic and phenotypic diversity, has long been the mainstay of conservation efforts (Eizaguirre and Baltazar-Soares, 2014). A central goal of conservation is the long-term persistence of viable populations, so that species and populations can respond to environmental pressures. The International Union for the Conservation of Nature (IUCN) frames it’s mission as ‘to influence, encourage and assist societies throughout the world to conserve the integrity and diversity of nature and to ensure that any use of natural resources is equitable and ecologically sustainable’[1]. Here, I argue that the ‘integrity’ of nature is classically interpreted as genetic integrity and conservation efforts are often targeted towards maintaining species, populations and habitats. Some of the key metrics for success in this field are population distribution and abundance, as well as genetic diversity and habitat restoration (IUCN, 2012). This thesis challenges the modern conservation rubric, where biodiversity is primarily defined through genetic diversity and geographic distribution and explores whether ‘within species diversity’[2] should include another important aspect of population heterogeneity; non-human culture.

---

[1] https://www.iucn.org/theme/global-policy/about

[2] Convention on Biological Diversity, Article 2: "Biological diversity" means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.

This chapter outlines the development of a process to explore the available evidence on non-human culture as it relates to conservation activities. The collaborations that followed helped identify gaps in knowledge, from which a conceptual framework was synthesised, which also informed the theoretical research presented in this thesis.

Sociality, conservation and marine mammals

Given limitations to the resources available for conservation and time pressures for managers, in ever changing environments, behavioural ecology has long been argued to be important for conservation efforts (Anthony and Blumstein, 2000; Berger-Tal et al., 2011; Caro and Durant, 1995; Greggor et al., 2016). A systematic survey of published research examined the different axes of behaviour and conservation and found a great deal of variation in the ways in which behaviour has been used to assist conservation efforts (Berger-Tal et al., 2016). This review recommended that researchers should focus on examining those interactions between conservation and behaviour that show promise, specifically by translating theory into testable predictions (Berger-Tal et al., 2016).

Anthropogenic threats to marine mammals have been well documented (Avila et al., 2018; Lascelles et al., 2014; Nelms et al., 2021). These threats can be synergistic, for example, for a population of eastern north Pacific long-beaked common dolphins (*Delphinus delphis capensis*), modelling predicts that cumulative effects from some sub-lethal stressors may exceed the effects of even a significant lethal stressor such as bycatch (Ashe et al., 2021). In addition, the cumulative effects of anthropogenic stressors, including climate change, may be particularly acute in small populations (e.g. beluga (*Dephinapterus leucas*) (Lesage, 2021).

Understanding how such threats interface with different aspects of behaviour and sociality, adds another layer of complexity. Examining two stressors, historical commercial whaling and climate change for some populations of baleen whales using a climate-biological coupled model, it has been argued that predicted declines could be reduced where there is plasticity in range size and migration (Tulloch et al., 2019).

But, accumulating sufficiently high-resolution data to quantify the extent and qualify the nature of individual variation and heterogeneity within and among populations and social groups remains a challenge, particularly for species on the brink of extinction, or at low population densities. While many published articles note that it is necessary to look beyond genetic processes when it comes to conservation management of socially complex species (for example in bottlenose dolphins (*Tursiops aduncus*) (Chabanne et al., 2021; Frère et al., 2010), and sperm whales (*Physeter macrocephalus*) (Pace et al., 2018)), the outstanding question remains: which aspect of sociality may be the most salient for informing conservation efforts and are there underlying processes that could be broadly applied?

To address this question, I began by reviewing evidence that social structure, social information use, culture and behavioural syndromes may have implications for the conservation of marine mammals (Brakes and Dall, 2016). Sutherland (1998), suggested 20 areas in which research on behavioural ecology could make a significant contribution to conservation efforts. Given the intervening decades, I reviewed and expanded Sutherland's list and applied this to the conservation of marine mammals, to establish which aspects of their behaviour and sociality to focus on in relation to conservation (Brakes and Dall, 2016). Having reviewed the available evidence, and given the breadth of this field, here I focus on one key issue for which there is emergent evidence that has potential for improving conservation: the role of social learning and non-human cultures. I summarize some of the key points as they relate to social learning and culture from that review in the extracts in Appendix 1.1.

From individuals to populations

Social networks provide the substrate across which social learning can be transmitted (Whitehead and Lusseau, 2012). While new methods for defining association criteria are evolving (Tavares et al., 2022), research on the position of individuals within social networks (i.e. the number or the strength of their social connections), can influence how likely a social group is to fragment when a key individual is removed (e.g., in killer whale (*Orcinus orca*) populations (Williams and Lusseau, 2006)). Similarly, how well connected an individual is can have implications for the condition of their wider social group following translocation (for e.g. in translocated African elephants (*Loxodonta africana*)). In addition, the reproductive success of male bottlenose dolphins (*Tursiops aduncus*) has also been linked to their male-male social bonds and social integration (Gerber et al., 2022). Given the multi-faceted manner in which social structure links individuals, social groups and populations (Kulahci and Quinn, 2019), it has been argued that population social structure is a ‘fundamental biological dimension that affects a wide range of ecological and evolutionary processes’ (Kurvers et al., 2014).

Croft *et al.* argue that “improving our ability to scale up from individuals to the population by establishing why certain patterns of association develop and how inter-individual association patterns affect population-level structure will revolutionize our understanding of the function, evolution, and implications of social organization” (Croft et al., 2008).

Network based diffusion analysis (NBDA) provides a powerful tool for analyzing how social learning is transmitted across a social network (Allen et al., 2013; Franz and Nunn, 2009). But, as yet, there is no methodology for analyzing how social learning influences the processes of population dynamics. Caswell *et al*.’s ‘problem of heterogeneity’ (Caswell et al., 2018), can be considered within this context and is a key motivation for the theoretical work in this thesis; specifically in relation how social learning and non-human culture generates heterogeneity that interfaces with population dynamics.

Social learning, culture and population dynamics

Social learning has been defined as any learning process that is facilitated by the observation of, or interaction with, another animal or its products (Heyes, 1994; Hoppitt and Laland, 2008; Whitehead and Rendell, 2015). It involves the transmission of information from one individual (the model) to another (the observer), which results in the observer learning the behaviour, (for details of the sensory channels and mechanism of social learning see Chapter 3 and (Kendal et al., 2018)). Social learning can be regarded as a cheap way of obtaining valuable information, given the constraints of individual learning (Rendell et al., 2011). It is the process that can lead to local cultural variants of behaviour, that can persist over time, sometimes over generations as non-human culture. In this work I use a broad definition of non-human culture (hereafter, culture), to allow for the identification of behaviours of relevance to conservation. Culture is defined here as: information or behaviours shared within a group and acquired from conspecifics through some form of social learning (Fragaszy and Perry, 2003; Whitehead and Rendell, 2015).

There are many ways in which the processes of social learning and non-human culture can interface with conservation efforts. For example, where it results in fine scale social structure (R. Esteban et al., 2016; Kurvers et al., 2014; Williams and Lusseau, 2006), which can influence social dynamics and potentially vital rates (Wild et al., 2019b). These influences may be 'synergistic or opposing and warrant a more sophisticated approach towards managing social species, particularly those which exhibit social transmission' (Brakes and Dall, 2016). For further examples and a detailed exploration of these processes see Chapter 3.

Quantifying how social learning and culture influence the dynamics of social groups and populations may yield important insights for conservation. Examining how these social processes influence vital rates (mortality, fertility, dispersal, age structure and sex ratio) and population dynamics may be key for management. Collectively, these vital rates determine population abundance and are therefore salient to conservation efforts. Social learning can, *inter alia*, increase the probability of locating food, accessing breeding patches, avoiding predators, or developing specialised foraging strategies (Brakes et al., 2021). This may improve individual fitness and - when such benefits are conferred to sufficient individuals across a social group - can have implications for vital rates within social units (Wild et al., 2019b).

An important consideration is the threshold for significant penetration of a socially learned behaviour within a social group or population for demographic effects to be detected. Such thresholds may be both context and behaviour specific. From a conservation perspective, the behavioural domain of a socially learned behaviour may also be relevant e.g., transmission of play behaviour is likely less (immediately) significant for survival or reproduction than transmission of a novel foraging strategy (although it is unknown whether certain play behaviours may act as a distinguishing feature between social groups - an ‘ethnic marker’ - or could develop a demographically significant role (Bossley et al., 2018)). Distilling how the effects of social learning scale up to have population level effects can be challenging. In this thesis I focus on exploring how one particular social learning strategy, direct-bias (after Boyd and Richerson, 1985), also known as content bias (Kendal et al., 2018), influences survival and reproduction, both within cultural units and across a wider population (see Chapters 4 and 5).

Social learning and vital rates

The value to reproduction of sharing accumulated knowledge is demonstrated in species such as killer whales and short-finned pilot whales (*Globicephala macrorhynchus*), where females exhibit post-reproductive lifespan (PRLS) - a very rare life-history stage in vertebrates. Complete reproductive cessation during an adult life stage seems counter-intuitive to propagation, and although multiple interacting mechanisms may result in PRLS (Croft et al., 2015), it is thought to have evolved in these species primarily as the result of benefits conferred from grandmothers transmitting social information to their descendants (Croft et al., 2017; Johnstone and Cant, 2010).

The transmission of social information may also have more subtle effects on reproduction than simply access to resources, or information on risk. Western Australian bottlenose dolphins which use tools (sponges) to forage (Sargeant and Mann, 2009), transmit this behaviour vertically from females to their calves. But ‘sponging’ also serves an affiliative grouping function, where ‘spongers’ appear to be more ‘cliquish’ and prefer to associate with other ‘spongers’ (Mann et al., 2012). It has been posited that this affiliative behaviour may have implications for how (and how rapidly) novel behaviours spread within and between social groups. It has also been suggested that social relationships between females may confer reproductive prowess through a type of homophily in which females with calves associate with other females with calves and that genetic and social effects interact to influence individual fitness (Frère et al., 2010). Similarly, social factors, including individual associations were found to influence reproductive success in bottlenose dolphins in the North Sea (Robinson et al., 2017), demonstrating that social learning can be intertwined with other aspects of sociality.

Sperm whales (*Physeter macrocephalus*), forage principally in the mesopelagic ocean and have multilevel social structure (Whitehead et al., 2012) with female social units forming larger scale dialect groups distinguished by unique clicking patterns or codas, termed vocal clans (Whitehead, 2003). Codas are socially learnt and transmitted along maternal lines, together with other aspects of behaviour, such as movement patterns, with apparent consequences for foraging success (Gero et al., 2016; Rendell et al., 2012; Rendell and Whitehead, 2003). These dialects therefore provide a cultural marker for each clan. Foraging variation amongst clans can lead these sub-populations to respond differently to environmental change. Members of two sperm whale clans studied off the Galapagos Islands showed differential responses to the El Niño oceanographic phenomenon. During the more frequent cool years, the 'Regular' clan showed higher feeding success than the 'Plus-one' clan. In contrast, during years with warmer El Niño conditions, the 'Plus-one' clan had more feeding success (Whitehead and Rendell, 2004). There is also evidence for differences in reproductive success between clans, which is thought to be associated with these socially learned foraging strategies (Marcoux et al., 2007; Whitehead and Rendell, 2015). Difference in surface-time coordination and the quality of social relationships, likely resulting from clan segregation, may influence alloparental care giving, potentially scaling up to different calf survival rates between clans (Cantor and Whitehead, 2015). While the influence of social learning on reproductive success is apparent, it is not yet clear how environmental changes influencing feeding success impact clan survival; such information is essential for understanding population dynamics within clans and across the species. For further examples of how social learning may influence vital rates across a range of taxa, see Chapter 3[3].

Resilience, density dependence and other demographic processes

There are many factors that can influence how social learning is transmitted across and between populations. Transmission of social learning through a population may be facilitated or constrained by: the type of social structure (Whitehead and Lusseau, 2012); the degree of conformity within the population (Aplin et al., 2015); which individual is exhibiting the behaviour (model-based

---

[3] See also and the following extensive supplementary material from Brakes et al., 2021: https://royalsocietypublishing.org/doi/suppl/10.1098/rspb.2020.2718

bias) (Kulahci and Quinn, 2019); frequency dependent bias; and content bias (Whitehead and Rendell, 2015). Population stability may also be an important factor for social transmission (Kurvers et al., 2014).

Density dependent processes may also influence the propagation of socially learned and other sources of social information. The Allee effect has been described as a ‘positive relationship between any component of individual fitness and either numbers or density of conspecifics’(Stephens et al., 1999). Effective transfer of information through a network - for example, finding food - can become compromised at low population densities. The Allee effect can reduce functional effectiveness of information transfer between individuals at low density (Jackson et al., 2008; Somers et al., 2008), (see Chapter 3).

For species that learn socially the potential for rapid spread of innovations, inhibition of adaptive behaviour through conformism and even the spread of maladaptive behaviour, can provide within generation opportunities, or limitations (Whitehead, 2010). These complex facets are not well accounted for in modern conservation policy and practice (see Chapter 2). Considering the way in which social learning can influence resilience in populations may provide valuable insights. It has been proposed that resilience in biological systems should be considered as having two key features: resistance and recovery (bivariate measurement and analysis of change in state and return time) (Hodgson et al., 2015). Resistance describes the instantaneous impact of external disturbance. Whereas, recovery involves the internal processes which return a system back toward equilibrium (Hodgson et al., 2015). Applying this approach to assess resilience of species that learn socially, it can be argued that social learning has a role in the recovery aspect of resilience, by providing opportunities for adaptive behaviours to spread in response to environmental change (e.g., Ansmann et al., 2012); or conversely, preventing the spread of adaptive behaviour as the result of socially learned conformity, potentially hindering recovery (Whitehead, 2010). Social learning may also have a subtle, but complex role in resistance to disturbance as the result of knowledgeable elders acting as repositories of social knowledge, e.g., in killer whales and African elephants (Croft et al., 2017; McComb et al., 2001). The interplay between these two components of resilience, and features such as precariousness (i.e., how far a population is from a tipping point, past which it could not recover (Hodgson et al., 2016)) provide fertile ground for exploring the multifaceted influence of social learning on group and population dynamics (see Chapter 6).

It has been argued that while efforts to connect conservation biology with behavioural ecology have been discussed for many years, theoretical advances in this area have been slower to catch up (Caro, 2007). The objective of the theoretical explorations in this thesis (Chapters 4, 5 and 6) are to unravel the interface between cultural transmission and population dynamics, specifically as they relate to conservation activities, thus connecting conservation biology and behavioural ecology through theory.

Aims and structure of thesis

First, I describe some of the patterns and processes of non-human culture that may be relevant to conservation. Then I develop theoretical models to explore insights that may be gained from considering aspects of social learning and non-human culture which may influence population dynamics and thus could increase the efficacy and efficiency of conservation.

To begin this research, I organised a joint workshop with the Convention on the Conservation of Migratory Species of Wild Animals (CMS) and Whale and Dolphin Conservation (WDC), to bring together international experts to explore these aspects of sociality and conservation; first for cetaceans (2014) and later for wider vertebrate taxa (2018). The workshops reviewed the available evidence, with the objective of informing how these data may be relevant to conservation management. The 2014 workshop initiated a stream of work under CMS (described in Chapter 2) and the chapters that follow were informed by discussion during these workshops.

This research highlighted some key gaps in theoretical understanding of the relationship between social learning and population level processes of relevance to conservation efforts. Examining the available evidence, for a wider range of vertebrate taxa beyond marine mammals, it became evident that the research on social learning and non-human culture was primarily empirical field or lab-based studies. To further develop understanding, the next stage was to synthesis in detail the available evidence to elucidate some of the underlying processes in play. This meta-research (Chapter 3) provided helpful guidance on the types of processes and scenarios that may be important and enabled the development of a conceptual framework for conservation policy makers and practitioners. However, there remained a need to increase the predictive power of conservation models, through better understanding of the interface between cultural processes, population dynamics and conservation. Therefore, to strengthen the theoretical foundations of the field (through verbal and mathematical theory), I next focused on developing models that would increase understanding of the dual dynamics of cultural transmission and population dynamics (Chapters 4, 5 and 6). The aim of these models was to improve understanding of the dual dynamics of cultural transmission and population dynamics, to elucidate how social learning can provide either increased resilience or create vulnerabilities.

To ground the theoretical research, I begin in Chapter 2 by exploring the interface between social learning and non-human culture for current conservation policy and practice, by considering non-human culture within the context of existing international conservation policy fora. This is then followed by the development of a framework for incorporating these aspects of heterogeneity into research, policy and practice (Chapter 3). Diving deeper into the underlying causes of the effects observed, I then take a process-based approach and explore the interaction between population dynamics and cultural transmission (Chapter 4) and consider the implications for conservation (Chapter 5), including the possibility that maladaptive culture can spread within social groups (Chapter 6). Finally, I consolidate these findings, consider remaining gaps in knowledge and suggest further areas for future research (Chapter 7).

The central proposition of this thesis is that non-human culture can interface with population dynamics to generate patterns and processes which can cause population level effects and thus inform conservation science, policy and practice:

"*The population level processes that are important for conservation are functions of the aggregated behaviour of individuals. Thus, understanding how individuals act and react, can help us better understand them as components in larger complex systems, as collective elements of societies, and thereby better* *predict collective outcomes at higher levels of system complexity*" (Brakes and Rendell, 2022).

In some of the following chapters of this thesis the term 'we' is used as per publication standard and for consistency, this by no means that this thesis is not my own work.

CHAPTER 2

Conservation and culture: science, policy and practice

Despite the burgeoning evidence for the complexity of animals' social lives and in particular social learning and animal culture (Whiten, 2017a), across a range of taxa and behavioural domains (Aplin et al., 2013; Hobaiter et al., 2014; Mueller et al., 2013; Riebel et al., 2015), there has been scant exploration of how the emergent understanding of these complex systems could be in incorporated into management advice through domestic and international conservation fora. To address the disconnect between emergent science and conservation policy, two workshops on animal culture and social complexity were held under the auspices of the Convention on the Conservation of Migratory Species of Wild Animal (CMS). The objective of these workshops was to review the available evidence and distil common themes, so that new recommendations in this field could be offered. Key experts in the field were identified and the workshops were based on a facilitation framework, in which participants were sub-divided into relevant issue or taxon based sub-groups, presented with focus questions and encouraged to collaborate on two key tasks: firstly, identifying evidence for how animal culture interfaces with conservation; and secondly, developing a conceptual framework for integrating animal culture into conservation management.

The first workshop (CMS, 2014), focused on gathering evidence from cetaceans and evaluating the conservation implications. The second workshop (CMS, 2018), spread the net wider to consider evidence and implications from a broader range of vertebrate taxa, including other mammals, birds, fishes and reptiles (see supplementary material in Brakes et al., (2019) for links to the workshop reports and the resultant CMS resolutions).

Given the developing biodiversity crisis (Casetta et al., 2019; Singh, 2002) and the limited financial resources available for conservation activities, the primary objective of these workshops was to build competency within this multilateral environmental agreement for evaluating how the processes of social learning and emergent animal culture could be utilised to augment or improve the effectiveness and the efficiency of the conservation of animals that learn socially. This chapter argues that social learning and animal culture can be important for *how* conservation is conducted, in terms of rapid assessment techniques, reintroductions or education and *how* specific biological processes may influence conservation outcomes. But it is also argued here that in some circumstances animal culture can be important for defining *what* to conserve, by accounting for cultural segregation when evaluating units to conserve.

Following the 2018 workshop a Policy Forum article for the journal *Science* was developed to highlight the interface between social learning and animal culture for current conservation policy and practice and discuss this emergent field within the context of existing international conservation policy fora and legal frameworks. This article was published in 2019 and is reproduced in its entirety here, with supplementary material provided online. The next chapter (Chapter 3), then demonstrates how some of these insights were synthesized to provide a conceptual framework for conservation scientists, policy-makers and practitioners.

Animal cultures matter for conservation

Understanding the rich social lives of animals benefits international conservation efforts

Philippa Brakes, Sasha R. X. Dall, Lucy M. Aplin, Stuart Bearhop, Emma L. Carroll, Paolo Ciucci, Vicki Fishlock, John K. B. Ford, Ellen C. Garland, Sally A. Keith, Peter K. McGregor, Sarah L. Mesnick, Michael J. Noad, Giuseppe Notarbartolo di Sciara, Martha M. Robbins, Mark P. Simmonds, Fernando Spina, Alex Thornton, Paul R. Wade, Martin J. Whiting, James Williams, Luke Rendell, Hal Whitehead, Andrew Whiten, Christian Rutz

Author affiliations are listed in the supplementary materials.

Science, 8 March 2019, Volume 363, Issue 6431, [DOI: 10.1126/science.aaw3557]

*Corresponding author. E-mail: p.brakes@exeter.ac.uk; christian.rutz@st-andrews.ac.uk

An African elephant matriarch (center) can lead, and shape the success of, a family for three decades or more. [Photo: V. Fishlock, Amboseli Trust for Elephants]

Animal culture, defined as “information or behavior—shared within a community—which is acquired from conspecifics through some form of social learning” (Whitehead and Rendell, 2015), can have important consequences for the survival and reproduction of individuals, social groups, and potentially, entire populations (Whitehead, 2010; Whitehead and Rendell, 2015). Yet, until recently, conservation strategies and policies have focused primarily on broad demographic responses and the preservation of genetically defined, evolutionarily significant units. A burgeoning body of evidence on cultural transmission and other aspects of sociality (Whiten, 2017a) is now affording critical insights into what should be conserved (going beyond the protection of genetic diversity, to consider adaptive aspects of phenotypic variation), and why specific conservation programs succeed (e.g., through facilitating the resilience of cultural diversity) while others fail (e.g., by neglecting key repositories of socially transmitted knowledge). Here, we highlight how international legal instruments, such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS), can facilitate smart, targeted conservation of a wide range of taxa, by explicitly considering aspects of their sociality and cultures.

Consequences of social knowledge

An important aspect of social learning is the speed with which new behaviors can potentially spread through populations, with effects that may be positive (e.g., adaptive exploitation of a new food source) or negative (e.g., increasing conflict with humans, such as when sperm whales learn to remove fish from longlines) (Whitehead, 2010). Transmission can be mediated by an inherent propensity to adopt innovations (e.g., “lobtail” feeding in humpback whales (Whitehead and Rendell, 2015)), or curbed by cultural conservatism (e.g., southern resident killer whales’ persistent foraging specialization on Chinook salmon (Whitehead, 2010)).

Social learning can result in the emergence of subpopulations with distinctive behavioral profiles, erecting social barriers, as observed in distinct vocal clans of sperm whales (see the Figure). Culturally mediated population structure has important implications for conservation efforts (Garland et al., 2015), as it can influence species-wide phenotypic diversity and adaptability to changing conditions (Keith and Bull, 2017). In some cases, such as humpback or blue whale song, cultural variation can reflect demography and facilitate more efficient, or less invasive, assays of contemporary genetic population structure (Garland et al., 2015; Whitehead and Rendell, 2015). Most profoundly, culture can play a causal role in establishing and maintaining distinct evolutionary trajectories (Foote et al., 2016).

Another consequence of social learning can be the in-creased importance of key individuals as repositories of accumulated knowledge, making their targeted protection particularly important for the persistence of social units. For example, the experience of African elephant matriarchs (see the photo) has been shown to positively influence the fertility rates of younger females in their social group, through the transmission of information about the social and ecological landscape (McComb et al., 2001). Yet, traditional approaches to species conservation often prioritize younger individuals for their direct reproductive potential.

Positive conservation outcomes can depend on the restoration of cultural knowledge. For example, because whooping cranes learn migratory routes socially, human surrogates in ultralight aircraft can guide naïve, captive-bred birds along their first migration, potentially boosting the effectiveness of reintroduction programs (Mueller et al., 2013; Teitelbaum et al., 2018). Similarly, without the benefit of socially inherited knowledge, bighorn sheep and moose translocated to unfamiliar habitats can take generations to master the skill of tracking the seasonal distribution of high-quality forage (Jesmer et al., 2018). Social learning can also be exploited to ameliorate human-wildlife conflict, for example, by artificially “seeding” desirable behavior, such as avoidance of particular foods or sites (Greggor et al., 2017; Whiten, 2017a).

To improve the efficacy of conservation efforts, we there-fore argue that it is critical to consider the interplay between social structure and the transmission of social information. This may be particularly important if different categories of individuals vary in their propensity to innovate, or are more likely to be copied by naïve group members (Greggor et al., 2017). In some cases, populations may be structured into distinct cultural units with differing resource requirements. For instance, cultural transmission of vocal patterns among sperm whales in the Eastern tropical Pacific results in distinct vocal clans (Whitehead and Rendell, 2015) (see the Figure). Clans vary in their feeding success during El Niño and La Niña oceanographic cycles (Whitehead and

Rendell, 2015), meaning that if these cycles increase, as predicted under climate change, population-level impacts may not be uniform.

Cetaceans, and beyond

Despite mounting evidence that aspects of sociality can have far-reaching implications for wildlife conservation, international policy forums—where most large-scale conservation strategies are conceived—have so far not engaged substantially with the challenges and opportunities presented by this new scientific perspective. A notable exception is the CMS Scientific Council, which has conducted work at the interface of cutting-edge science and international policy-making.

The CMS signatories work to develop collaboration be-tween range states for the conservation of species that move across jurisdictional boundaries. They agree to support research, to endeavor to provide immediate protection for migratory species listed in CMS Appendix I, and to work toward developing agreements for the conservation and management of migratory species in CMS Appendix II. Although, like many other international agreements, CMS does not have a compliance mechanism, its standing committee is in the process of critically reviewing the impacts of its decisions, to im-prove effectiveness (background CMS documents are available in the supplementary materials).

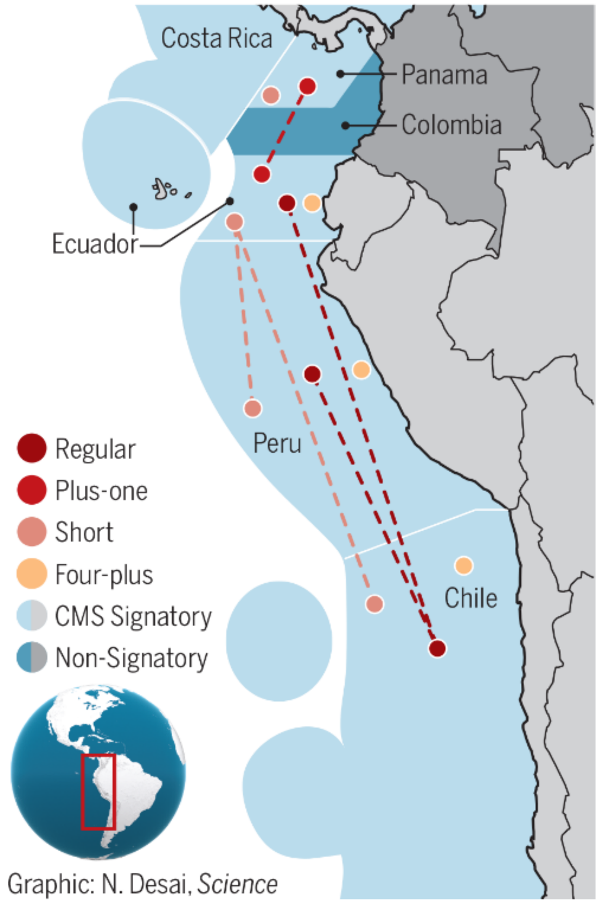
Impetus for an animal culture initiative was provided by a growing body of evidence for social learning and culture in cetaceans that raised important questions about how best to conserve these animals (Whitehead et al., 2004). The CMS Scientific Council’s pre-existing expertise in evaluating threats to aquatic mammals made CMS a natural avenue for examining these issues further. In 2014, a formal consultation revealed an extensive range of circumstances in which social structure, social learning, and cultural variation in whales and dolphins can affect the planning or outcomes of conservation efforts. This culminated in the adoption of a ground-breaking resolution, through which the CMS signatories formally acknowledged the importance of social learning and culture for the conservation of some highly social species.

Following the 2014 resolution, the CMS Scientific Council established an expert group to broaden the scope of this initiative beyond cetaceans. The group determined that social learning has conservation relevance across a wide range of vertebrate taxa, including birds, fishes, and many marine and terrestrial mammals (Whitehead and Rendell, 2015; Whiten, 2017a). At a 2018 cross-taxa CMS culture workshop in Parma, Italy, the authors of the present article reviewed relevant evidence, with a particular focus on species in which social learning has the potential to strongly influence migratory behavior, habitat use, foraging, or interaction with human activities. On the basis of this work, we recommend, among other things (for details, see table S1): augmenting the designation of evolutionarily significant units; conserving individuals that are critical repositories of social knowledge; refining the criteria used for identifying and prioritizing species and populations for assessment; improving reintroduction schemes through strategic management of social knowledge; planning effective mitigation strategies for anthropogenic impacts using aspects of sociality; systematically cataloging the dimensions of cultural diversity; and raising awareness about the value of conserving animal cultures.

The overall aim of this initiative is to maximize the efficacy of conservation efforts through enhanced consideration of sociality in general, and social learning and (both adaptive, and seemingly arbitrary) cultural processes in particular. Under-standing the im-portance of behavioral diversity will benefit conservation policies both when assessing the status of potentially vulnerable populations (e.g., when delineating units to conserve, by accounting for cultural segregation) and when devising effective conservation strategies (e.g., by identifying key repositories of social knowledge). Achieving these ambitious goals will require a considerable amount of work. For example, although there is broad agreement that successful reintroduction programs require individuals to be behaviorally competent (Mueller et al., 2013), for many species it will still be necessary to establish the degree to which key behaviors are socially learned (e.g., migratory routes in birds (Meyburg et al., 2017; Teitelbaum et al., 2018)). To facilitate progress, we highlight a few additional opportunities, both in terms of particular species that may merit further consideration and promising research approaches.

Sperm whale vocal clans

Subpopulations in the eastern tropical Pacific. Clan names are derived from their culturally transmitted vocal dialects. Colored lines indicate confirmed movements of photo-identified individuals of known clans across jurisdictional boundaries (conceptual map, not to scale). See supplementary materials.



Graphic: N. Desai, *Science*

The CMS encourages its signatories to engage in collective conservation measures through its “concerted action” mechanism. This process is particularly relevant when considering collaboration between range states for gathering and sharing data on cultural diversity for populations that move predictably across national borders. In 2017, CMS adopted a concerted action for Eastern tropical Pacific sperm whales (see the Figure). A variety of species may benefit from similar consideration, to evaluate the importance of aspects of their sociality for their conservation. This includes species as diverse as cod (not currently listed in the CMS Appendices), which appear to socially learn migratory routes, and chimpanzees (recently listed in the CMS Appendices), where a culture of nut-cracking tool use thrives in a small area of Western Africa (see Fig. S1), yet spans multiple national jurisdictions and may provide access to an important food source during the dry season (Whiten, 2017a).

An important challenge is to identify those populations, or social units, that would most benefit from our proposed approach, and to predict how specific biological processes may influence conservation outcomes (Greggor et al., 2017). Recent studies illustrate how innovative rapid-assessment techniques could aid the identification of distinct cultural units, which may be particularly vulnerable (e.g., as a result of socially learned foraging strategies). Where socially transmitted traits - such as foraging tactics (and hence resource requirements) and vocal behavior - covary (Whitehead and Rendell, 2015), it may be possible to document cultural variation with well-established, inexpensive survey protocols (Garland et al., 2015). Another approach is to harness new survey technologies, such as autonomous motion-triggered cameras, as exemplified by a recent attempt to chart putative cultural variation in wild chimpanzees (Kuehl et al., 2016) in the face of urgent threats from habitat destruction and poaching (see Fig. S1). In addition, appropriately parameterized formal models may provide reliable predictions about the impact of specific conservation interventions on sociocultural processes (Keith and Bull, 2017). The field of animal social learning is now sufficiently mature to provide key parameters for robust modelling of some systems, where relevant data are available from long-term field studies and controlled experiments.

Moving forward

Our growing understanding of the conservation relevance of cultural variation urges that scientists and policy-makers collaborate closely to ensure that policy is informed by the latest scientific advances. Many cultural systems are highly complex, and the conservation impact of cultural processes is context dependent, necessitating careful case-by-case consideration. Recommendations from the Parma workshop will inform discussions at the November 2019 Meeting of the Sessional Committee of the CMS Scientific Council and the 2020 CMS Conference of the Parties in India. A key challenge will be to determine if evidence warrants explicitly recognizing some distinct cultural units listed in the CMS Appendices, and how insights from this work can be used to inform conservation efforts across the entire CMS portfolio of agreements.

Within the broader context of international wildlife law (Trouwborst et al., 2017), it is important to consider the relevance of animal culture for scientific assessments and policy decision-making across a range of relevant multilateral environmental agreements, such as the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) and the Convention on Biological Diversity (CBD). We see opportunities to extend our approach beyond species and issues currently covered by CMS, for example, when assessing the sustainability of exports and trade through CITES processes. Such consideration is timely, because 2020 is the final year of the United Nations Decade on Biodiversity, when governments will negotiate the Post-2020 Biodiversity Framework. Given the prevalence of social learning and cultures across a wide range of taxa, a comprehensive, integrated approach is essential to maintaining the natural diversity and integrity of Earth's rich ecosystems.

Acknowledgements

We are grateful to the CMS executive secretary and the CMS secretariat for organizing the Parma workshop; the hosts and sponsors of the workshop (the Appennino Tosco-Emiliano National Park, the Fondazione Monteparma, and the Principality of Monaco); M. Prideaux for helpful policy discussions; S. Smart for graphic design; and the experts that have supported this initiative. G.N.d.S. is the CMS Conference of the Parties Appointed Councillor for Aquatic Mammals. F.S. is the chair of the CMS Scientific Council and is the councillor for Italy. J.W. is the UK scientific councillor for CMS and works for the Joint Nature Conservation Committee, which is a statutory adviser to the UK Government.

Supplementary materials

www.sciencemag.org/cgi/content/full/science.aaw3557/DC1

10.1126/science.aaw3557

[NB: references have been collated into the main reference list for this thesis]

CHAPTER 3

A conceptual framework for integrating animal culture into conservation

Evidence gathering and collaboration on non-human culture and conservation (Chapter 2), highlighted the need to gain a better conceptual understanding of the conditions under which animal cultures interface with conservation.

Both the 2014 and 2018 workshops examined evidence that social learning and animal culture could increase resilience (Hodgson et al., 2015), either through: resistance to exogenous pressures, e.g., by facilitating a switch in prey type in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (Ansmann et al., 2012); or recovery through endogenous mechanisms, e.g., through the transmission of advantageous innovations in a changing environment, such as blue tits (*Cyanistes caeruleus*) piercing the foil lid of milk bottles to feed on cream (Aplin et al., 2015; Fisher and Hinde, 1949); or by buffering against environmental stochasticity, as seen in socially transmitted tool-use in Indo-Pacific bottlenose dolphins (Wild et al., 2019b). There was also evidence that social learning and animal culture could increase vulnerability, e.g., through foraging specialization in killer whales (*Orcinus orca*) (Ford and Ellis, 2006; Whitehead, 2010); or could lead to precipitous decline at low population densities, e.g., the potential for Allee effect in dispersing oceanic fish such as herring (*Clupea*) and cod (*Gadus*) (Fernö et al., 2011; Rogers et al., 2018), or foraging griffon vultures (genus *Gyps*) (Jackson et al., 2008).

Further, there was evidence that key individuals within a social unit may act as repositories of social knowledge, e.g., in African elephants (*Loxodonta africana*) (McComb et al., 2001) and that loss of key individuals could have population-level effects that can last for decades (Shannon et al., 2013). In contrast, there was also evidence that social learning could provide opportunities for effective practical intervention, for example by seeding a social unit or population with lost social knowledge (Mueller et al., 2013), or by manipulating behaviour to reduce conflict in wildlife-human interactions, e.g. to reduce crop raiding (Chiyo et al., 2012; King et al., 2009).

To improve the depth of understanding of the potential costs and benefits under different scenarios, a synthesis of the broad range of available evidence of social learning interfacing with conservation issues, across diverse vertebrate taxa, was developed. The goal was to advance this field by placing this evidence within the context of existing conservation rubrics and elucidate some of the underlying processes.

This chapter investigates the available evidence and suggests how existing datasets could be re-examined in light of evidence on animal culture by exploring common behavioural contexts in which social learning and culture can be critical to assess (e.g., foraging and migration) and discusses relevant methodologies. It then explores how social learning may influence population viability and may provide an important resource for responses to anthropogenic change. Finally, the insights from this work enabled the development of a conceptual framework for this field, which was published in the journal *Royal Society Proceeding B* (Brakes et al., 2021). This article is reproduced here*.* In addition to the examples highlighted in the main manuscript, there are extensive additional examples and case studies from a broad range of taxa in the supplementary material (see: https://royalsocietypublishing.org/doi/suppl/10.1098/rspb.2020.2718).

A deepening understanding of animal culture suggests lessons for conservation

Philippa Brakes[1,2], Emma L. Carroll[3,4], Sasha R. X. Dall[1], Sally A. Keith[5], Peter K. McGregor[6], Sarah L. Mesnick[7,8], Michael J. Noad[9], Luke Rendell[4,10], Martha M. Robbins[11], Christian Rutz[12], Alex Thornton[1], Andrew Whiten[13], Martin J. Whiting[14], Lucy M. Aplin[15,16], Stuart Bearhop[1], Paolo Ciucci[17], Vicki Fishlock[1,18], John K. B. Ford[19], Giuseppe Notarbartolo di Sciara[20], Mark P. Simmonds[21,22], Fernando Spina[23], Paul R. Wade[24,25], Hal Whitehead[26], James Williams[27] and Ellen C. Garland[4,10]

Proc. R. Soc. B 288: 20202718.

https://doi.org/10.1098/rspb.2020.2718

Affiliations:

[1]Centre for Ecology and Conservation, Biosciences, College of Life and Environmental Sciences, University of Exeter, Cornwall TR10 9FE, UK

[2]Whale and Dolphin Conservation, Brookfield House, Chippenham, Wiltshire SN15 1LJ, UK

[3]School of Biological Sciences, University of Auckland, Auckland 1010, New Zealand

[4]Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews KY16 8LB, UK

[5]Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, UK

[6]ISPA - Instituto Universitário, 1149-041 Lisboa, Portugal

[7]Marine Mammal and Turtle Division, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037, USA

[8]Scripps Institution of Oceanography, UC San Diego, La Jolla, CA 92093-0203, USA

[9]Cetacean Ecology and Acoustics Laboratory, School of Veterinary Science, The University of Queensland, QLD 4343, Australia

[10]Centre for Social Learning and Cognitive Evolution, School of Biology, University of St Andrews, St Andrews KY16 9TH, UK

[11]Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

[12]Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews KY16 9TH, UK

[13]Centre for Social Learning and Cognitive Evolution, School of Psychology and Neuroscience, University of St Andrews, St Andrews KY16 9JP, UK

[14]Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

[15]Max Planck Institute of Animal Behavior, Radolfzell, 78315, Germany

[16]Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, 78467, Germany

[17]Department of Biology and Biotechnologies, University of Rome La Sapienza, 00185, Roma, Italy

[18]Amboseli Trust for Elephants, Langata 00509, Nairobi, Kenya

[19]Department of Zoology, University of British Columbia, Vancouver BC, Canada

[20]Tethys Research Institute, 20121 Milano, Italy

[21]Bristol Veterinary School, University of Bristol, Bristol BS40 5DU, UK
[22]Humane Society International, London N1 7LY, UK
[23]Istituto Superiore Protezione Ricerca Ambientale (ISPRA), I-40064 Ozzano Emilia (BO), Italy
[24]Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA Fisheries, Seattle, WA 98115, USA
[25]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98105, USA
[26]Biology Department, Dalhousie University, Halifax, Nova Scotia, B3H4R2, Canada
[27]Joint Nature Conservation Committee, Monkstone House, Peterborough PE1 1JY, UK

Corresponding authors: P.Brakes@exeter.ac.uk, e.carroll@auckland.ac.nz and ecg5@st-andrews.ac.uk

Abstract

A key goal of conservation is to protect biodiversity by supporting the longterm persistence of viable, natural populations of wild species. Conservation practice has long been guided by genetic, ecological and demographic indicators of risk. Emerging evidence of animal culture across diverse taxa and its role as a driver of evolutionary diversification, population structure and demographic processes may be essential for augmenting these conventional conservation approaches and decision-making. Animal culture was the focus of a ground-breaking resolution under the Convention on the Conservation of Migratory Species of Wild Animals (CMS), an international treaty operating under the UN Environment Programme. Here, we synthesize existing evidence to demonstrate how social learning and animal culture interact with processes important to conservation management. Specifically, we explore how social learning might influence population viability and be an important resource in response to anthropogenic change, and provide examples of how it can result in phenotypically distinct units with different, socially learnt behavioural strategies. While identifying culture and social learning can be challenging, indirect identification and parsimonious inferences may be informative. Finally, we identify relevant methodologies and provide a framework for viewing behavioural data through a cultural lens which might provide new insights for conservation management.

1. Introduction

A key goal of conservation is to ensure the adaptive potential and long-term persistence of viable populations by maintaining genetic and phenotypic diversity (Eizaguirre and Baltazar-Soares, 2014). To achieve this, it is necessary to identify population units in need of conservation, and identify, evaluate and mitigate threats. Standard rubrics for defining units to conserve rely on identifying groups with distinct evolutionary or demographic trajectories (Figure 1). International and national conservation frameworks and laws consider the threat status of units to conserve through the assessment of population trajectories, abundance, range dynamics and extinction risk (e.g. IUCN Red List, Endangered Species Act (USA)). We argue that considering animal social learning and animal culture (hereafter ‘culture’) could augment these conventional conservation approaches and decision-making, by informing the identification of units to conserve and assessing their viability.

The importance of behaviour for conservation biology has been increasingly recognized (Greggor et al., 2016; Ryan, 2006). However, a systematic review of the literature reveals learning and social behaviours were ‘rarely considered’ in wildlife conservation and management (Berger-Tal et al., 2016, p. 744). Our objective is to provide a practical framework to enable conservation managers to consider how culture may impact the viability and structure of certain animal populations and influence animals’ responses to conservation strategies. We start by defining animal social learning and culture. We then explore how these processes may influence the transmission of behaviours related to survival and reproduction, and thus provide evidence that social learning might influence demographic processes in a way that impacts population persistence and viability. Next, we delve deeper into the interface of social learning and culture across several behavioural contexts (Figure 2). We provide examples where the linkages between conservation and social learning have been demonstrated for endangered species. However, to further elucidate some of the underlying cultural and demographic processes, we also provide examples from species of lower conservation concern, to assist researchers and practitioners in identifying scenarios where social learning may be important for the conservation of endangered species, or for distinct population segments.

Finally, we provide a framework (Figure 3) to guide the integration of culture and social learning into current conservation and management efforts for social species.

Acknowledging the bias in the existing literature towards the most studied species, which are often more social and/or viewed as cognitively ‘advanced’, we highlight the crucial role that cultural transmission can play in guiding effective conservation responses. For example, this was recently achieved through the integration of culture and sociality into aspects of the management framework of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) (Brakes et al., 2019) (electronic supplementary material S1). ‘Concerted Actions’ approved by the Parties to the treaty, based on cultural data now inform the conservation management of eastern tropical Pacific sperm whales (*Physeter macrocephalus*) and ‘nut-cracking’ western chimpanzees (*Pan troglodytes verus*) (electronic supplementary material, S1, S4a, S4c) under CMS. Importantly, the aim is not to divert resources from critical conservation needs, or towards cultural species, but to apply scientific knowledge from this field to advance conservation priorities and assist conservation practice.

2. Social learning and culture

Social learning has been defined as any learning process that is facilitated by the observation of, or interaction with, another animal or its products (Heyes, 1994; Hoppitt and Laland, 2008; Whitehead and Rendell, 2015). An individual may learn new behaviour, like how to open a nut, asocially. Social learning, in contrast, involves the transmission of information from one animal (model) to another (observer), which results in the observer learning the behaviour. Social learning can occur along differing sensory channels (e.g. visual, olfactory) and through a variety of mechanisms such as local enhancement and emulation (Hoppitt and Laland, 2008) (electronic supplementary material, S2, glossary). Socially learnt behaviour can flow via: vertical transmission from parent to offspring; oblique transmission from older to younger, often unrelated, individuals; horizontal transmission between peers of the same generation (Cavalli-Sforza and Feldman, 1981); and even between species (Damas-

Moreira et al., 2018). All except the first of these pathways of transmission differ significantly from the dynamics of genetic transmission in the spread of behaviours. It should be noted that, like genetic variation, socially learnt behaviour can be adaptive, non-adaptive or neutral with respect to fitness (Whiten, 2019). However, unlike genetic inheritance, in many circumstances, social learning can facilitate the rapid transmission of behaviour across a diversity of contexts including foraging, migration routes and mate choice (Carroll et al., 2015; Gruber et al., 2019; Van De Waal et al., 2013; Warner, 1988; Wild et al., 2019b), with potentially significant implications for conservation management.

Social learning may also lead to the transmission of information through groups, giving rise to local behavioural (cultural) variants that persist over time and generations. Culture is defined here as information or behaviours shared within a group and acquired from conspecifics through some form of social learning (Fragaszy and Perry, 2003; Whitehead and Rendell, 2015). While this is a broad definition, it allows researchers to identify and measure potential cultural behaviours of conservation value (Whitehead and Rendell, 2015). Culture and its critical foundation, social learning, are observed in a wide variety of different social systems (see (Whiten, 2017a)). While socially learnt behaviour—and in some cases culture—have increasingly been documented across a wide range of invertebrate and vertebrate species (Whiten, 2017a), many adaptive behaviours do not require social input to develop. Conversely, socially learnt behaviour does not necessarily generate sustained or stable cultures, if, for example, it is related to transient resources. Nevertheless, group-wide behavioural variants (or their products) can be assessed to evaluate the possibility that they are socially learnt from conspecifics.

The precautionary principle (electronic supplementary material, S2, glossary) should be applied when assessing the conservation significance of behavioural patterns against the strength of evidence for social learning. For example, in species with endangered populations, information on social learning should rapidly be incorporated into management plans if there is suggestive evidence that these processes might play a role in survival or reproductive rates, even if it is not conclusive (Kasuya, 2008). In many species, it is difficult to determine the mechanism of social learning through observation alone. Nevertheless, in a small number of species, including bluehead wrasse (*Thalassoma bifasciatum*), great tits (Parus major), meerkats (*Suricata suricatta*), vervet monkeys (*Chlorocebus aethiops*) and chimpanzees, controlled studies have provided strong evidence that behaviours spread through groups and over generations via social learning (Aplin et al., 2015; Thornton and Malapert, 2009; Van De Waal et al., 2013; Warner, 1988; Whiten et al., 2007). Such work represents a 'gold standard' of evidence for social learning and culture. However, these controlled studies may have ethical implications, or may not be feasible, particularly in the wild or in endangered species, where observed patterns of behavioural expression can instead be used to infer the presence of cultural processes (Garland et al., 2011; Schuppli and van Schaik, 2019; van Schaik, 2009). Indeed, controlled studies can be vital for informing conservation by shaping our understanding of the fundamental principles of social learning and cultural transmission, and how they interface with demographic processes (e.g. anti-predator and survival training (Kierulff et al., 2012)).

One common tool to detect the presence of culture is the ethnographic method or the method of exclusion, where cultural processes are inferred if ecological and genetic processes can be ruled out (Schuppli and van Schaik, 2019). This may reveal a regionally distributed checkerboard of behavioural variants through the examination of multiple populations or social groups spread across the landscape (e.g. (Garland et al., 2011; Whiten et al., 1999)). However, the exclusion method is vulnerable to both over and under-attribution of cultural causes where researchers fail to recognize subtle environmental factors shaping individual plasticity or genetic change. For example, chimpanzees' use of long versus short stems to dip for ants was originally thought independent of habitat differences (Whiten et al., 1999), but later detailed studies suggested the choice reflected local variations in the severity of ants' defensive biting (Humle and Matsuzawa, 2002). Conversely, the approach may neglect cultural behaviours that are adaptations to different local environments (Schuppli and van Schaik, 2019), such as tool use to crack shellfish in long-tailed macaques (*Macaca fascicularis*) (Luncz et al., 2019).

Correlational studies can identify culturally transmitted behaviours where social learning experiments are not possible (e.g. (Carroll et al., 2015)). For example, if the vertical transmission is suspected to play a role in learning foraging strategies, correlations can be assessed between neutral genetic markers, as proxies for relatedness or parental lineages, and stable isotope markers, as proxies for foraging patterns (e.g. (Carroll et al., 2015)). It can be parsimonious to infer that social learning plays a role if a correlation is detected, particularly in species with multiple or generalist foraging strategies which suggest behavioural plasticity or phenotypic variation within a population, or in species where social learning has been previously observed. Vertical culture may be reasonably inferred as a determinant of foraging behaviour, if there is a strong correlation between the foraging measure and a uniparentally inherited genetic marker (e.g. mtDNA) that is unlikely to influence foraging directly (Krützen et al., 2005). Correlation between functional nuclear DNA markers and foraging behaviour could be indicative of a genetic component to the behaviour, but gene-culture coevolution can also create such patterns (Foote et al., 2016).

This approach has been questioned in the past due to the assumption that genetics plays a strong role in determining many behaviours (Laland and Janik, 2006). However, the patterns of genetic diversity within populations and species are shaped by the demographic, adaptive and stochastic processes that govern genetic drift, gene flow, mutation and Darwinian selection. In this context, the genetic component of behavioural traits is considered to be shaped by many genes that often have only small effect sizes and moderate heritability (Bubac et al., 2020). Neutral genetic markers typically used to assess relatedness and parentage are, by definition, less likely to be influenced by Darwinian selection than genes underpinning behavioural variants. While it is sometimes possible to conclusively rule out genetic effects in the described scenario by cross-fostering experiments to discover if they acquire their adopted or biological parents' foraging strategy (Sheppard et al., 2018; Slagsvold and Wiebe, 2007), this is often not ethical or feasible for endangered species.

Culture can be one of many influences that shape behaviour and new modelling approaches now integrate ecological, social and genetic factors into analyses of behavioural variation (e.g. (Hoppitt et al., 2010)). For example, network-based diffusion analysis (NBDA) has been used to investigate the social transmission of behaviours in chimpanzees (Hobaiter et al., 2014), humpback whales (*Megaptera novaeangliae* (Allen et al., 2013; Franz and Nunn, 2009)) and bottlenose dolphins (*Tursiops* sp. (Wild et al., 2019a)) by quantifying the extent to which social network structure explains the spread of behaviour (Hoppitt et al., 2010).

There is no one-size-fits-all method to identify social learning or culture. Feasibility, financial or ethical constraints make it unlikely that some behaviours would ever be definitively shown to be socially learnt. While the inference approaches listed above do not directly test social learning through experiments, they can provide robust, parsimonious inference for the presence of cultural processes underpinned by social learning based on patterns of behavioural expression. Identifying social learning *per se* is important whether or not this social learning gives rise to local cultural variation. Social learning can be a cause, a consequence or a marker of phenotypic diversity, of demography and vital rates, of population genetic structure, and of ecological niche separation (e.g. (Carroll et al., 2014; Riesch et al., 2012)). Conservation outcomes depend on demographic processes. If social learning can influence demography, then it follows that conservation practitioners may benefit from considering cultural processes.

A.

Unit	Definition	Example in conservation framework
Evolutionary significant unit (ESU)	Evolutionary units that show genetic or heritable phenotypic distinctiveness, and that demonstrate isolation, such that there is a restricted flow of information that determines genotype or phenotypes, from other such units [62,63]	IUCN species or sub-species; Canadian Designatable units
Demographically independent population (DIP)	Internal demographic processes (births, deaths) more important to population persistence than migration [60,61]	IUCN subpopulation: distinct groups between which there is little demographic or genetic exchange; US MMPA; IWC populations; Australian EPBC populations
Cultural variant (CV)	The particular form or variant of the cultural trait (behaviour) displayed by a group or population (derived from [9])	Varies depending on context: can be within, among or equivalent to DIP or ESU. Shown here within DIP (see figure 2 for other examples)

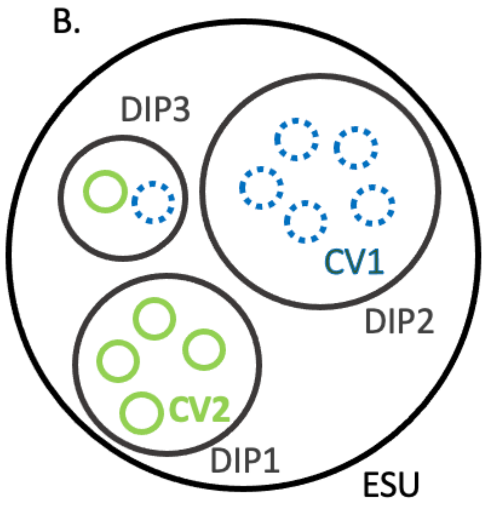


Figure 1. (a) Description and overview of conservation units (ESUs, DIPs and CVs) and how they are used in current conservation frameworks. (b) Example of the potential relationship between ESUs, DIPs and CVs: one ESU comprises three DIPs of different sizes, with two CVs found at different frequency in each of the DIPs. (For Figure references see: doi.org/10.1098/rspb.2020.2718)

3. Conservation through the lens of social learning and culture

Given the conservation challenges associated with rapid environmental change and habitat degradation, maintaining the long-term persistence of viable natural populations requires conservationists to focus on maximizing survival prospects and reproductive outputs of individuals, social groups and populations. To illustrate the links between these demographic parameters and social learning, we draw on examples from a wide variety of species, of the varying threat level. The processes elucidated in these examples have relevance for the management of many species, regardless of their conservation status. Indeed, while some examples in this section may not be of immediate conservation concern, many countries actively manage species and populations to avoid them slipping into such categories; therefore, understanding the influence of culture on demographic processes is highly relevant. Multiple sources of social information can generate the diversity of responses to resource availability and predation pressures (Chiyo et al., 2012; Schakner et al., 2014). What conservation relevant insights might be overlooked by assuming that populations—and social groups—are behaviourally homogeneous? We contend that increasing evidence on social learning and culture provides novel perspectives for addressing this question.

Social learning can create phenotypic variation among individuals and groups that can lead to differences in locating food, developing and propagating specialized foraging strategies, accessing important habitat or avoiding predators or other risks (Whiten, 2017a). Such differences can generate variation in individual fitness within a population and—when such benefits are conferred widely across a social group—can influence vital rates and structure populations (Keith and Bull, 2017; Mcgregor et al., 2000). First, cultural knowledge may act as a buffer, providing an opportunity to flexibly exploit environments in periods of resource scarcity. Second, in spatially variable environments, social learning can act to ‘fine-tune’ behaviour to local conditions, a ‘resident knowledge’ that transient or inexperienced individuals cannot exploit, unless they are able to learn from residents (Slagsvold and Wiebe, 2007). Third, innovations in response to novel challenges and opportunities can spread via social learning to establish new cultural behaviours, providing a route to exploit new resources (Aplin et al., 2015). In one of the most famous examples of innovation spread, great and blue (*Cyanistes caeruleus*) tits learnt to break the foil tops of milk bottles delivered to doorsteps and drink the cream beneath, a behaviour that subsequently spread across Britain and Ireland (Fisher and Hinde, 1949). However, cultural constraints can also limit the spread of adaptive behaviour, depending on the species and context (e.g. (Whitehead, 2010)).

Quantifying how social learning and culture generate behavioural variation and influence the dynamics of social groups and populations can yield important insights for conservation by examining effects on vital rates. Distilling precisely how social learning and culture can scale up to influence abundance and density, and thus population dynamics, under different scenarios, is challenging. A practical starting point is examining the influence of social learning on two key vital rates—survival and reproduction—as well as the central conservation question of what units to conserve. How population resilience may be impacted is explored in electronic supplementary material, S3.

a) Influence of social learning on survival

Building on innovative research on model organisms (Aplin et al., 2015; Hobaiter et al., 2014; Thornton and Malapert, 2009), consideration and utilization of social learning has proved important for increasing survival in managed populations (Greggor et al., 2016) (electronic supplementary material, S4a). In the case of golden lion tamarins (*Leontopithecus rosalia*), survival rates of reintroduced animals were initially extremely low (13%) (Stoinski et al., 2003). An intensive post-release programme involving supplemental feeding and nest-site provisioning allowed reintroduced animals to survive for long enough to learn basic life skills, doubling survival rates. The offspring of these captive-born re-introduced animals then showed a survival rate of 70%, suggesting that social learning and scaffolding from elders can make a critical contribution to survivorship during reintroductions (Kierulff et al., 2012). In another example, to maximize post-release survival of captive reared critically endangered Hawaiian crows (*Corvus hawaiiensis*), young birds are conditioned to recognize a potential natural predator, the Hawaiian hawk (*Buteo solitarius*), and to exhibit context-appropriate anti-predator behaviour (A. L. Greggor *et al*., unpublished data). In addition to learning to avoid danger, Hawaiian crows may socially learn key skills required to forage efficiently, communicate in a species-typical manner and breed successfully (Rutz et al., 2016) (see electronic supplementary material, S4a). These examples illustrate the importance of seeking to maintain individuals as ‘repositories of knowledge’ that may span a number of behavioural contexts and ensuring individuals scheduled for release are behaviourally competent, thus impacting conservation success.

Social learning can also provide access to novel, high quality forage, potentially via less energy expenditure than through individual exploration. Socially learnt foraging strategies can also buffer against adverse effects of environmental variability. For example, long-term behavioural studies show bottlenose dolphins in Western Australia have multiple foraging strategies, including socially learnt use of sponges as tools to help extract prey (Sargeant and Mann, 2009). A recent marine heatwave led to a 5.9% and 12.2% decrease in the survival rate of dolphins that did and did not use tools, respectively. These data indicate that socially transmitted tool use may have buffered a section of the population against the cascading effects of habitat loss on prey species (Wild et al., 2019b). More broadly, this example highlights how survival in bottlenose dolphins is linked to phenotypic variation. This lesson may be applicable to the conservation and management of other species that show heterogeneity in foraging strategies that could stem from social learning.

b) Influence of social learning on reproduction

Variation in reproductive output among females in a population can provide a quantifiable indicator of population health (Robinson et al., 2017) and can be influenced by social learning in complex ways across different scales. For example, individual female bottlenose dolphins in Brazil that specialize in socially learnt cooperative foraging with fishermen may have a fecundity advantage related to increased seasonal prey resources (Bezamat et al., 2020). At a group scale, the sharing of social information by experienced older African elephant (*Loxodonta africana*) matriarchs increases group survival and reproductive success, by providing information on the level of threat posed by elephants from other social groups and by predators in the wider environment (McComb et al., 2001). Management plans should incorporate the understanding that matriarchs act as ‘repositories of knowledge’ and that the loss of these individuals (e.g. culling or translocation) can have population-level impacts that persist for decades (Shannon et al., 2013).

Considering broader population units, sperm whale social units cluster into ‘clans’ identified by acoustic dialects. Reproductive success varies between clans, which is thought to be associated with socially learnt foraging strategies (Marcoux et al., 2007; Whitehead and Rendell, 2015) and perhaps alloparental care patterns (Cantor and Whitehead, 2015), with potential population-level consequences. Foraging variation among clans can lead sub-populations to respond differently to environmental change, such as the El Niño oceanographic phenomenon. Noting this differential success between acoustic clans, in 2017 the Parties to CMS agreed a Concerted Action to further explore the implications of the clan structure for the conservation of sperm whales in the eastern tropical Pacific (CMS, 2017). While the influence of social learning on reproductive success is apparent, it is not yet clear how environmental changes influencing feeding success impact clan survival; such information is essential for understanding population dynamics within clans and across the species.

c) Influence of social learning and culture on units to conserve

Social learning and culture can promote demographic isolation between groups or populations with relevance to management and conservation demographically independent populations (DIPs); Figures 1 and 2 (Ryan, 2006)(Whitehead, 2010). For example, killer whales (*Orcinus orca*) can exhibit highly conservative socially learnt prey specializations to the extent that separate, endangered fish-eating Southern Resident killer whale social units forage on fish (e.g. chinook salmon, *Oncorhynchus tshawytscha*) specific to individual river systems (Ford and Ellis, 2006). The population abundance of this social unit has declined along with its preferred prey. This reliance on a single river system and cultural reluctance to switch food sources clearly links the importance of understanding foraging culture with conservation management. This demographic isolation can also lead to genetic divergence and speciation through mechanisms such as assortative mating (Whitehead et al., 2019). Figure 2 highlights examples where culture provides valuable data on the delineation of units to conserve at different scales (DIPs

(Morin and Dizon, 2018; Wade and Angliss, 1997) and evolutionary significant units (ESUs) (Whitehead et al., 2019, 2004)). We direct readers to recent reviews (Whitehead et al., 2019; Whiten, 2019) that delve into the role of culture as an evolutionary force leading population segments towards distinct evolutionary trajectories as ESUs (Figure 1) (Crandall et al., 2000; Riesch et al., 2012) and highlight the role of gene–culture coevolution in this process.

Behavioural context	Species [reference*]	Socially learnt behaviour	Implications	Mitigation strategy	Conservation policy
Foraging	Killer whales [31]	Conservative foraging strategies and vocal dialects	Unlikely to switch to alternative prey source when prey preference depleted	Managed as distinct cultural units	Committee on the Status of Endangered Wildlife in Canada (COSEWIC) DIP, MMPA, ESA
	Chimpanzees [79]	Nut-cracking foraging strategy	Potential access to additional food source during dry season when fruit is scarce	Investigation of potential benefits or costs of nut-cracking behaviour	CMS Concerted Action: collaboration across range states
	Meerkats [20]	Social learning and teaching of foraging strategy to young	Pups learn to locate and recognise prey, and handle difficult/potentially dangerous prey e.g., scorpions	Disturbance that interrupts pathways of transmission may reduce population survival	Within population cultural variant
	Elephants [43]	Crop-raiding leads to negative human-wildlife conflict	Older males protect and guide younger males; experienced fence breakers serve as repositories of knowledge	'Cultural arms race' requiring ever-adapting management	
	Griffon vultures [80]	Locate food in chain reaction of information transfer	Visual contact with a number of conspecifics required to achieve efficient foraging	Successful reintroduction: early-stage supplemental food and simultaneous release large numbers individuals in same location	IUCN designated critically endangered
	Bottlenose dolphins [14]	Multiple socially learnt foraging strategies	Higher survival rate for tool-using dolphins during heat wave	Manage 'sponging', 'shelling' cultural units	Within-population cultural variant
	Golden lion tamarins [26]	Knowledge of forage and predator avoidance	Reintroduction survival rates extremely low - failed to forage effectively and recognise predators	Food provisioning and nest-sites: reintroduced animals survive long enough to socially learn basic life skills	Reintroduce with wild elders
Migration/Movement	Whooping cranes [67]	Socially learnt migratory routes	Increased survival resulting from social learning of migration to suitable habitat	Reintroduction: use social learning mechanisms to seed migratory routes; social learning important in multiple behavioural contexts	
	Cod and herring [81]	Learning established migratory routes from adults	If ratio juveniles to adults too high oblique transmission interrupted; reduced offspring survival and reproduction	Stochastic events required to reintroduce recent released fish to migratory routes	
	Bighorn sheep [71]	Green wave surfing (synching movements with waves of plant growth)	Translocated sheep fail to migrate when moved into unfamiliar landscapes	Potential to harness emulation or local enhancement by intervening to seed knowledge in a sub-set of individuals	
	Right whales [12]	Socially learnt migratory destinations	Unknown flexibility to migration route and destination - high human use areas increase ship strike, noise pollution	Vessel restrictions e.g., Boston harbour, for migrating North Atlantic right whales	Southern right whale wintering grounds considered DIPs (IWC, New Zealand & Australian domestic legislation), MMPA, ESA
	Beluga whales [82]	Socially learnt migratory routes and destinations; socially learnt avoidance of ice entrapment	Exploitation may disrupt beluga societies, impact ability for populations to recover and recolonise habitats where extirpated	Maintain viable populations in all habitats, protect migration corridors, continued protection from direct exploitation	Fisheries and Oceans Canada, Wildlife Management Boards, IWC, MMPA, ESA
Communication	Sperm whales [55]	Acoustic codas identify populations; provide proxy for foraging strategy; cultural clans have different movement patterns	Differential foraging success in different oceanographic conditions; movement patterns important for how clans mitigate effects of El Nino-like events	Manage acoustic clans as units to conserve	CMS Concerted Action: multiple range states collecting data, MMPA, ESA
	Humpback whales [25]	Horizontal transmission of song variants; vocal markers for populations	Male sexual display - disruption may impact reproduction but details unclear	Rapid assessment tool for identifying and assessing population connectivity; identification of units to conserve	Could be incorporated by IWC; MMPA, ESA
	New Caledonian crows [83]	Vocal dialects	Some aspects of tool-assisted foraging behaviour may be socially transmitted, with potential fitness consequences	Vocal dialects may provide 'markers' for rapidly mapping variation in tool-related behaviour	
	Corn buntings [84]	Vocal dialects indicate breeding population; lack of clear dialects indicate recent recolonisation, relative unsuitability of habitat	Both sexes breed within natal dialect, behaviourally fragmenting continuous population; low settlement density, lack clear dialects indicate habitat suitability	Potentially a rapid assessment tool for habitat quality and population connectivity	Could be used by national conservation bodies to assess effective population size/habitat suitability

Figure 2. Some examples linking social learning across behavioural contexts, to vital rates and conservation policy. Implications: implications for reproduction, survival or adaptation. Mitigation strategy: mitigation strategy linked to animal culture. *Additional references per species are provided in electronic supplementary material, table S2. Image credits – Chris Huh: humpback whale, killer whale, right whale, sperm whale (https://creativecommons.org/licenses/by-sa/3.0/). (For Figure references see: doi.org/10.1098/rspb.2020.2718)

4. Ecological studies through the lens of social learning and culture

Evidence for social learning can be identified across several behavioural contexts, perhaps most commonly across the contexts of foraging, migration and communication. These contexts are often the focus of conservation actions. Therefore, our aim is to provide a roadmap to understand the contexts under which social learning may be relevant and to consider ways the field can contribute to promoting conservation outcomes. We hope the examples (electronic supplementary material, S4a–c; Figure 2) will encourage readers to re-examine their data using a cultural lens to investigate whether social learning is important for managing and conserving their species.

a) Foraging

Social learning plays a vital role in the development of foraging behaviour in many species. Where foraging strategies are socially learnt, innovations can spread rapidly through a social group, facilitating the exploitation of new resources in the environment. For example, young male elephants learn crop-raiding techniques from experienced older males (Chiyo et al., 2012) leading to negative conservation outcomes (Figure 2). Alternatively, cultural conservatism may lead to an inability to switch prey species despite dwindling resources, as changing foraging techniques to exploit alternative prey may be costly. Failure to recognize that species with multiple foraging cultures may have multiple resource requirements (e.g. killer whales (Whitehead, 2010)) could undermine conservation efforts.

Direct assessment of diet can be achieved through observations of feeding or using morphological or DNA-based assessments of prey remains found in scat, stomach contents or lavages (e.g. (Tim Tinker et al., 2012)). Stable isotope or fatty acid analyses of tissue or scat can be used to infer foraging location and trophic level (West et al., 2006), where opportunities for direct observations are limited. In one recent example, stable isotope analysis of whisker samples provided strong evidence that young banded mongooses (*Mungos mungo*) inherit their foraging niche from specific (non-parent) adult cultural role models (Sheppard et al., 2018). Importantly, intraspecific foraging specialization may have real-world consequences for survival and reproduction for endangered species (see electronic supplementary material, S4a). For example, multiple lines of evidence have now established nut-cracking, a foraging specialization limited to sub-populations of critically endangered Western chimpanzees, as a socially learnt and culturally transmitted behaviour that may be essential to survival through the dry season when the fruit is scarce. Noting this specialization and the critically endangered status of these sub-populations, in 2020, the Parties to CMS agreed a Concerted Action to further explore the implications of nut-cracking culture for the conservation of this species (electronic supplementary material, S1 and S4a).

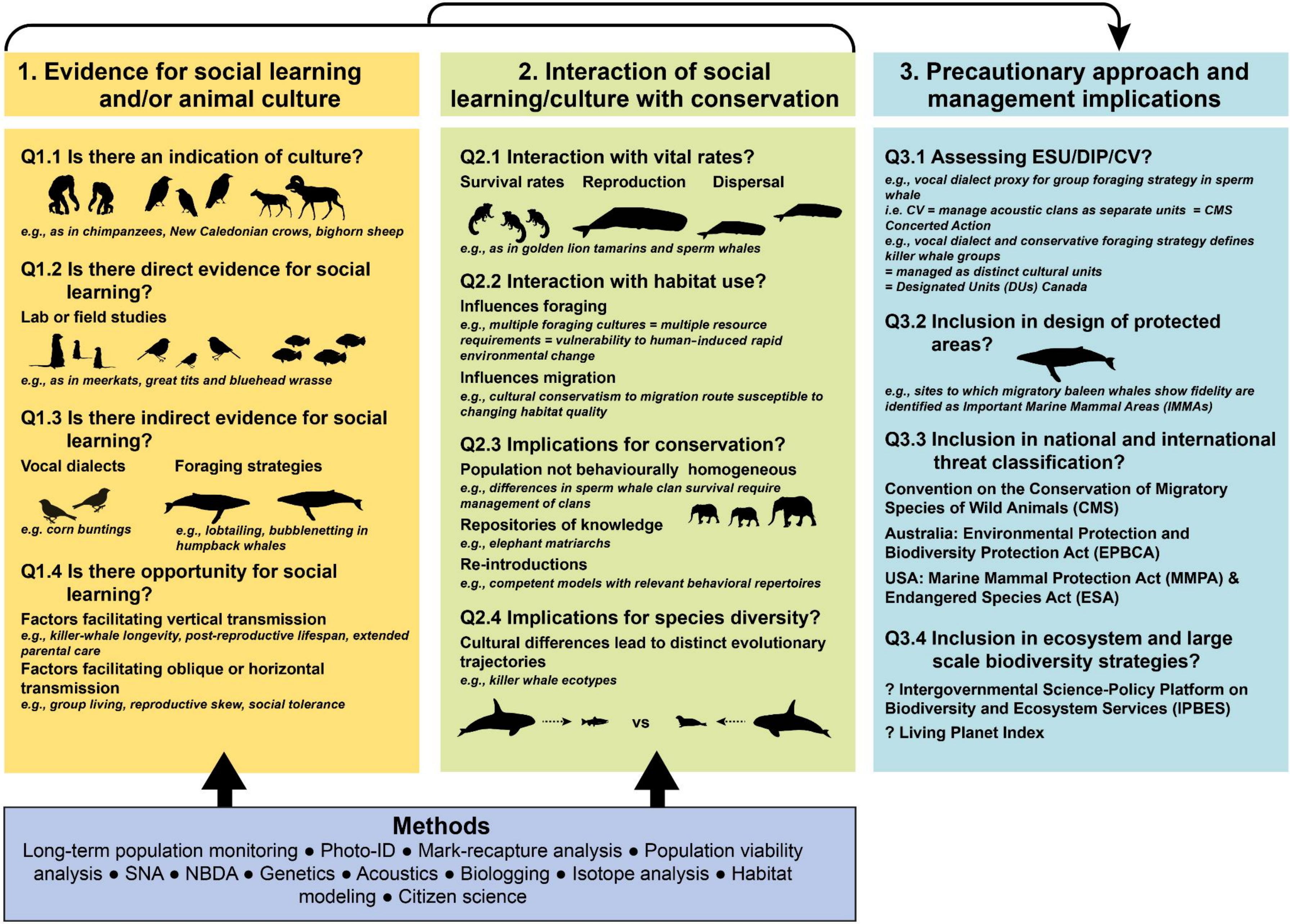
b) Migration

In some group-living species or those with extended periods of parental care, the first migration of an individual’s life is often with conspecifics. The migration route and/or site learnt can therefore be horizontally transferred from conspecifics (Harrison et al., 2010) or vertically transmitted from parent to offspring (e.g. in whooping cranes, *Grus americana* (Mueller et al., 2013) and southern right whales, *Eubalaena australis* (Carroll et al., 2015): Figure 2), helping ensure that offspring are able to find ephemeral resources in highly patchy environments (Switzer, 1993). Individuals can maintain these socially learnt migratory behaviours across time, leading to a form of cultural conservatism, which can be of relevance to conservation. For example, migratory route fidelity influences management unit designation and the spatially patchy recovery from the hunting of some baleen whale species (Carroll et al., 2014).

Migration movements have been studied directly using field observations and marking methods (e.g. genotypes and photo-identification), and indirectly using stable isotopes and DNA from tissue (Baker et al., 1990; Carroll et al., 2015). Genetic pedigrees have been combined with long-term field data, for example, to demonstrate fine-scale extended kin structure at migratory destinations in light-bellied Brent geese (*Branta bernicla hrota*), supporting the hypothesis that site choice has a cultural component (Harrison et al., 2010). Increasingly, migration movements are studied directly using animal-attached bio-loggers, which provide high-quality fine-scale movement data (Rutz and Hays, 2009), used to infer links between breeding, stopover and feeding grounds. For example, translocation experiments exploring the cultural basis of migratory behaviour, such as those conducted on big horn sheep (*Ovis canadensis*) and moose (*Alces alces*), provide strong evidence for the importance of cultural behaviour for conservation reintroductions (Jesmer et al., 2018) (electronic supplementary material, S4b). Similar patterns are found comparing genetic relatedness and proxies for foraging grounds, such as stable isotopes, in cetacean species (e.g. (Carroll et al., 2015); Figure 2; electronic supplementary material, S4b). Adults with migratory experience and knowledge of suitable habitats may be particularly important as ‘knowledgeable individuals’ for reintroduction efforts or for preserving existing populations.

c) Communication

Vocal communication—the transfer of information or influence between individuals using sound signals—is routinely studied within the context of social learning and culture using acoustic recordings often supplemented with genetic, identification marks and bio-logging information to provide context (e.g. (Rendell et al., 2012)). Comparisons of vocal differences among groups or populations can require large geographic ranges to be covered, and long-term monitoring for those species that change their vocalizations over time (e.g. via cultural evolution; see electronic supplementary material, S4c). Group-specific or geographic dialect differences become apparent when examining displays across a region and can be used as a cost-effective measure in rapid assessment of population structure (Mcgregor et al., 2000). In many cases, cultural conformity to a vocal display within a group appears a key factor in the formation and maintenance of dialects (Lachlan et al., 2018). Acoustic clans in sperm and killer whales offer clear examples of vocal dialects defining groups to conserve, with linkages to vital rates and a CMS Concerted Action in the former, and COSEWIC DIP, USA MMPA and ESA management protection in the latter (Figures 2 and 3; electronic supplementary material, S4c). Such vocal differences can be very long lasting and/or lead to reproductive isolation between populations, correlating with genetic differences (e.g. (Ford, 1991; Rendell et al., 2012)). Finally, severe population declines can result in loss of song culture, as shown in critically endangered regent honeyeaters (*Anthochaera phrygia*) (Crates et al., 2021); cultural decline may be a precursor to extinction thus providing an important conservation indicator (Crates et al., 2021).



1. Evidence for social learning and/or animal culture

Q1.1 Is there an indication of culture?

e.g., as in chimpanzees, New Caledonian crows, bighorn sheep

Q1.2 Is there direct evidence for social learning?

Lab or field studies

e.g., as in meerkats, great tits and bluehead wrasse

Q1.3 Is there indirect evidence for social learning?

Vocal dialects

e.g. corn buntings

Foraging strategies

e.g., lobtailing, bubblenetting in humpback whales

Q1.4 Is there opportunity for social learning?

Factors facilitating vertical transmission
e.g., killer-whale longevity, post-reproductive lifespan, extended parental care

Factors facilitating oblique or horizontal transmission
e.g., group living, reproductive skew, social tolerance

2. Interaction of social learning/culture with conservation

Q2.1 Interaction with vital rates?

Survival rates **Reproduction** **Dispersal**

e.g., as in golden lion tamarins and sperm whales

Q2.2 Interaction with habitat use?

Influences foraging
e.g., multiple foraging cultures = multiple resource requirements = vulnerability to human-induced rapid environmental change

Influences migration
e.g., cultural conservatism to migration route susceptible to changing habitat quality

Q2.3 Implications for conservation?

Population not behaviourally homogeneous
e.g., differences in sperm whale clan survival require management of clans

Repositories of knowledge
e.g., elephant matriarchs

Re-introductions
e.g., competent models with relevant behavioral repertoires

Q2.4 Implications for species diversity?

Cultural differences lead to distinct evolutionary trajectories
e.g., killer whale ecotypes

3. Precautionary approach and management implications

Q3.1 Assessing ESU/DIP/CV?

e.g., vocal dialect proxy for group foraging strategy in sperm whale
i.e. CV = manage acoustic clans as separate units = CMS Concerted Action
e.g., vocal dialect and conservative foraging strategy defines killer whale groups
= managed as distinct cultural units
= Designated Units (DUs) Canada

Q3.2 Inclusion in design of protected areas?

e.g., sites to which migratory baleen whales show fidelity are identified as Important Marine Mammal Areas (IMMAs)

Q3.3 Inclusion in national and international threat classification?

Convention on the Conservation of Migratory Species of Wild Animals (CMS)

Australia: Environmental Protection and Biodiversity Protection Act (EPBCA)

USA: Marine Mammal Protection Act (MMPA) & Endangered Species Act (ESA)

Q3.4 Inclusion in ecosystem and large scale biodiversity strategies?

? Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)

? Living Planet Index

Methods

Long-term population monitoring ● Photo-ID ● Mark-recapture analysis ● Population viability analysis ● SNA ● NBDA ● Genetics ● Acoustics ● Biologging ● Isotope analysis ● Habitat modeling ● Citizen science

Figure 3. A conceptual framework for incorporating evidence and inference on social learning and animal culture into conservation policy and practice (silhouettes indicate examples discussed in main text and electronic supplementary material; see text for details). Image credits—Chris Huh: humpback whale, killer whale, sperm whale; Kent Sorgon: wrasse (https://creativecommons.org/licenses/by-sa/3.0/).

5. Conceptual framework and future directions

Maintaining the adaptive potential and ensuring the longterm persistence of viable natural populations requires conservation managers to focus on maximizing the survival prospects and reproductive outputs of individuals, social groups and populations. An understanding of animal social learning and culture has significant potential to help maximize the impact and efficiency of conservation efforts (electronic supplementary material, table S1). Specifically, understanding linkages between culture and vital rates, cultural evolution, and adaption to rapid global change, will be critical for incorporating culture into management plans. Central to the approach we advocate here is a need to understand the circumstances under which social learning and culture are likely to impact population viability through phenotypic variation (Figures 1–3, §3). Additionally, we argue that social learning and culture can be important indicator (§3c) and a resource for resilience in the face of anthropogenic change (Figure 2). Social learning and thus cultural evolution may provide opportunities for adaptive behaviours to spread in response to environmental change (Ansmann et al., 2012). Conversely, social learning may prevent the spread of adaptive behaviour, potentially hindering recovery, if conformity is high or some other mechanism promotes cultural ‘conservatism’ (e.g. killer whale (Whitehead, 2010)). It may also have a subtle and complex role in resistance to disturbance as the result of knowledgeable elders acting as repositories of social knowledge, as for example in African elephants and killer whales (Croft et al., 2017; McComb et al., 2001). The examples given here are relevant to endangered species, but may also provide insights for those species not currently of conservation concern; managers work to ensure that populations do not decline into threatened status, after all.

Identifying culture and social learning is challenging. While there are a growing number of relatively well-studied species, in the majority of cases, detailed behavioural data are sparse. Indirect identification and parsimonious inferences
(e.g. correlation) may therefore be informative. With this perspective in mind, Figure 3 provides a framework to guide the integration of data on culture and socially learnt behaviour into current conservation management, and electronic supplementary material, table S1 provides specific recommendations. Within this framework, the first step is to review the evidence, or opportunity, for culture or social learning. Second, how social learning/culture may interact with demographic processes and impact conservation efforts is evaluated and suitable assessment tools are proposed. Third, we suggest how culture could be brought into current conservation frameworks and assessments. For example, if data show that culture or social learning is influencing vital rates of discrete social groups, it could be integrated into population viability analyses. Thus, where salient, phenotypic variation arising from cultural, as well as ecological and genetic processes, could be informative for assessing demographic separation between potential units to manage and conserve (Ryan, 2006), and incorporated into national and international conservation frameworks (e.g. IUCN), following published examples (Figure 2).

This framework is intended to help guide practitioners towards ‘future-proofing’ populations by conserving both cultural variation and the capacity for innovation and social learning to maximize the resilience of vulnerable populations. Human activities can both threaten existing cultures and provide a catalyst for new cultural behaviour (Gruber et al., 2019). The COVID-19 anthropause may provide an opportunity to examine—with an unusual degree of control—the role of social learning in species’ responses to significant environmental perturbation (Rutz et al., 2020). We argue resilience relies on preserving three building blocks of cultural capacity: demography and phenotypic variation; social network structure and population connectivity. Given that such an approach is common to preserving other aspects of biological diversity, and that culture and social learning can interface in multiple ways with conservation efforts, we recommend that the IUCN establish a cross-taxa specialist group to incorporate such information into IUCN assessments. It is only through enhanced collaboration between scientists, conservation practitioners and policy makers that animal culture and social learning can be embedded into conservation practice and policy.

Data accessibility. This article has no additional data.

Authors' contributions. P.B., E.C.G. and E.L.C. co-wrote the manuscript and developed ideas for the figures and tables, with core writing contributions from S.R.X.D., S.A.K., P.K.M., S.L.M., M.J.N., L.R., M.M.R., C.R., A.T., A.W. and M.J.W. All co-authors contributed to the development of ideas and provided feedback on the manuscript.

Competing interests. We declare we have no competing interests.

Funding. Funding and support as follows: Whale and Dolphin Conservation to P.B.; Royal Society New Zealand Rutherford Discovery Fellowship to E.L.C; Radcliffe Fellowship, Radcliffe Institute for Advanced Study, Harvard University, and Biotechnology and Biological Sciences Research Council grant no. [BB/S018484/1] to C.R.; Human Frontier Science Program grant no. [RGP00049] to A.T.; Royal Society University Research Fellowship grant no. [UF160081] to E.C.G.

Acknowledgements. This manuscript is the result of discussions during a 2018 CMS Workshop on Conservation Implications of Animal Culture and Social Complexity, Parma, Italy. We are grateful to the late Bradnee Chambers, former CMS Executive Secretary, for his encouragement and the CMS secretariat for organizing the Parma workshop; the hosts and sponsors of the workshop (the Appennino Tosco-Emiliano National Park, the Fondazione Monteparma, and the Principality of Monaco); the experts that have supported this initiative; and Vivian Ward for the graphic design of Figure 3.

CHAPTER 4

Content biased social learning and population dynamics

Abstract

Evidence for cultural transmission within and between social units is emerging across a variety of taxa. A range of techniques have been developed for detecting social learning of specific behavioural traits within and between wild populations. Nevertheless, given the emergent understanding in this field and the challenges associated with gathering high resolution data across multiple cultural generations, evidence for the influence of cultural transmission on population dynamics are in shorter supply. Using simulations of a model system of two interacting cultural units, the tension between the simultaneous dynamics of cultural transmission and demographic process are explored. Insights are provided on how a directly-biased social learning strategy (or content bias) can influence concurrent demographic processes. A simple stage-structured population with two discrete cultural units that are coupled through content biased transmission is considered. Using population projection matrices (PPMs), the coupled cultural units are simultaneously projected, to explore the implications for population dynamics and persistence. It is shown that the strength of transmission can influence not only the movement towards an informed cultural unit, but how the benefits to socially learned information that improves survival or reproduction can interface in a complex manner with population dynamics.

1. Introduction

Multiple sources of social information, including social learning, can shape social groups and their response to resource availability and predation pressures (Gil et al., 2017). Given the burgeoning evidence for social learning across a broad range of vertebrate taxa (Whiten, 2017a), a key question is how do the processes of social learning interact with population dynamics?

In addition to the influence of exogenous factors demonstrated in Figure 1, such as resource availability under changing environmental conditions, some endogenous processes may also influence whether cultural groups thrive or decline. For example, cultural transmission may result in individuals moving between cultural groups (e.g. from a naive state to an informed state) (Cantor and Whitehead, 2013). In this case, if being informed confers an advantage to vital rates (e.g. survival or reproduction) then the interplay between cultural transmission and the demography of cultural units may be complex.

Examining the interplay between culture and demographic process in human populations, previous theoretical research demonstrated the value of exploring demographic structure and cultural transmission in concert, particularly for explaining domain-specific cultural behaviour as it changes over an individual's lifetime and in shaping patterns of cultural evolution (Fogarty et al., 2019). Similarly, examining connectivity between human populations, modelling work suggests that the interactions between populations not only facilitates cultural transmission, but it may also generate a positive-feedback loop that can drive acceleration in cultural accumulation (Creanza et al., 2017).

It is demonstrably the case that cumulative culture in the form of technology has increased the vital rates of humans, from the agricultural revolution to genetic research (Lehmann and Feldman, 2009; Richerson and Boyd, 2005). While there is scant evidence for cumulative culture in non-humans, there is evidence that socially mediated behaviour can influence survival and reproduction in other taxa (e.g. in killer whales (*Orcinus orca*), (Ruth Esteban et al., 2016; Vélez-Espino et al., 2015) and sperm whales (*Physeter macrocephalus*) (Cantor and Whitehead, 2015; Marcoux et al., 2007)).

Distilling precisely how social learning and culture can scale up to influence abundance and density, and thus population dynamics, under different conservation scenarios, is challenging. Given the relationship between the transmission of some cultural behaviour and vital rates, a practical staring point is examining the influence of social learning on survival and reproduction (Brakes et al., 2021), and exploring how this may effect population resilience (see Chapter 5).

To explore some of this complexity, in this Chapter a simple stage-structured population with two discrete units that are coupled through social transmission is considered. Using population projection matrices (PPMs), the cultural units are coupled through the movement of naive individuals to the informed cultural unit as the result of directly biased, or content based, cultural transmission (after Boyd and Richerson, 1985) and then simultaneously projected. The focus here is on content biased social learning, given the relevance of the transmission of behaviours such as foraging strategies for conservation, as described in the previous chapter (Brakes et al., 2021).

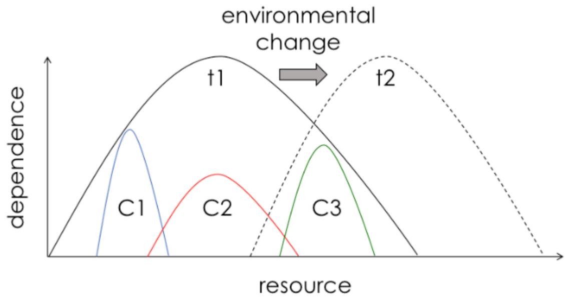


Figure 1. A schematic representation of the vulnerability of social groups with different cultural foraging cultures in the face of environmental change (reproduced from (CMS, 2018)). Cultural units (C1, C2, C3) consume distinct resources due to socially learnt specialisation of foraging strategies. Under a scenario of environmental change (e.g., increased temperatures), the resource base can shift over time (from t1 to t2) and create vulnerability dependent on the potential for cultural units to track and exploit new resources. In the example here, environmental change will result in loss of C1 and persistence of C3, whilst the persistence of C2 will depend on its capacity to forage for resources that are currently consumed with low probability.

2. **The model**

Consider two coupled, two-stage cultural units: $\boldsymbol{x_n}$, the naive cultural unit and $\boldsymbol{x_k}$, the informed cultural unit. Both units are comprised of juveniles (*J*) and adults (*A*) thus:

$$\boldsymbol{x_n} = \begin{pmatrix} J_n \\ A_n \end{pmatrix} \qquad \boldsymbol{x_k} = \begin{pmatrix} J_k \\ A_k \end{pmatrix}$$

The population biology of the naive unit is determined by the population projection matrix (PPM) $\mathbf{M_n}$ and the informed unit by $\mathbf{M_k}$ (Fig. 2b). The theoretical cultural units are sympatric and are linked through the movement of naive individuals ($\boldsymbol{x_n}$) to the informed cultural unit ($\boldsymbol{x_k}$) as the result of social learning of a novel foraging strategy (Fig. 2a).

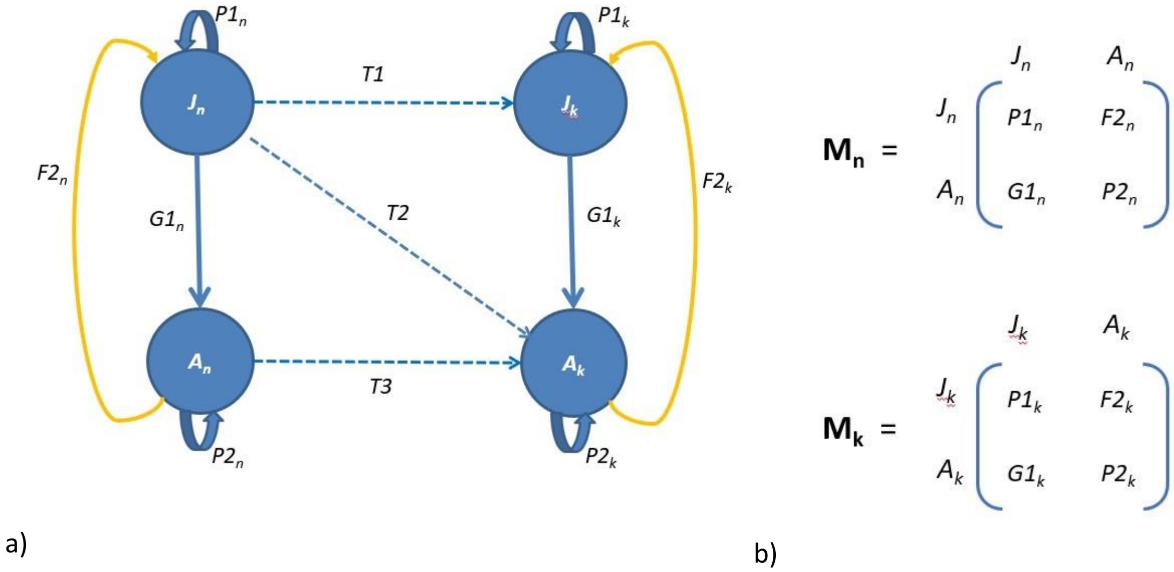


Figure 2. a) Life-cycle graph for two cultural units ($\boldsymbol{x_n}$ and $\boldsymbol{x_k}$), where juveniles and adults can move between knowledge states, from naive to informed (e.g. J_n to J_k). The transmission can be facilitated via transmission routes *T1*, *T2* or *T3* (see Table 1). *T1* represents horizontal transmission between juveniles, or vertical or oblique transmission from informed adults; *T2* represents vertical or oblique transmission from informed adults, or horizontal transmission from informed juveniles, which results in naive juveniles transitioning to informed adults; and *T3* represents horizontal transmission between adults. Note that in the wild, movement of naïve juveniles to informed (i.e. J_1 to J_2) may be the result of either knowledge transmission via *T1* and/or *T2* (i.e. horizontal and/or vertical or oblique transmission). b) Population projection matrices for cultural units $\boldsymbol{x_n}$ and $\boldsymbol{x_k}$ with transition between stages as identified in a).

The acquisition of knowledge is captured by transmission rates between naive and informed cohorts and these can be manipulated depending on the transmission pathways to be modelled (Table 1). At each time step, social learning can result in juveniles and/or adults moving from the naive unit ($\boldsymbol{x_n}$) to the informed unit ($\boldsymbol{x_k}$), depending on the transmission route (T).

Table 1. Social learning transmission pathways in coupled two PPM model

	Cohort transition	**Transmission pathway**
T_1	J_1 to J_2	Since juveniles can learn socially from any source, this pathway can involve horizontal, or oblique social learning (in any combination)
T_2	J_1 to A_2	As above
T_3	A_1 to A_2	Horizontal transmission between adults

Directly biased transmission (copy ‘what’ strategy)

A simple model of directly biased transmission of a dichotomous trait (or content bias (Kendal et al., 2018)), after Boyd and Richerson (1985) (eq 5.2) is considered. For two cultural variants c and d, there are two cultural ‘parents’ and both have equal weight in the transmission process, with parameter B representing the effect of directly biased transmission (where $0 \leq B \leq 1$). The frequency of variant d before transmission is p and the frequency following transmission (p') is calculated by the equation:

$p' = p + Bp(1-p)$ [after: Boyd and Richerson (1985)] (1)

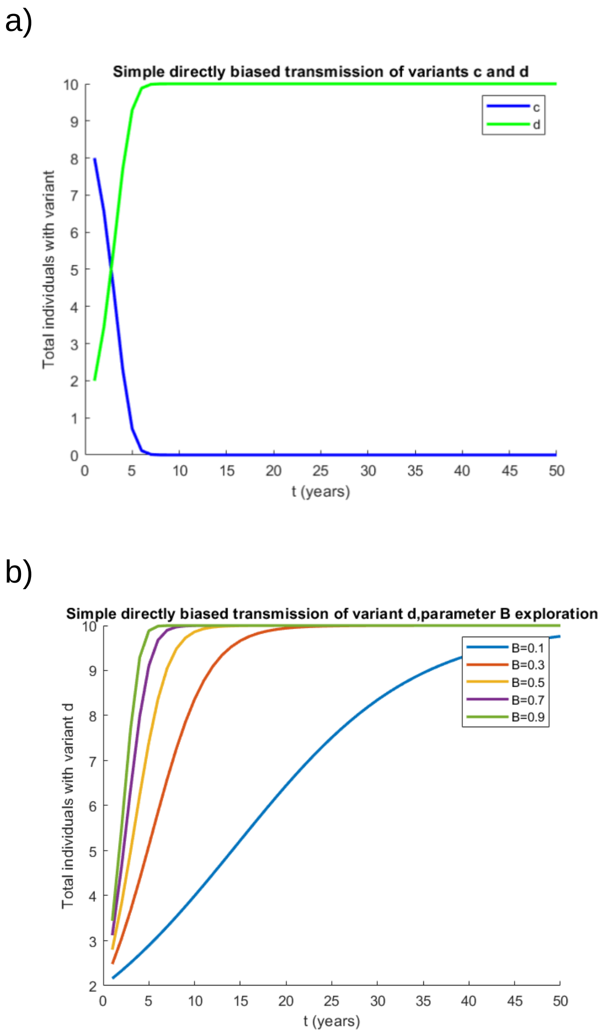


Figure 3. Parameter space exploration for simple content biased transmission of variants *c* and *d* (after Boyd and Richerson (1985)) for a total population of ten individuals. The initial condition is set as *d*=2, *c*=8. The number of individuals with variant *c* decreases as individual switch to variant *d*, which varies according to the strength of parameter *B* where a) *B*=0.9 and b) 0 ≤ *B*≤ 1.

A parameter space exploration for *B* shows how the magnitude of this parameter shapes the transmission of cultural variant *d* (Fig. 3b). For example, B=0.9 would represent a very high transmission rate, in which the majority of the cultural unit uptake the new cultural variant over a short period, such as a novel foraging strategy transmitted under environmental constraints, such as a shortage of prey. Boyd and Richerson (1985) suggest this can be considered a model of vertical transmission. Given the concept of ‘cultural parents’ it is argued here that this type of simple directly/content biased transmission can also be applied to horizontal transmission between juveniles or adults, or to oblique transmission between adults and juveniles. This directly biased transmission function assumes that the overall population for each stage remains constant following transmission, as individuals are reallocated between variants. This function is inserted into the model such that cultural transmission takes place following the demographics of the initial population projection (such that J_n+J_k and A_n+A_k are the same before and after transmission). The transmission then updates the demographics of the cultural units in each time step (Figure 4).

In the interests of parsimony, the model includes the following assumptions:

a) all transmission (movement between $\boldsymbol{x_n}$ and $\boldsymbol{x_k}$) is the result of content-biased social learning and that there is no trial and error learning (Rendell et al., 2010);
b) there is no migration into, or emigration out of the overall population;
c) there is ‘even’ connectivity between individuals;
d) informed adults (A_k) birth offspring (J_k) via $F2_k$ (Fig. 2a), which become informed in the first time step;
e) copying of the variant is fidelity-neutral but content sensitive (Morin and Miton, 2018);
f) each demographic time step equates to one cultural generation;
g) that there is no density dependence or environmental constraint to transmission.

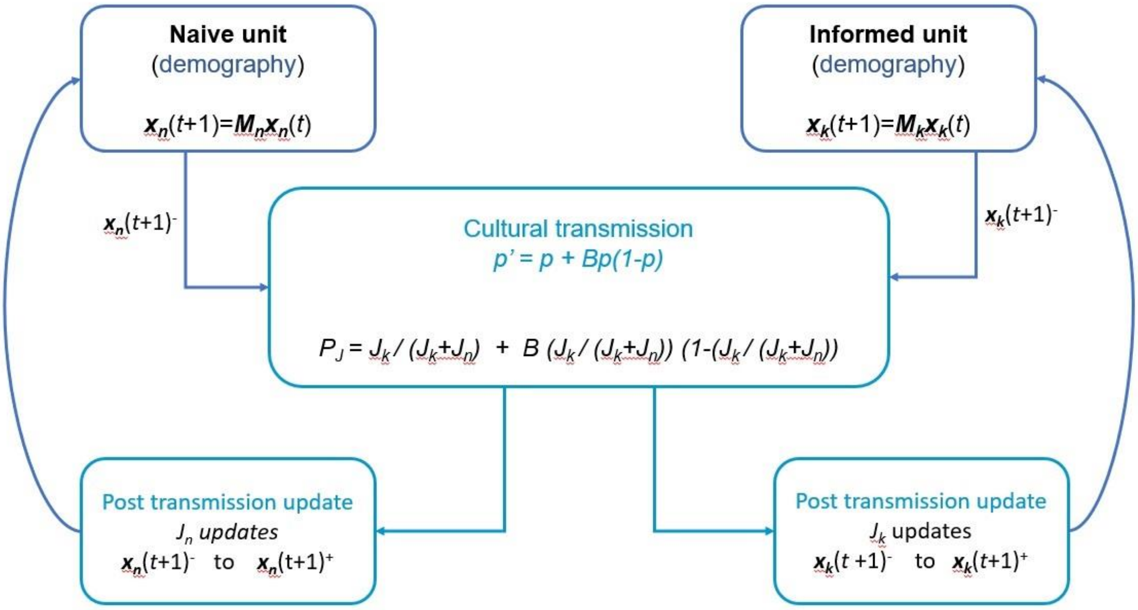


Figure 4. Schematic for population projections for $\boldsymbol{x}_n$ and $\boldsymbol{x}_k$ following content-biased transmission between the two cultural units. Here horizontal cultural transmission between juveniles is shown. The cultural unit is first projected (e.g. $\boldsymbol{x}_n(t+1)^-$). Following cultural transmission, the unit structure is updated before the next time step (e.g. $\boldsymbol{x}_n(t+1)^+$). Note: P_J is the new proportion of informed juveniles in the overall population following cultural transmission; '–' denotes unit before cultural transmission at time t and; '+' denotes unit following cultural transmission at time t.

Combining the coupled two PPM model with simple content biased transmission, under this scenario of transmission the key drivers for the propagation of the cultural variant of interest are the proportion (p) of the focal cultural variant (in this case informed individuals in $\boldsymbol{x}_k$), interfacing with demography of the projection matrix. This can be written as:

$$\begin{tikzcd}
\boldsymbol{x}_n(t) \arrow[r, "\text{demography}"] & \boldsymbol{x}_n^-(t+1) \arrow[r, "\text{transmission}"] & \boldsymbol{x}_n^+(t+1) \arrow[r, "\text{update}"] & \boldsymbol{x}_n(t+1)
\end{tikzcd}$$

$$\begin{tikzcd}
\boldsymbol{x}_k(t) \arrow[r] & \boldsymbol{x}_k^-(t+1) \arrow[r] & \boldsymbol{x}_k^+(t+1) \arrow[r] & \boldsymbol{x}_k(t+1)
\end{tikzcd}$$

These dynamics are next explored by examining the interplay between population dynamics and cultural transmission using some empirical PPMs.

3. Model exploration for content-biased social learning

To test this model, a two-stage PPM for a declining sperm whale population was selected from the literature (Gero and Whitehead, 2016)) [**PPM 1.1**]. To explore the possible advantages of cultural transmission, a declining population was selected to explore how cultural transmission interfaces with population dynamics. The naive cultural unit is governed by the parameters in **PPM 1.1**. This starting PPM is then used to generate PPMs for the informed cultural unit where the vital rates (survival of juveniles, survival of adults, or adult fecundity) are increased respectively. Here the advantage of cultural information (i.e., moving from the naive to the informed cultural unit) is assumed to confer demographic advantage to the informed unit through these respective increases in vital rates, i.e., the cultural information is adaptive. The increase in survival rates (*P1* and *P2*) cannot be greater than 1 (since 1 infers a 100% probability of survival). Whereas, the increase in adult fecundity (*F2*) can be improved through cultural transmission to some biologically plausible upper bound (which will vary according to species).

The social learning sperm whales exhibit multi-level social structure (Cantor and Whitehead, 2015) with enduring acoustic clans. But these clans may exhibit dynamic ranges, where large-scale range shifts are thought to be mediated through cultural transmission (Cantor et al., 2016). In this model it is assumed that individuals can switch freely between the two cultural units (naive or informed). These units do not necessarily represent broader acoustic sperm whale clans, but the transmission of information within an acoustic clan, where there is finer scale cultural structuring as the result of culturally transmitted information, for example long-line depredation (Schakner et al., 2014).

$$\begin{array}{ccc} & \text{calves} & \text{adults} \\ \text{calves} & 0.7451 & 0.0621 \\ \text{adults} & 0.0870 & 0.9495 \end{array} \quad [\textbf{PPM 1.1}]$$

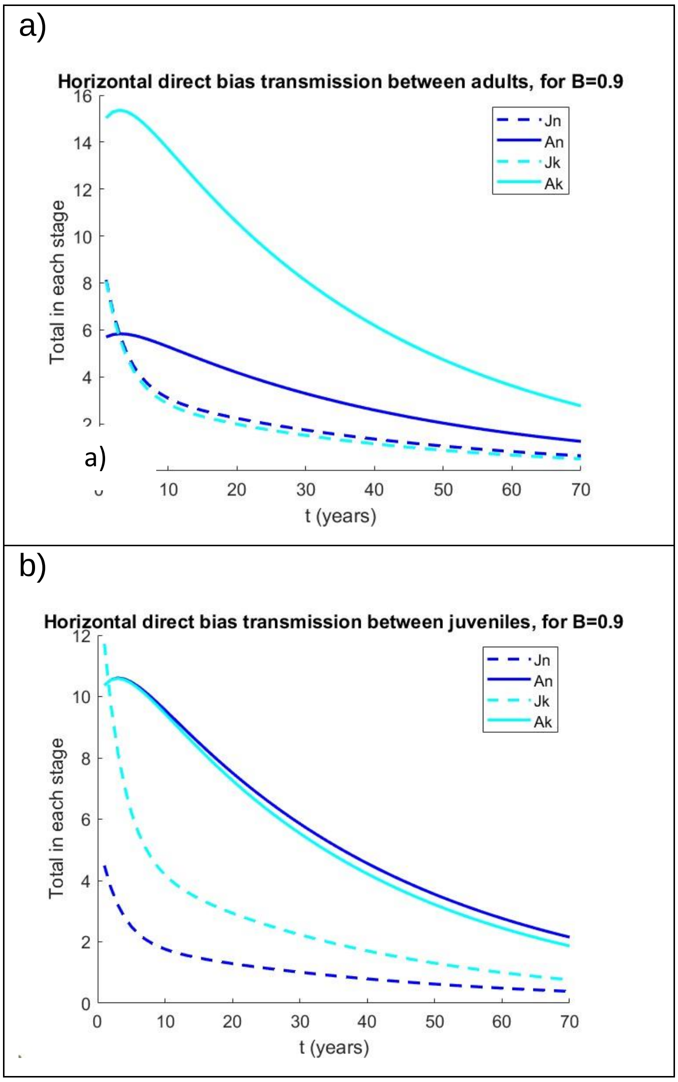


Figure 5: a) Projection of two initial cultural units consisting of 10 individuals in each age class (juveniles J_n and J_k, adults A_k and A_n) projected using **PPM 1.1**, with horizontal direct bias transmission between adults from naive population (A_n) to informed population (A_k). b) Projection for juveniles, using the same initial condition and allowing for social learning as juveniles with transitions between calves from the naive unit (J_n) to informed unit (J_k)).

As one might expect, a high transmission rate (B=0.9) between adults (Fig.5a) initially results in a dramatic increase in the informed adult unit, but both units decline over time. This indicates that despite the transmission between populations, the declining population dynamics which is governed by the same growth rate, $\lambda = 0.9732$ (PPM 1.1), continues to drive the population towards zero. However, the initial boost to the informed population resulting from cultural transmission slows this trajectory. Similarly, a high transmission rate (*B*=0.9) between calves (Fig.5b) initially results in a dramatic increase in the informed calf population (as calves are converted from the naive to the informed unit), but both units decline over time.

Investigating the effects of population structure, simulations for randomly selected initial population structures reveal the same overall pattern i.e. despite the high transmission rate (*B*=0.9) the declining population dynamics (driven by **PPM 1.1**) ultimately determining the outcome for these cultural units (Fig. 5 and 6).

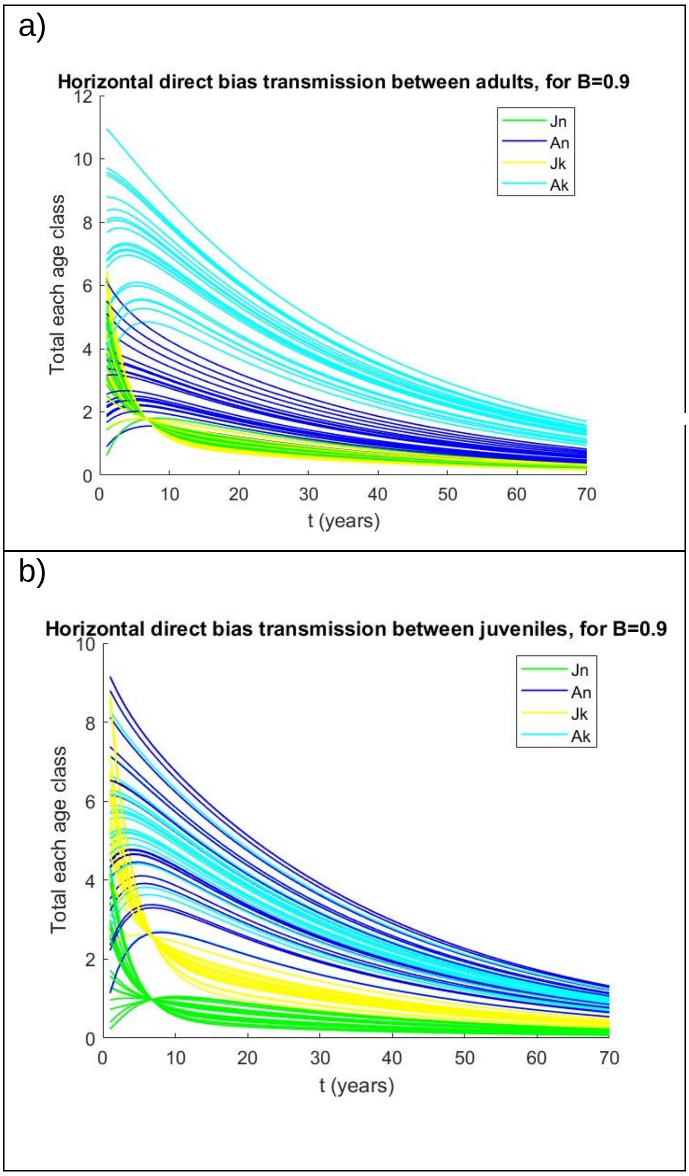


Figure 6: Simulations of directly biased transmission, *B*=0.9 between a) adults, and b) juveniles, for 20 randomly selected initial population structures with a total initial population of 10 individuals across two stages (using **PPM 1.1**).

As the result of direct biased transmission between adults, an increase in A_k is clearly visible (Fig. 6a). However, note that transmission between calves under the same scenario produces interesting transients in calf dynamics (Fig. 6b). These transient dynamics are explored further in Chapter 5.

Despite high transmission rates (*B*=0.9) the population parameters (**PPM 1.1**) apparently dominate the asymptotic, long-term outcomes for these cultural units. However, beyond the transmission of relatively content neutral cultural information (i.e., content that has no influence on survival or reproduction), next the consequences of cultural transmission that results in a benefit to vital rates is investigated.

Perturbation of vital rates

Taking this example of a declining mammalian population ([**PPM 1.1**]), the interplay between population dynamics and cultural transmission in this coupled system is explored by perturbation of the vital rates. The vital rates of the informed population are perturbed by adding 10% to the survival of the juveniles ($P1_k$), the survival of the adults ($P2_k$), or the reproduction of the adults ($F2_k$), respectively (Fig. 7).

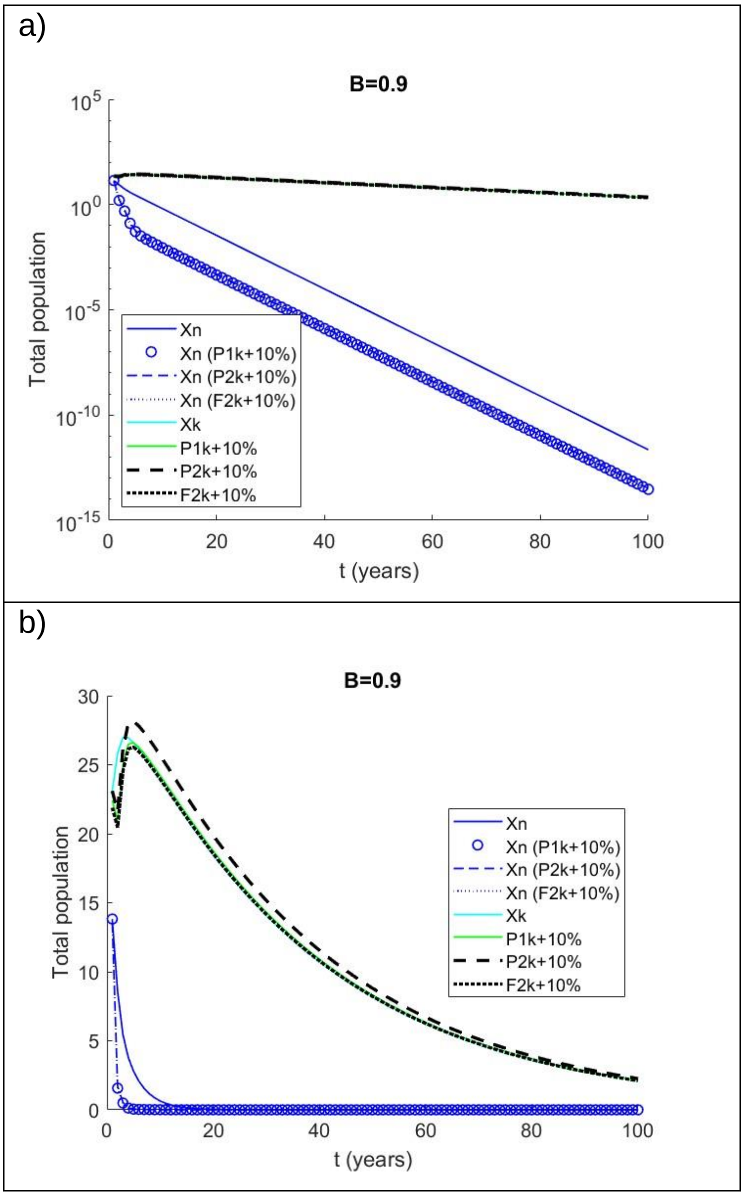


Figure 7. Projection for a declining mammalian population [**PPM 1.1**] with two cultural units, where the vital rates are perturbed such that the informed cultural unit has a 10% increase in: survival of juveniles ($P1_k$); survival of adults ($P2_k$); or fertility in adults ($F2_k$). The projection is provided for: a) cultural transmission between adults (log plot), B=0.9; and (b) cultural transmission between adults, B=0.9.

In this example, when the simple social learning function is applied for transmission between the naive ($\boldsymbol{x_n}$) and informed ($\boldsymbol{x_k}$) populations (Fig. 7 a and b), the naïve unit declines much more rapidly than the informed unit, as the result of both the benefit of the increase in vital rates to $\boldsymbol{x_k}$ and the boost from conversions from $\boldsymbol{x_n}$ to $\boldsymbol{x_k}$.

Exploring dynamics for other species PPMs

To examine these coupled dynamics further a range of scenarios for growing and declining mammalian and avian populations are considered (Fig. 8). Examples were extracted from the database COMADRE[4] (Table 2), (see Appendix 4.2 for R and MATLAB scripts). In the same way as in the sperm whale example, it is assumed that being informed is advantageous, which results in one of the entries in the original PPM (juvenile survival, adult survival or adult fecundity) increasing.

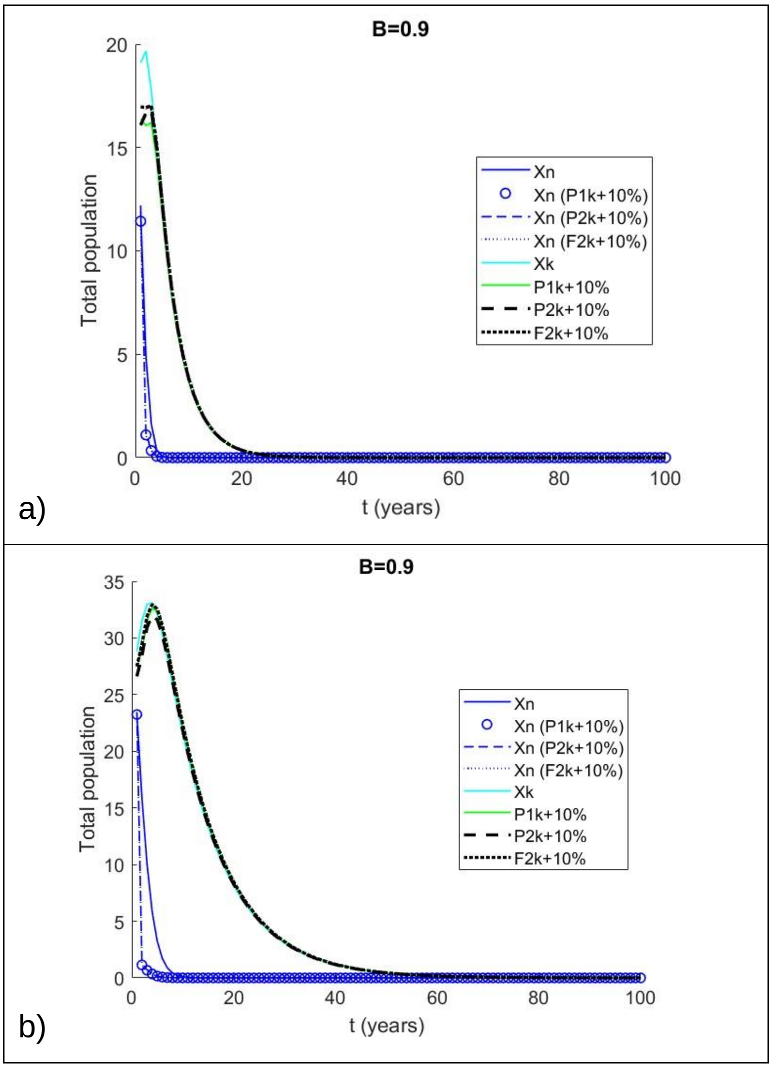
Table 2. Two stage PPMs for declining mammal and bird populations, extracted from COMADRE database.

Tamiasciurus douglasii, Douglas squirrel (Schumaker et al., 2004) $\mathbf{x_n} \begin{pmatrix} 0 & 0.75 \\ 0.2 & 0.6 \end{pmatrix}$ $\lambda = 0.7899$	*Passer domesticus*, House sparrow (Maclean et al., 2008) $\mathbf{x_n} \begin{pmatrix} 0.44 & 1.57 \\ 0.13 & 0.47 \end{pmatrix}$ $\lambda = 0.9070$	*Forpus passerines*, Green-rumped parrot (Sandercock and Beissinger, 2002) $\mathbf{x_n} \begin{pmatrix} 0.5805 & 0.6627 \\ 0 & 0.7612 \end{pmatrix}$ $\lambda = 0.7612$
Hirundo rustica, Barn swallow (Gruebler et al., 2014) $\mathbf{x_n} \begin{pmatrix} 0 & 3.06 \\ 0.1633 & 0.4758 \end{pmatrix}$ $\lambda = 0.9837$	*Vermivora chrysoptera*, Golden winged warbler (Bulluck et al., 2013) $\mathbf{x_n} \begin{pmatrix} 0.32 & 0.64 \\ 0.214 & 0.427 \end{pmatrix}$ $\lambda = 0.7474$	*Physeter macrocephalus*, sperm whale (Gero and Whitehead, 2016) $\mathbf{x_n} \begin{pmatrix} 0.7451 & 0.0621 \\ 0.0870 & 0.9495 \end{pmatrix}$ $\lambda = 0.9732$

---

[4] COMADRE Animal Matrix Database (2022). Available from: https://www.compadre-db.org [27 Jan 2022, Version 4.21.8.0]

In the following projections, cultural unit $\boldsymbol{x_n}$ is set to the empirical PPM, with initial growth rate (λ) calculated. Then the survival of the informed juveniles ($P1_k$), survival of informed adults ($P2_k$) and fertility rate of informed adults ($F2_k$) in the informed cultural unit ($\boldsymbol{x_k}$) are each increased by 10%, respectively, increasing the growth rate (Fig. 8). In all the B=0.9, to simulate a high rate of transmission between the two units. Both units have an initial condition of 10 juveniles and 10 adults in the starting population.



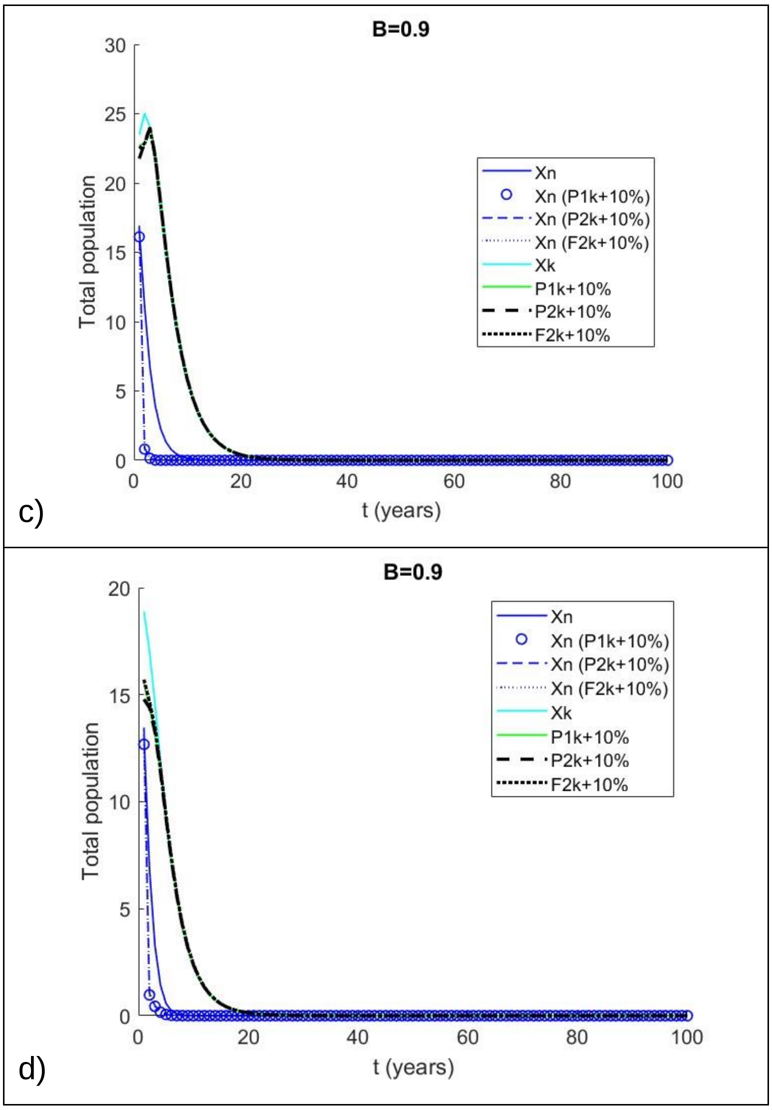


Figure 8. Vital rate perturbation projections for 2-stage mammalian and avian PPMs, with parameter B=0.9, for a) Douglas squirrel, b) house sparrow, c) green rumped parrot, and d) golden-winged warbler.

These plots show that, as one might expect, there is an advantage to the informed cultural unit $\boldsymbol{x_k}$, through the increase in vital rate in each perturbation. However, these plots also indicate this advantage to the informed cultural unit also generates more complex dynamics in these coupled systems than one would anticipate from a system driven solely by the parameters of the PPM, without cultural transmission between the two units (for further examples see Appendix 4.1).

By coupling the two cultural units with this social learning function, naive individuals are redistributed from the naive to the informed cultural unit. Through this process, the social learning function drives the ‘conversion’ towards the unit with the beneficial cultural behaviour. Therefore, it can be anticipated that an increase in vital rates of the informed population may exacerbate the benefit of this transmission, as the informed unit grows and continues to convert increasing numbers of individuals. The projections in Fig. 7 and 8 (and Appendix 4.1) show that is indeed the case. For a growing population (i.e. $\lambda > 1$), in this coupled system a 10% increase in any of the three vital rates of the informed unit ($P1_k$, $P2_k$ or $F2_k$) causes the naive unit to decline rapidly, while the informed unit grows (e.g. coyote, bob cat and Adelie penguin, Appendix 4.1).

For a declining initial population (i.e. $\lambda_1 < 1$), the initial benefit to the informed cultural unit can clearly be observed (e.g. house sparrow and green-rumped , Fig. 8). This is the result of conversion from the declining naive unit, which boosts the informed unit in the short-term. However, the informed unit can rapidly reach a peak, as the result of both the naive unit crashing (with the benefit of conversions being lost) and the population dynamics of the system driving the unit back toward decline, following this initial boost.

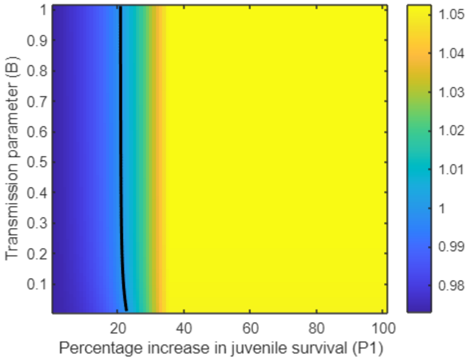
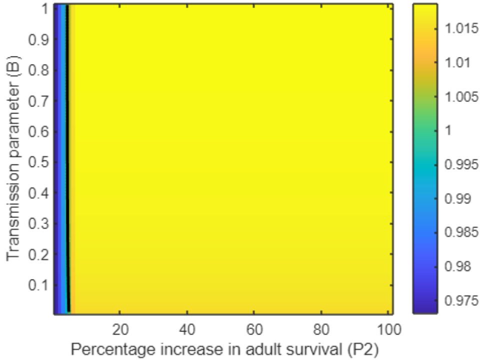
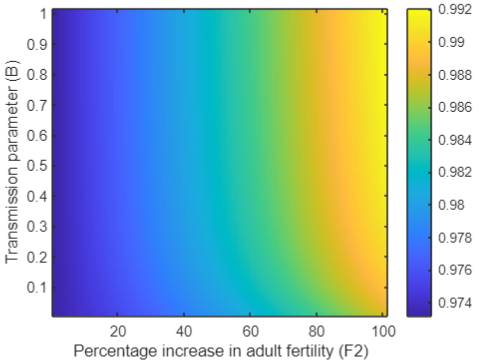
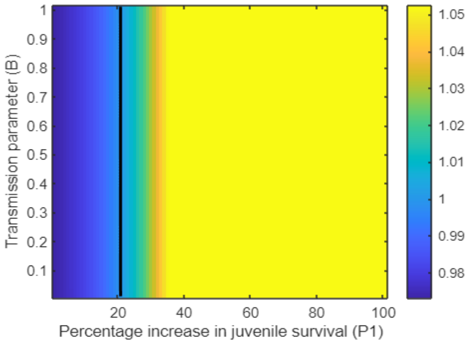
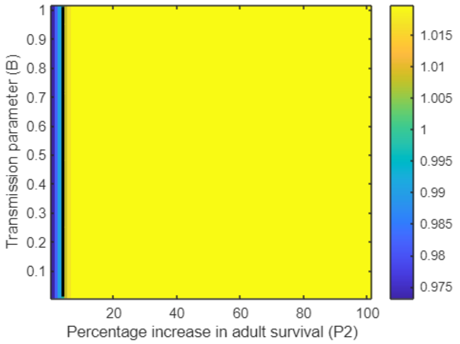
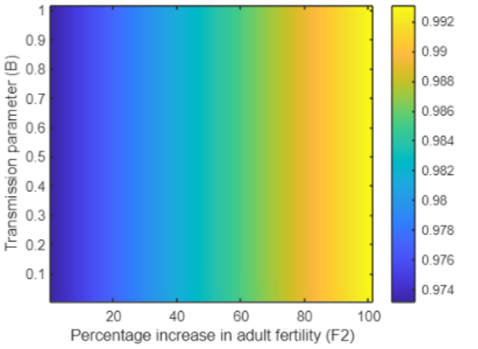
Exploring optimal threshold for population growth

To better understand the coupled dynamics of this system, a series of simulations were undertaken using the parameters for a declining sperm whale population, **PPM 1.1** as the starting point. A parameter space exploration was undertaken for a range of percentage improvements in vital rates, in concert with a range of strengths of transmission parameter (B=0 to 1), for horizontal transmission between adults (Fig. 9) and then for non-vertical social learning as juveniles (Fig. 10).

The simulations were run for a range of initial conditions, to explore the optimal threshold between the coupled dynamics of the increase in transmission parameter (B) and the improvement in vital rates of the informed cultural unit, $P1_k$, $P2_k$ and $F2_k$ respectively, to bring about growth in the overall population, i.e. $\lambda > 1$.

A contour line was fitted in each simulation where λ=1, to identify the threshold at which the previously declining overall population ($\boldsymbol{x_n} + \boldsymbol{x_k}$), becomes stable and beyond which (λ>1), it transitions into a growing population.

i) Horizontal transmission between adults

	$P1_k$ perturbed	*$P2_k$* perturbed	*$F2_k$* perturbed
A			
B			

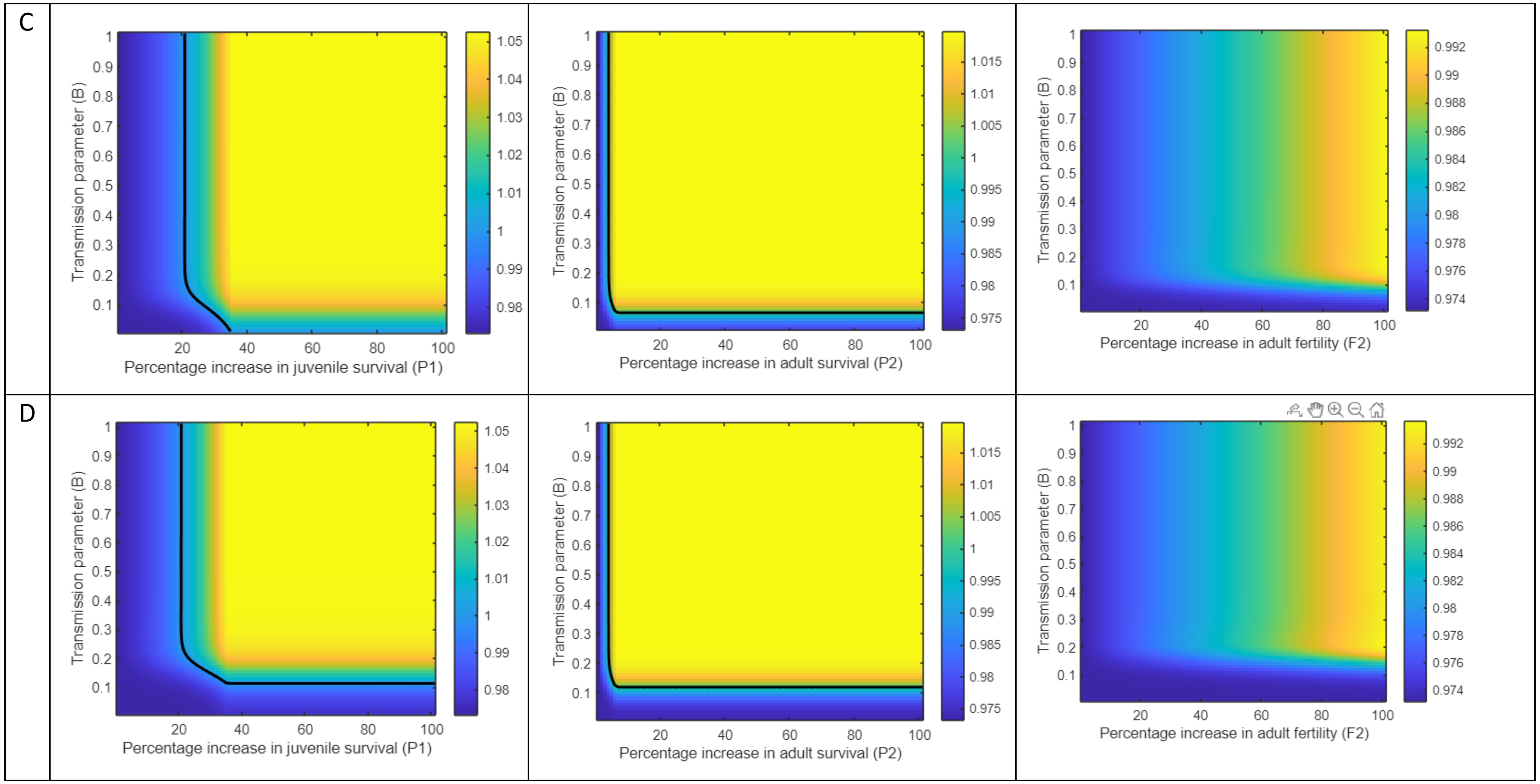
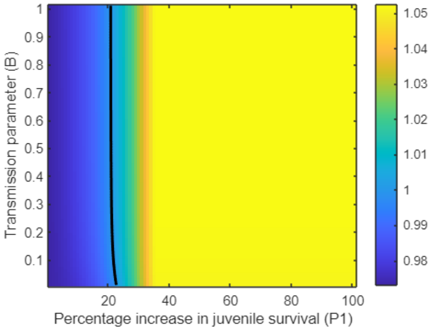
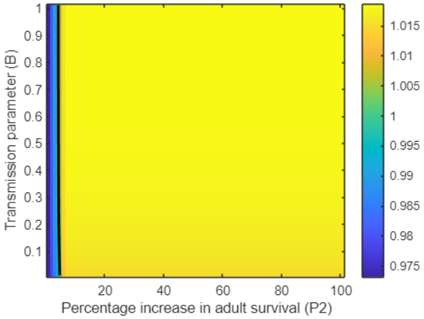
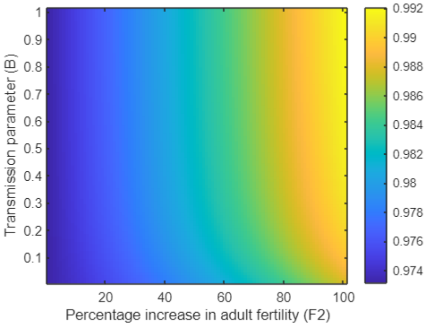
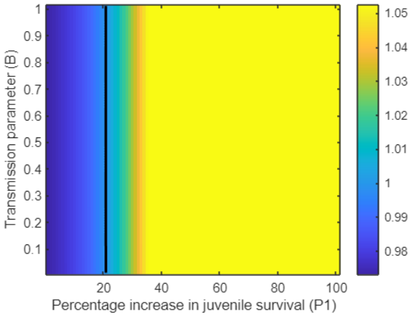
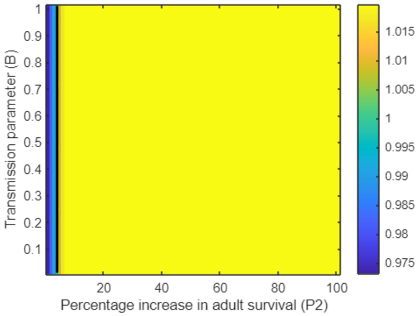
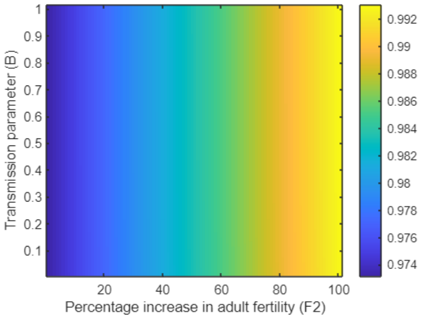


Figure 9. Parameter space exploration for percentage increase in survival and fertility following horizontal transmission between adults through directly-biased social learning in a declining sperm whale population. Colour bar represents value of λ.

Population set with the following initial conditions: (A) J_n=10, A_n=10, J_k=10, A_k=10; (B) J_n=4, A_n=10, J_k=40 A_k=800; (C) J_n=40 A_n=800, J_k=4, A_k=10; and (D) J_n=400, A_n=8000, J_k=4, A_k=10.

ii) Non-vertical social learning as juveniles

	$P1_k$ perturbed	$P2_k$ perturbed	$F2_k$ perturbed
A			
B			

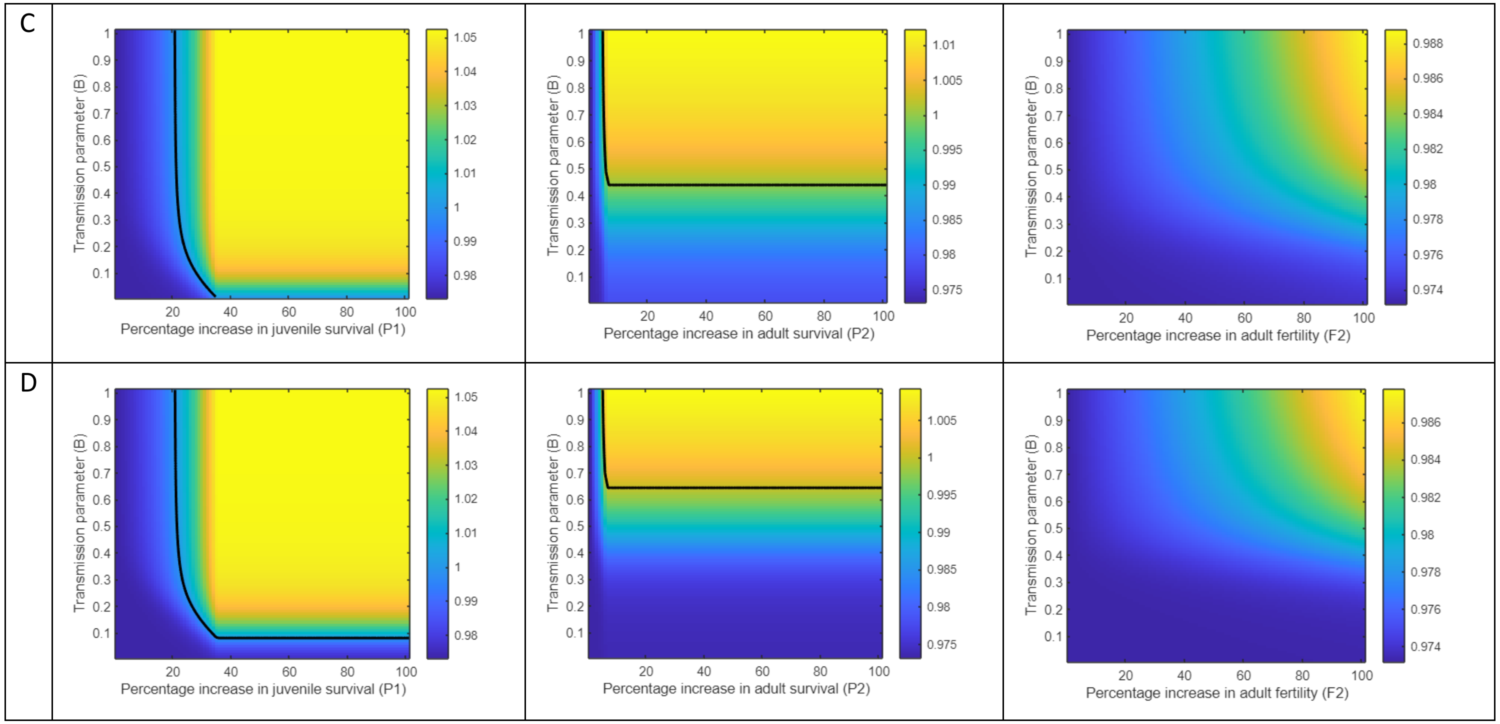
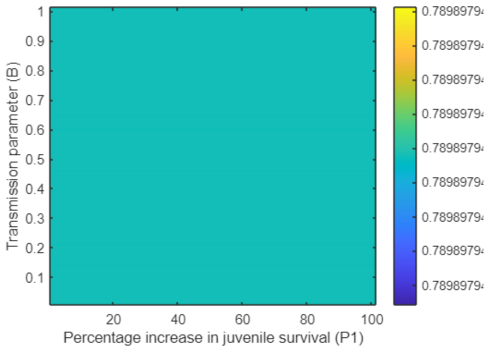
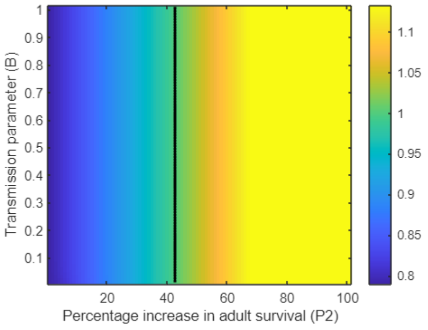
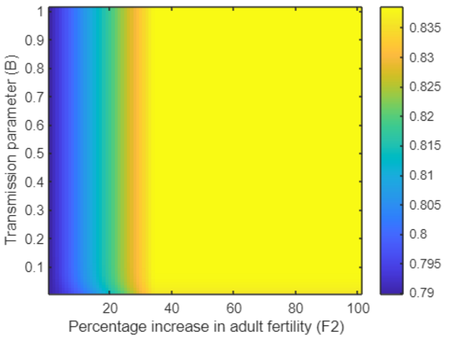
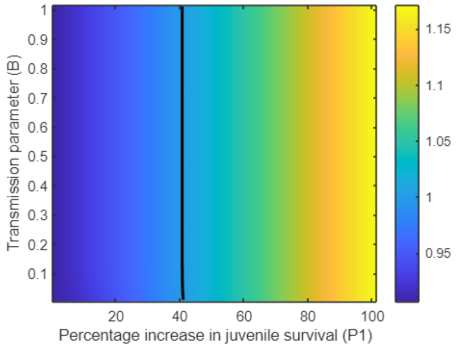
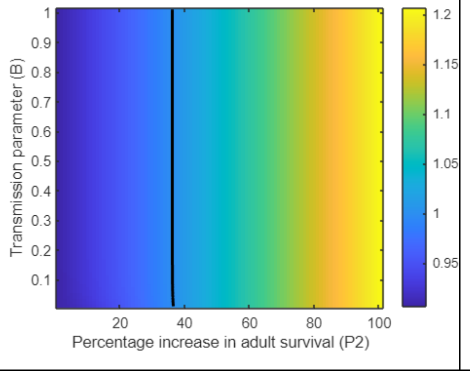
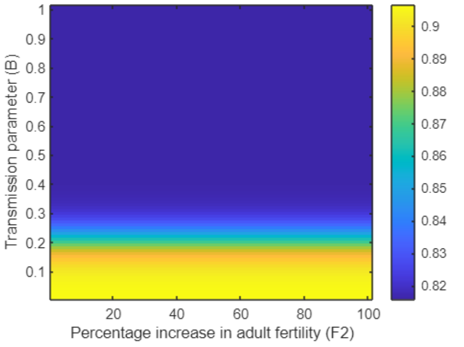
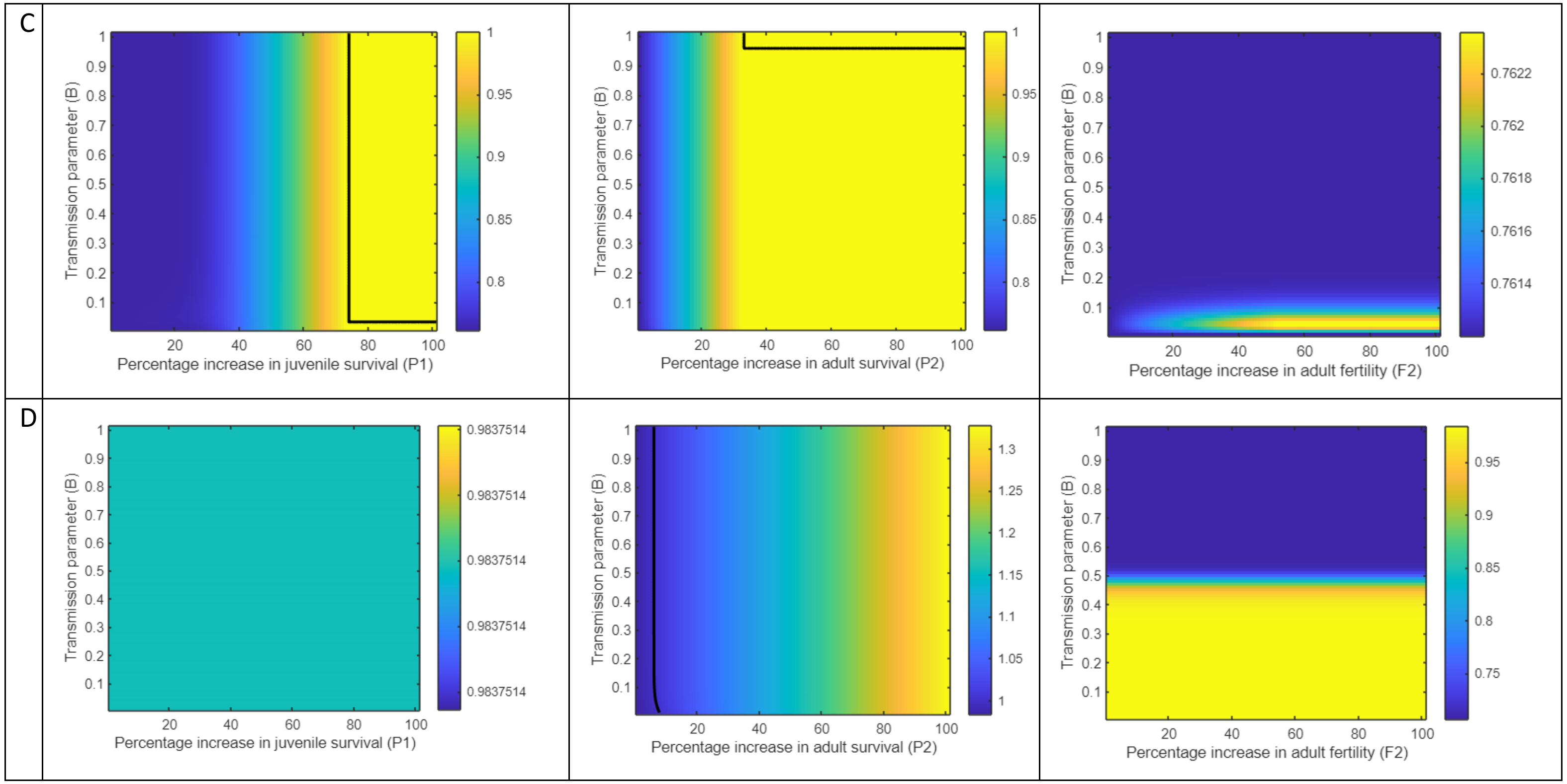


Figure 10. Exploration of sperm whale perturbations with non-vertical social learning as juveniles for the following initial conditions: (A) J_n=10, A_n=10, J_k=10, A_k=10; (B) J_n=4, A_n=10, J_k=40 A_k=800; (C) J_n=40, A_n=800, J_k=4, A_k=10; and (D) J_n=400, A_n=8000, J_k=4, A_k=10. Colour bar represents value of λ.

To explore these dual dynamics further, simulations were also conducted using the PPM examples in Table 2. The initial conditions were set as in the previous simulations, for the purpose of comparison, for horizontal transmission between adults only.

<u>iii) horizontal transmission between adults for other species</u>

	$P1_k$ perturbed	$P2_k$ perturbed	$F2_k$ perturbed
A			
B			


C
Transmission parameter (B)
Percentage increase in juvenile survival (P1)
Percentage increase in adult survival (P2)
Percentage increase in adult fertility (F2)
1
0.95
0.9
0.85
0.8
0.7622
0.762
0.7618
0.7616
0.7614
D
0.9837514
1.3
1.25
1.2
1.15
1.1
1.05
0.75

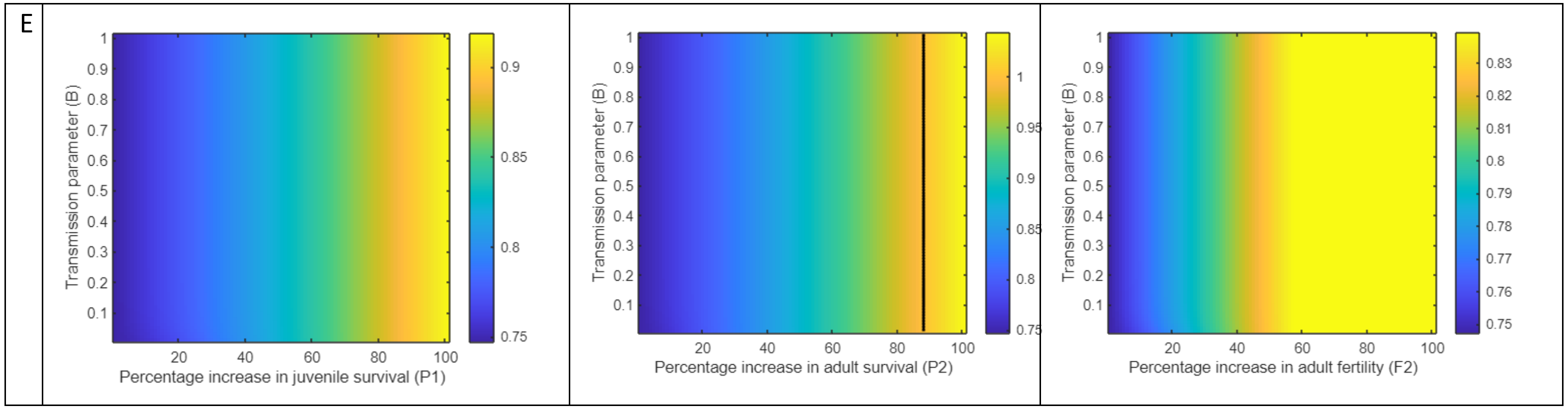


Figure 11. Parameter space exploration for percentage increase in survival and fertility with horizontal transmission between adults, through directly-biased social learning for a range of different taxa: (A) Douglas squirrel (initial λ=0.7899); (B) house sparrow (initial λ=0.9070); (C) green-rumped parrot (initial λ=0.7612); (D) barn swallow (initial λ=0.9837); (E) golden winged warbler (initial λ=0.7474). Note, in all cases, J_n=10, A_n=10, J_k=10, A_k=10 (i.e. total initial population =40) is the initial condition. Colour bar represents value of λ.

Interpreting these heatmaps, the black contour line indicates a threshold where the combination of incremental change in transmission (*B*), coupled with percentage increase in specific vital rate, results in a stable population, where λ =1. Where the contour line is vertical, this indicates that there is a threshold for growth that is associated with a specific percentage change to the vital rate under perturbation. Where the contour is horizontal, this indicates a threshold for the transmission rate that will tip the system from declining into growing.

The predominance of vertical contour lines (λ =1), in these simulations, indicates that in many of these scenarios it is the percentage change in the specific vital rate that tips the system into growth, rather than effects of the coupled transmission. However, in scenarios where the populations have higher overall initial abundance (C and D), the effects of transmission on the threshold for λ =1 became more apparent (Fig. 9 and 10).

Comparing the plots in Fig. 9c (transmission between adults) and Fig.10c (transmission between juveniles) it is notable that an increase in the survival of the informed adults ($P2_k$) shifts the threshold for growth to approximately *B*=0.44 for a percentage increase in adult survival >5%, whilst the transmission is between juveniles (Fig. 10c). Whereas, this threshold for transmission is much lower (c. *B*<0.1 with an increase in adult survival <5%) when transmission is between adults (Fig. 9c).

The relative abundance of the informed unit to the naive unit in the initial population also appears to play a role in determining the threshold for the combination of the transmission and the vital rate parameters to bring about growth. This may be the result of an initial condition with more naive individuals than informed, i.e. the system has to pass a threshold of transmission before the benefits of the contribution of transmission and vital rate improvement together shift the population from declining to increasing. This may operate as a type of Allee effect (Allee, 1931; Stephens et al., 1999) at low population densities in this system.

But stage structure may also be an important factor in determining the threshold for growth in this system. For example, the overall initial population abundance in scenarios B and C (Fig. 9 and 10) where the relative initial proportions between the naive and informed cultural units are reversed, i.e., in scenario B there are 60 times more informed than naive individuals in the initial population. Whereas, under scenario C there are 60 times more naive than informed individuals in the initial population.

It is also notable that in some simulations, there is no point at which the population starts to grow, despite 100% increase in vital rates. This is the case in the sperm whale simulations for fertility (Fig. 9 and 10), where no contour is visible for any of the simulations with percentage changes to $F2_{k.}$ This is also true for 100% incremental increase in $F2_k$ for the other species for which simulations were conducted (Fig. 11). Interestingly, increasing transmission parameter (B) in the house sparrow, green-rumped parrot and barn swallow simulations for $F2_k$ appears to move the population away from growth, rather than towards it (see for example the green-rumped parrot simulation, where the optimum window for reducing decline is shown in yellow) (Fig. 11). These results are somewhat counter-intuitive and warrant future exploration as they may be the result of the coupled dynamics of this system, but may also relate to the life history of the species, as expressed through the PPM parameters.

Discussion

The coupling of these, two-stage cultural units with a simple model of social learning has produced some complex and unexpected results. In some instances, as anticipated the model shows that where one unit has benefits to their vital rates as a result of social learning, linking this informed unit to a naive unit through content biased social learning can, under certain parameter regimes, result in an overall benefit to the total population as individuals are converted from the naive unit to the informed unit. This is as expected, given the combination of the transmission and benefits from increased vital rates.

However, this coupling can also create some complex dynamics, in both the longer-term (asymptotic) and short-term (transient) dynamics of the system. This chapter has focused on the asymptotic dynamics and the transient dynamics are explored further in Chapter 5.

It has been argued that knowledge may benefit a cultural unit (see Chapter 3 for multiple examples). By explicitly linking the population of cultural units through directly biased social learning, it has been possible here to gain some insights, not only on how social learning can create ‘conversions’ to new cultural units, but also on some of the complex behaviour of a system when transmission is coupled with population dynamics.

The asymptotic dynamics in Figures 5 and 6, for example, are driven predominantly by **PPM 1.1**, which is parametrised for a declining population of sperm whales, where an initial simulated population of 40 tends towards zero over 100 years. This is the result of the negative growth rate, $\lambda = 0.9732$ (**PPM 1.1**). Despite cultural transmission and movement between the cultural units, in this scenario the cultural transmission is content neutral, so there is no direct positive or negative effect on survival or fertility rates from the cultural transmission. As a result, the overall outcome is predominantly driven by the population parameters in **PPM 1.1**.

Under scenarios where cultural transmission results in modest (+10%) improvement to either survival or fertility (Figures 7 and 8) the interplay between cultural dynamics and the driving population parameters become more complex. For growing populations, (i.e., $\lambda > 1$), as expected, a 10% increase in survival or fertility in the informed unit drives an increase in the informed unit. This creates steady growth in the informed unit, which after multiple generations (60 to 80 years) can result in exponential growth (e.g., coyote, bob cat and Adelie penguin, Appendix 4.1). In contrast, whilst an initial boost to an informed unit of a declining population may be observed (e.g. house sparrows, Figure 8b), this may only last a few generations, with the long-term population dynamics over 100 years being driven towards zero by the overall negative growth rate.

To better understand these processes a parameter space exploration for the interaction between incremental increase in vital rates and cultural transmission was conducted (Figures 9 to 11). This demonstrates how different parameter regimes can tip a population from declining into growing (or vice versa). Depending on which vital rate is perturbed ($P1_k$, $P2_k$, or $F2_k$), the outcome is contingent on the interplay between transmission and change to vital rates. This highlights how life history parameters, such as time spent by an organism in a specific developmental stage and probability of surviving (and/or reproducing) and aging into the next stage, can influence how cultural information is transmitted across a population. For example, if cultural transmission of a specific foraging strategy resulted in increased survival in reproductive adults (P_2) within a cultural unit, these informed adults may 'boost' the population by continuing to reproduce for longer, with the added benefit (positive feedback) of continuing to transmit the skills associated with the advantageous foraging strategy.

The optimal parameter regime for growth ($\lambda \geq 1$), as well as being dependent on the transmission parameter (B) and incremental change in vital rates, is also contingent on a third parameter: relative abundance of the naive ($\mathbf{x_n}$) and informed ($\mathbf{x_k}$) units in the initial population. For example, in Figures 9 and 10, as the number of naive individuals ($\mathbf{x_n}$) in the initial population is increased relative to the number of informed individuals ($\mathbf{x_k}$) (scenarios C and D), the threshold for λ to tip into growth ($\lambda \geq 1$) is not only contingent on the percentage increase in survival (P_1 or P_2), but also the strength of the transmission parameter B. Under these scenarios, there are only a small number of informed individuals relative to the naive population and the rate of transmission (B) must also be over a certain threshold for the positive effects of the increase in survival resulting from cultural transmission to bring about population growth. Such considerations may be important in interventions such as reintroductions, where the relative abundance of informed to naive individuals can influence success as survival strategies are shared (e.g., Jackson et al., 2008; Kierulff et al., 2012). Stage structure, i.e. the relative abundance of juveniles to adults in each cultural unit may also be important and warrant further exploration. But overall abundance ($\boldsymbol{x_n} + \boldsymbol{x_k}$) may be highly relevant, as per the Allee effect. How these complex dynamics might be utilized in a wild setting is discussed in the next chapter, where the conservation implications of these findings are explored further.

Arguably, the parameter regimes required to 'tip' a population into growth (or decline) in this system are very specific and contingent on a number of variables. It is interesting that by taking a simple social learning model and applying this to PPM projections in a coupled system results in these complex outcomes (May, 1976). These complex dynamics are explored further in Chapters 5 and 6.

To better understand these complex processes, managers can be encouraged to incorporate the following into conservation assessments for species that learn socially:

i) explore the temporal and spatial patterning created by cultural transmission within these populations and prioritise research on how specific cultural variants may influence vital rates and habitat use;

ii) gather data on the propagation of cultural variants across social networks and evaluate the relative abundance of informed to naive units, to help elucidate the thresholds for transmission and vital rate parameters to bring about growth in wild populations;

iii) where possible, determine the route of social transmission (horizontal, vertical, or oblique) and whether this is ubiquitous across the population, or in isolated cultural units.

Conclusion

This model system with two cultural units shows that coupling stage structed population dynamics with a simple form of social learning can have a range of effects, depending on the parameter regime. The strength of the transmission parameter can influence not only the movement towards the informed population in this system (and thus the outcomes for both cultural units), but also can influence how the benefits to adult survival or reproduction of a particular cultural trait interfaces with population dynamics. It is notable that these effects can be demonstrated with only a 10% increase in adult survival or reproduction, which perhaps could provide opportunity in some conservation settings to manipulate transmission parameters to capitalise on marginal gains in survival or reproduction for the benefit of wider populations. Further, it may be important to further explore other transmission routes (as per Fig. 2a) and some of the transient dynamic under certain parameter regimes (for example in the Douglas squirrel example). These shorter-term, transient dynamics are the focus of the next chapter, as they may be particularly relevant for responses to rapid environmental change and effective conservation intervention.

Considering these findings for asymptotic dynamics, here it has been shown that a cultural variant with rapid transmission (*B*=0.9), comparable to a cultural fad that might pass quickly through a population, has a very different impact on population dynamics than the spread of a cultural variant with a much lower transmission rate (*B*=0.1). The relative abundance of cultural units, as well as stage structure can also influence how social learning propagates across such system and at very low population densities the benefits of cultural transmission between cultural units may be suppressed. This system does not include any density dependence and limits to growth, as inherent in real world systems and this system has also focused on culturally transmitted behaviour that is adaptive. The interface between these dual dynamics of cultural transmission and population dynamics in density dependent systems, as well as the transmission of information that is not adaptive are the focus of Chapter 6.

CHAPTER 5

Conserving cultural populations: management options

Abstract

The cultural structuring of populations presents a considerable challenge for conservation policy makers and practitioners. Given that cultural units may require different resources, or respond differently to conservation intervention, animal culture creates a conundrum of how best to focus limited resources on conserving populations that are culturally heterogenous and whose dynamics may be complex. Here three management options are explored using a coupled system with two interacting cultural units that are linked through directly-biased social learning (see Chapter 4). The first option is to expend effort conserving the more vulnerable cultural unit with less adaptive cultural behaviour. The second option is to manipulate the transmission of cultural variants to maintain overall populations as stable or growing for longer whilst further conservation intervention can be deployed. Or, thirdly, managers may attempt to maintain cultural diversity in the overall population by expending equal effort on both cultural units. These options are explored for a range of scenarios and taxa. Simulations show that transmission rate, relative abundance and stage structure of cultural units, in addition to effects of socially learned information on survival, together create a complex of parameters than can influence both asymptotic and transient dynamics in these systems, making predicting outcomes challenging. Since the fates of the two cultural units in this model system are intrinsically bound through the endogenous process of social learning, it is concluded that the most conservative course of action may often be option 3, particularly where data on the other parameters are difficult to obtain. A notable exception may be reintroduction efforts, where some of these parameters can more readily be manipulated.

Introduction

The current rationale for conservation is to conserve biological diversity, by conserving the adaptive potential of species (Eizaguirre and Baltazar-Soares, 2014). But how does phenotypic diversity influence overall biological diversity and what aspects of behavioural phenotypic diversity, including cultural diversity, are adaptive? Where should conservationists focus effort to achieve the best outcomes for both behavioural and genetic diversity? Where populations are culturally heterogenous, how can the processes of cultural transmission be maximised to achieve the most efficient conservation outcomes? Further, what insights and opportunities might be overlooked by neglecting to account for cultural heterogeneity and instead assuming that populations and social groups are behaviourally homogenous?

Social learning of behavioural variants - and any resulting culturally-generated phenotypic diversity - may influence population viability, demography and evolutionary or adaptive potential by allowing social information to spread between parents and offspring, and through social groups, but also by structuring populations (Mcgregor et al., 2000; Whitehead, 2010). For example, social learning can drive foraging specialisation in sympatric groups, which in turn can influence evolutionary potential and lead to niche partitioning, as demonstrated in killer whales (*Orcinus orca*) and bottlenose dolphins (*Tursiops* sp.) (Ansmann et al., 2012; Foote et al., 2016; Whitehead et al., 2019). This can result in superficially cryptic population structure, e.g., where effective population size of partitioned, socially isolated cultural groups may be less than indicated via naive census survey. Thus, standard genetic or geographic delineation between populations may be insufficient for the conservation of some cultural species (Brakes et al., 2021).

While social learning can facilitate the spread of important innovations, it can also hinder the transmission of adaptive behaviour and conservatism can lead to cultural variants which are no longer ecologically advantageous being maintained (Barrett et al., 2019). This chapter focuses on the transmission of ecologically advantageous, or adaptive socially learned information (for an exploration of the transmission of maladaptive cultural traits, see Chapter 6).

Given that conservation resources and practical options can often be limited, the challenge for conservation managers is to understand the best way to apply limited resources to culturally heterogenous populations. In a population with two distinct cultural units, linked by directly biased social learning (as described in the previous chapter), the underlying question then emerges: is it more productive to conserve the informed cultural unit with adaptive information and higher vital rates and the greater likelihood of persisting; or is it better to conserve the naive cultural unit with lower vital rates and lower likelihood of persisting? Generally, if an approach based on conserving genetic diversity is applied, one might assume that the answer is to protect the cultural unit with the lower vital rates which are leading to a more rapid decline, or to protect the cultural unit with the lower abundance, (since these are the standard parameters used to help calculate thresholds in current conservation paradigms). This option might be chosen on the basis that, on first inspection, this seems a logical approach to help maintain cultural diversity within the population.

On the other hand, one might take the approach of considering that where a cultural unit is declining, this may indicate that the culture being propagated may be either less adaptive or even maladaptive for the current social or ecological conditions. In human societies there is good evidence for culture driving population collapse and this phenomenon has been well documented, e.g. Rapa Nui, Easter Island (Diamond, 2005; Tainter, 1988). Using this rationale, it could be argued that less effort should be spent on conserving a smaller, declining cultural unit (concede defeat) and instead, more effort should be spent on conserving the larger cultural unit, which is more likely to thrive as the result of either greater abundance or more favourable vital rates. More favourable vital rates would make this unit likely to be better adapted to the current environment, because this cultural adaptation has provided some advantage, (through either survival or reproduction) so is either increasing, or at least declining at a slower rate, which may make conservation intervention more plausible.

This is a significant conundrum for conservation managers when faced with burgeoning data on cultural heterogeneity across populations (Whiten, 2017a), but only limited resources to help maintain entire demographic and genetic populations, let alone cultural units. It is demonstrably the case that there is no one size fits all solution to the conservation of cultural populations (see Chapter 3). One added complication, as demonstrated by the research in this thesis, is that while an informed cultural unit with higher vital rates can increase very rapidly as the result of both more favourable populations dynamics and cultural transmission, resulting in conversion from a naive cultural unit, under certain parameter regimes, this increase can also be limited by the conversion rate from the naive unit (Chapter 3). Under such a scenario, with directly biased social learning, where individuals can move freely between cultural units, the future of both cultural units within the wider population are intertwined, through the coupling of population dynamics and transmission.

Transmission

Taking the model and parameters described in the previous chapter (Chapter 4), it is worth considering the effect on the coupled horizontal transmission and population dynamics for a range of transmission strengths, i.e., for a cultural trait where the conversion of individuals is slower (B=0.1), through to a cultural variant that is transmitted faster across the population (B=0.9), such as a fad (Whitehead, 2010).

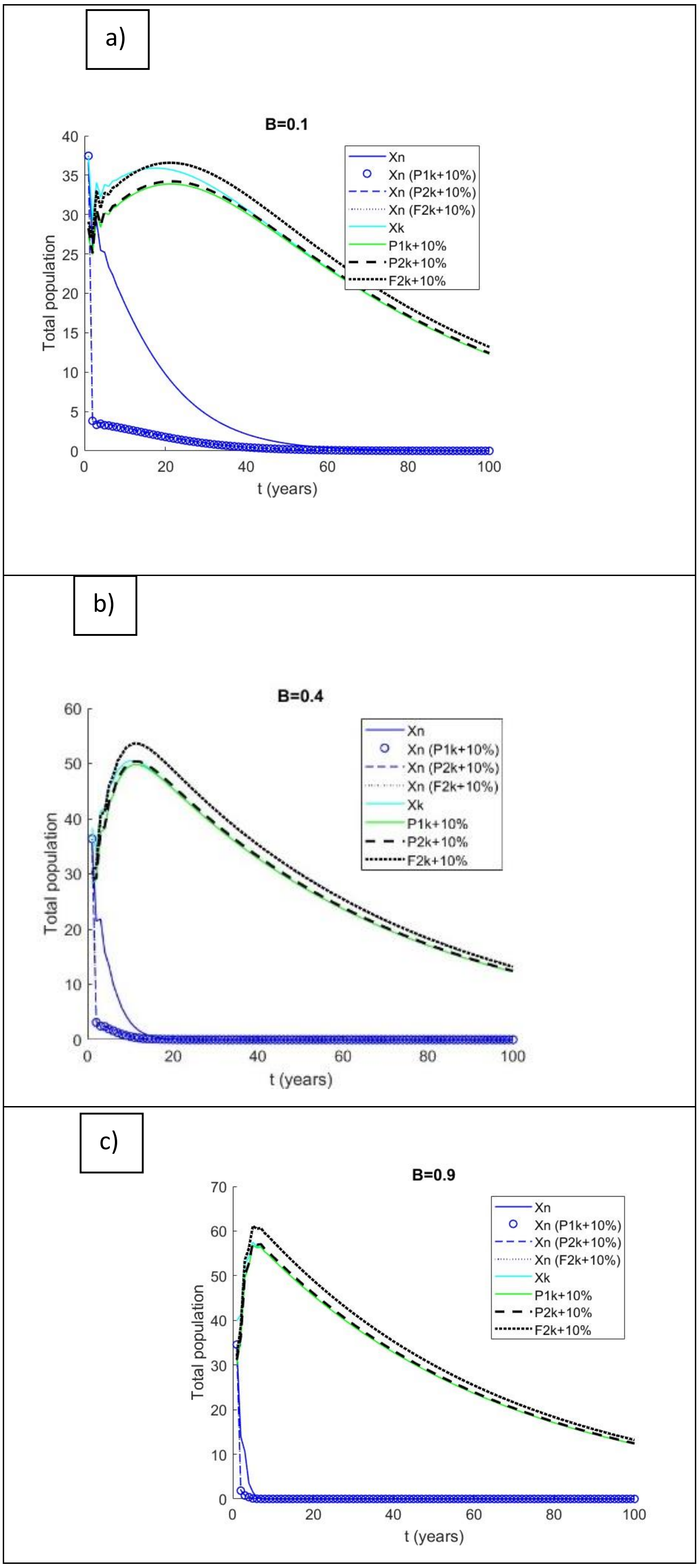


Figure 1. Barn swallow PPM example (see Chapter 4) with an initial population of J_n=10, A_n=10, J_k=10 and A_k=10 providing exploration of the effects of transmission parameter *B*, for a) *B*=0.1, b) *B*=0.4 and c) *B*=0.8

This example shows that if there is high transmission rate between two cultural units (*B*=0.9) and only a small pool of individuals for conversion from the naive unit, there may initially be a pronounced peak in the informed unit (Fig. 1c). However, transient dynamics that cause a temporary peak in abundance may give conservation managers a false sense of security in the short-term, as the peak may pass quickly and the overall population may rapidly move back into decline (e.g., in the well documented case of the Dungeness crab, *Cancer magister* (Higgins et al., 1997; Ludwig et al., 1978)).

Recalling the parameter space exploration for transmission parameter *B*, (Fig.3, Chapter 4), as one might expect, at lower levels of transmission the rate of decline of the naive unit is slower, in the barn swallow example (Fig. 1a), as there is a lower rate of conversion to the informed unit. Given that the informed unit has higher vital rates (resulting from the benefits of socially learned information), one might anticipate that a more rapid conversion to the unit with the higher vital rates would be of the greatest benefit. However, when *B*=0.1 (Fig. 1a), the peak of the informed unit is flattened, such that the informed unit does not begin to decline until some ten years later than when *B*=0.4 (Fig. 1b).

The positive effect on the informed unit of decreasing the transmission parameter, which reduces transmission towards the informed unit, is somewhat counter intuitive. The effect is that while the maximum peak of the informed unit is lower in terms of population abundance for *B*=0.1, transmission is sustained for longer and the population continues to grow or remains stable for longer (Fig 1a).

Conservation options

Given these facets of transmission, here, three possible options to tackle the conservation management conundrum are suggested. First, rather than focus effort on the unit with the more adaptive culture, which may be more likely to thrive, instead effort is spent on maintaining the cultural unit with less adaptive cultural behaviour. The naive unit has the greater threat to existence and the objective is to slow the rate of decline of this cultural unit. The rationale here is to capitalise on the transmission and the conversions to the adaptive behaviour, whilst conserving the individuals available to ‘boost’ the more adaptive culture through conversions. This strategy, (Option 1, Table 1) is to conserve the less adaptive, or potentially even maladaptive culture.

Table 1. Possible options for the conservation of culturally heterogenous populations

Option 1	Rather than focus effort on conserving the more adaptive cultural behaviour, conserve cultural unit that is in faster decline or with less adaptive cultural behaviour
Option 2	Manipulate the transmission rate between the cultural units, to decrease the rate of decline
Option 3	Focus equal effort on conserving both cultural units with the objective of maintaining cultural heterogeneity

A second option, (Option 2, Table 1) is to manipulate the transmission rate between the two cultural units. The objective would not necessarily be to increase the conversion rate, as one might expect, in terms of speeding up the number of individuals converting to the better adapted culture as this may actually result in the informed unit rapidly increasing, but then crashing (Fig 1c). Instead, it is suggested here that in some circumstances, it may be better to slow the transmission rate to the adaptive culture. This is fundamentally counter-intuitive. We might assume that growth of adaptive behaviour will assist population growth. However, in this coupled system, what may happen is that the better adapted unit may grow and have a boost from conversion of naive individuals. But, depending on the parameter regime, this may be short lived. By slowing down the transmission rate, it may be possible to flatten the curve and slow down the speed at which the informed unit peaks. By reducing the transmission rate and slowing down the speed at which the naive individuals are being converted to informed, that may reduce the speed at which the naive cultural unit crashes. Although, the informed population may not reach the same maximum peak abundance, it may peak later, resulting in the informed cultural unit remaining stable for longer, or at least declining less rapidly. The question is then what is the difference in total population abundance under such a scenario and are there optimal thresholds which conservation policy makers and practitioners could use to calculate the best course of action?

Nevertheless, the manipulation of transmission rate can have practical challenges in a wild setting. It may also be difficult to identify which individuals are associated with a particular cultural unit, which could provide practical challenges for option 1. This may be the case, for example, if the two cultural units are sympatric and the delineation between cultural units cannot easily be determined through individual behavioural observations. Therefore, a third option may be to simply focus effort on conserving the entire population and its cultural heterogeneity. As demonstrated in Chapter 4, the coupling of transmission and population dynamics can lead to complex dynamics (particularly when there is density dependence in the system, see Chapter 6). The rationale in option 3 (Table 1) is that since the fates of the two cultural units are undoubtedly interwoven, through the complex dynamics associated with the interactions between the transmission and the population dynamics, the most conservative course of action may be to apply conservation effort to both units.

To test the viability of these three options, simulations were undertaken for a range of scenarios.

Option 1 – conserve the naive unit

In Chapter 4, the benefits of adaptive cultural transmission on vital rates for an informed cultural unit were examined. In contrast, here, using the same coupled model, the benefits of expending conservation effort on a declining naive cultural unit ($\boldsymbol{x_n}$) are explored. Recalling that in this system, social learning drives individuals from the naive to the informed cultural unit, incremental increases to the vital rates of the naive unit can be considered a proxy for successful conservation mitigation for the naive unit. For example, conservation activities to reduce bycatch or entanglement of a particular cultural unit, which increase survival (Bezamat et al., 2021; Wade et al., 2012).

Under this scenario the population dynamics of the naive cultural unit are perturbed to compare the effects of the transmission parameter B, for the overall population abundance for a declining population. Revisiting the example of a theoretical declining sperm whale (*Physeter macrocephalus*) population from Chapter 4, based on [PPM 1.1] (Gero and Whitehead, 2016), a parameter space exploration for *B* of the relative advantage of an increase upto +35% survival of juvenile sperm whales is constructed for B=0.1, 0.3, 0.5, 0.7 and 0.9 respectively. Thus, enabling the exploration of the effect on overall population abundance (Fig. 2).

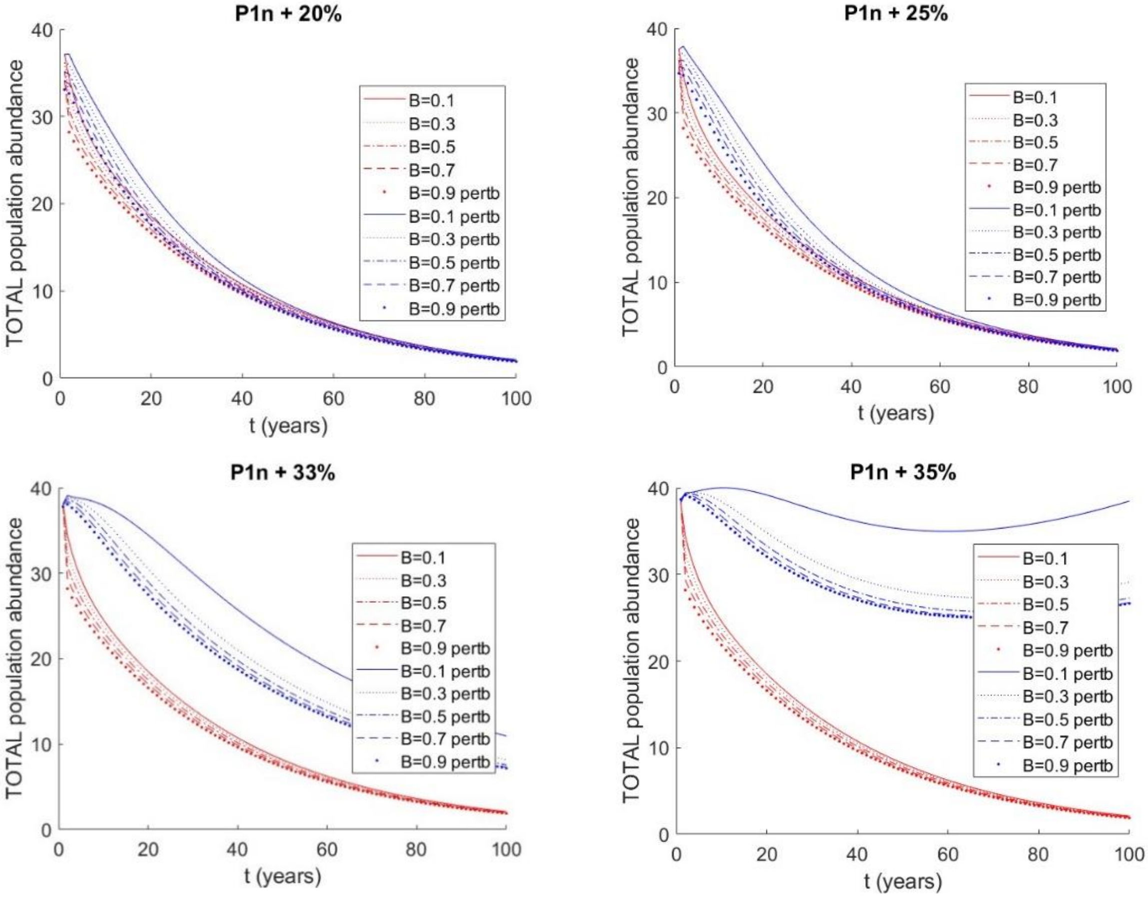


Figure 2. Parameter space exploration for transmission parameter *B*, with naive juvenile survival (*P1n*) perturbed by 20%, 25%, 33% and 35%. Red indicates overall population abundance for the non-perturbed populations for each value of *B*. Blue indicates the overall population abundance for the perturbed naive unit ($\boldsymbol{x_n}$), for each value of *B*.

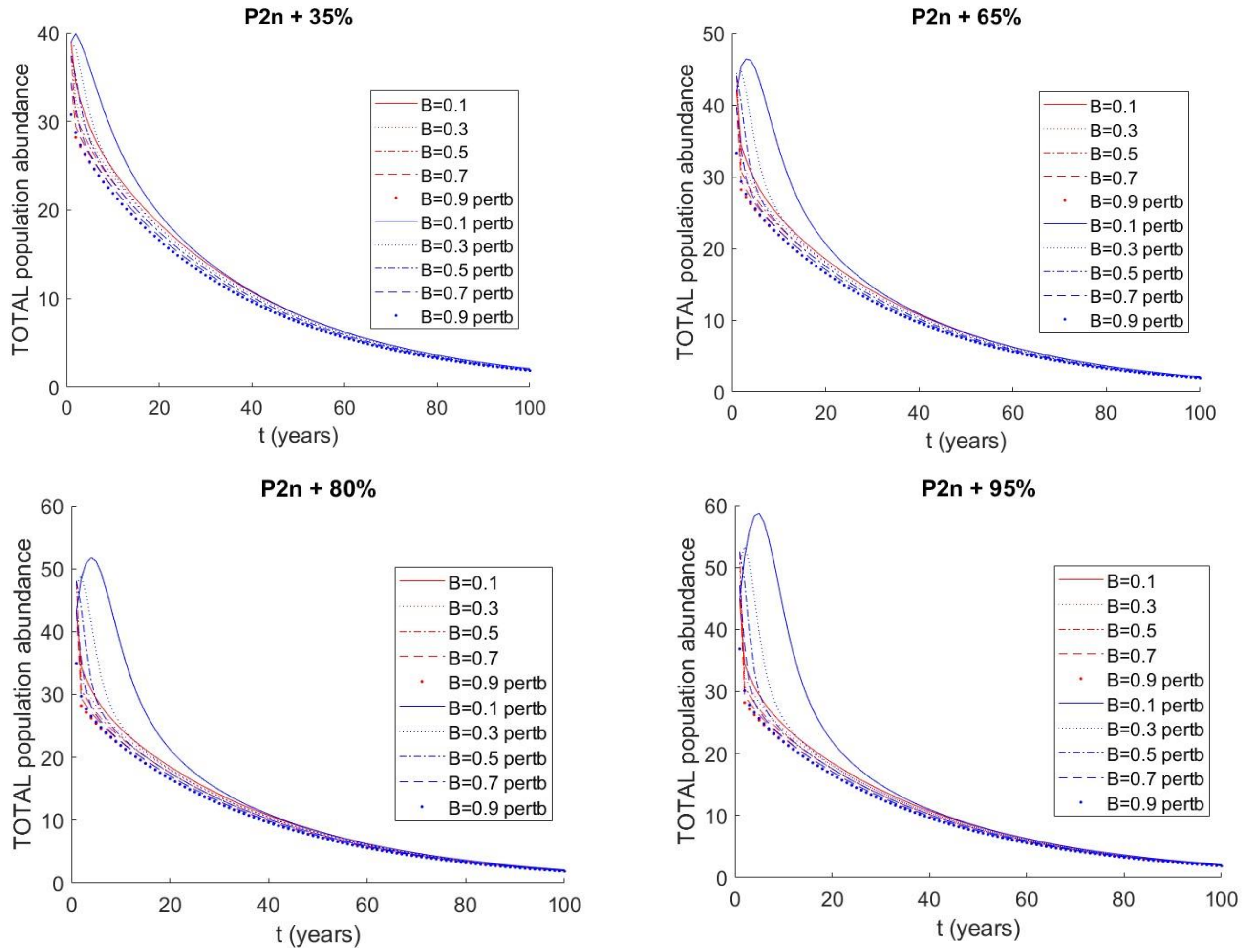


Figure 3. Parameter space exploration for transmission parameter *B*, with naive adult survival (*P2n*) perturbed by 35%, 65%, 80%, 95%. Red indicates overall population abundance for the non-perturbed populations for each value of *B*. Blue indicates the overall population abundance for the perturbed naive unit ($\boldsymbol{x_n}$), for each value of *B*.

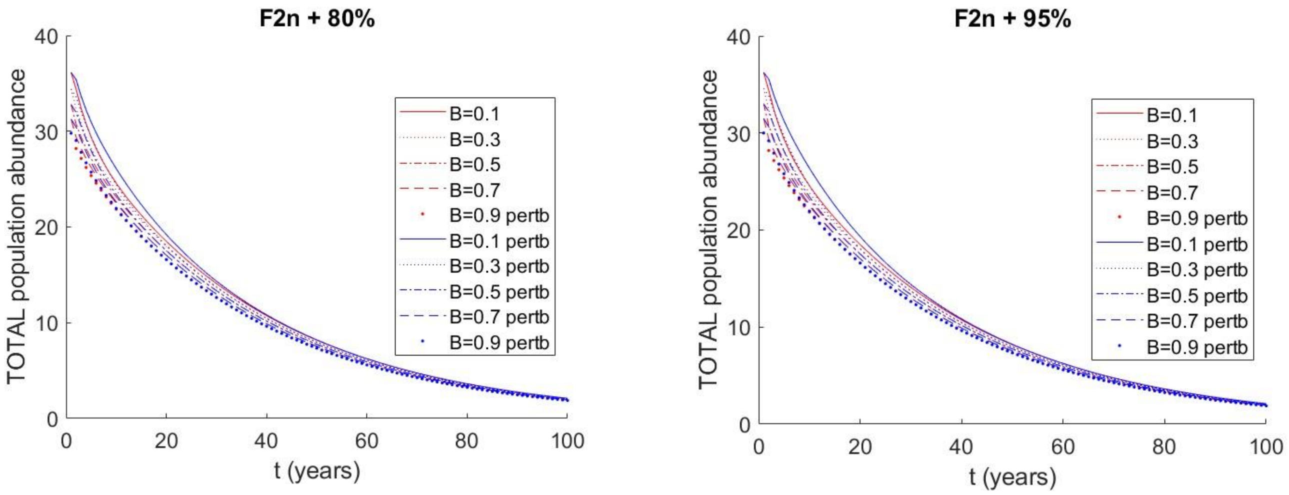


Figure 4. Parameter space exploration for transmission parameter *B*, with naive adult fecundity (*F2n*) perturbed by 80% and 95%. Red indicates overall population abundance for the non-perturbed populations for each value of *B*. Blue indicates the overall population abundance for the perturbed naive unit ($\boldsymbol{x_n}$), for each value of *B*.

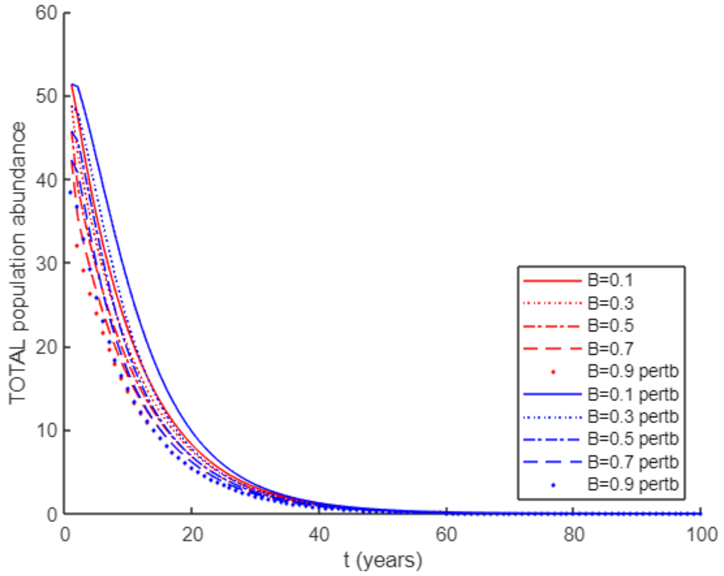
Whilst it might be anticipated that under this model system, increasing the vital rates of $\boldsymbol{x_n}$ would have a benefit to the overall population, because the $\boldsymbol{x_n}$ unit is being driven towards $\boldsymbol{x_k}$ through directly biased social learning (Chapter 4), it does not necessarily follow that increasing the survival rate of $\boldsymbol{x_n}$ (as a proxy for conservation mitigation), would bring about the same effect. This is because the naive unit is also being depleted by conversion to the informed unit. Figure 2 shows that even a 25% increase in survival of juveniles can increase overall abundance in the population, with a 35% increase in $P1_n$ resulting in the population switching to growth in the long-term. This is an excellent example of how social learning is an endogenous process, with potential latent effects.

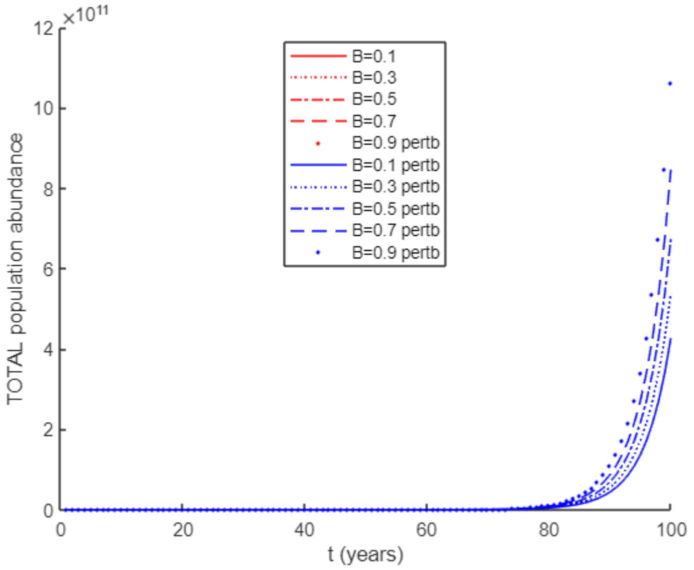
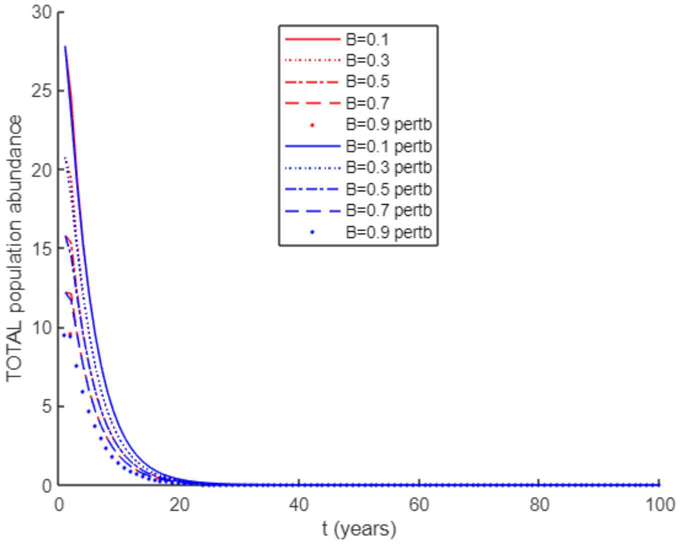
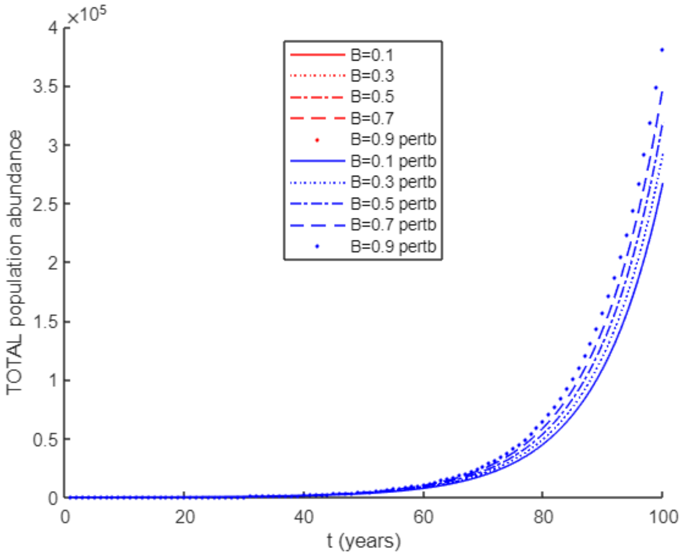
This would indicate that focusing conservation effort to improve the survival rates of a naive unit, that is disadvantaged because it does not have the benefit of adaptive knowledge, can still assist an overall population in becoming stable or growing (particularly when transmission is low, e.g., *B*=0.1, Fig. 2). It is notable that in this sperm whale example, smaller percentage increases to naive juvenile survival ($P1_\mathrm{n}$), has a much larger effect on bringing the overall population into stability than a larger percentage increases to adult survival

($P2_n$), and even implausibly large increases to adult fertility ($F2_n$) of 80% to 95%.

Option 2 – manipulate transmission

Manipulating transmission rates in wild population may be challenging. But for some conservation interventions, such as reintroductions, manipulating transmission rate may be possible by introducing a higher density of demonstrators, or for species that forage through local enhancement, through simultaneous release of a larger number of individuals, e.g. in griffon vultures (genus *Gyps*), (Jackson et al., 2008). To investigate these dynamics further, investigations were conducted for a range of other mammal and bird species using the PPM examples in Chapter 4 (Chapter 4, Table 1 and Appendix 4.1), to explore the effects of increasing juvenile survival in these very different taxa and how the transmission rate influences outcomes (Fig. 5).

Species and source	**Exploration of transmission parameter *B***
House sparrow (*Passer domesticus*) P_1+35% (Maclean et al., 2008)	

Coyote (*Canis latrans*) P_1+35% (Schumaker et al., 2004)	
Douglas squirrel, (*Tamiasciurus douglasii*) P_1+35% (Schumaker et al., 2004)	
Helmeted honey eater (*Lichenostomus melanops cassidix)* P_1+35% (Baxter et al., 2006)	

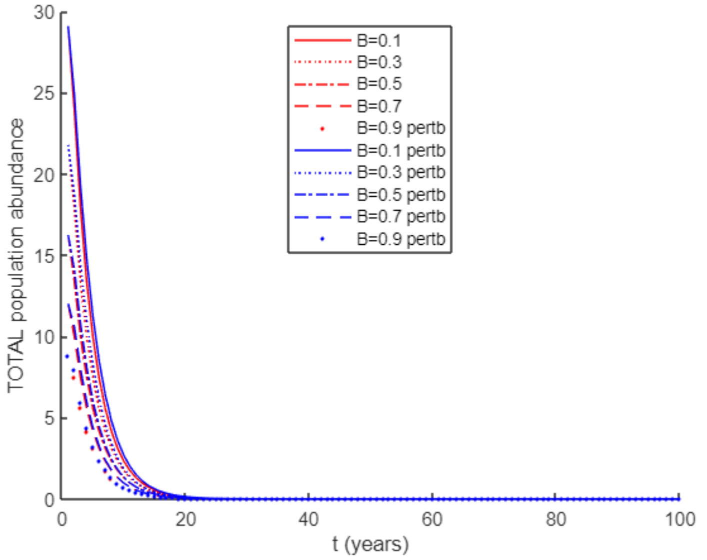
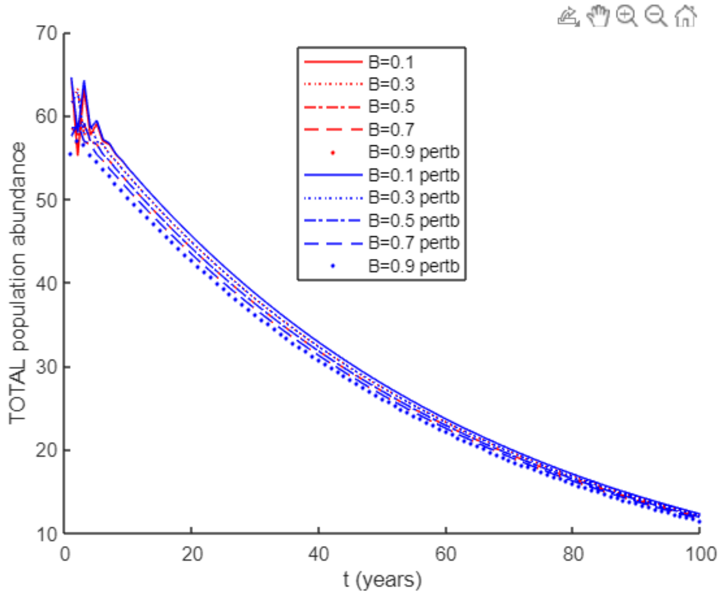
Golden winged warbler (*Vermivora chrysoptera*) P_1+35% (Bulluck et al., 2013)	
Barn swallow, (*Hirundo rustica*) P_1+35% (Gruebler et al., 2014)	

Figure 5. Parameter space exploration for transmission parameter *B*, with naive juvenile survival (*P1n*) perturbed by +35%. Red indicates overall population abundance for the non-perturbed populations for each value of *B*. Blue indicates the overall population abundance for the perturbed naive unit ($\boldsymbol{x_n}$), for each value of *B*.

The result in Figures 2 to 5 indicate that when an overall population is in decline, a lower transmission rate (*B*=0.1) from $\boldsymbol{x_n}$ to $\boldsymbol{x_k}$ results in slower decline in overall population abundance. Whereas, when a population is growing, a higher transmission rate (*B*=0.9), results in higher total abundance. One might reasonably assume that higher transmission towards a more adaptive state (through social learning), would result in an increase in overall population abundance. This was shown to be the case for the coyote and helmeted honeyeater examples (Fig. 5), both growing populations. However, in the sperm whale, house sparrow, Douglas squirrel, golden-winged warbler and barn swallow examples modelled, in fact it was setting the transmission parameter lowest (B=0.1) that resulted in highest overall abundance. It is notable that these populations are all declining and it may be that reducing the conversion from $\boldsymbol{x_n}$ - which under this scenario has biological advantage as the result of human intervention (as per option 1) - results in a lower decline in the now advantaged naive unit. This highlights how conservation managers may need to make decisions based on the feasibility of manipulating transmission or vital rates in a certain cultural unit. Again, these dynamics are not straightforward, and it may be a combination of several parameters beyond simply the transmission rate, including the parameters for the PPMs, and the stage structure of the two units that are driving these contrasting dynamics. To further elucidate these complex dynamics the relationship between stage structure of the two cultural units and transmission rate are explored by investigating their combined effect on transient dynamics.

Transient dynamics

To further elucidate this coupled system, next the transient dynamics of the system are inspected more closely, to evaluate how stage structure and transmission rate together influence the transient envelope (Stott et al., 2011). To begin, a range of initial conditions for the example sperm whale population (PPM 1.1) (Gero and Whitehead, 2016) were simulated, with a focus on the first ten years, to capture transient dynamics within a time relevant to conservation managers.

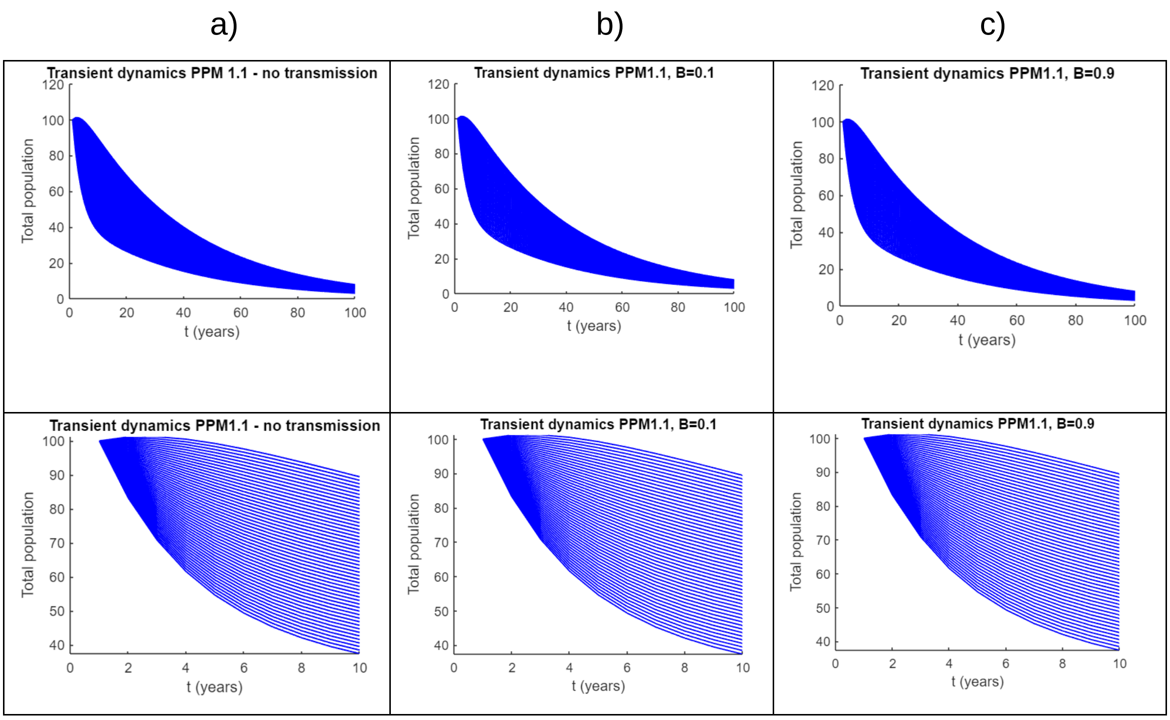


Figure 6. Transient dynamics for a) initial total population of 100, for stage structed populations with initial condition J_0 = 1 to 100, A_0= 100 - J_0, for sperm whale PPM 1.1, with B=0, i.e., no cultural transmission; b) two cultural units $\mathbf{x_n}$ and $\mathbf{x_k}$ where the initial population is distributed evenly, $\mathbf{x_n}$ =50 and $\mathbf{x_k}$ =50, with initial conditions J_{n0} = 1 to100, A_{n0}= 100 – J_{n0} and J_{k0} = 1 to 100, A_{k0}= 100 – J_{k0}, with cultural transmission parameter B=0.1; and c) B=0.9.

In Figure 6, the vital rates for both $\mathbf{x_n}$ and $\mathbf{x_k}$ cultural units were set the same (i.e., $\mathbf{Mx_n}$ = $\mathbf{Mx_k}$) to explore the transient envelope. Although there is horizontal transmission between the two units (Fig. 6b and 6c) both cultural units have the same PPM parameters and there appears to be little effect on the transient envelope from transmission under this scenario. Next the effects of perturbing adult survival rate ($P2_k$) in unit $\mathbf{x_k}$ for a range of stage structures and transmission rates were explored (Fig.7) and similarly for juvenile survival ($P1_k$), (Fig. 8).

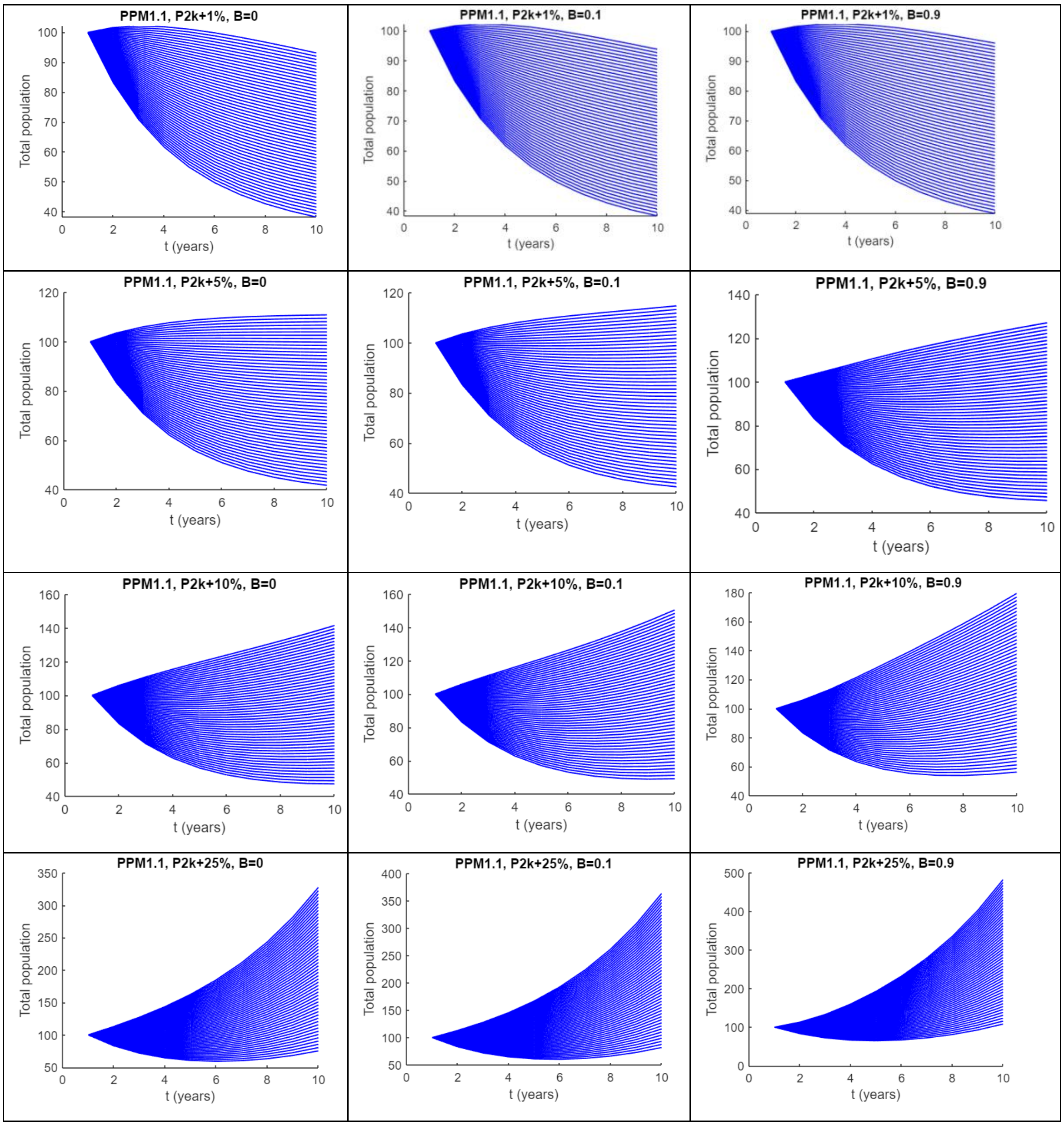


Figure 7. Transient dynamics for initial total population of 100, with two cultural units $\mathbf{x_n}$ and $\mathbf{x_k}$, where the initial population is distributed evenly, $\mathbf{x_n}$ =50 and $\mathbf{x_k}$ =50, with initial conditions J_{n0} = 1 to 100, A_{n0}= 100 – J_{n0} and J_{k0} = 1 to 100, A_{k0}= 100 – J_{k0}. Sperm whale PPM 1.1, cultural transmission parameter B= 0, 0.1 or 0.9. Horizontal cultural transmission is between adults and adult survival rate of the informed unit is perturbed ($P2_k$ +1%, +5%,+10% and +25%).

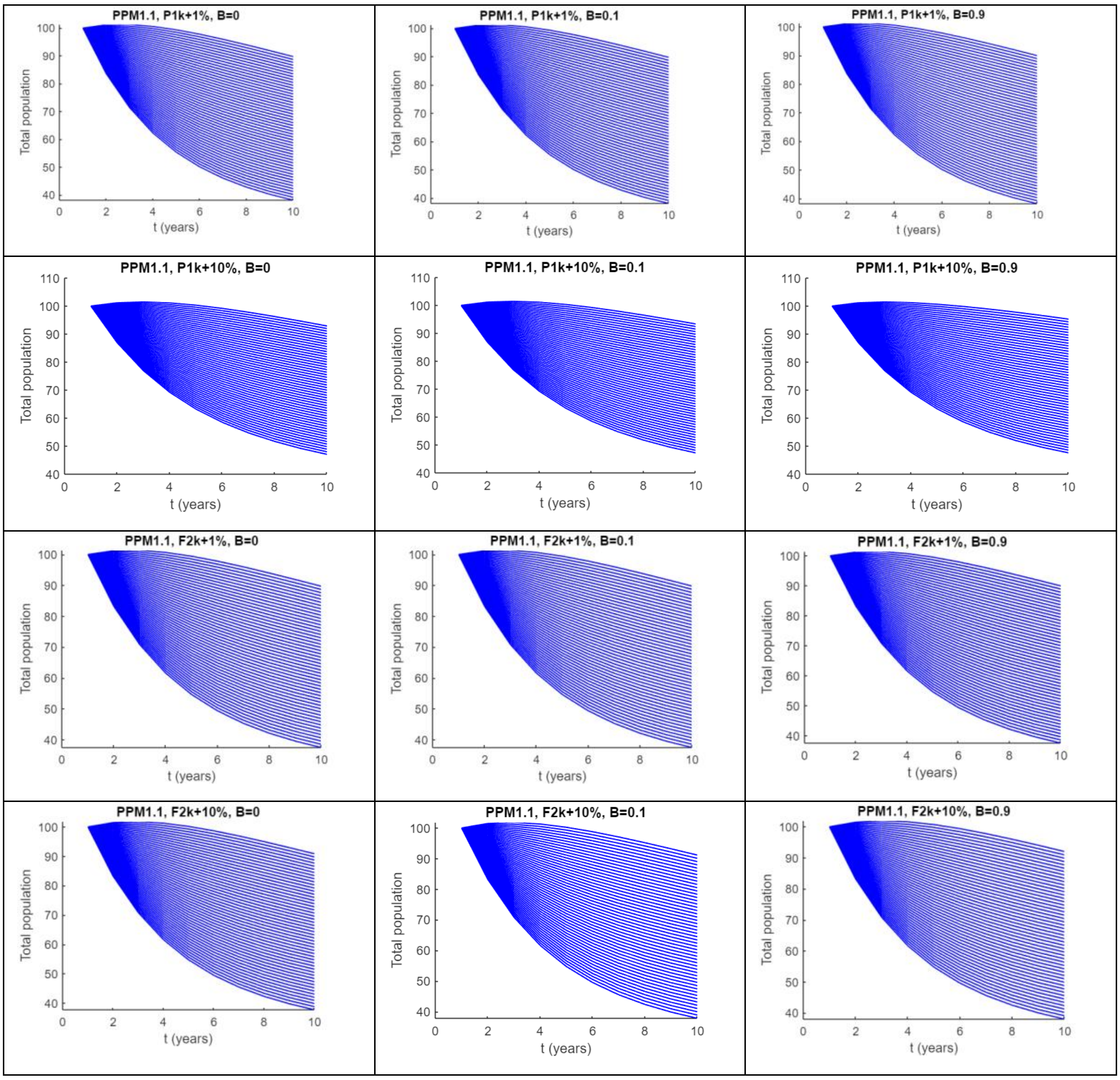


Figure 8. Transient dynamics for initial total population of 100, with two cultural units $\mathbf{x}_\mathbf{n}$ and $\mathbf{x}_\mathbf{k}$ where the initial population is distributed evenly, $\mathbf{x}_\mathbf{n}$=50 and $\mathbf{x}_\mathbf{k}$=50, with initial conditions J_{n0} = 1 to 100, A_{n0}= 100 – J_{n0} and J_{k0} = 1 to 100, A_{k0}= 100 – J_{k0}. Sperm whale PPM 1.1, cultural transmission parameter B= 0, 0.1 or 0.9. Horizontal cultural transmission is between adults and juvenile survival rate of the informed unit is perturbed ($P1_k$ +1% and 10%) and adult fertility (F2+ 1% and 10%).

As one might anticipate, the perturbation of vital rates of the informed adults (Fig. 7) has a greater impact on both the transient envelop and abundance than the perturbation of vital rates of the informed juveniles (Fig. 8), because the horizontal transmission in this scenario is between adults. To explore the transient envelope for the different stages under a range of potential initial conditions, further simulations were conducted for initial conditions where the total abundance $\mathbf{x_n} \neq \mathbf{x_k}$ (Fig. 9), to better replicate the stages of a particular cultural variant moving across a population through horizontal transmission.

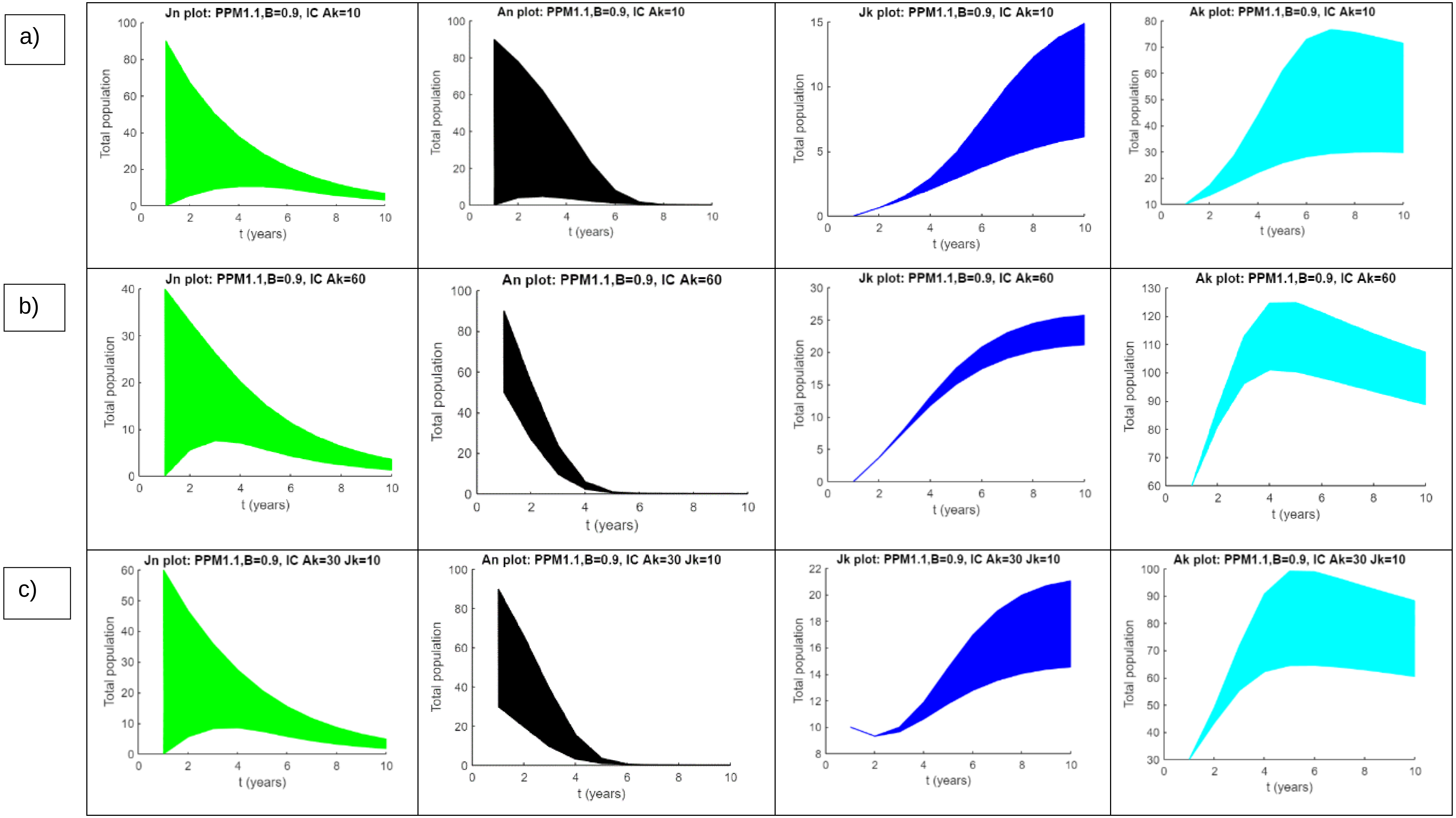


Figure 9. a) IC A_k=10, J_k= 0; b) IC A_k=60, J_k= 0; and c) IC A_k=30 and J_k= 10.

Transient bounds provide the best- and worst-case scenario of transient change in population density and the 'transient envelop' represents a range of possible population densities captured within these bounds (Stott et al., 2011). The comparison of transient envelopes for even a small range of initial stage structures (Fig. 9) demonstrates the effect of these coupled dynamics on creating a wide transient envelope for J_n and A_n up to t=4. As $\boldsymbol{x_k}$ grows, as the result of conversion to the informed unit through transmission, coupled with the PPM parameters, at approximately t=4 the transient envelope for J_k and A_k increases dramatically.

Option 3 – maintain cultural diversity

Conservation managers and practitioners may hope to utilise the processes of social learning to increase survival or reproduction in wild populations and ideally benefit from better understanding of the coupled dynamics discussed here. But these explorations hint at some very complex dynamics from which it may be challenging to distil salient overarching management advice (see Chapter 6 for an analysis of the complex dynamics emerging from the simpler case of a scalar population). In this coupled system the outcomes are contingent on: transmission rate; PPM parameters (including any change to vital rates arising from adaptive socially learned information); relative abundance of $\boldsymbol{x_n}$ and $\boldsymbol{x_k}$; as well as stage structure. Therefore, offering guiding principles for conserving culturally heterogenous populations based on anticipated population dynamics may still be out of reach.

These challenges may be exacerbated by the fact that many of these parameters can be difficult to measure and monitor in wild populations. As a result, in some instances, the best advice to managers may be to work to ensure that cultural diversity is maintained within populations to facilitate the emergence of adaptive cultural variants.

However, there may be some species and conservation settings, such as reintroductions where the manipulation of vital rates, relative abundance, stage structure or transmission can reliably be measured and manipulated. Nevertheless, realistically manipulating vital rates in the wild can be very difficult, so a focus on manipulating transmission rates to help boost populations may be more achievable in some conservation settings.

Given these limitations, the third conservation option outlined in this chapter may be the most practical option, i.e., to consider that cultural diversity itself may in some instances be key to keeping culturally structured populations stable, particularly in the face of rapidly changing environments. Whilst maladaptive cultures may not ultimately lead to population stability and growth, their occurrence may provide segments of a population (cultural units) the opportunity to test the viability of alternative socially learned behaviours. This process can occur intra-generationally, i.e., much more rapidly than the inter-generational processes of natural selection, which can assist resilience in rapidly changing environments. As described in Chapter 6, even cultural units with maladaptive cultures may provide a pooled resource for conversion to more adaptive culture, which may also influence the dynamics of a more adaptive cultural trait.

It was argued in Chapter 3, that it may be important to consider ‘future-proofing’ populations by conserving the *capacity* for innovation and social learning to give rise to new adaptive cultures. Human activities can both threaten existing cultures and provide a catalyst for new cultural behaviour (Gruber et al., 2019) and cultural diversity may help buffer some of these effects (Brakes et al., 2021). Evidence for the benefits of conserving cultural diversity has been provided by population of bottlenose dolphins in Western Australia which suffered a marine heatwave. Diversity of foraging strategies among cultural units showed that survival rates in a segment of the population with socially learned tool use, buffered these dolphins against the cascading effects of the heatwave on habitat and prey availability (Wild et al., 2019b). This example provides clear evidence of the value of maintaining cultural diversity to increase resilience in increasingly perturbed environments. However, for cultural diversity to be maintained managers must consider how the capacity for innovations and new cultures to arise can be safeguarded, by conserving phenotypic variation, social network structure and population connectivity (Brakes et al., 2021).

For example, in the eastern tropical Pacific, at least four separate acoustic clans of sperm whales have been identified with varying feeding success between clans in different oceanographic conditions (as determined by surface defecation rate) (Whitehead and Rendell, 2015). To better understand the interplay between cultural transmission and demography in these acoustic clans, a region-wide network of researchers has been established to collaborate on the collection of higher resolution data on these clans, to inform conservation efforts through a ‘concerted action’ under CMS (CMS, 2017; Brakes et al., 2019; *pers comms* A. Eguiguren).

Similarly, it has been suggested that nut-cracking may provide extra-nutrients in the dry season for a some chimpanzees in West Africa (Whiten, 2017a). Efforts to determine how diverse cultural traits in this species interface with conservation are ongoing under a ‘concerted action’ under CMS (Brakes et al., 2021) and through the IUCN.

Arguably, deciding how best to conserve culturally structured populations may have wider considerations than just the interface of the culture with population dynamics and any possible efficiencies that could be gained. There may also be philosophical considerations regarding the protection of specific cultures, that involve calculations beyond conservation efficiencies (Carvalho et al., 2022) and these are addressed in the concluding discussion of this thesis.

Conclusion

The question of how best to conserve culturally heterogenous populations remains a challenge. This is due to the range of parameters that can influence both asymptotic and transient dynamics when population dynamics are coupled with cultural transmission. A simplistic approach of conserving a cultural unit that has more adaptive culture (as expressed here as a higher survival rate), whilst neglecting a cultural unit that does not, or may even have been transmitting undesirable behaviour (such as engagement with fishing vessels), may overlook important, complex aspects of the interaction between population dynamics and cultural transmission. This means that no ‘one size fits all’ solutions are available for advising on the conservation of culturally structured populations and these considerations becomes vastly more complex when a population has more than two cultural units, or a wider variety of cultural traits that can impact survival, reproduction or dispersal. Finally, the effects of density dependency to cultural variants and limits to growth, as in real-world systems have not yet been explored in this coupled system and are examined in the next chapter.

CHAPTER 6

Cultural bistability, exclusion and chaos in a scalar population

In the previous two chapters (Chapter 4 and 5) it has been shown how culture can generate complex dynamics in a stage structured population. The same social learning strategy (direct bias, after Boyd and Richerson 1985) is next explored in a scalar population for a range of parameter regimes.

In this chapter, the tension between the concurrent processes of cultural transmission and population dynamics are again examined, but here the importance of cultural diversity in compensating for the inevitable risk of maladaptive or costly cultural variants arising is explored. It is shown here how, maladaptive cultural variants, which one might assume would be self-limiting if they are costly to vital rates, can potentially dominate in a simple two variant system. The conditions under which ‘cultural exclusion’, cultural tipping points and chaos can arise are also explored and the consequences for wild populations and human political systems are discussed. This chapter has been prepared for submission to *Royal Society Proceedings B* and supplementary material is provided in Appendices 6.1 and 6.2.

From risky foraging traditions to alternative facts: cultural transmission and population dynamics

Philippa Brakes[a,b], Sasha R.X. Dall[a], and Stuart Townley[c]

[a]Centre for Ecology and Conservation, Biosciences, College of Life and Environmental Sciences, University of Exeter, Cornwall TR10 9FE, UK; [b]Whale and Dolphin Conservation, 38 St Paul Street, Brookfield House, Chippenham, Wiltshire, SN15 4RN, UK; [c]Department of Mathematics, College of Engineering, Mathematics and Physical Sciences, University of Exeter, TR10, Cornwall, UK

Abstract

Social learning of cultural variants can allow populations to adapt to changing environments. Social learning occurs on ecological time scales concurrently with population dynamics. We explore the population level consequences of these interwoven processes. Using simple socially-coupled population maps, we show that directly-biased social learning of a dichotomous cultural trait can dramatically influence population dynamics. We demonstrate that biologically costly cultural variants can predominate, or persist in populations, if they are transmitted at higher rates than they are removed by demographic costs. We find conditions for ‘cultural bi-stability’ (coexistence of adaptive and maladaptive cultures), and potential maladaptive ‘cultural exclusion’. We demonstrate that small changes in cultural transmission rates can have profound effects on the propagation of cultural variants (from cultural hysteresis with tipping points which ‘flip’ the system between variants non-reversibly, to chaotic population dynamics). We discuss the potential implications of our analysis for wildlife conservation and human political systems, demonstrate the importance of cultural diversity to guard against maladaptive variants and suggest areas for future research.

Keywords: social learning | population dynamics | maladaptive culture | foraging | alternative facts

Introduction

The ability of organisms to respond to their environment by gathering information is a prerequisite for life. Information coded into DNA through the processes of natural selection can be passed between generations. During their lifetimes, organisms can also acquire information by learning individually, or benefit from the experience of their peers through social learning, providing intra-generational opportunities for information transfer and behavioural adaptation (horizontal transmission). Socially learned behaviour can also be passed down from parents or other elders to juveniles (vertical or oblique transmission) (Cavalli-Sforza and Feldman, 1981; Hoppitt and Laland, 2008). Social learning can be defined as any learning process that is influenced by the observation of, or interaction with, another animal or its products (Heyes, 1994; Hoppitt and Laland, 2008; Whitehead and Rendell, 2015). The evolutionary value of intra- and inter-generational information transmission through some form of social learning is supported by burgeoning evidence of how widespread the processes of social learning are across vertebrate taxa (Whiten, 2017a).

Information or behaviour that is acquired through some form of social learning from conspecifics, has been termed ‘animal culture’ (Fragaszy and Perry, 2003; Whitehead and Rendell, 2015), (hereafter ‘culture’ will be used to describe both human and non-human culture). Culture has been described as a second inheritance system (Boyd and Richerson, 1985; Whiten, 2005), which provides opportunities for rapid adaptation to changing social or ecological conditions. The evolution of cultures and the causes and consequences of cultural evolution are the focus of a growing body of work (Kuijper et al., 2021; Mesoudi, 2021; Mesoudi et al., 2016; Whiten, 2017b, 2005), with the interplay between genes and cultural transmission described as gene-culture coevolution (Feldman and Laland, 1996; Whitehead, 2017; Whitehead et al., 2019).

One aspect of cultural transmission that has received considerably less attention is the influence of social learning on shorter-term population dynamics (Brault and Caswell, 1993; Fogarty et al., 2013; Whitehead and Ford, 2018), which may be relevant for a range of different issues, from conservation

(Brakes et al., 2021) to human rights (Almqvist, 2005). Given that social learning can influence vital rates such as reproduction and survival (Kierulff et al., 2012; Paxton et al., 2019; Wild et al., 2019b) it is salient to examine inter-generation dynamics resulting from cultural transmission. Fogarty et al. (2013) investigated the role of cultural transmission for human demography. Using an age structured Leslie-type model they explored the transmission of a single dichotomous cultural trait that affected age-specific fertility and mortality. They argued that, intuitively, vertical learning alone cannot support trait fixation or demographic changes, since “if the offspring of parents carrying the trait are fewer, the trait will soon die out under a pure vertical learning regime”. Introducing a small amount of horizontal or oblique transmission, in addition to vertical transmission, they found that oblique and horizontal transmission can accelerate the spread of a cultural variant and increase population growth and equilibrium frequency more rapidly than vertical transmission alone (Fogarty et al., 2013). This research demonstrated that when a cultural trait is strongly transmitted this can cause large-scale demographic change.

Learning from others provides a potentially rapid mechanism for responding appropriately to changes in the environment. However, this is not infallible. It can cause the carryover of behaviour that is no longer relevant in a changing environment (Barrett et al., 2019), or sources other than genetic parents can result in maladaptive cultural variants being transmitted (Richerson and Boyd, 2005). Such maladaptive behaviour decreases the vital rates (survival and/or reproduction), i.e. the Darwinian fitness, of the actor (e.g., in human societies, ‘cult of personality’ leading to the social transmission of misinformation (McMillan, 2016; Yamey and Gonsalves, 2020)). In some wild populations, the consequences of maladaptive behaviour spreading can be challenging to determine (e.g., depredation from long-line fisheries by some toothed whale species is socially learned, but the population level impacts are not well understood (Baird et al., 2014; Fader et al., 2021; Schakner et al., 2014).

The fact that maladaptive cultural variants can predominate seems counter-intuitive, since maladaptive behaviour should, by definition, be self-limiting. However, somewhat paradoxically, for cultural variation to effectively track environments (both intra- AND inter-generationally), maladaptive cultural variants are inevitable. Natural selection cannot eliminate the spread of maladaptive cultural variants because it takes time and effort to evaluate the veracity of socially-acquired behaviour. This has been described as the ‘costly information hypothesis’ in which maladaptive cultural variants result from population-level evolutionary trade-offs that are intrinsic to adaptation via cultural transmission (Richerson and Boyd, 2005). This hypothesis predicts that maladaptive cultural variants are likely to arise under a wide range of circumstances.

The challenge then is to elucidate the inter-weaving of population-level processes and cultural transmission. To explore the tension between the transmission of adaptive or maladaptive cultural variants and population dynamics, we adopted a novel approach. We formalise the hypothesis that biologically costly cultural variants can predominate (or be maintained in populations) if they are transmitted at higher rates (e.g. within generations) than they are removed (among generations) by demographic costs. We then examine how the social learning of a dichotomous cultural trait may influence population dynamics for two scalar populations.

Boyd and Richerson describe a simple model of directly biased transmission of a dichotomous trait (Boyd and Richerson, 1985), for content bias, which can also be described as a copy ‘what’ strategy (Kendal et al., 2018). They consider two cultural variants, with two cultural ‘parents’, where both have equal weight in the transmission process. Parameter b represents the effect of directly biased transmission (where $0 \leq b \leq 1$) and can be tuned according to transmission strength of the variant. The frequency of the focal variant before transmission is p and the frequency following transmission (p') is calculated by the equation:

$$p' = p + bp(1 - p) \qquad [1]$$

(after Boyd and Richerson, 1985, eq. 5.2).

We extend this formulation of directly-biased transmission between two socially linked populations to explore dynamics and equilibria of a maladaptive cultural variant being transmitted across a naive population. We present a theory of cultural exclusion and further examine the conditions under which such cultural transmission can result in chaos.

Cultural Bistability – Cultural Exclusion

We consider two populations, modelled by scalar linear maps:

$$x^{-}(t+1) = \alpha x^{+}(t)$$

$$y^{-}(t+1) = \beta y^{+}(t).$$

Here α is the growth rate of the "x population", β is the growth rate of the "y population" and $x^{+}(t)$, resp. $x^{-}(t+1)$ and $y^{+}(t)$, resp. $y^{-}(t+1)$ represent the abundance of x and y before, resp. after, the biology (in this case population growth) occurring over one time-step from t to $t+1$ (Figure 1).

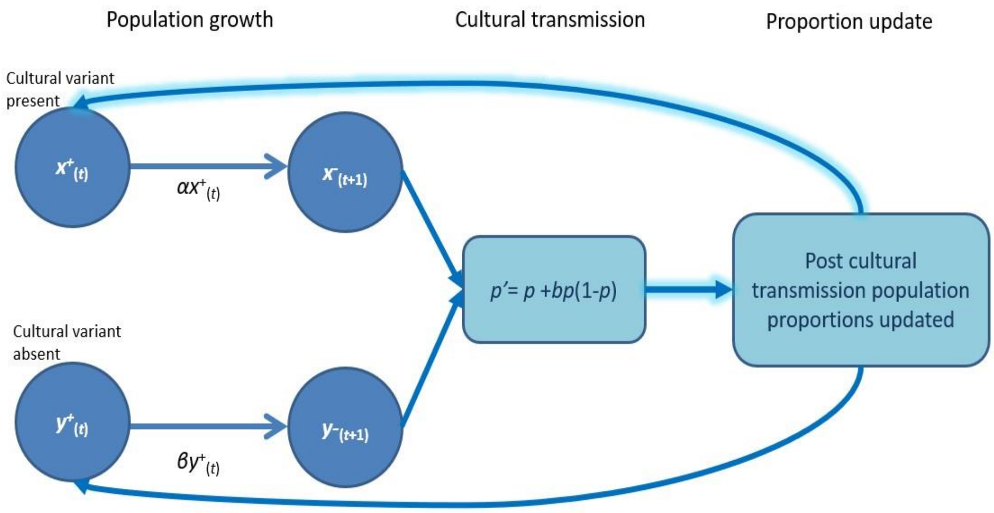


Figure 1. Schema of two populations modelled by scalar linear maps that are coupled by directly biased cultural transmission (after Boyd & Richerson1985). Highlighted arrow indicates transmission of the cultural variant, with a proportion of the population becoming knowledgeable post scalar transformation, as the result of directly biased cultural transmission.

The population with state *x* might represent a population with a maladaptive cultural variant (present) and *y* a population without the maladaptive cultural variant (absent). Or *x* might carry a cultural trait ξ and *y* a cultural trait η. The relative growth rate ρ

$$\rho = \frac{\beta}{\alpha}$$

which provides the rate of convergence to stability, is the main focus of our analysis as it captures an important region of the parameter space for the populations in which the maladaptive variant is either present or absent.

Following population growth/decline, the pre (−) cultural transmission proportion

$$p^{-}(t + 1) = \frac{x^{-}(t + 1)}{x^{-}(t + 1) + y(t + 1)}$$

is adjusted using the Boyd-Richerson model Eq. (1) to yield an updated proportion

$$p^{+}(t+1) = F_{b,p}\left(p^{+}(t)\right), \qquad [2]$$

where

$$F_{b,p}(p) = \frac{(b+1)p}{(\rho - (\rho - 1)p)} - \frac{bp^2}{(\rho - (\rho - 1)p)^2}$$

The update of proportion given by Eq. (2) always admits the two equilibria

$p = 0 \qquad p = 1$

and when $b < \rho - 1$, a third equilibrium

$$p = \rho\,\frac{(\rho - 1 - b)}{(1 - \rho)^2} \qquad [3]$$

A linearised stability analysis (see Appendix 6.1) shows that:

1. if $b > \rho - 1$, then $p = 1$ is stable and $p = 0$ is unstable;

2. if $b < (\rho - 1)/\rho$, then $p = 0$ is stable and $p = 1$ is unstable;
3. if $(\rho - 1)/\rho < b < \rho - 1$, then $p = 0$ and $p = 1$ are stable and the third equilibrium given by Eq. (3) is unstable

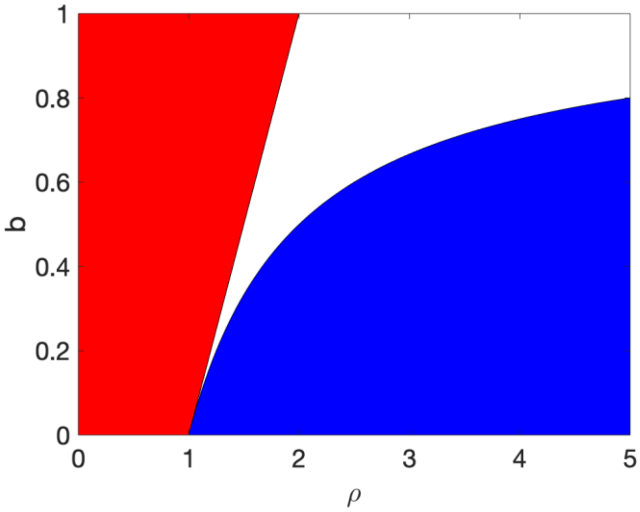


Figure 2. Depiction of stable and unstable equilibrium proportions: Red region, 0 and 1 only equilibria, *p* = 0 is unstable, *p* = 1 is stable; Blue region, 0 and 1 only equilibria, *p* = 1 is unstable, *p* = 0 is stable; White region, both *p* = 0 and *p* = 1 are stable equilibria, separated by an unstable, co-existence equilibrium *p* ∈(0,1) (see Appendix 6.1).

These results (Figure 2) demonstrate, as one might anticipate that if the *x* population with an adaptive variant present has a higher growth rate, i.e. $\rho < 1$, then *p* = 1 is stable, i.e. $p(t) \to 1$, and the adaptive variant dominates. In this case, cultural transmission reinforces the biological advantage of higher growth rate for the *x* population.

However, if *x* is moderately maladaptive, i.e. the ratio of growth rates $\rho \in (1,2)$, then with low cultural transmission $b < (\rho - 1)/\rho$, *p* = 0 is stable, i.e. $p(t) \to 0$, and the *y* population, without the maladaptive variant, dominates. If cultural transmission $b > \rho - 1$, then $p = 1$ is stable and the maladaptive variant dominates. For intermediate values of b where $((\rho - 1)/\rho) < b < \rho - 1$, there is a **cultural bistability** in which both $p = 0$ and $p = 1$ are stable. In this case, if the initial population is initially low in the maladaptive variant, specifically $p(0) < p^*$, where p^* is given by (Eq. 3), then the population without the maladaptive variant dominates. But if the initial population has a high proportion with the maladaptive variant, specifically $p(0) > p^*$, then the maladaptive variant dominates. In this case, there is a complex trade-off between the advantage of cultural transmission for the x population and the biological advantage of higher growth for the y population.

However, for more maladaptive variants, i.e. if the ratio of growth rates $\rho > 2$, then with low cultural transmission $b < (\rho-1)/\rho$, $p = 0$ is stable and the naive population (without the maladaptive variant) dominates. But with $b > (\rho - 1)/\rho$, there is again a **cultural bistability** as above in which both $p = 0$ and $p = 1$ are stable.

Where there is cultural bistability we see something similar to “competitive exclusion”, what we might call **cultural exclusion**, whereby for some initial conditions a maladaptive cultural variant may dominate and for other initial conditions a more adaptive, or biologically useful cultural variant dominates. If the initial growth rate of the population with a maladaptive variant is high, then with a high transmission rate this can result in ‘cultural exclusion’, with the maladaptive variant dominating. In contrast, if the population with the maladaptive variant has a moderate growth rate (i.e. $2 < \rho < 1$), for lower rates of cultural transmission ($b < (r - 1)/r$) this can result in cultural bi-stability, where both populations can be argued to have secured a ‘cultural niche’, which is stable (for any given value of b).

Cultural Bistability – Cultural Hysteresis

Often, bistability in a system is associated with hysteresis. Hysteresis leads to non-reversible dynamics. Looking at Figure 2, and setting $\rho \approx 1.5$. Then as we increase b from $b = 0$ to $b = 1$, then we pass from $p = 0$ being stable, to both $p = 0$ and $p = 1$ being stable to only $p = 1$ being stable. In this case, if the change in the parameter is slower than the dynamics of the system, then the proportion p will track the equilibrium $p = 0$. This will persist until the parameter b takes us into the red region at $b = b^{*}$ where the system flips to the $p = 1$ stable equilibrium. Now decrease b from $b = 1$ to $b = 0$, then we pass from $p = 1$ being stable, to both $p = 0$ and $p = 1$ being stable to only $p = 0$ being stable. In this case, the proportion p will track the equilibrium at $p = 1$. This will persist until the parameter b takes us into the blue region at $b = b^{**}$ where the system flips to the $p = 0$ stable equilibrium. Because $b^{**} < b^{*}$, this creates a hysteresis loop (Figure 3).

Such hysteresis effects are common, for example in climate systems (Lenton and Williams, 2013) where a tipping point is effectively irreversible on reasonable time scales. In terms of culture, suppose that cultural pressures increasingly favour the $p = 1$ equilibrium, i.e. b increases. Then the system flips to a $p = 1$ equilibrium at $b \approx 0.8$. Now suppose these cultural pressures are reversed so that b now decreases. Then the system flips to a $p = 0$ equilibrium but only when $b \approx 0.3$. For example, in a binary electoral system, this creates a memory or latency effect in the system. If the popular vote switches from left to right as a result of right-favouring media, then reversing this switch requires more left-leaning “campaigning” effort (see discussion).

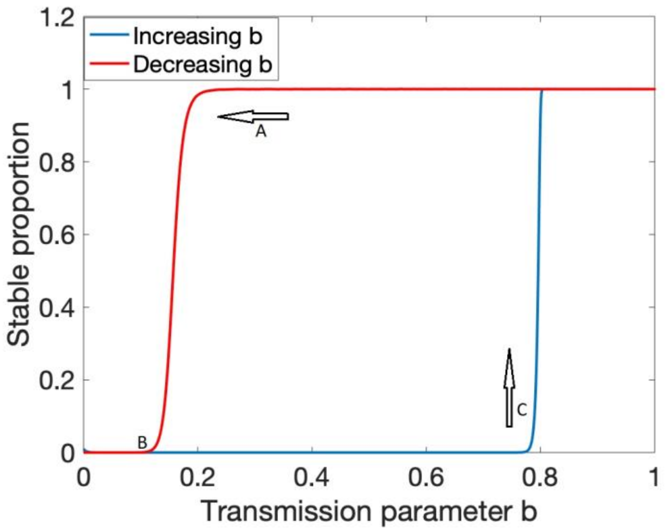


Figure 3. Depiction of hysteresis in a cultural system. Blue curve – as *b* increases the system flips from $p = 0$ to $p = 1$ at $b \approx 0.8$ (arrow C). Red curve – as *b* decreases (arrow A) the system flips from $p = 1$ to $p = 0$ at $b \approx 0.2$ (point B).

Cultural transmission as a route in and out of chaos

To further examine the tension between population dynamics and cultural transmission we explored transmission under a range of population scenarios. It is often assumed that socially transmitted innovative behaviour that provides a fitness benefit to those who learn the innovation, may also benefit the entire population as the behaviour spreads. However, there can be tension between the transmission of novel behaviour and the effects on population dynamics. As well as the risk of propagation of maladaptive behaviour (as shown here), innovation can also lead to over exploitation of resources and result in what we argue is a '**cultural trap**'. Over exploitation as the result of cultural transmission of adaptive variants could theoretically result in population declines, as some culturally transmitted traits may only be adaptive under a range of population and environmental parameters.

We have seen here that even with linear, i.e. density independent growth, cultural transmission can have a significant impact on qualitative outcomes. In real world systems we anticipate that some cultural variants may be density dependent.

For example, culturally transmitted foraging strategies may be limited by prey availability (e.g., in fish-eating killer whales (*Orcinus orcs*) (Foote et al., 2016; Ford and Ellis, 2006) and tool-using long-tailed macaques (Luncz et al., 2017)). This indicates that for some cultural variants there may be a carrying capacity as the result of ecological constraints. We explore a density dependent scenario, to provide more realistic limits to growth resulting from intrinsic carrying capacity for cultural variants and demonstrate how our analysis can be extended beyond a presence/absence evaluation of cultural variants, to consider competition between, potentially multiple, variants.

We consider populations with intrinsic carrying capacities modelled by logistic maps:

$$x^-(t+1) = r_1 x^+(t)\left(1 - \frac{x^+(t)}{k_1}\right)$$

$$y^-(t+1) = r_2 y^+(t)\left(1 - \frac{y^+(t)}{k_2}\right),$$

with growth rates r_1 and r_2 and carrying capacities k_1 and k_2 respectively, coupled as above by directly biased cultural transmission, after Boyd and Richerson (Boyd and Richerson, 1985)

$$p^+(t+1) = p^-(t+1) + bp^-(t+1)\big(1 - p^-(t+1)\big).$$

Note that the two populations are coupled only via cultural transmission and that the density dependence of the two populations is independent.

We explore the impact of cultural transmission as a bi-furcation in various scenarios. In the absence of cultural transmission, it is well known that a logistic map, with growth rate *r*, admits a transition from extinction, to a persistent steady state, through a sequence of period-doubling and ultimately chaos, as the parameter *r* passes, resp., through $r = 1$, $r = 3$ and up to $r \approx 3.56$ (Strogatz, 2015; Alligood, Sauer and Yorke, 1996).

We fix the carrying capacities – $k_1 = 1$, $k_2 = 1.2$ and consider:

1. $r_1 = 0.9$, $r_2 = 1.5$ corresponding to an x population declining to zero and a y population with persistent steady state (Figures 3 and 4, Top left);
2. $r_1 = 3.6$, $r_2 = 1.1$ corresponding to an x-population in chaos and a y population with persistent steady state (Figures 3 and 4, Top right);

3. $r_1 = 1.5$, $r_2 = 3.6$ corresponding to an x population with persistent steady state and y population in chaos (Figures 3 and 4, Bottom left);

4. $r_1 = 2.6$, $r_2 = 2.4$ corresponding to both x and y populations having persistent steady states (Figures 3 and 4, Bottom right).

Figure 4 (Top left), where $r_1 = 0.9$, $r_2 = 1.5$, and the associated equilibrium plot (Figure 5, Top left), which provides the abundance of the populations, rather than proportions, show that at low levels of cultural transmission ($b < 0.38$) the x population is zero and the y population has a persistent steady state ($p = 0$ stable). But as the transmission parameter b increases ($0.38 < b < 0.6$) then both x and y populations are persistent, but in varying proportions. The populations then reach a point where they are in approximately equal abundance. At $b > 0.6$ a threshold of transmission is reached, which causes the y population to decline to zero. The result is that both populations die out, but in such a way that the x population dominates during the decline (i.e. the y population is declining to zero, faster than the x population) (Figure 6). These plots show that there is an optimum region for transmission, where the transmission rate is not too strong, but just strong enough ($0.38 < b > 0.6$) that the persistence of both cultures is achieved. But if the transmission rate is higher ($b > 0.6$) then the proportion favours the x population, such that there is too much conversion to the x population (which is now a failing population), such that both populations decline towards zero, but the *y* population declines faster than the *x* population.

In Figures 4 and 5 (Top right) we start with an *x* population in chaos and a *y* population with a persistent steady state. As the cultural transmission increases, so eventually the *y* population is overwhelmed and dies out. The cultural transmission parameter *b* is acting in a similar way to enhanced growth rate, so it is pushing the *x* population beyond chaos. In Figures 4 and 5 (Bottom left) we swap *x* and *y* over and start with a *y* population in chaos and an *x* population with a persistent steady state. As cultural transmission increases, the persistent steady population dynamics overcome the chaotic dynamics resulting in a period-halving transition out of chaos to both populations achieving persistent steady states. Thus, we have shown that by coupling a chaotic population to a steady population, with directly biased cultural transmission from the stable population (i.e. such that *x* abundance increases), can bring both populations into a steady state.

In Figures 4 and 5 (Bottom right) we start with both systems exhibiting persistent steady states. As cultural transmission increases so the system traverses through a sequence of period doubling into culture induced chaos. This means the system switches predictably between different proportions of the two cultural variants within the population. But within the chaotic regime the proportion of each cultural variant is chaotic and so unpredictable. For example, if the cultural traits were voting preferences for a bi-party political system, then cultural transmission between political affiliations under this scenario could lead to chaotic affiliations.

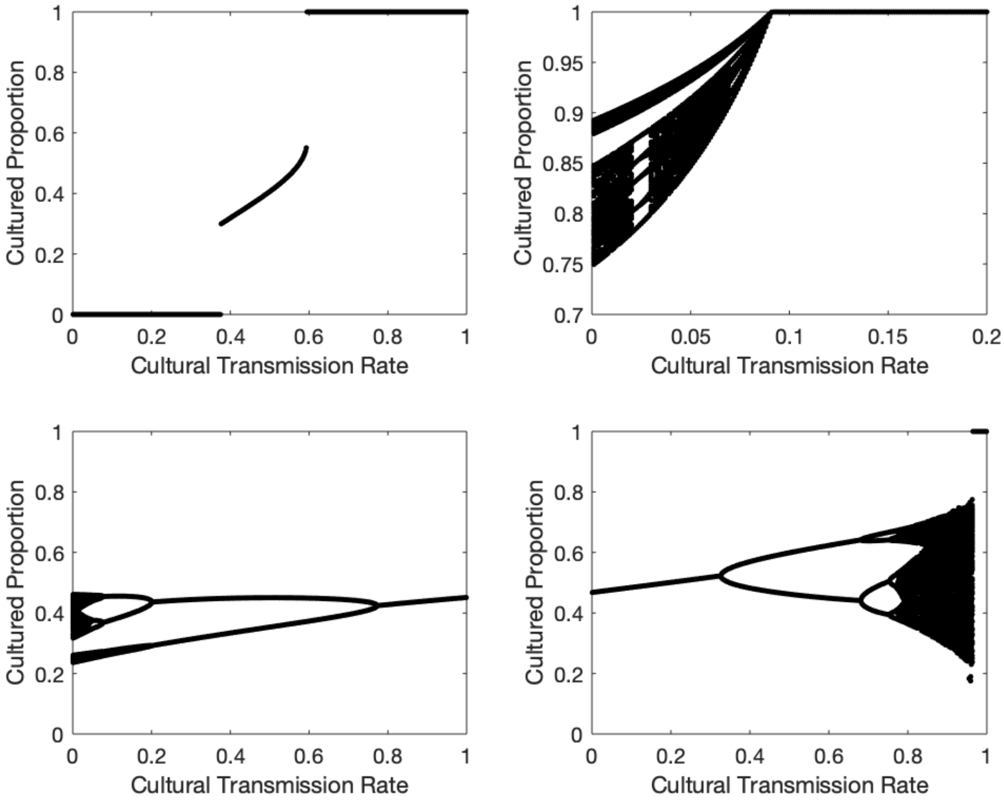


Figure 4. The proportion (*p*) of the *x* population relative to the strength of transmission (*b*) under a range of scenarios. k_1 = 1, k_2 = 1.2. Top left: r_1 = 0.9, r_2 = 1.5; Top right: r_1 = 3.6, r_2 = 1.1; Bottom left: r_1 = 1.5, r_2 = 3.6; Bottom right: r_1 = 2.6, r_2 = 2.4. See also corresponding plots in Fig. 5.

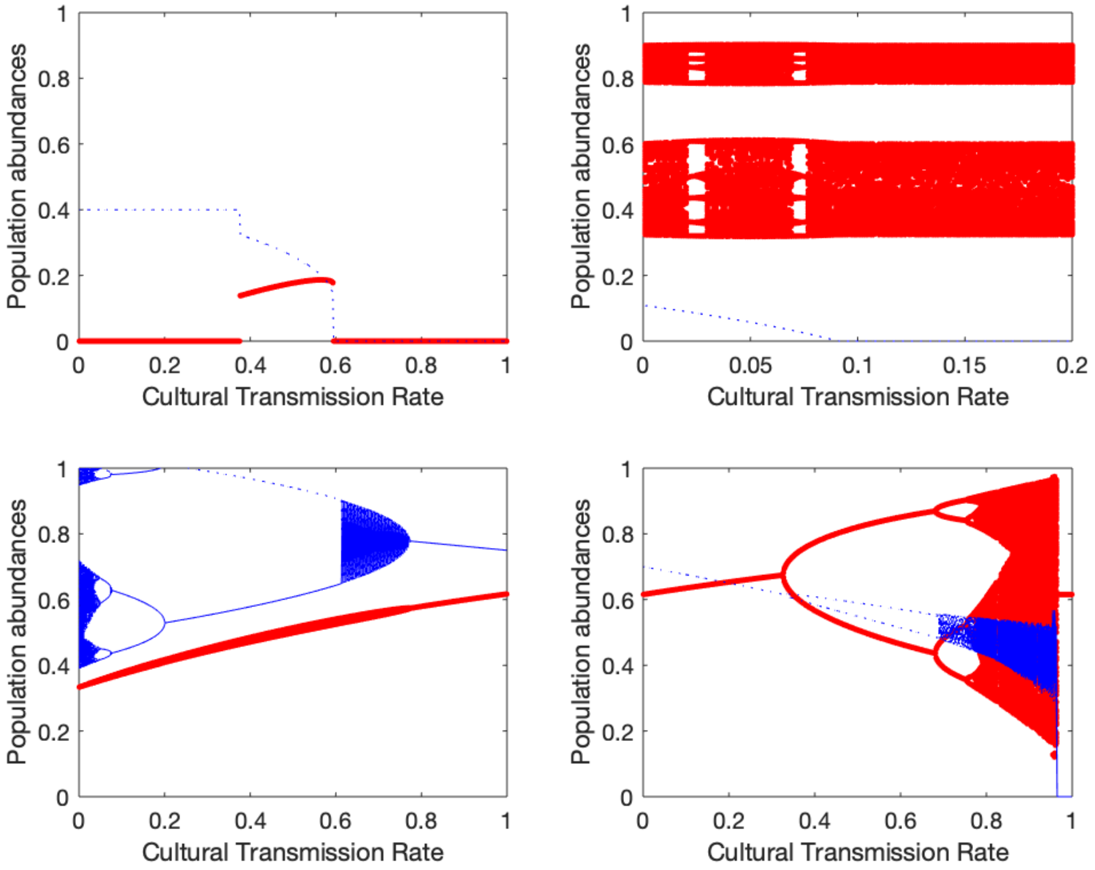


Figure 5. In corresponding plots, Fig. 5 provides the steady state equilibrium plot of the two populations (red for *x*, blue for *y*) relative to *b*, under the same scenarios in Fig 4.

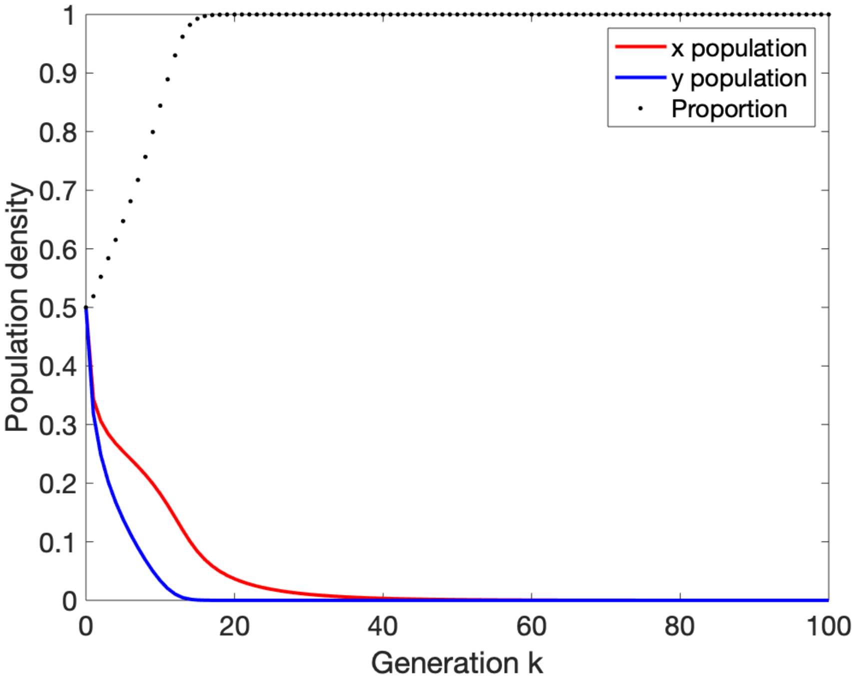


Figure 6. Inter-generational population density plot (*b* = 0.8) for the scenario under Fig 4 – Top left. This plot shows that as both populations are declining towards zero, the *y* population reaches zero before the *x* population under this scenario.

4. Discussion

Social learning provides a rapid mechanism for adopting adaptive behaviour in changing environments. But there are important trade-offs. Social information can be received from individuals other than parents and some social learning strategies, such as conformity or prestige bias, may have unavoidable, maladaptive side effects (Richerson and Boyd, 2005). Social learning can be considered maladaptive when it: limits the spread of adaptive behaviour (Boyd and Richerson, 1995; Giraldeau et al., 2002); leads to the acquisition of inaccurate or outdated behaviour, which hinders adaptive responses (Whitehead and Richerson, 2009); or when environmental factors limit faithful social transmission (Ward et al., 2008).

There is burgeoning interest in cultural evolution and the dynamics of gene-culture coevolution (Whitehead et al., 2019). But given the intra- and inter-generation time scales of cultural transmission, and relevance for issues such as conservation (Brakes et al., 2021), we have taken a novel approach by exploring the effects of a simple model for directly-biased (Boyd and Richerson, 1985), copy 'what' (Kendal et al., 2018), strategy of cultural transmission of a maladaptive variant on shorter-term population dynamics. By examining these concurrent processes (population growth, captured by ρ, and cultural transmission, captured by b), we show that cultural transmission can favour one population over another depending on the relative growth rates of the two populations and the strength of transmission. We show that in a system where individuals can freely switch between variants, the spread of maladaptive behaviour can lead to a cultural bistability (where both adaptive and maladaptive variants can co-exist). Significantly, from the perspective of ecological outcomes, we also show that under certain initial conditions a maladaptive cultural variant could dominate in what we describe as cultural exclusion (Figure 1).

We have shown that in addition to the strength of transmission (b), the relative proportion of the two cultural variants (p), as well as the ratio of the growth rates of the two populations (ρ) can have significant impacts on how cultural transmission propagates between two populations. As expected, if a specific cultural variant is associated with higher population growth rates, then that variant dominates, as cultural transmission reinforces the biological advantage of the higher vital rates. However, our analysis also demonstrates that, depending on the parameter regime, the strength of transmission (b) and the relative growth rate of the two populations (ρ), either cultural bistability can predominate, or the population with a maladaptive cultural variant can dominate at population dynamic equilibrium. This seems counter-intuitive to our understanding of maladaptive behaviour, which we might assume, by definition, is self-limiting. Nevertheless, by modelling the two concurrent processes of population growth and cultural transmission we show that there is a complex trade-off between the transmission rate (captured through parameter *b*) and the relative growth rate (ρ) of the two populations carrying the different cultural variants. This can result in ’cultural exclusion’, or cultural bistability where both populations secure a ’cultural niche’.

We also show that this bistability is associated with a hysteresis, where the population growth is dependent on both present and past inputs, i.e., the system has a ‘memory’ of recent inputs, or there is a latency effect in the system, which influences the outputs (Figure 3). An example from human culture might be a two-party electoral system, where the size of the populations supporting two parties, R and S, are both growing. If party R conducts a widespread propaganda campaign (increasing the transmission parameter *b* to 0.8), this dramatically ‘flips’ the overall population to predominantly supporting party R (arrow C, Figure 3). However, if party S then runs a counter-propaganda campaign the systems does not ‘flip’ back towards predominantly supporting party S (arrow A, Figure 3), until the transmission of party R propaganda has massively reduced (below 0.2, point B, Figure 3).

Further, from the perspective of species conservation, it has been argued that whether or not a species response to anthropogenic changes in the environment is adaptive or maladaptive is, at least in part, dependent on its past environment (Barrett et al., 2019). The demonstration of a hysteresis in our two variant system supports the idea that there may be latency in some cultural systems and that the history of a cultural variant – and its consequences for population dynamics – may to some extent be contingent on the history of the system.

The transmission of a cultural variant may also be constrained by aspects of the environment, from prey availability or access to social media. Figures 4 and 5 show that coupling two persistent populations with cultural transmission can result in chaos (Figures 4 and 5, Bottom right). Whereas, coupling a chaotic population and a persistent population with cultural transmission, the chaotic population can be moved into a persistent, harmonious state (Figures 4 and 5, Bottom left), with potential implications for managing populations. Alternatively, under a scenario coupling a chaotic population with a persistent population, cultural transmission resulting in movement from the persistent population to the chaotic population results in the dominance of the chaotic population and the previously harmonious population declines to zero (Figures 4 and 5, Top left). Finally, when a persistent population is coupled to a declining (but not chaotic) population with cultural transmission, depending on the strength of transmission (b), either the persistent population dominates, both populations persist or, when the strength of transmission is high ($b > 0.6$), the population that is declining dominates, but both populations decline to zero (Figures 4 and 5, Top left).

This example, (Figure 4 Top left), shows how transmission of a maladaptive cultural variant could be tolerated, so that both populations could persist for ($0.38 < b < 0.6$). However once transmission of the maladaptive behaviour reaches a certain threshold (here $b > 0.6$), both populations decline to zero. There are potentially many foraging, reproductive, religious or political examples that could be explored in this context. For example, some behaviourally plastic species, such as bottlenose dolphins (*Tursiops* spp.) can switch between foraging strategies, exploiting the foraging opportunity provided by human activities (Ansmann et al., 2012; Daura-Jorge et al., 2012). Theoretically, if anthropo-dependence on a maladaptive foraging strategy which increased entanglement rates, with lethal effects (or potentially even sub-lethal effects) were to propagate, then beyond a certain threshold of transmission, both the original foragers and the maladaptive anthropo-dependent foragers would decline, but with proportionally more of the dolphins undertaking the maladaptive behaviour.

In our two-variant analysis, the population with the less adaptive cultural variant had a higher growth rate, but a lower carrying capacity, than the other to simulate a culturally transmitted foraging strategy on prey with increased nutritional value with benefits for survival and/or reproduction, but that can only support a small population compared with the population following the original foraging strategy. At low transmission rates ($b < 4$) the proportions of each variant in the overall population stabilises (Figure 4, Bottom right). As the transmission rate increases slightly the proportions bifurcate into a period two orbit, where proportions of each cultural variant flip back and forth over each time step. As the transmission rate is increased beyond $b = 0.6$, we encounter a period four, eight, 16 orbit etc., until the system reaches chaos, in which case there are no stable proportions of the cultural variants. We note that such chaos can only be induced in systems where individuals can freely switch between cultural variants (e.g., in culturally fluid systems).

In contrast, we have demonstrated how culturally mediated over exploitation of resources could lead to a culture trap. It has been suggested that further research in this area may yield important insights for understanding how cultural transmission may influence wildlife populations response to anthropogenic changes to the environment (Barrett et al., 2019). We have also shown that two persistent, non-chaotic populations, coupled by cultural transmission can transition to chaos (Figures 4 and 5). It is perhaps surprising that this simple process of directly biased cultural transmission causes chaos, far below the parameter values required to achieve chaos in these populations without cultural transmission. Without cultural transmission, one would expect that the population would transition into period doubling when $r > 3$ and that for $1 < r < 3$ the population would remain stable and persistent. However, the result of coupling these logistic maps with cultural transmission is that the threshold for period doubling and chaos is reduced below $r > 3$. Notably, the degree of chaos is increased as the transmission parameter (b) in increased.

We have focused on a mechanism for direct biased (copy ‘what’ (Kendal et al., 2018)) strategy, but of course individuals can learn socially using multiple sources and various strategies across a range of behavioural domains. Thus, future analyses might usefully consider other learning biases, such as conformity, prestige bias, or frequency dependence. We have also assumed in our theoretical social system that individuals may switch between cultural variants without constraint. In addition, our analysis is limited to social transmission between conspecifics, but there is some evidence for social learning from heterospecifics (e.g. predator risk (Ito and Mori, 2010) or the location of foraging habitat (Farine et al., 2015)). So there is ample scope for future explorations to consider the effect of different social learning strategies, behavioural plasticity, or individual differences, on the propagation of maladaptive cultural variants within and between populations. Further, how density dependence may result in a carrying capacity for particular cultural variants and the possibility of ‘cultural traps’ also warrants further investigation. It has been argued that ‘Darwin’s ability to account for maladaptation was more important than his ability to account for adaptations’ (Richerson and Boyd, 2005). The inevitability and potential consequences of maladaptive cultural variants make them an important target for research in relation to the processes of population dynamics, particularly since the processes influencing the propagation of maladaptive cultural variants operate on different timescales and are potentially even more multi-faceted than the processes which limit the transmission of maladaptive genes. It is generally considered that the greater the number of possible cultural variants to choose from, the higher the chances are of acquiring the ‘best’ variant (i.e., most adaptive variant for the current environment) in the population (Richerson and Boyd, 2005).

Boyd and Richerson suggest that ‘The price we pay for our promiscuous lust for adaptive information is playing host to sometimes spectacularly pathological cultural variants’ (Richerson and Boyd, 2005). In our dichotomous, two variant system, we demonstrate the potential risks associated with having only two cultural variants to choose from, particularly if one is maladaptive. Our research shows the importance of maintaining cultural diversity, both in the wild, but also across human political and social systems, since maladaptive cultural variants are inevitable and may propagate. For example, the transmission of propaganda about Covid19, through ‘alternative facts’ or deep fakes on social media (Yamey and Gonsalves, 2020). Beyond the propagation of maladaptive variants, we have also shown that coupling two populations through a simple social leaning rule can have unexpected consequences for population dynamics, bringing populations into and out of stability.

This work emphasises the importance of accurately assessing transmission rates for cultural variants in empirical data sets and considering the limits to and feedback on their growth. While transmission rates themselves may be dynamic, we suggest that this approach could be used to further explore the dynamics of cultural transmission of specific cultural variants within human and non-human societies and examine how this could lead to the instability or breakdown of cultural systems under certain parameter regimes.

Acknowledgements: The authors would like to thank Dr Thomas Currie for helpful comments on a previous draft

CHAPTER 7

General Discussion and Future Directions

Overview

The central proposition of this thesis is that non-human culture can interface with population dynamics to generate patterns and processes which can cause population level effects and thus inform conservation science, policy and practice. Culture can provide insights on both *how* conservation is conducted and *what* managers should be aiming to conserve (the ‘unit to conserve’). To better understand how non-human culture and conservation interface a process was developed under a multi-lateral environmental agreement, to generate a large-scale collaboration between researchers, across regions and across vertebrate taxa, to gather evidence for the multifaceted manner in which social learning and non-human culture interfaces with conservation. A synthesis of the available evidence led to the development of a conceptual framework for conservation and culture (Brakes et al., 2021). Examining the emergent patterns, I then developed theoretical models to explore some of the underlying processes involved in how culture interfaces with conservation and population dynamics. I have explored the transmission of both adaptive and maladaptive cultural variants and consider the implications for conservation activities and beyond.

In this final chapter I provide further context for the insights gained from this research and consider the implications for conservation science, policy and practice. I also consider philosophical aspects of conserving non-human cultures and finally, suggest areas for future research.

Conserving cultural species

In April 2021 the United Nations General Assembly adopted a resolution which highlighted the need to protect biodiversity, to help humanity achieve the millennium development goals[5]. I argue that the burgeoning evidence on non-human culture warrants a re-examination of the concept of biodiversity, with fine scale structuring of populations that can arise as the result of non-human culture.

A key objective of conservation is to maintain heritable variation and adaptive evolvability (Whiten, 2021). The aim of conservation policy makers is to determine the most salient unit to conserve to achieve the best conservation or sustainability outcomes. Delineating populations is a primary consideration and can be informed by data on genetics, population structure, movement between populations and non-human culture (Brakes et al., 2021). These data enable the estimation of abundance and trends which can inform threat status (IUCN, 2012) and prioritisation. An important element in this process - particularly the case for cetaceans given the challenges associated with accurate abundance estimates for these species (Taylor et al., 2007) - is estimating the degree of uncertainty associated with these estimates (Ashe et al., 2021). To calculate uncertainty, managers must consider a wide range of factors that include endogenous population processes and the exogenous influence of the environment affecting population dynamics. Given the evidence that non-human culture can generate both heritable variation and cultural structuring of populations (Whitehead, 2010; Whiten, 2021), social learning (the process which can generate non-human culture) is arguably an important endogenous process for evaluating uncertainty in population assessments.

The concept of the evolutionary significant unit (ESU) was developed in response to the need to establish units that conservation managers and practitioners should aim to conserve (Crandall et al., 2000; Whitehead et al., 2004). ESUs focus specifically on genetic or heritable phenotypic distinctiveness, within units that demonstrate isolation, such that there is a restricted flow of information that determines genotype or phenotypes, from other such units (Crandall et al., 2000; Whitehead et al., 2004). Whereas, a demographically independent population (DIP) is focused specifically on internal demographic processes (births and deaths) that are more important to population persistence than migration (Morin and Dizon, 2018; Wade and

---

[5] United Nations General Assembly, 75th Session, Agenda Item 19, Sustainable Development, Resolution A/RES/75/271. Nature knows no boarders: transboundary cooperation – a key factor for biodiversity conservation, restoration and sustainable use

Angliss, 1997). In addition, a cultural variant (CV) is a particular form or variant of a cultural trait displayed by a group or population (Cavalli-Sforza and Feldman, 1981). It has since been argued that after genetics, culture may be the second most important process for shaping phenotypic diversity within and between populations (Whitehead and Rendell, 2015). Since social learning can create heterogeneity within populations which can result in cultural structuring of populations, it has been argued here that this can inform the 'unit to conserve'. The question then for conservation managers is what are the risk involved in assuming that cultural populations are homogeneous? If managers attempt to incorporate culture into conservation assessments, what criteria should they use to decide which units to prioritise, given the complex dynamics between culture and population dynamics explored here?

Modelling insights

Previous metapopulation research showed that social learning which slows responses to anthropogenic threats can contribute to population decline (Hale et al., 2015). A review of social learning and adaptive responses to human induced rapid environmental change (HIREC), noted that 'More empirical and modelling work on consequences of social learning for population… dynamics and for eco-evolutionary dynamics should be valuable and exciting' (Barrett et al., 2019). Taking up this gauntlet, the modelling research undertaken in this thesis aims to illuminate some of the processes that may bring about such a decline when social learning interfaces with population dynamics. This research also demonstrate how social learning can create opportunities and contribute to resilience through the spread of adaptive culturally transmitted variants.

By exploring the tension between the simultaneous dynamics of cultural transmission and demography for a particular social learning strategy (direct bias, after Boyd and Richerson 1985), it was possible to show how the manipulation of transmission by conservation practitioners could be used to capitalise on marginal gains in survival or reproduction, for the benefit of the wider population (Chapter 4). In practice, seeding social information, either though human demonstrators (e.g., whooping cranes (Mueller et al., 2013)), or conspecific demonstrators (e.g., golden lion tamarins, (Kierulff et al., 2012)) has been shown to greatly enhance some reintroduction efforts, at least in the short-term. Similarly, for species that forage through local enhancement, such as griffon vultures, simultaneous release of a larger number of individuals improved release success by creating a chain reaction of foraging (Jackson et al., 2008). Understanding the type of social learning that is the focus of conservation efforts and whether this is driven for example by ontology (e.g., imprinting chicks), density of demonstrators, frequency of occurrence of the behaviour, prestige bias or another copying rule is key to understanding how transmission rates may be practically manipulated in the wild. Ideas include, ensuring there are sufficient competent demonstrators, as for reintroduction of golden lion tamarins (Kierulff et al., 2012), or ensuring that those individuals that act as repositories of social knowledge (McComb et al., 2001) are protected.

Further, the timing of conservation intervention may be an important consideration in populations where cultural transmission results in transient population dynamics (Chapter 5) and social learning, which is an endogenous population process, may have potential latent effects. It was also possible to establish conditions for cultural bistability, but also cultural exclusion, similar to the idea of competitive exclusion, where under certain parameter regimes one cultural variant will dominate in a population (Chapter 6). Under certain parameter regimes, this bistability can also lead to a hysteresis loop, where for example in human culture, a small amount of negative publicity can only be recovered by a large amount of good public relations activity (e.g., MMR vaccine (Petts and Niemeyer, 2004)). By introducing density dependence into this system it was also possible to demonstrate how cultural transmission can induce chaos in an otherwise stable system (Chapter 6).

Another matter which merits further consideration is the issue of how behavioural plasticity may relate to the propagation of non-human cultures and scale up to have population level consequences. In the coupled system explored here, individuals can switch freely between cultural variants, which can lead to cultural bi-stability, or even cultural exclusion (Chapter 4). The ability for some species to be able to switch opportunistically between cultural variants in the face of anthropogenic stressors or where new opportunities arise, has often been assumed to provide resilience (i.e., resistance to perturbation (Hodgson et al., 2015)). For example, behavioural plasticity in bottlenose dolphins (*Tursiops aduncus*) when a ban to trawl fishing caused a switch in foraging activity

(Ansmann et al., 2012). Nevertheless, if a maladaptive cultural variant is being propagated (as per Chapter 6), then in some circumstances adopting the maladaptive variant could be a disadvantage. In which case cultural conservatism, as seen in the foraging strategies of killer whale (*Orcinus orca*) populations (Whitehead, 2010), would be a safer strategy. Despite the risks of depleted prey base for such specialists, this conservatism reduces the risk of adopting a maladaptive cultural variant. Therefore, it is postulated here that perhaps one advantage to conservatism is avoiding the risk of chaos ensuing (as per Chapter 6) as the result of individual switching back and forth between cultural variants. However, the trade-off is that conservatism may limit a population's ability to respond by adopting a new cultural variant when the carrying capacity of a particular cultural behaviour is exceeded.

One important difference between culture and population dynamics is that culture is measured by proportion in each cultural unit, whereas populations are driven by abundance. It is shown here how costly (or maladaptive) cultural variants can predominate, or persist in populations, if they are transmitted at higher rates than they are removed by demographic costs (Chapter 6). This supports the conclusion that rather than specifically focussing on conserving one cultural variant, conservation managers should work to conserve cultural diversity and the capacity for new adaptive cultures to arise (Chapter 5).

While the value of developing theory in this field, amid ever pressing threats to the natural world, could be questioned. This observation from an anniversary edition of the journal *Theoretical Population Biology* provides useful context: "…theoretical work in population biology often proceeds in relative obscurity over many years, as theory frameworks are refined, sometimes well ahead of their time in relation to the associated empirical science, and sometimes breaking through to empirical applications only after substantial effort to communicate the work in different, less mathematical forms." It is hoped that the insights developed here on these dual dynamics and on the potential for cultural exclusion, cultural bistability, tipping points and transition to chaos, may provide useful steppingstones for future theoretical and empirical studies in this field.

Implications for conservation policy and practice

Conservation managers and practitioners may be able to utilise the processes of social learning to increase survival or reproduction in wild populations and potentially benefit from deeper understanding of the processes in play (Brakes et al., 2021). The modelling work conducted here hints at some very complex dynamics from which it may be challenging to distil simple overarching management advice (see chapter 6 for an analysis of the complex dynamics emerging from the simpler case of a scalar population). In the simple coupled system in Chapter 4, the outcomes are contingent on: transmission rate; population projection matrix parameters (including any change to vital rates arising from adaptive social learning); relative abundance of cultural units; as well as population stage structure. Therefore, distilling overarching principles for conserving culturally heterogenous populations based on anticipated population dynamics may be impractical. Given the wide range of parameters which can influence outcomes, the best option remains a case-by-case approach, with the core objective of maintaining cultural diversity and the capacity for adaptive cultural variants to emerge by restoring and conserving the integrity of habitats.

It is argued here that there are significant risks associated with maintaining the *status quo* and assuming that populations are culturally homogenous. There may be distinct population segments arising from cultural variants that have specific ecological requirements, which may dictate how segments of the wider population and their habitats should be managed. Neglecting to recognise such heterogeneity may result in less efficient implementation of conservation mitigation efforts. Further, failure to monitor for maladaptive cultural variants, such as depredation, may be detrimental for the entire population if they are able to propagate (see Chapter 6).

But how should managers attempt to incorporate cultural heterogeneity into conservation assessments? It is recommended that longitudinal, high resolution behavioural research within and between populations will help to inform decision making and both direct and indirect lines of evidence (including phylogenetic inference) may be useful in evaluating the presence and effects of social learning (Brakes et al., 2021; Chapter 3, Figure 3). Given that non-human cultures can be either long-lasting or ephemeral and there may be multiple parameters that are beyond the control of managers (see Chapter 4 and 5), it is suggested here that best practice is to conserve the capacity for adaptive cultural variants to arise, as a source of resilience, by protecting diversity within habitats and behavioural heterogeneity within populations. For this long-term goal to be achieved, managers should work to prioritise the following two key elements. Firstly, the collection of behavioural data in endangered species that learn socially, particularly where there is evidence for cultural transmission influencing survival or reproduction. Secondly, applying insights on cultural transmission for conservation interventions such as reintroduction or translocations, e.g., where beneficial cultural information can be seeded into a population either through human or conspecific demonstrators. In addition, the broad field of human-wildlife interactions can also benefit from prioritising the role of social learning in mitigating conflicts such as crop raiding (Brakes et al., 2021).

Nevertheless, emergent evidence on non-human cultures begs the question, what is the best unit to conserve? Cole (1957) defined a population as ‘a biological unit at the level of ecological integration where it is meaningful to speak of a birth rate, a death rate, a sex ratio, and an age structure in describing the properties of the unit’ (Cole, 1957). It has been argued by Hammond et al. (Hammond et al., 2021), that this definition is difficult to implement for species such as marine mammals and it’s been suggested that a more practical definition by Krebs (1972) may be more useful: ‘a group of organisms of the same species occupying a particular space at a particular time… [its] boundaries … both in space and time are vague and in practice are usually fixed by the investigator arbitrarily’ (Krebs, 1972). In contrast, the International Union for the Conservation of Nature (IUCN), has adopted a broader definition of a population as the “Set of individuals from the same wild species that share the same habitat.” (IUCN, 2022).

There are many other definitions of the term population used in various management organisations, which relate to the specific focus of the organisation’s activities (Hammond et al., 2021). However, all such definitions fail to incorporate the heterogeneity which can arise as the result of cultural structuring of populations. Returning to Cole’s definition, cultural structuring can influence birth and death rate between cultural units (e.g., in bottlenose dolphins (*Tursiops aduncus*) (Wild et al., 2019b)). Only a small handful of international conservation bodies have even begun to grapple with how culture generates heterogeneity and what this implies for defining units to conserve (see Chapters 2 and 3). This research demonstrates the importance of collecting evidence for social learning within and between populations, particularly where cultural variants create discernible patterning and interface directly with vital rates (either positively, or negatively). This provides significant insights for the question of the 'unit of conserve'. The complex interactions between cultural transmission and population dynamics provide a strong imperative for researchers to gather high resolution behavioural data and for managers to recognise some culturally significant units as distinct population segments, or demographically independent units, where the data support these delineations (Brakes et al., 2021). Arguably, the precautionary principle should also be applied, as the simple fact is that non-human cultures are likely being lost at a much faster rate than they can be described.

Beyond providing insights for the unit to conserve, this research also shows how transient dynamics that can be generated through cultural transmission (Chapter 5), may influence the efficiency of some conservation measures. It has been argued that better understanding of how transient dynamics affect overall population dynamics is essential for predicting how human populations may response to environmental and social factors and their effects on projected population size (Nicol-Harper et al., 2018). Indeed, it has been suggested that understanding these shorter-term dynamics may also be valuable for effective sustainable development (UN, 2015). Arguably, the research presented here demonstrates that this may also be true for planning and conservation of non-human populations where cultural structuring within populations generates transient dynamics (Chapter 5).

The question of temporal stability of a cultural variant may also be an important consideration. Archaeological excavations in chimpanzee (*Pan troglodytes versus*) habitat in West Africa recovered evidence for nut-cracking, dating back to around 4,300 years ago (Mercader et al., 2007). A vertically transmitted cultural variant, that might be thousands of years old, may have survived and been refined across multiple generation because it has adaptive value. However, I have shown that even fad-style cultures, that are horizontally transmitted, which may be brief and/or temporally unstable, may still generate population level consequences under certain parameter regimes (Chapter 6).

Returning to the example of sperm whale (*Physeter macrocephalus*) acoustic clans in the easter tropical Pacific (see Chapter 2), the question for conservation policy makers is whether there is value in focusing effort on conserving a smaller, or potentially declining cultural unit (see Chapter 5). The answer is yes if the objective is to maintain cultural integrity of the wider population. The answer may also be yes, if the objective is to conserve cultural capacity, by conserving any latent cultural knowledge that may not be advantageous now but could become viable in a changing environment. The dual dynamics between cultural transmission and population dynamics explored in this thesis demonstrate that, when considering cultural populations, it is rarely as straightforward as assisting a cultural unit with adaptive knowledge to flourish, at the cost of a less adaptive, or maladaptive cultural unit failing. These findings support the proposition that the objective for conservation managers should be conserving cultural diversity and the capacity for adaptive culture to emerge.

The need for fine scale data on cultural variation in the wild also supports the call for further, higher resolution, longitudinal field data for marine mammal (Mann and Karniski, 2017) and other species (Harrison and van de Waal, 2022). Such studies may be essential for further developing understanding of the interface between non-human culture, population dynamics and conservation efforts and for testing theoretical findings with empirical data sets.

Received wisdom and other considerations

This research has focused primarily on the utility of non-human cultures, for either shaping how we define populations or practical aspects of how conservation is undertaken. It has previously been suggested that certain spectacular or unusual non-human behaviours, such as wildebeest (*Connochaetes* sp.) migrations or Japanese Macaques (*Macaca fuscata*) bathing in hot springs, may warrant special attention based simply on their uniqueness (Sutherland, 1998). But beyond utility and interest to humans the fact of non-human culture raises a deeper philosophical question: what do these non-human cultures mean to the species themselves? Although rhetorical, this question deserves consideration.

For humans, everything from our names, our clothes, our homes to how we communicate are all culturally transmitted. For each of us, our sense of identity is inevitably prescribed and proscribed by the rules and trends of our cultures. We value this diversity and have systems for protecting the intrinsic value of human cultures, as enshrined by the United Nations Education, Scientific and Cultural Organization (UNESCO). This organisation asserts that human cultural heritage extends beyond objects and monuments, but also includes ‘oral traditions, performing arts, social practices, rituals, festive events, knowledge and practices concerning nature and the universe or the knowledge and skills to produce traditional crafts’ (UNESCO, 2016), in what is termed intangible cultural heritage.

Humans have spent generations documenting our diverse cultures. However, we are still only in the foothills of describing and understanding the processes of non-human cultures. What our own, diverse cultures choose to do with this emergent knowledge on non-human cultural heterogeneity, besides re-evaluating conservation mandates, is an inherently philosophical question beyond the scope of this thesis. But it is hoped that some of the research presented here may be informative for subsequent dialogue on these matters.

Acknowledging the inherent challenges in adapting culture theory into conservation practice (Carvalho et al., 2022), I argue that better understanding of the consequences of cultural transmission for population dynamics may be essential for the conservation of some species or populations. It is precisely because cultural transmission can interface with “well established conservation metrics such as population size, viability and demography” (Carvalho et al., 2022), to increase population resilience or create vulnerability, that theoretical research can provide direction for empirical studies to elucidate how best to harness some of these processes for conservation benefit.

Future directions

Transmission of social learning through a population may be facilitated or constrained by: the type of social structure (Whitehead and Lusseau, 2012); the degree of conformity within the population (Aplin et al., 2015); which individual is exhibiting the behaviour (model-based bias) (Kulahci and Quinn, 2019); frequency dependent bias; fidelity of copying; the centrality of individuals (Kulahci and Quinn, 2019; Rendell et al., 2019); and content bias (Whitehead and Rendell, 2015). Population stability may also be an important factor for social transmission (Kurvers et al., 2014). This research focused on directly biased social learning (after Boyd and Richerson, 1985), but research on how these other aspects of cultural transmission interface with population dynamics is fertile ground for further research that could help advance this field.

In terms of conservation, taking into consideration non-human cultures may also enable the identification of unique habitats of relevance for specific cultural behaviours, e.g., stone rubbing beaches for killer whale (*Orcinus orca*) cultural unit (Ford, 2009). The Important Marine Mammal Area (IMMA) initiative under the IUCN (Tetley et al., 2022), has a number of criteria for identifying and classifying habitat. One criterion on special attributes, identifies areas of distinctiveness as 'Areas which sustain populations with important genetic, behavioural or ecologically distinctive characteristics'[6]. Arguably, unique cultural behaviour could qualify under this criterion as a behaviourally distinctive characteristic.

Given the findings of Chapter 6, another area for potential future research, is exploring how socially learned rules of engagement, which may result in what we regard in humans as 'moral' behaviour, may interface with population dynamics. Whitehead postulated that the fact that there is no evidence that the powerful echolocation clicks of sperm whales are directed at conspecifics in aggression, may be the result of a code of conduct in this species (Whitehead, 2003). Returning to the question of the interface between cultural transmission and population dynamics, one might interrogate the demographic consequences of cultural transmission of such rules and consider the population level consequences for rules of engagement or taboos being propagated across non-human populations through social learning.

---

[6] IMMA Criterion D – Special Attributes, Sub-criterion D1 - Distinctiveness

Conclusion

The reach of non-human culture into many areas of human activity is extensive (Whiten, 2021). Whether helping humans to obtain food (Bhattacharyya and Chakraborty, 2017; Daura-Jorge et al., 2012), shedding light on dynamics and perceptions within our own cultures (Marcel et al., 2019), or informing how to mitigate the effects of anthropogenic degradation of habitats and ecosystems (Bezamat et al., 2021). This second inheritance system (Whiten, 2017a) has been shown here to generate complex dynamics. There is no 'one size fits all' solution to understanding the interaction between conservation and non-human cultures. This work focused on one particular social learning strategy (directly-biased horizontal social learning), which revealed a wealth of complexity resulting from simultaneous cultural transmission and population dynamics. Nevertheless, it has been possible to identify parameter regimes where culture can generate bistability, tipping points (or hysteresis), chaos and, what is termed here, 'cultural exclusion'.

Sutherland noted that "the overwhelmingly important problem of humanity and biodiversity is the increase in human population". Given that often what we manage, rather than the species themselves, is human behaviour (Record, 2021), one of the greatest challenges for the decades ahead is how we can utilise understanding of human and non-human cultures to facilitate better outcomes for biodiversity and ourselves.

This research shows how perturbing cultural systems can result in complex outcomes and therefore supports the suggestion that 'removing an individual can sometimes be more consequential than a simple decline in census size' (Brakes and Rendell in press). For the effective conservation of cultural species, we can use our knowledge of the role of social learning to promote the acquisition and spread of fitness-related behaviour to design conservation policy that ensures that pathways of cultural transmission are maintained as much as possible. Although there are many challenges associated with this in practice, it is argued here that the most judicious course, given the complex interactions between culture and population dynamics is to work to conserve cultural diversity, within and between populations, as an essential source of adaptive behaviour.

Returning to Caswell's ‘problem of heterogeneity’ (Caswell et al. 2018), which highlights the challenge of unravelling how individual heterogeneity influences population dynamics, another challenge emerges: emergent understanding of finer scale diversity, from individual variation to non-human culture, also raises important scientific and philosophical questions about how we define biodiversity and what it is we should be aiming to conserve.

APPENDICIES

APPENDIX 1.1

Extracts from: Brakes, P and Dall, SRX (2016).

Marine mammal behaviour: a review of conservation implications

Front. Mar. Sci., 20 June 2016 | https://doi.org/10.3389/fmars.2016.00087

Introduction

The extant marine mammals are found in three Orders *Cetacea, Sirenia* and *Carnivora* (including suborder *Pinnipedia,* Family *Mustelidae* and Family *Ursidae*). These species inhabit a diverse range of habitats from river, brackish, mangrove and estuarine habitats, to coastal shallows and pelagic seas, with some even foraging at the edge of the abyssal plain. In addition, they have a diverse range of food items, from seagrass or zooplankton, through to fish, penguins and other marine mammals. As a result of their diverse niches, they exhibit a wide range of behaviors. Some of their behaviors have been studied in detail, whereas others remain more mysterious. For example, the exceptional migration of the baleen whales is well documented, while details about the more subtle, small-scale behavioral differences between marine mammals social groups is only now starting to emerge.

The importance of incorporating behavioral ecology into conservation efforts has long been argued for terrestrial mammals (Candolin and Wong, 2012; Caro and Durant, 1995; Sutherland, 1998), particularly where manipulations of the wild environment are possible to assist conservation efforts. The challenge that remains is to determine how insights into behavioral ecology can best be used to inform conservation efforts in the more alien marine environment.

Sociality and social learning are undoubtedly important considerations when conserving marine mammals. In 2010 Whitehead suggested that several factors complicate the conservation of species that learn socially, such as the rapid spread of novel behavior, the evolution of maladaptive behavior, or the inhibition of adaptive behavior (Whitehead, 2010). He argued that such factors have an influence on habitat suitability, responses to anthropogenic change and even genetic structures. This is reflected in an analysis which revealed that of the toothed whales (*Odontoceti*), four species showed evidence of decrease in birth rates following exploitation, highlighting the effects beyond the dynamics of individual removals (Wade et al., 2012).

Behavioral variation among populations and individuals also has the potential to influence responses to management efforts and to enhance or hinder conservation. For example, understanding sperm whale (*Physeter microcephalus*) depredation of sablefish from demersal longlines across the Alaskan fishery has only been possible with emerging knowledge about the scale and spread of this behavior and whether noise from fishing vessels may be providing an acoustic cue for these whales (Thode et al., 2015). While research on killer whale (*Orcinus orca*) response to an acoustic harassment device, to prevent long-line depredation, indicated habituation to the device (Tixier et al., 2015). However, despite being habituated to the device, exposure to the sound it produces while depredating lines may result in potentially harmful hearing damage (Tixier et al., 2015).

Small population extinctions

Genetic, ecological and behavioral factors can all contribute to making small populations particularly vulnerable to extinction. One of the most significant challenges for marine mammal conservation is determining demographically independent conservation units, based on acoustic, taxonomic, genetic, geographic, behavioral, social or ecological features (Parsons et al., 2015). In highly social species, behavior may play a particularly important role in differentiation between units to conserve and in understanding the mechanisms of population persistence or decline.

Social species may benefit from the presence of conspecifics in a number of ways including predation risk dilution, collective anti-predator vigilance, ‘selfish herd’ effects, predator confusion, cooperative foraging, resource defense, increased availability of suitable mates, allo-parental care and reduction of inbreeding (Krause and Ruxton, 2002; Stephens et al., 1999). Whilst a handful of marine mammal species are solitary, many are social for at least part of their life cycle and as numbers decrease the ability to raise the alarm, defend against predators, forage or breed cooperatively also generally declines. The Allee effect (Allee, 1931), which may result in precipitous decline, is defined as a positive relationship between any component of individual fitness and density of conspecifics (Stephens et al., 1999). But it is necessary to differentiate between component Allee effects (at the level of individual fitness) and demographic Allee effects (at the level of mean fitness), which may be important for predicting the persistence of small populations, particularly where a decrease in numbers results in reduced opportunities for cooperation. For example, obligate cooperative breeders rely on a minimum group size to subsist and studies in terrestrial mammals suggest that cooperative breeders (see Section 3) may be particularly susceptible to Allee effects. A new conceptual level, the group Allee effect, has been suggested for cooperative breeders (Angulo et al., 2013).

Smaller populations may also place limitations on the ability to find a suitable mate. This may be the result of changes in operational sex ratio as the population declines, which may be related to population density and changes in habitat, but other sexual selection pressures, such as the specifics of mate choice, may also have an influence on population growth rates, making smaller populations more prone to extinction. For example, there is evidence from sperm whaling records that following the reduction in abundance of larger males, that fertility rates were reduced (Clarke et al., 1980; Whitehead et al., 1997). Whether this reduced fertility rate was the result of female mate choice or other selection pressures is unknown.

Nevertheless, it has been suggested that in baleen whales, since male song may influence female mate choice, that preference for local or known dialects could theoretically cause pre-zygotic isolation between species, potentially a precursor to speciation (Beltman et al., 2004; Thornton and Clutton-Brock, 2011). Conversely, it has also been suggested that to avoid inbreeding depression female humpback whales may have a preference for novelty in song, which itself may drive the evolution of the males’ song (Parsons et al., 2008).

The matter of how to define a ‘small population’ has conventionally been resolved on genetic or geographic parameters (or both). Nevertheless, from the perspective of determining the influence of behavior for conservation efforts, delimiters based on specific behaviors may also be relevant for predicting population persistence. For example, Southern sea lions (*Otaria flavescens*), which have declined by over 90% in the Falkland Islands since the 1930s, exhibit two discrete foraging strategies; inshore and offshore. These strategies appear to be independent of intraspecific competition and are thought to be influenced by foraging site fidelity (Baylis et al., 2015). Using feeding strategies as a boundary between smaller sub-sets of the population may be a vital conservation tool.

In addition, of the three distinct populations of false killer whales (*Pseudorca crassiden*) recognized around the Hawaiian Islands, a significant difference in fisheries related scarring has been identified between these populations. This suggests that fisheries interactions are occurring at a higher rate in one population, with a bias towards females, suggesting that fisheries-related mortality is likely to be disproportionate across these distinct populations (Baird et al., 2014). Thus behavior is relevant for determining ‘distinct population segments’ (DSP) and it has been argued that attempts to limit DSPs to purely ‘evolutionarily significant units’ could compromise management efforts, since the use of demographic and behavioral data would be reduced (Pennock and Dimmick, 1997).

Species Isolation

Behavior, and in particular social learning, may be drivers for speciation (Beltman et al., 2004). But species isolation may cause genetic bottlenecks to develop or create independent evolutionary trajectories. Behavior itself, and particularly social information use, may cause effective population isolation to develop for population segments in sympatry (Riesch et al., 2012).

Extirpation has the potential to remove localized adaptations and potentially eliminate unique evolutionary paths. It has been suggested that for the morphologically and genetically distinct Maritimes walrus (*Odobenus* sp) localized extinction as a result of hunting, curtailed an evolutionary trajectory that would have enabled this species to evolve along a different path to other north Atlantic walrus (McLeod et al., 2014).

Dispersal in fragmented populations

The degradation of habitats can lead to the fragmentation of populations and remains an ongoing conservation issue. Key causes of population fragmentation in marine mammals are displacement, through noise, fishing, harassment or some other environmental stressor, or change in prey abundance or dispersal. Some species may be better equipped to adapt to differing food availability, for example through adapting foraging specializations (Ansmann et al., 2012; Tinker et al., 2008). But other species don't have this flexibility, sirenians are obligate seagrass feeders and thus may disperse into fragmented populations in search of new food patches following extensive damage to seagrass beds (Prins and Gordon, 2014).

Key to predicting how populations may fragment as a result of habitat degradation is an understanding of the range of possible dispersal behaviors. Sutherland (1998) noted a need for a better understanding of how animals search, sample and select new patches (or boarder habitat) and this remains a significant question for marine mammals. This is not only true for resident populations – versus more transient cohorts - but may also be relevant for understanding changes to migration patterns between critical feeding and breeding habitats. But interpreting responses to disturbance can be complex. Bejder et al. (2006) argue that incorrect application of the term habituation may result from situations where more sensitive individuals have already left a disturbed study area before assessment.

Fragmentation of social groups may be caused by other anthropogenic effects, such as hunting, bycatch or harassment. Dispersal behavior is also relevant to the rate and extent of the spread of disease. The rate of infection is dependent upon the frequency with which susceptible individuals come into contact with uninfected individuals. For example, elucidation of dispersal and social interactions may be important for predicting transmission of the phocine distemper virus epidemics across harbor seal populations (*Phoca vitulina*) in north-western Europe (Bodewes et al., 2013).

Predicting the consequences of environmental change

Predicting the consequences of environmental change is best understood by looking at the patterns of density dependent processes (Sutherland, 1996) i.e. how vital rates (such as mortality and fertility) are regulated by population density. To understand the role of behavior in some density dependent processes it is necessary to have data on the type of breeding systems, social structure and the transmission of social information within and between populations, as well as an understanding of individual decision making. Such data can be difficult to collect in the marine environment. Nevertheless, some studies provide insights into these processes and may provide opportunities for predicting the consequences of human-induced rapid environmental change (HIREC) (Sih et al., 2011) in marine environments.

Arguably the most pressing environmental issue of this era, which is increasingly being regarded as the ‘Anthropocene’ (Waters et al., 2016) - because within this epoch human activities are having significant global impact - is the rising atmospheric carbon dioxide and the resultant change in climate. This is producing discernable shifts in marine ecosystems, particularly in relation to temperature, circulation, stratification, oxygen content and acidification (Doney et al., 2012). From the perspective of marine mammal conservation, it has long been thought that these effects will be most acutely felt in the polar regions, which are particularly vulnerable to sea-ice retreat and which may be the destination of species migrating towards the poles as temperatures rise (Kovacs et al., 2011) . Whilst some marine mammals may be able to adapt more readily to rapid change, others may not (Moore and Huntington, 2008). For example, killer whales are now able to access new regions of the Artic as a result of receding sea ice. But as apex predators their presence may have an influence on other marine mammal populations such as beluga (*Delphinapterus leucas*) and bowhead whales (*Balaena mysticetus*) (Ferguson et al., 2010). It remains unknown whether this expansion of their range is opportunistic, or the result of undocumented environmental pressures.

Retaining cultural skills

Research on non-human culture has progressed a pace, particularly in cetaceans since Sutherland (1998) identified these original 20 areas of interest (see for example Rendell and Whitehead, 2001; Whitehead and Rendell, 2015). Social learning is a prerequisite for culture, which can be defined as: '*information or behavior - shared within a community – which is acquired from conspecifics through some form of social learning*' (Whitehead and Rendell, 2015, p.12). Social learning and culture are not only relevant to terrestrial conservation in terms of ensuring that captive-bred or translocated animals have the rights skills to survive in the wild (as Sutherland (1998) suggests), but culture is also now recognized as having important implications for the conservation of wild populations (CMS, 2014; Whitehead, 2010).

Whilst there are many types of learning, social learning is arguably the most relevant to the consideration of the conservation of marine mammals. Social learning can entail fewer costs to the individual than individual learning and enables novel behavior to spread rapidly, so adaptation can occur faster than through genetic change alone (Boyd and Richerson, 1985). HIREC may provide a number of novel cues and opportunities for social learning for marine mammals, generating unique selection pressures. It has been argued that 'a cognitive mechanism that causes avoidance of novel food is as encumbering as a specialized feeding apparatus that prevents an animal from eating that food'(Greggor et al., 2014, p.490). It can similarly be argued that the learning of a social norm and the drive to conform may likewise inhibit the spread of adaptive behavior, in a similar manner to neophobia (fear or dislike of anything new or unfamiliar).

But the occurrence and consequences of innovations can be difficult to predict. Malthus (1798) famously predicted that the projected increase in human populations would lead to 'vice and misery', but failed to account for the fact that humans had the capacity to innovate and socially transmit methods for increasing their own food supply (Davies et al., 2012). Nevertheless, caution should be applied when predicting how social learning may assist or hinder wildlife adaptation to change as there may be anthropogenic (Donaldson et al., 2012), ecological, cognitive (Greggor et al., 2014) or cultural (Whitehead, 2010) interactions and constraints in play. There is also evidence for individual variation in social learning within species and a continuum of phenotypic plasticity (i.e. a range of ways in which the genes can manifest in different environments) has been suggested (Mesoudi et al., 2016).

Social learning in marine mammals is most famously evidenced in the transmission of humpback whale song (*Megaptera novaeangliae*) (Garland et al., 2011; Noad et al., 2000) and more recently through the spread of a novel feeding method, known as 'lobtail feeding' (Allen et al., 2013). The occurrence of these two apparently independent elements of social learning suggest that this species can maintain more than one independently evolving culture (Allen et al., 2013).

Social transmission and cultural constraints may influence conservation outcomes. North Atlantic right whales (*Eubalaena glacialis*) have shown a very poor recovery following intensive whaling during the 16th and 17th Centuries. Right whales are now almost entirely absent in the waters of Labrador (Katona and Kraus, 1999). It is thought that whilst oceanic climate change may play a role in this lack of recovery, perhaps the removal of such a significant proportion of the population through whaling destroyed cultural knowledge about critical habitat, or other significant cultural knowledge that may be inhibiting recovery (Whitehead et al., 2004).

Also, since baleen whale calves are thought to learn migratory routes and likely other habitat knowledge from their mothers, such as the location of critical feeding or breeding habitat, or areas of high predator density, some may be more reluctant to explore new areas, culminating in slower range recovery following extirpation (Baker et al., 2013; Carroll et al., 2011, 2014; Clapham et al., 2008). It has been suggested that loss of cultural knowledge and resultant limited range recovery may be one factor inhibiting a recovery of the North Atlantic right whale population (Mate et al., 1997). This has been demonstrated for southern right whales (*Eubalaena australis*) where, following extensive whaling, the remaining populations are now limited to two distinct feeding areas as a result of maternally directed site fidelity, despite the availability of other suitable feeding habitat (Carroll et al., 2016, 2014).

Research on the social structure of migrating beluga whales (*Delphinapterus leucas*), an odontocete species, also suggests that cultural conservatism enables social groups to learn migratory routes. However, a potential cost may be that this conservatism could impede the re-colonization of extirpated areas (Colbeck et al., 2013).

As well as ecological cultural knowledge, conservative cultures, in which individuals must conform in order to ‘fit in’, may lead to the suppression of novel behaviors. Conformist cultures may inhibit adaptive learning, with preference for cultural norms potentially suppressing ecologically useful behavioral adaptations, or leading to valuable habitats being overlooked (Whitehead, 2010). A striking example of this is provided by the southern resident population of killer whales which feed preferentially on chinook salmon (*Oncorhynchus tshawytscha*) (Ford and Ellis, 2006). It is argued that since these killer whales seem very reluctant to use a variety of other prey-items available to them, this conformist prey specialization may be a constraint on the population’s resilience, since it is contingent on the availability of the salmon (Ford et al., 2010; Whitehead, 2010). In addition to prey preferences, cultural conformism may also inhibit an individual’s adaptive use of space, through dispersal or migration. For example, it has been suggested that killer whales may continue to use traditional areas despite increases in chemical and noise pollution (Osborne, 1999).

Whitehead suggest that in some instances cultural behavior may be maladaptive (Whitehead, 2010) and that mass stranding of species such as the highly social pilot whales may be at least partly be associated with conformist cultures (Rendell and Whitehead, 2001). Nevertheless, there are many other possible causes of mass stranding and the difficulty in such instances is to separate out anthropogenic, cultural and other natural causes.

Sutherland (1998, p.804) noted: ‘A better understanding of cultural evolution would have considerable consequences for conservation’. Although social learning has been identified in many terrestrial mammals (Thornton and Clutton-Brock, 2011), research on social learning and investigation into potential unique cultures in other marine mammals species besides cetaceans is limited. This is an area where directed examination of social transmission across all marine mammal species would likely benefit conservation efforts in the future.

Behavioral manipulations

Successful mitigation of environmental threats and identification of critical habitat requires a good understanding of the behavioral ecology of the species and population specific behavior. Some instances of behavioral manipulation in marine mammals arise as the result of opportunistic interaction with humans, although these may not necessarily be directly associated with conservation efforts, they may have conservation implications.

Interactions with human activities, such as co-operative fishing (Daura-Jorge et al., 2012), trawling (Ansmann et al., 2012; Chilvers and Corkeron, 2001; Pace et al., 2011), depredation (i.e. taking fish from fishing gear) (Ruth Esteban et al., 2016), provisioning or begging (Donaldson et al., 2012; Mann and Kemps, 2003), can provide a novel foraging niche, which marine mammals can learn to utilize through social transmission. As a result there is a risk of social groups becoming dependent on these human activities, in what has been termed ‘anthropo-dependence’ (CMS, 2014).

Exploitation

Patterns of exploitation are influenced by the behavior of both hunters and their prey (Sutherland, 1998). Similarly, the distribution of whaling vessels has been compared with the ecological theory of ideal free distribution, in which the number of individuals that will aggregate in various patches of resource is proportional to the amount of resource available in each patch. However, records of sperm whaling in the Galapagos Islands in the 1800s, suggest a violation of the ideal free distribution. It is speculated that this may be a result of inaccuracies in the information available to these early whalers (Whitehead and Hope, 1991).

For many marine mammals the history of hunting is well chronicled, but the numbers taken is often less well documented (Ivashchenko et al., 2011; Ivashchenko and Clapham, 2015) . As a result determining pre-exploitation abundance can be challenging and controversial. For example, models for mDNA sequence variation provide estimates for North Atlantic fin (*Balaenoptera physalus physalus*) and humpback (*Megaptera novaeangliae*) whale populations 6 to 20 times higher than present day populations (Roman and Palumbi, 2003).

One important potential behavioral issue of concern for exploited marine mammals is the buffer effect, where at low densities individuals concentrate in the best habitat, but at higher densities are more dispersed over a wider area

(Brown, 1969). This can give a false indication of abundance to hunting communities searching in localized areas of high density, whilst the overall population may be in decline. This may be an important consideration in the geo-political wrangling between whalers, scientists and governments, and in decision making on protection of polar bear habitat (Rode et al., 2014). Sutherland (1998) contends that it is precisely this effect that led to the confidence of the fishing community which brought about the collapse of the Atlantic cod (*Gadus morhua*) fishery off the eastern-coast of Canada. Marine mammal conservation efforts will doubtless benefit from improved knowledge of dispersal trends, particularly in relation to changing environments and patchy distribution of resources.

21.1 Consequences of environmental changes on behavior

The implications of behavior for conservation of marine mammals have been reviewed here extensively. But Sutherland (1998) also argued that it is important to consider the implications of environmental change on behavior itself. Specifically it is important to consider how environmental change, including exploitation, may create selection pressures that may influence marine mammal behavior.

Acknowledging the limitations of the data reviewed, Wade et al. (2012) argue that odontocetes (toothed cetaceans) may be less resilient than mysticetes (baleen whales) to overexploitation. In contrast, research on the restructuring of a dolphin population following a change in human use of the environment from trawling to post-trawling periods within Moreton Bay, Australia, showed that since the reduction in trawling the social networks of the two social groups had become less differentiated and that previous partitioning into two communities disappeared (Ansmann et al., 2012). These contrasting findings highlight the complexity with which social dynamics may be influenced by differing anthropogenic environmental change and how some species and populations may demonstrate adaptability and be more robust to change, whereas others may be less resilient. This complexity may be further compounded by the synergistic manner in which some anthropogenic threats may operate, making forecasting the consequences for behavior a greater challenge.

Marine mammals inhabit a vast array of habitats and as a result threats from HIREC are myriad. It is also important to consider the spatio-temporal scale of the species in question when assessing changes in behavior as a result of environmental factors (Lomac-Macnair and Smultea, 2016).

1 Further considerations

Whilst the synergies between behavioral ecology and conservation science have blossomed in the years since Sutherland (1998) raised the issue of disconnect between these two fields, the examination of his 20 key areas of interest shows that there is still a considerable way to go for behavioral ecology to be fully incorporated into conservation science and policy making for marine mammals.

In addition to the 20 key areas raised by Sutherland, there are arguably a number of other emerging issues in behavioral ecology that also warrant consideration for marine mammals, including different social learning mechanisms, social structure, social role and personality.

Social information and fine scale social structure (R. Esteban et al., 2016; Kurvers et al., 2014; Williams and Lusseau, 2006) may strongly influence social dynamics and potentially vital rates. These influences may be synergistic or opposing and warrant a more sophisticated approach towards managing social species, particularly those which exhibit social transmission.

How social segments within marine mammal populations are connected and how information flows between them also requires further elucidation (for example see: Filatova et al., 2013; Rendell et al., 2012), particularly since multi-level societies may have differing behavioral responses to anthropogenic change (Cantor et al., 2015; Whitehead et al., 2012). The roles of individuals within their social groups and even the ontogeny of senescence may have important implications for survivorship and conservation (Brent et al., 2015).

Since maintaining behavioral diversity is important for adaptation to novel environments, one of the principle goals of conservation, beyond conserving genetic biodiversity, should also be to conserve a wide range of behaviors and in some populations this may also include protecting discrete cultural units.

Understanding behavioral plasticity is also undoubtedly an important consideration for predicting how a species may respond to changes in their environment. The degree of plasticity within behavioral repertoires may provide important opportunities for adaptation (Ansmann et al., 2012; Mann et al., 2012). Although resilience as a result of behavioral plasticity may act as a buffer to ecological change, there is also concern that behavioral adaptation could mask emerging ecological issues. For example, whilst a species may switch prey in the face of ecological pressures, if such buffers then become exhausted the consequences of change could be more rapid (CMS, 2014). This highlights the need to monitor changes in prey choice for endangered species that exhibit a high degree of behavioral plasticity.

In addition to the more general characterization of a species overall behavioral plasticity, behavioral syndromes, consistent individual differences in behavior (CIDs or personality variation) may influence individuals' ability to cope with novel conditions (Sih et al., 2004). For example, individuals with flexible, exploratory, bold or aggressive behavioral tendencies may be able to cope better with HIREC (Sih et al., 2011). However, in captivity there are concerns that reduced behavioral diversity and selection for personality traits that better suit the captive environment may lead to propagation of personality types and behavior that is ill-suited for the wild, potentially reducing viability for successful release (Carere and Maestripieri, 2013).

For a discussion on the consequences of animal personality for population persistence and social dynamics see (Wolf and Weissing, 2012). However, empirical studies into personality variation in wild marine mammals are rare (see for example: Estes et al., 2003; Twiss et al., 2012) and are likely to remain so for some of the more enigmatic species, such as the beaked whales. But even for those more accessible marine mammals whose behavioral repertoires and ecology are well researched it is important not to conflate behavioral polymorphism with personality variation. An empirical framework for evaluating personality variation has been suggested to avoid such pitfalls (Dall and Griffith, 2014).

Conclusion

There is no doubt that a better understanding of the behavioral ecology of many marine mammals is important for their conservation. It is difficult to envision any approach towards conserving a population of modern humans, which merely preserved their genetic integrity and did not also consider their behavior. We have some understanding and experience of the complexity of human decision making: amid our different cultures, environments and circumstances we make choices about what to eat, who to socialize with, where to live, how many offspring to have etc. All of which can influence our fertility rates and survival.

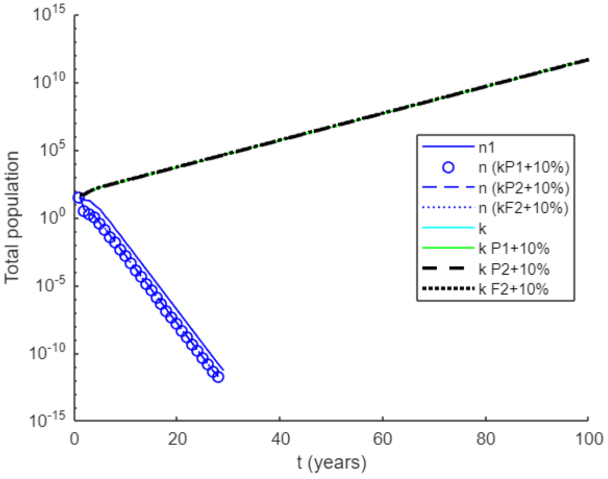
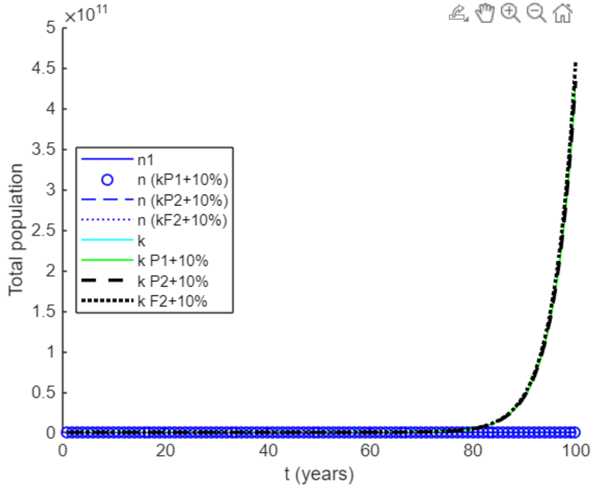
Similarly, while efforts to conserve marine mammal biodiversity focus strongly on maintaining genetic integrity and diversity, the emerging evidence indicates that sociality and behavioral diversity may also be central to individual, social group and population viability. The challenge ahead is teasing out the most relevant factors and understanding how to incorporate this new knowledge into management models and conservation efforts for marine mammals.

For references see full online version:
https://doi.org/10.3389/fmars.2016.00087

APPENDIX 4.1

Vital rate perturbation projections for 2-stage mammalian and avian PPMs with social learning

Following on from the examples in Chapter 4, projections based on PPMs for further mammals and avian populations are provided here.

Species and source for n_1	**Perturbation <u>with</u> transmission, log plot, *B*=0.9**	**Perturbation <u>with</u> transmission, *B*=0.9**
Canis latrans, Coyote (Schumaker et al. 2004) $\mathbf{x}_n \begin{pmatrix} 0 & 2.8 \\ 0.29 & 0.61 \end{pmatrix}$ $\lambda_n = 1.2563$		

<table>
<tr>
<td>

Lynx rufus,

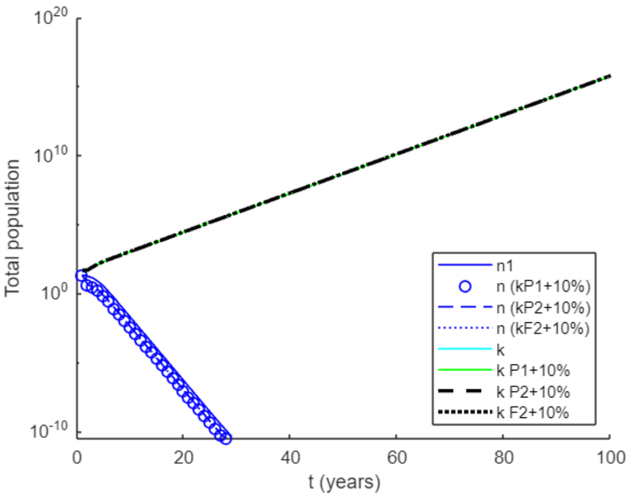
Bob cat

(Schumaker et al. 2004)

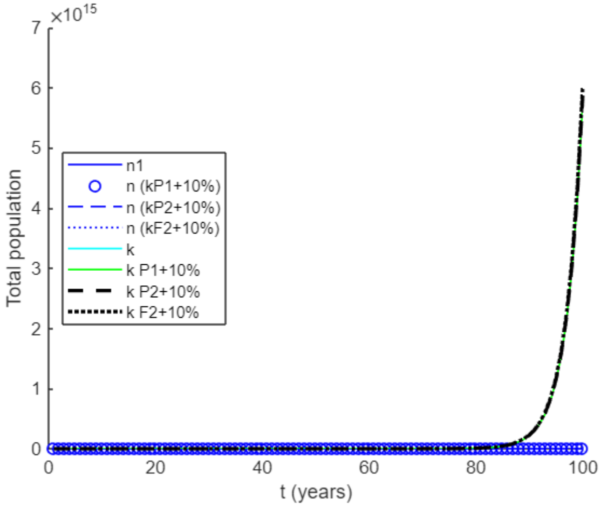
$\mathbf{x}_n \begin{pmatrix} 0 & 1.4 \\ 0.689 & 0.689 \end{pmatrix}$

$\lambda_n = 1.3853$

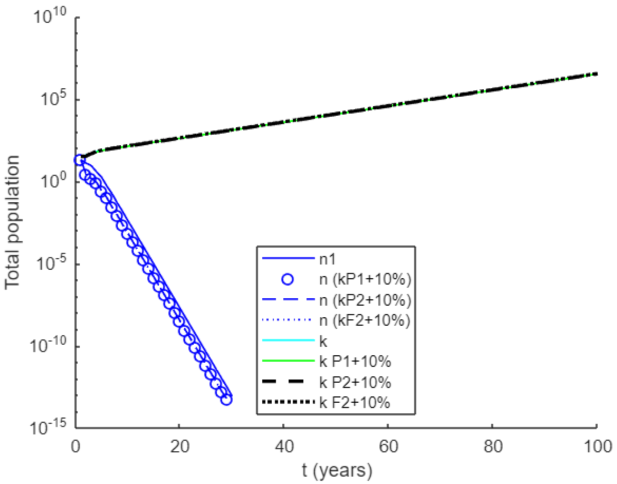
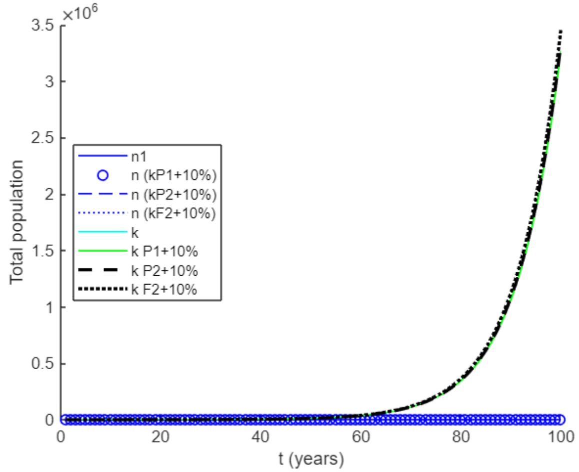
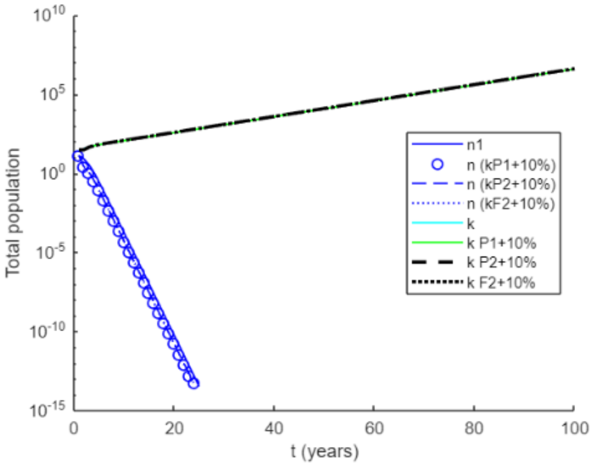
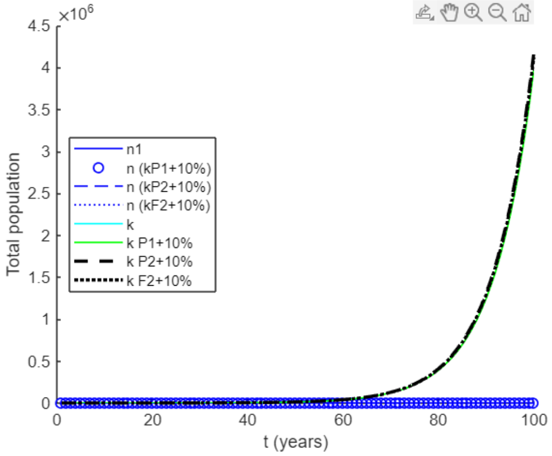
</td>
<td>

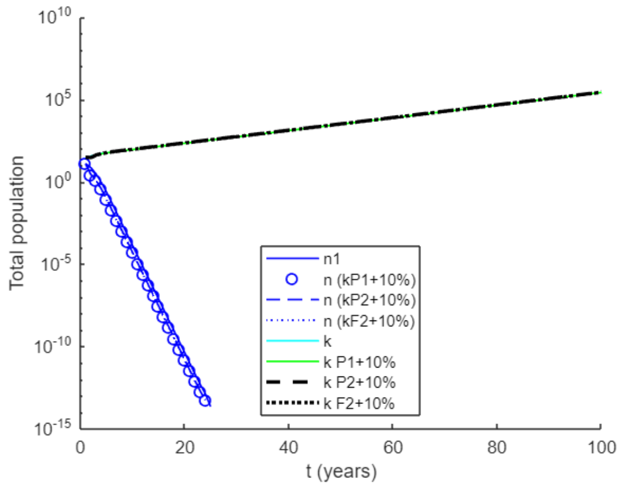
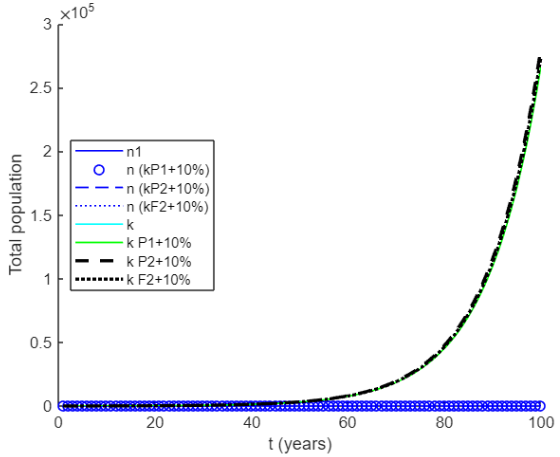


</td>
<td>



</td>
</tr>
</table>

Vulpes vulpes, Red fox (Schumaker et al. 2004) **x_n** $\begin{pmatrix}0 & 1.49\\0.48 & 0.48\end{pmatrix}$ $\lambda_n = 1.1191$		
Pygoscelis adeliae, Adelie penguin (Hinke et al. 2017) **x_n** $\begin{pmatrix}0 & 0.6\\0.53 & 0.84\end{pmatrix}$ $\lambda_n = 1.1231$		

Lichenostomus melanops cassidix, Helmeted honey eater (Baxter et al. 2006) $\mathbf{x_n} \begin{bmatrix} 0 & 0.4 \\ 0.8 & 0.8 \end{bmatrix}$ $\lambda_n = 1.0928$		

APPENDIX 4.2

CITATION FOR R Packages: Jones, Owen R., Patrick Barks, Iain M. Stott, Tamora D. James, Sam C. Levin, William K. Petry, Pol Capdevila, et al. 2021. “Rcompadre and Rage – Two R Packages to Facilitate the Use of the COMPADRE and COMADRE Databases and Calculation of Life History Traits from Matrix Population Models.” bioRxiv. doi: 10.1101/2021.04.26.441330.

CITATION for COMADRE database: COMADRE Animal Matrix Database (2022). Available from: https://www.compadre-db.org [27 Jan 2022, Version 4.21.8.0].

R code for 2 stage PPM query of COMADRE database

```
#Query to extract 2stage PPMs from COMADRE database
#call up the package
library(Rcompadre)
#Fetch most recent version from comadre-db.org
comadre <- cdb_fetch("comadre")

#Subset metadata based on query criteria
#Here subset only Mammalian species with matrix dimension <3
y <- subset(comadre, Class == "Mammalia" & MatrixDimension <3)
#Returns 65 PPMs (as of 04/04/22)

#Export results (y) to Excel
#First install writexl package and call to library
install.packages("writexl")
library(writexl)
#write y to a dataframe for export to Excel
df<- data.frame(y)
#Assign df to file destination
write_xlsx(df,"C:\\Users\\Philippa Brakes\\Desktop\\Mammal_PPMs.xlsx")
```

MATLAB Code

```
%Two PPM model with simple directly biased transmission
%individuals disperse between the 2 units as result of transmission
%Directly-biased transmission after Boyd and Richerson 1985
%PPM data from Whitehead & Gero 2015


clc
clear


%Dimensions of the model


    % 2 stages - across 2 PPMs (one for naives (pop1) and one for
    % informed (pop2))

    % POP1
    % Cn = naive calves
    % An = naive adults

    %POP2
    % Ck = informed calves
    % Ak = informed adults
```

```
% MATRIX CONSTRUCTION
% TWO STAGE-CLASSIFIED PROJECTION MATRICES


PPM1=[0.7451 0.0621; 0.0870 0.9495] %
PPM2=[0.7451 0.0621; 0.0870 0.9495] % set equal initially


%calc dominant eigenvalue and eigenvector for both PPMs
[V1 D1] = eig(PPM1);
[w1 d1] = eigs(PPM1,1);
lambda1=d1


[V2 D2] = eig(PPM2);
[w2 d2] = eigs(PPM2,1);
lambda2=d2


 total1=zeros(4,100);
 total2=zeros(4,100);
```

```
%Setting up initial population
pop1=zeros(8,100); %naive under the different parameter regimes
pop2=zeros(2,100); %initial k
pop3=zeros(2,100); %k with P1 perturbed
pop4=zeros(2,100); %k with P2 perturbed
pop5=zeros(2,100); %k with F2 perturbed


pop1(:,1)= [10;10;10;10;10;10;10;10];
pop2(:,1)= [10;10];
pop3(:,1)= [10;10];
pop4(:,1)= [10;10];
pop5(:,1)= [10;10];


%setting equal to original PPM2, prior to perturbation
PPM2P1=PPM2;
PPM2P2=PPM2;
PPM2F2=PPM2;


%Exploring perturbation of vital rates (increase by x%)
%starting population
for Perturb=2:4 %first original PPM2=PPM2

    if Perturb==2
       PPM2P1(1,1)=PPM2(1,1)*0.10+(PPM2(1,1)) %increase P1 x%
    elseif Perturb==3
       PPM2P2(2,2)=PPM2(2,2)*0.10+(PPM2(2,2)) %increase P2 x%
    else Perturb==4
       PPM2F2(1,2)=PPM2(1,2)*0.10+(PPM2(1,2)) %increase F2 x%
    end


end
```

```
%Project population
B=0.9;  % set transmission parameter B >0 to positively distribute An to
Ak
for t=1
pop1(1:2,t)= PPM1*pop1(1:2,t); %projection for t=1 naive
pop1(3:4,t)= PPM1*pop1(3:4,t);
pop1(5:6,t)= PPM1*pop1(5:6,t);
pop1(7:8,t)= PPM1*pop1(7:8,t);
pop2(:,t)= PPM2*pop2(:,t); %informed projection, no perturbation
pop3(:,t)= PPM2P1*pop2(:,t);%informed projection, P1 perturbed
pop4(:,t)= PPM2P2*pop2(:,t);%informed projection, P2 perturbed
pop5(:,t)= PPM2F2*pop2(:,t);%informed projection, F2 perturbed


%Transmission for adults using PPM2
p1=pop2(2,t)/(pop1(2,t)+pop2(2,t)); %p1 proportion of informed
```

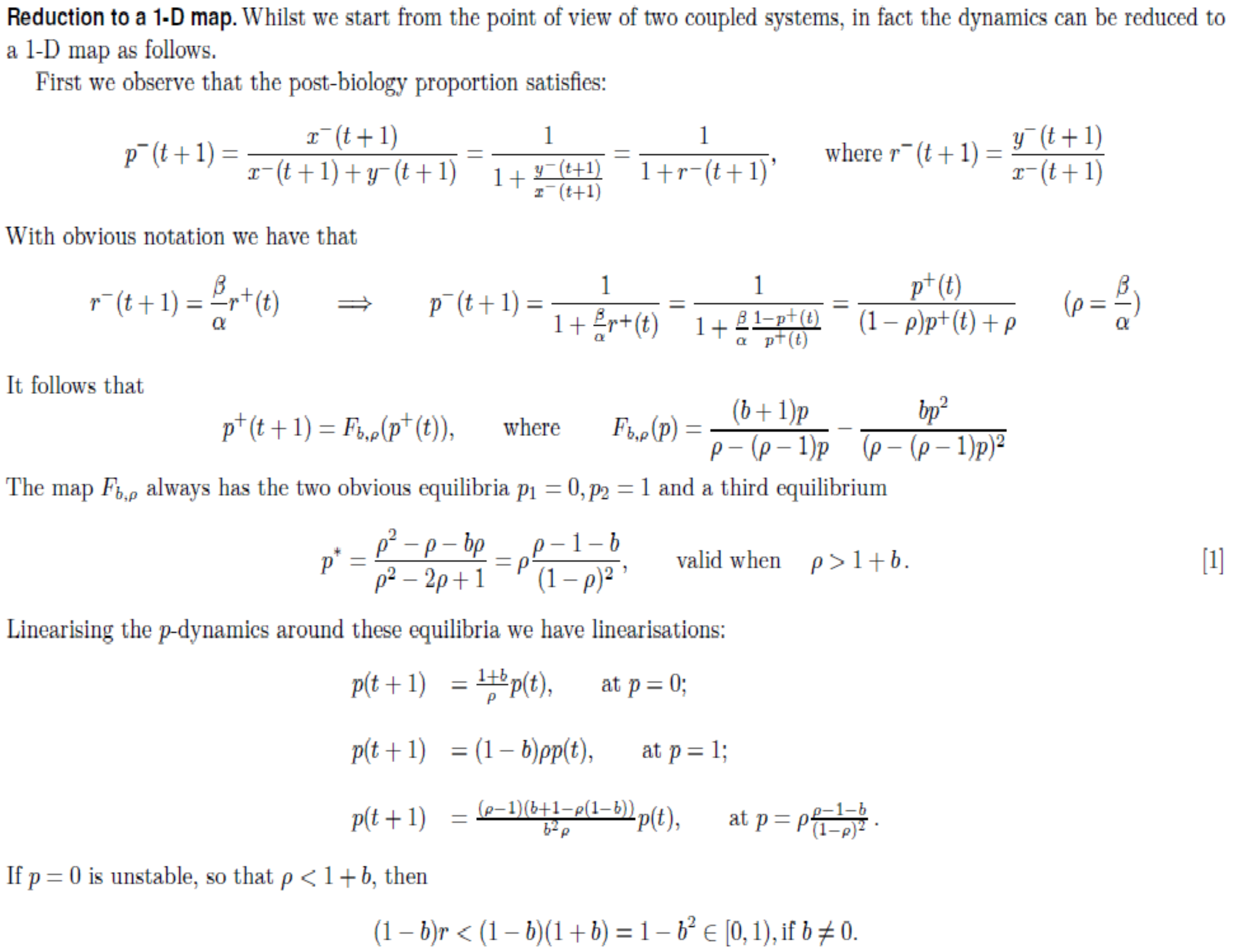
```
p1=p1+(B*p1*(1-p1)); %transmission
newpop2(2,t)=p1*(pop1(2,t)+pop2(2,t)); %new proportion * total pop
%NB: SL function assumes total An + Ak remains constant
pop1(2,t)=pop1(2,t)+pop2(2,t)-newpop2(2,t);
pop2(2,t)=newpop2(2,t);

%Transmission for adults using PPM2P1
p2=pop3(2,t)/(pop1(4,t)+pop3(2,t));
p2=p2+(B*p2*(1-p2)); %transmission
newpop3(2,t)=p1*(pop1(4,t)+pop3(2,t));
pop1(4,t)=pop1(4,t)+pop3(2,t)-newpop3(2,t);
pop3(2,t)=newpop3(2,t);

%Transmission for adults using PPM2P2
p3=pop4(2,t)/(pop1(6,t)+pop4(2,t));
p3=p3+(B*p3*(1-p3));
newpop4(2,t)=p3*(pop1(6,t)+pop4(2,t));
pop1(6,t)=pop1(6,t)+pop4(2,t)-newpop4(2,t);
pop4(2,t)=newpop4(2,t);

%Transmission for adults using PPM2F2
p4=pop5(2,t)/(pop1(8,t)+pop5(2,t));
p4=p4+(B*p4*(1-p4));
newpop5(2,t)=p1*(pop1(8,t)+pop5(2,t)); %new proportion * total pop
pop1(8,t)=pop1(8,t)+pop5(2,t)-newpop5(2,t);
pop5(2,t)=newpop5(2,t);

%summing stages following transmission
total1(1,t)=pop1(1,t)+pop1(2,t); %pop1 after transmission with k(PPM2)
total1(2,t)=pop1(3,t)+pop1(4,t); %pop1 after transmission with k(PPM2P1)
etc.
total1(3,t)=pop1(5,t)+pop1(6,t);
total1(4,t)=pop1(7,t)+pop1(8,t);
total2(1,t)=pop2(1,t)+pop2(2,t); %pop2 (PPM2)after transmission with n
total2(2,t)=pop3(1,t)+pop3(2,t); %pop2 (PPMP1) after transmission n etc.
total2(3,t)=pop4(1,t)+pop4(2,t);
total2(4,t)=pop5(1,t)+pop5(2,t);
   end

for t=2:100 %total projection interval
pop1(1:2,t)= PPM1*pop1(1:2,t-1);  %projection for rest of naive pop
pop1(3:4,t)= PPM1*pop1(3:4,t);
pop1(5:6,t)= PPM1*pop1(5:6,t);
pop1(7:8,t)= PPM1*pop1(7:8,t);
pop2(:,t)= PPM2*pop2(:,t-1);  %informed projection, no perturbation
pop3(:,t)= PPM2P1*pop2(:,t-1);%informed, P1 perturbed
pop4(:,t)= PPM2P2*pop2(:,t-1);%informed, P2 perturbed
pop5(:,t)= PPM2F2*pop2(:,t-1);%informed, F2 perturbed


%Transmission for adults, PPM2
p1=pop2(2,t)/(pop1(2,t)+pop2(2,t));
p1=p1+(B*p1*(1-p1));
newpop2(2,t)=p1*(pop1(2,t)+pop2(2,t));
```

```
pop1(2,t)=pop1(2,t)+pop2(2,t)-newpop2(2,t);
pop2(2,t)=newpop2(2,t);

%Transmission for adults, PPM2P1
p2=pop3(2,t)/(pop1(4,t)+pop3(2,t));
p2=p2+(B*p2*(1-p2));
newpop3(2,t)=p1*(pop1(4,t)+pop3(2,t));
pop1(4,t)=pop1(4,t)+pop3(2,t)-newpop3(2,t);
pop3(2,t)=newpop3(2,t);

%Transmission for adults, PPM2P2
p3=pop4(2,t)/(pop1(6,t)+pop4(2,t));
p3=p3+(B*p3*(1-p3));
newpop4(2,t)=p1*(pop1(6,t)+pop4(2,t));
pop1(6,t)=pop1(6,t)+pop4(2,t)-newpop4(2,t);
pop4(2,t)=newpop4(2,t);


%Transmission for adults, PPM2F2
p4=pop5(2,t)/(pop1(8,t)+pop5(2,t));
p4=p4+(B*p4*(1-p4));
newpop5(2,t)=p1*(pop1(8,t)+pop5(2,t));
pop1(8,t)=pop1(8,t)+pop5(2,t)-newpop5(2,t);
pop5(2,t)=newpop5(2,t);

%summing stages for total pop
total1(1,t)=pop1(1,t)+pop1(2,t); %pop1 after transmission with k(PPM2)
total1(2,t)=pop1(3,t)+pop1(4,t); %pop1 after transmission with k(PPM2P1) etc.
total1(3,t)=pop1(5,t)+pop1(6,t);
total1(4,t)=pop1(7,t)+pop1(8,t);
total2(1,t)=pop2(1,t)+pop2(2,t);
total2(2,t)=pop3(1,t)+pop3(2,t);
total2(3,t)=pop4(1,t)+pop4(2,t);
total2(4,t)=pop5(1,t)+pop5(2,t);
end

%Plot pop1 (naive) and pop2 (informed) following transmission
hold on
    plot (total1(1,:), "b", "LineWidth", 1)
    plot (total1(2,:), "bo", "LineWidth", 1)
    plot (total1(3,:), "b--", "LineWidth", 1)
    plot (total1(4,:), "b:", "LineWidth", 1)

    plot(total2(1,:), "c", "LineWidth", 1)
    plot(total2(2,:), "g", "LineWidth", 1)
    plot(total2(3,:), "k--", "LineWidth", 2)
    plot(total2(4,:), "k:", "LineWidth", 2)
%set(gca, 'YScale', 'log') %setting y-axis to log scale
    ax = gca;
    ax.FontSize = 12;
    hold off
    xlabel("t (years)"), ylabel("Total population")
    %title('Transmission between cultural units')
```

```
    title("B=0.9")
    legend ('Xn', 'Xn (P1k+10%)', 'Xn (P2k+10%)', 'Xn (F2k+10%)', 
'Xk','P1k+10%', 'P2k+10%', 'F2k+10%' )
     legend('Location', 'northeast')
```

Appendix 6.1

Reduction to a 1-D map (extracted from LaTeX):



Reduction to a 1-D map. Whilst we start from the point of view of two coupled systems, in fact the dynamics can be reduced to a 1-D map as follows.

First we observe that the post-biology proportion satisfies:

$$p^-(t+1) = \frac{x^-(t+1)}{x^-(t+1)+y^-(t+1)} = \frac{1}{1+\frac{y^-(t+1)}{x^-(t+1)}} = \frac{1}{1+r^-(t+1)}, \qquad \text{where } r^-(t+1) = \frac{y^-(t+1)}{x^-(t+1)}$$

With obvious notation we have that

$$r^-(t+1) = \frac{\beta}{\alpha} r^+(t) \qquad \Longrightarrow \qquad p^-(t+1) = \frac{1}{1+\frac{\beta}{\alpha}r^+(t)} = \frac{1}{1+\frac{\beta}{\alpha}\frac{1-p^+(t)}{p^+(t)}} = \frac{p^+(t)}{(1-\rho)p^+(t)+\rho} \qquad (\rho = \frac{\beta}{\alpha})$$

It follows that

$$p^+(t+1) = F_{b,\rho}(p^+(t)), \qquad \text{where} \qquad F_{b,\rho}(p) = \frac{(b+1)p}{\rho-(\rho-1)p} - \frac{bp^2}{(\rho-(\rho-1)p)^2}$$

The map $F_{b,\rho}$ always has the two obvious equilibria $p_1 = 0, p_2 = 1$ and a third equilibrium

$$p^* = \frac{\rho^2-\rho-b\rho}{\rho^2-2\rho+1} = \rho\frac{\rho-1-b}{(1-\rho)^2}, \qquad \text{valid when} \qquad \rho > 1+b. \qquad [1]$$

Linearising the p-dynamics around these equilibria we have linearisations:

$$\begin{aligned} p(t+1) &= \tfrac{1+b}{\rho}p(t), && \text{at } p = 0; \\ p(t+1) &= (1-b)\rho p(t), && \text{at } p = 1; \\ p(t+1) &= \tfrac{(\rho-1)(b+1-\rho(1-b))}{b^2\rho}p(t), && \text{at } p = \rho\tfrac{\rho-1-b}{(1-\rho)^2}. \end{aligned}$$

If $p = 0$ is unstable, so that $\rho < 1+b$, then

$$(1-b)r < (1-b)(1+b) = 1-b^2 \in [0,1), \text{if } b \neq 0.$$

REFERENCES

Allee, W.C., 1931. Animal Aggregations. A study in General Sociology. University of Chicago Press. https://doi.org/10.5962/bhl.title.7313

Allen, J., Weinrich, M., Hoppitt, W., Rendell, L., 2013. Network-based diffusion analysis reveals cultural transmission of lobtail feeding in humpback whales. Science 340, 485–8. https://doi.org/10.1126/science.1231976

Alligood,K.T, Sauer, T., Yorke, J., 1996. Chaos: An Introduction to Dynamical Systems. Springer-Verlag New York.

Almqvist, J., 2005. Human Rights, Culture, and the Rule of Law, Human Rights, Culture, and the Rule of Law. Hart Publishing. https://doi.org/10.5040/9781472563422

Ansmann, I.C., Parra, G.J., Chilvers, B.L., Lanyon, J.M., 2012. Dolphins restructure social system after reduction of commercial fisheries. Anim. Behav. 84, 575–581. https://doi.org/10.1016/j.anbehav.2012.06.009

Anthony, L.L., Blumstein, D.T., 2000. Integrating behaviour into wildlife conservation: The multiple ways that behaviour can reduce N(e). Biol. Conserv. 95, 303–315. https://doi.org/10.1016/S0006-3207(00)00037-9

Aplin, L.M., Farine, D.R., Cockburn, A., Thornton, A., 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. Nature 518, 538–541 https://doi.org/10.1038/nature13998

Aplin, L.M., Sheldon, B.C., Morand-Ferron, J., 2013. Milk bottles revisited: Social learning and individual variation in the blue tit, *Cyanistes caeruleus*. Anim. Behav. 85, 1225–1232. https://doi.org/10.1016/j.anbehav.2013.03.009

Ashe, E., Williams, R., Clark, C., Erbe, C., Gerber, L.R., Hall, A.J., Hammond, P.S., Lacy, R.C., Reeves, R., Vollmer, N.L., 2021. Minding the Data-Gap Trap: Exploring Dynamics of Abundant Dolphin Populations Under Uncertainty. Front. Mar. Sci. 8, 1–10. https://doi.org/10.3389/fmars.2021.606932

Avila, I.C., Kaschner, K., Dormann, C.F., 2018. Current global risks to marine mammals: Taking stock of the threats. Biol. Conserv. 221, 44–58. https://doi.org/10.1016/j.biocon.2018.02.021

Baird, R.W., Mahaffy, S.D., Gorgone, A.M., Cullins, T., McSweeney, D.J., Oleson, E.M., Bradford, A.L., Barlow, J., Webster, D.L., 2014. False killer whales and fisheries interactions in Hawaiian waters: Evidence for sex bias and variation among populations and social groups. Mar. Mammal Sci. 31, 579–590. https://doi.org/10.1111/mms.12177

Baker, C.S., Palumbi, S.R., Lambertsen, R.H., Weinrich, M.T., Calambokidis, J., O’Brien, S.J., 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. Nature 344, 238–240.

Barrett, B., Zepeda, E., Pollack, L., Munson, A., Sih, A., 2019. Counter-Culture: Does Social Learning Help or Hinder Adaptive Response to Human-Induced Rapid Environmental Change? Front. Ecol. Evol. 7, 1–18. https://doi.org/10.3389/fevo.2019.00183

Baxter, P., McCarthy, M., Possingham, H.P., Menkhorst, P., McLean, N., 2006. Accounting for Management Costs in Sensitivity Analyses of Matrix Population Models. Conserv. Biol. 20, 893–905. 10.1111/j.1523-1739.2006.00378.x

Berger-Tal, O., Blumstein, D.T., Carroll, S., Fisher, R.N., Mesnick, S.L., Owen, M.A., Saltz, D., St Claire, C.C., Swaisgood, R.R., 2016. A systematic survey of the integration of animal behavior into conservation. Conserv. Biol. 30, 744–753. https://doi.org/10.1111/cobi.12654

Berger-Tal, O., Polak, T., Oron, a., Lubin, Y., Kotler, B.P., Saltz, D., 2011. Integrating animal behavior and conservation biology: a conceptual framework. Behav. Ecol. 22, 236–239. https://doi.org/10.1093/beheco/arq224

Bezamat, C., Castilho, P. V., Simões-Lopes, P.C., Ingram, S.N., Daura-Jorge, F.G., 2020. Reproductive parameters and factors influencing calf survival of bottlenose dolphins that engage in a unique foraging cooperation with fishermen. Mar. Biol. 167, 1–12. https://doi.org/10.1007/s00227-019-3611-4

Bezamat, C., Hammond, P.S., Castilho, P. V., Simões-Lopes, P.C., Daura-Jorge, F.G., 2021. Dolphin population specialized in foraging with artisanal fishers requires zero-bycatch management to persist. Aquat. Conserv. Mar. Freshw. Ecosyst. 1–13. https://doi.org/10.1002/aqc.3694

Bhattacharyya, M., Chakraborty, K., 2017. Of honeyguides and humans - a unique interspecific association formed over honey. Sci. Cult. 83, 103–107.

Bossley, M., Steiner, A., Brakes, P., Shrimpton, J., Foster, C., Rendell, L., 2018. Tail walking in a bottlenose dolphin community : the rise and fall of an arbitrary cultural ‘ fad .’ Biol. Lett. 20180314. https://doi.org/10.1098/rsbl.2018.0314

Boyd, R., Richerson, P.J., 1995. Why does culture increase human adaptability? Ethol. Sociobiol. 16, 125–143. https://doi.org/10.1016/0162-3095(94)00073-G

Boyd, R., Richerson, P.J., 1985. Culture and the Evolutionary Process. University of Chicago Press.

Brakes, P., Carroll, E.L., Dall, S.R.X., Keith, S.A., Mcgregor, P.K., Mesnick, S.L., Noad, M.J., Rendell, L., Robbins, M.M., Rutz, C., Thornton, A., Whiten, A., Whiting, M.J., Aplin, L.M., Bearhop, S., Ciucci, P., Fishlock, V., Ford, J.K.B., Notarbartolo, G., Simmonds, M.P., Spina, F., Wade, P.R., Whitehead, H., Williams, J., Garland, E.C., Carroll, E.L., Garland, E.C., 2021. A deepening understanding of animal culture suggests lessons for conservation. Proceeding R. Soc. B 20202718. https://doi.org/10.1098/rspb.2020.2718

Brakes, P., Dall, S.R.X., 2016. Marine Mammal Behavior : A Review of Conservation Implications. Front. Mar. Sci. 3, 87. https://doi.org/10.3389/fmars.2016.00087

Brakes, P., Dall, S.R.X., Aplin, L.M., Bearhop, S., Carroll, E.L., Ciucci, P., Fishlock, V., Ford, J.K.B., Garland, E.C., Keith, S.A., McGregor, P.K., Mesnick, S.L., Noad, M.J., Notarbartolo di Sciara, G., Robbins, M.M., Simmonds, M.P., Spina, F., Thornton, A., Wade, P.R., Whiting, M.J., Williams, J., Rendell, L., Whitehead, H., Whiten, A., Rutz, C., 2019. Animal cultures matter for conservation. Science 363, 1032–1034.

https://doi.org/10.1126/science.aaw3557

Brakes, P. and Rendell, L. 2022. Conservation relevance of individuals and societies. In: Notarbartolo di Sciara, G., Würsig, B. (eds) Marine Mammals: the Evoloving Human Factor. Ethology and Behavioural Ecology of Marine Mammals. Springer, Cham. doi.org/10.1007/978-3-030-98100-6_3

Brault, S., Caswell, H., 1993. Pod-specific demography of killer whales (Orcinus orca). Ecology 74, 1444–1454. https://doi.org/10.2307/1940073

Bubac, C.M., Miller, J.M., Coltman, D.W., 2020. The genetic basis of animal behavioural diversity in natural populations. Mol. Ecol. 29, 1957–1971. https://doi.org/10.1111/mec.15461

Bulluck, L., Buehler, D., Vallender, R., Robertson, R.J., 2013. Demographic comparison of Golden-Winged Warbler (*Vermivora chrysoptera*) populations in northern and southern extremes of their breeding range. Wilson J. Ornithol. 125, 479–490. https://doi.org/10.1676/12-154.1

Cantor, M., Whitehead, H., 2015. How does social behavior differ among sperm whale clans? Mar. Mammal Sci. 31, 1275–1290. https://doi.org/10.1111/mms.12218

Cantor, M., Whitehead, H., 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 368, 20120340. https://doi.org/10.1098/rstb.2012.0340

Cantor, M., Whitehead, H., Gero, S., Rendell, L., 2016. Cultural turnover among Galápagos sperm whales. R. Soc. Open Sci. 3, 160615. https://doi.org/10.1098/rsos.160615

Caro, T., 2007. Behaviour and conservation: a bridge too far? Trends Ecol. Evol. 22, 394–400. https://doi.org/DOI:10.1016/j.tree.2007.06.003

Caro, T.M., Durant, S.M., 1995. The importance of behavioural ecology for conservation biology: examples from serengeti carnivores, in: Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. pp. 451–472.

Carroll, E.L., Baker, C.S., Watson, M., Alderman, R., Bannister, J., Gaggiotti, O.E., Gröcke, D.R., Patenaude, N., Harcourt, R., 2015. Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand. Sci. Rep. 5, 16182. https://doi.org/doi.org/10.5061/dryad.cc2kq

Carroll, E.L., Rayment, W.J., Alexander, A.M., Baker, C.S., Patenaude, N.J., Steel, D., Constantine, R., Cole, R., Boren, L.J., Childerhouse, S., 2014. Reestablishment of former wintering grounds by New Zealand southern right whales. Mar. Mammal Sci. 30, 206–220. https://doi.org/10.1111/mms.12031

Carvalho, S., Wessling, E.G., Abwe, E.E., Almeida-Warren, K., Arandjelovic, M., Boesch, C., Danquah, E., Diallo, M.S., Hobaiter, C., Hockings, K., Humle, T., Ikemeh, R.A., Kalan, A.K., Luncz, L., Ohashi, G., Pascual-Garrido, A., Piel, A., Samuni, L., Soiret, S., Sanz, C., Koops, K., 2022. Using nonhuman culture in conservation requires careful and concerted action. Conserv. Lett. e12860. https://doi.org/10.1111/conl.12860

Casetta, E., Marques da Silva, J., Vecchi, D., 2019. From Assessing to Conserving Biodiversity. Springer. https://doi.org/10.1007/978-3-030-10991-2

Caswell, H., de Vries, C., Hartemink, N., Roth, G., van Daalen, S.F., 2018. Age × stage-classified demographic analysis: a comprehensive approach. Ecol. Monogr. 88, 560–584. https://doi.org/10.1002/ecm.1306

Cavalli-Sforza, L.L., Feldman, M.W., 1981. Cultural Transmission and Evolution: A Quantitative Approach. Princeton University Press.

Chabanne, D.B.H., Allen, S.J., Sherwin, W.B., Finn, H., Krützen, M., Louis, M., 2021. Inconsistency Between Socio-Spatial and Genetic Structure in a Coastal Dolphin Population. Front. Mar. 7, 1–14. https://doi.org/10.3389/fmars.2020.617540

Chiyo, P., Moss, C.J., Alberts, S.C., 2012. The Influence of Life History Milestones and Association Networks on Crop-Raiding Behavior in Male African Elephants. PLoS One 7, e31382. https://doi.org/10.1371/journal.pone.0031382.t002

CMS, 2018. Report of the CMS Workshop on Conservation Implications of Animal Culture and Social Complexity, Parma, Italy, 12-14 April 2018. https://doi.org/UNEP/CMS/ScC-SC3/Inf.8

CMS, 2017. Concerted Action for sperm whales (*Physeter macrocephalus*) of the eastern tropical Pacific UNEP/CMS/Concerted Action 12.2.

CMS, 2014. Report of the CMS Scientific Council Workshop on the Conservation Implications of Cetacean Culture, Convetion on Migratory Species, London, April 2014

Cole, L.C., 1957. Sketches of general and comparative demography. Cold Springs Harb. Symp. Quant. Biol 22, 1–15. https://doi.org/10.1101/sqb.1957.022.01.004

Crandall, K.A., Bininda-Emonds, O.R.P., Mace, G.M., Wayne, R.K., 2000. Considering evolutionary processes in conservation biology. Trends Ecol. Evol. 15, 290–295. https://doi.org/10.1016/S0169-5347(00)01876-0

Crates, R., Langmore, N., Ranjard, L., Stojanovic, D., Rayner, L., Ingwersen, D., Heinsohn, R., 2021. Loss of vocal culture and fitness costs in a critically endangered songbird. Proc. R. Soc. B Biol. Sci. 288. https://doi.org/10.1098/rspb.2021.0225

Creanza, N., Kolodny, O., Feldman, M.W., 2017. Greater than the sum of its parts? Modelling population contact and interaction of cultural repertoires. J. R. Soc. Interface 14. https://doi.org/10.1098/rsif.2017.0171

Croft, D.P., Brent, L.J.N., Franks, D.W., Cant, M.A., 2015. The evolution of prolonged life after reproduction. Trends Ecol. Evol. 30: 407-16 https://doi.org/10.1016/j.tree.2015.04.011

Croft, D.P., James, R., Krause, D.J., 2008. Exploring Animal Social Networks. Princeton University Press.

Croft, D.P., Johnstone, R.A., Ellis, S., Nattrass, S., Franks, D.W., Brent, L.J.N., Mazzi, S., Balcomb, K.C., Ford, J.K.B., Cant, M.A., 2017. Reproductive Conflict and the Evolution of Menopause in Killer Whales. Curr. Biol. 27, 298–304. https://doi.org/10.1016/j.cub.2016.12.015

Damas-Moreira, I., Oliveira, D., Santos, J.L., Riley, J.L., Harris, D.J., Whiting, M.J., 2018. Learning from others: An invasive lizard uses social information from both conspecifics and heterospecifics. Biol. Lett. 14, 20180532. https://doi.org/10.1098/rsbl.2018.0532

Daura-Jorge, F.G., Cantor, M., Ingram, S.N., Lusseau, D., Simões-Lopes, P.C., 2012. The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biol. Lett. 8, 702–5. https://doi.org/10.1098/rsbl.2012.0174

Diamond, J., 2005. Collapse: How societies choose to fail or succed. Viking Press.

Eizaguirre, C., Baltazar-Soares, M., 2014. Evolutionary conservation-evaluating the adaptive potential of species. Evol. Appl. 7, 963–967. https://doi.org/10.1111/eva.12227

Esteban, R., Verborgh, P., Gauffier, P., Giménez, J., Foote, A.D., de Stephanis, R., 2016. Maternal kinship and fisheries interaction influence killer whale social structure. Behav. Ecol. Sociobiol. 70, 111–122. https://doi.org/10.1007/s00265-015-2029-3

Esteban, Ruth, Verborgh, P., Gauffier, P., Giménez, J., Guinet, C., de Stephanis, R., 2016. Dynamics of killer whale, bluefin tuna and human fisheries in the Strait of Gibraltar. Biol. Conserv. 194, 31–38. https://doi.org/10.1016/j.biocon.2015.11.031

Fader, J.E., Elliott, B.W., Read, A.J., 2021. The Challenges of Managing Depredation and Bycatch of Toothed Whales in Pelagic Longline Fisheries: Two U.S. Case Studies. Front. Mar. Sci. 8, 123. https://doi.org/10.3389/fmars.2021.618031

Farine, D.R., Aplin, L.M., Sheldon, B.C., Hoppitt, W., 2015. Interspecific social networks promote information transmission in wild songbirds. Proc. R. Soc. B Biol. Sci. 282, 20142804. https://doi.org/10.1098/rspb.2014.2804

Feldman, M.W., Laland, K.N., 1996. Gene-culture coevolutionary theory. Trends Ecol. Evol. 11, 453–457. https://doi.org/10.1016/0169-5347(96)10052-5

Fernö, A., Huse, G., Jakobsen, P.J., Kristiansen, T.S., Nilsson, J., 2011. Fish

Behaviour, Learning, Aquaculture and Fisheries, in: Fish Cognition and Behavior. Wiley-Blackwell, Oxford, UK, pp. 359–404. https://doi.org/10.1002/9781444342536.ch16

Fisher, J., Hinde, R.A., 1949. The opening of milk bottles by birds. Br. Birds 42, 347–357.

Fogarty, L., Creanza, N., Feldman, M.W., 2019. The life history of learning: Demographic structure changes cultural outcomes. PLoS Comput. Biol. 15, 1–15. https://doi.org/10.1371/journal.pcbi.1006821

Fogarty, L., Creanza, N., Feldman, M.W., 2013. The role of cultural transmission in human demographic change: An age-structured model. Theor. Popul. Biol. 88, 68–77. https://doi.org/10.1016/j.tpb.2013.06.006

Foote, A., Vijay, N., Avila-Arcos, M., Baird, R., Durban, J., Morin, P., Fumagalli, M., Gibbs, R., Hanson, B., Korneliussen, T., Martin, M., Robertson, K., Sousa, V., Vieira, F., Vinar, T., Wade, P., Worley, K., Excoffier, L., Gilbert, T., Wolf, J., 2016. Genome-culture coevolution promotes rapid divergence in the killer whale. Nat. Commun. 7, 11693. https://doi.org/10.1101/040295

Ford, J.K.B., 2009. Killer whale: Orcinus orca, in: Encyclopedia of Marine Mammals. Elsevier Ltd, pp. 650–657. https://doi.org/10.1016/B978-0-12-373553-9.00150-4

Ford, J.K.B., 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Can. J. Zool. 69, 1454–1483. doi.org/10.1139/z91-20

Ford, J.K.B., Ellis, G.M., 2006. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. Mar. Ecol. Prog. Ser. 316, 185–199. 10.3354/meps316185

Fragaszy, D.M., Perry, S. (Eds.), 2003. The Biology of Traditions: models and evidence, The Biology of Traditions. Cambridge University Press, Cambridge. https://doi.org/10.1017/cbo9780511584022

Franz, M., Nunn, C.L., 2009. Network-based diffusion analysis: a new method for detecting social learning. Proc. R. Soc. B Biol. Sci. 276: 1829-1836 https://doi.org/10.1098/rspb.2008.1824

Frère, C.H., Krützen, M., Mann, J., Connor, R.C., Bejder, L., Sherwin, W.B., 2010. Social and genetic interactions drive fitness variation in a free-living dolphin population. Proc. Natl. Acad. Sci. U. S. A. 107, 19949–54. https://doi.org/10.1073/pnas.1007997107

Garland, E.C., Goldizen, A.W., Lilley, M.S., Rekdahl, M.L., Garrigue, C., Constantine, R., Hauser, N.D., Poole, M.M., Robbins, J., Noad, M.J., 2015. Population structure of humpback whales in the western and central South Pacific Ocean as determined by vocal exchange among populations. Conserv. Biol. 29, 1198–1207. https://doi.org/10.1111/cobi.12492

Garland, E.C., Goldizen, A.W., Rekdahl, M.L., Constantine, R., Garrigue, C., Hauser, N.D., Poole, M.M., Robbins, J., Noad, M.J., 2011. Dynamic horizontal cultural transmission of humpback whale song at the ocean basin scale. Curr. Biol. 21, 687–691. https://doi.org/10.1016/j.cub.2011.03.019

Gerber, L., Connor, R.C., Allen, S.J., Willems, E.P., Wittwer, S., 2022. Social integration influences fitness in allied male dolphins. Curr. Biol. 32, 1664–1669. https://doi.org/https://doi.org/10.1016/j.cub.2022.03.027

Gero, S., Whitehead, H., 2016. Critical decline of the eastern Caribbean sperm whale population. PLoS One 11, 1–11. https://doi.org/10.1371/journal.pone.0162019

Gero, S., Whitehead, H., Rendell, L., 2016. Individual , unit and vocal clan level identity cues in sperm whale codas. R. Soc. Open Sci. 3, 1–12. https://doi.org/10.1098/rsos.150372

Gil, M.A., Emberts, Z., Jones, H., St. Mary, C.M., 2017. Social Information on Fear and Food Drives Animal Grouping and Fitness. Am. Nat. 189, 227–241. https://doi.org/10.1086/690055

Giraldeau, L., Valone, T.J., Templeton, J.J., 2002. Potential disadvantages of using socially acquired information. Philos. Trans. R. Soc. London. Ser. B Biol. Sci. 357, 1559–1566. https://doi.org/10.1098/RSTB.2002.1065

Greggor, A.L., Berger-Tal, O., Blumstein, D.T., Angeloni, L., Bessa-Gomes, C., Blackwell, B.F., St Clair, C.C., Crooks, K., de Silva, S., Fernández-Juricic, E., Goldenberg, S.Z., Mesnick, S.L., Owen, M., Price, C.J., Saltz, D., Schell, C.J., Suarez, A. V., Swaisgood, R.R., Winchell, C.S., Sutherland, W.J., 2016. Research Priorities from Animal Behaviour for Maximising Conservation Progress. Trends Ecol. Evol. 31, 953–964. https://doi.org/10.1016/j.tree.2016.09.001

Greggor, A.L., Thornton, A., Clayton, N.S., 2017. Harnessing learning biases is essential for applying social learning in conservation. Behav. Ecol. Sociobiol. 71, 16. https://doi.org/10.1007/s00265-016-2238-4

Gruber, T., Luncz, L., Mörchen, J., Schuppli, C., Kendal, R.L., Hockings, K., 2019. Cultural change in animals: a flexible behavioural adaptation to human disturbance. Palgrave Commun. 5, 1–9. https://doi.org/10.1057/s41599-019-0271-4

Gruebler, M., Korner-Nievergelt, F., Naef-Daenzer, B., 2014. Equal nonbreeding period survival in adults and juveniles of a long-distant migrant bird. Ecol. Evol. 4, 756–765. 10.1002/ece3.984

Hale, R., Treml, E.A., Swearer, S.E., 2015. Evaluating the metapopulation consequences of ecological traps. Proceeding R. Soc. B 282, 201492930. https://doi.org/10.1098/rspb.2014.2930

Hammond, P.S., Francis, T.B., Heinemann, D., Long, K.J., Moore, J.E., Punt, A.E., Reeves, R.R., Sepúlveda, M., Sigurðsson, G.M., Siple, M.C., Víkingsson, G., Wade, P.R., Williams, R., Zerbini, A.N., 2021. Estimating the Abundance of Marine Mammal Populations. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.735770

Harrison, R.A., van de Waal, E., 2022. The unique potential of field research to understand primate social learning and cognition. Curr. Opin. Behav. Sci. 45, 101132. https://doi.org/doi.org/10.1016/j.cobeha.2022.101132

Harrison, X., Tregenza, T., Inger, R., Colhoun, K., Dawson, D., Gudmundsson, G., Hodgson, D.J., Horsburgh, G.J., McElwaine, G., Bearhop, S., 2010. Cultural inheritance drives site fidelity and migratory connectivity in a long-distance migrant. Mol. Ecol. 19, 5484–5496. https://doi.org/10.1111/j.1365-294X.2010.04852.x

Heyes, C.M., 1994. Social learning in animals: categories and mechanisms. Biol. Rev. Camb. Philos. Soc. 69, 207–31.

Higgins, K., Hastings, A., Sarvela, J.N., Botsford, L.W., 1997. Stochastic dynamics and deterministic skeletons: population behaviour of Dungeness Crab. Science 276, 1431–1435. https://doi.org/https://doi.org/10.1126/science.276.5317.1431

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., Gruber, T., 2014. Social Network Analysis Shows Direct Evidence for Social Transmission of Tool Use in Wild Chimpanzees. PLoS Biol. 12, e1001960. https://doi.org/10.1371/journal.pbio.1001960

Hodgson, D., McDonald, J.L., Hosken, D.J., 2016. Resilience Is Complicated, but Comparable: A Reply to Yeung and Richardson. Trends Ecol. Evol. 31, 3–4. https://doi.org/10.1016/j.tree.2015.11.003

Hodgson, D., McDonald, J.L., Hosken, D.J., 2015. What do you mean, “resilient”? Trends Ecol. Evol. 30, 503-6 https://doi.org/10.1016/j.tree.2015.06.010

Hoppitt, W., Boogert, N.J., Laland, K.N., 2010. Detecting social transmission in networks. J. Theor. Biol. 263, 544–555. https://doi.org/10.1016/j.jtbi.2010.01.004

Hoppitt, W., Laland, K.N., 2008. Social Processes Influencing Learning in Animals: A Review of the Evidence. Adv. Study Behav. 38, 105–165. https://doi.org/10.1016/S0065-3454(08)00003-X

Humle, T., Matsuzawa, T., 2002. Ant-dipping among the chimpanzees of Bossou, Guinea, and some comparisons with other sites. Am. J. Primatol. 58, 133–148. https://doi.org/10.1002/ajp.10055

Ito, R., Mori, A., 2010. Vigilance against predators induced by eavesdropping on heterospecific alarm calls in a non-vocal lizard oplurus cuvieri cuvieri (Reptilia: Lguania). Proc. R. Soc. B Biol. Sci. 277, 1275–1280. https://doi.org/10.1098/rspb.2009.2047

IUCN, 2022. Glossary of Definitions [WWW Document]. URL https://www.iucn.org/%0Asites/dev/files/iucn-glossary-of-definitions_en_2021.05.pdf (accessed 5.5.22).

IUCN, 2012. IUCN Red List categories and criteria, version 3.1, second edition. IUCN, Gland and Cambridge.

Jackson, A. L., Ruxton, G.D., Houston, D.C., 2008. The effect of social facilitation on foraging success in vultures: a modelling study. Biol. Lett. 4, 311–313. https://doi.org/10.1098/rsbl.2008.0038

Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B., Hurley, M.A., Mcwhirter, D.E., Miyasaki, H.M., Monteith, K.L., Kauffman, M.J., 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. Science 361, 1023–1025. https://doi.org/10.5061/dryad.8165qv5

Johnstone, R., Cant, M., 2010. The evolution of menopause in cetaceans and humans: the role of demography. Proc. Biol. Sci. 277, 3765–71. https://doi.org/10.1098/rspb.2010.0988

Kasuya, T., 2008. Cetacean biology and conservation: A Japanese scientist’s perspective spanning 46 years - The Kenneth S. Norris Lifetime Achievement Award Lecture. Presented on 29 November 2007 Cape Town, South Africa. Mar. Mammal Sci. 24, 749–773. https://doi.org/10.1111/j.1748-7692.2008.00230.x

Keith, S.A., Bull, J.W., 2017. Animal culture impacts species’ capacity to realise climate-driven range shifts. Ecography 40, 296–304. https://doi.org/10.1111/ecog.02481

Kendal, R.L., Boogert, N.J., Rendell, L., Laland, K.N., Webster, M., Jones, P.L., 2018. Social Learning Strategies: Bridge-Building between Fields. Trends Cogn. Sci. 22, 651–665. https://doi.org/10.1016/j.tics.2018.04.003

Kierulff, M C M, Ruiz-Miranda, C.R., de Oliveira, P.P., Beck, B.B., Martins, A., Dietz, J.M., Rambaldi, D.M., Baker, A.J., 2012. The Golden lion tamarin Leontopithecus rosalia: A conservation success story. Int. Zoo Yearb. 46, 36–45. https://doi.org/10.1111/j.1748-1090.2012.00170.x

King, L.E., Lawrence, A., Douglas-Hamilton, I., Vollrath, F., 2009. Beehive fence deters crop-raiding elephants. Afr. J. Ecol. 47, 131–137.

https://doi.org/10.1111/j.1365-2028.2009.01114.x

Krebs, C.J., 1972. Ecology: The Experimental Analysis of Distribution and Abundance, Harper Int. ed. Harper and Row, New York, NY.

Krützen, M., Mann, J., Heithaus, M.R., Connor, R.C., Bejder, L., Sherwin, W.B., 2005. Cultural transmission of tool use in bottlenose dolphins. Proc. Natl. Acad. Sci. U. S. A. 102, 8939–43. https://doi.org/10.1073/pnas.0500232102

Kuehl, H.S., Kalan, A.K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., Jones, S., Kehoe, L., Regnaut, S., Tickle, A., Ton, E., Van Schijndel, J., Abwe, E.E., Angedakin, S., Agbor, A., Ayimisin, E.A., Bailey, E., Bessone, M., Bonnet, M., Brazolla, G., Buh, V.E., Chancellor, R., Cipoletta, C., Cohen, H., Corogenes, K., Coupland, C., Curran, B., Deschner, T., Dierks, K., Dieguez, P., Dilambaka, E., Diotoh, O., Dowd, D., Dunn, A., Eshuis, H., Fernandez, R., Ginath, Y., Hart, J., Hedwig, D., Heegde, M. Ter, Hicks, T.C., Imong, I., Jeffery, K.J., Junker, J., Kadam, P., Kambi, M., Kienast, I., Kujirakwinja, D., Langergraber, K., Lapeyre, V., Lapuente, J., Lee, K., Leinert, V., Meier, A., Maretti, G., Marrocoli, S., Mbi, T.J., Mihindou, V., Moebius, Y., Morgan, D., Morgan, B., Mulindahabi, F., Murai, M., Niyigabae, P., Normand, E., Ntare, N., Ormsby, L.J., Piel, A., Pruetz, J., Rundus, A., Sanz, C., Sommer, V., Stewart, F., Tagg, N., Vanleeuwe, H., Vergnes, V., Willie, J., Wittig, R.M., Zuberbuehler, K., Boesch, C., 2016. Chimpanzee accumulative stone throwing. Sci. Rep. 6, 22219. https://doi.org/10.1038/srep22219

Kuijper, B., Leimar, O., Hammerstein, P., McNamara, J.M., Dall, S.R.X., 2021. The evolution of social learning as phenotypic cue integration. Phil. Trans. R. Soc. B 376, 20200048. https://doi.org/10.1101/2020.10.30.358028

Kulahci, I.G., Quinn, J.L., 2019. Dynamic Relationships between Information Transmission and Social Connections. Trends Ecol. Evol. 34, 545–554. https://doi.org/10.1016/j.tree.2019.02.007

Kurvers, R.H.J.M., Krause, J., Croft, D.P., Wilson, A.D.M., Wolf, M., 2014. The evolutionary and ecological consequences of animal social networks: emerging issues. Trends Ecol. Evol. 29, 326–335. https://doi.org/10.1016/j.tree.2014.04.002

Lachlan, R.F., Ratmann, O., Nowicki, S., 2018. Cultural conformity generates extremely stable traditions in bird song. Nat. Commun. 9, 2417. https://doi.org/10.1038/s41467-018-04728-1

Laland, K.N., Janik, V.M., 2006. The animal cultures debate. Trends Ecol. Evol. 21, 542–547. https://doi.org/10.1016/j.tree.2006.06.005

Lascelles, B., Notarbartolo, G., Sciara, D., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E., Llewellyn, F., Louzao, M., Ridoux, V., Tetley, M.J., 2014. Migratory marine species : their status , threats and conservation management needs. Aquat. Conserv. Mar. Freshw. Ecosyst. 24, 111–127. https://doi.org/10.1002/aqc.2512

Lehmann, L., Feldman, M.W., 2009. Coevolution of adaptive technology, maladaptive culture and population size in a producer-scrounger game. Proc. R. Soc. B Biol. Sci. 276, 3853–3862. https://doi.org/10.1098/rspb.2009.0724

Lenton, T.M., Williams, H.T.P., 2013. On the origin of planetary-scale tipping points. Trends Ecol. Evol. 28, 380–382.

Lesage, V., 2021. The challenges of a small population exposed to multiple anthropogenic stressors and a changing climate: The St. lawrence estuary beluga. Polar Res. 40, 5523. https://doi.org/10.33265/polar.v40.5523

Ludwig, D., Jones, D., Holling, C., 1978. Quantitative analysis of insect outbreak systems: the spruce budworm and forest. J. Anim. Ecol. 47.

Luncz, L. V., Gill, M., Proffitt, T., Svensson, M.S., Kulik, L., Malaivijitnond, S., 2019. Group-specific archaeological signatures of stone tool use in wild macaques. Elife 8, 1–21. https://doi.org/10.7554/eLife.46961

Luncz, L. V., Tan, A., Haslam, M., Kulik, L., Proffitt, T., Malaivijitnond, S., Gumert, M., 2017. Resource depletion through primate stone technology. Elife 6, e23647. https://doi.org/10.7554/eLife.23647

Maclean, M., Carslake, D., Evans, M., Townley, S., Hodgson, D., 2008. The usefulness of sensitivity analysis for predicting the effects of cat predation on the population dynamics of their avian prey. Ibis 150, 100–113.

Mann, J., Karniski, C., 2017. Diving beneath the surface: long-term studies of dolphins and whales. J. Mammal. 98, 621–630. https://doi.org/10.1093/jmammal/gyx036

Mann, J., Stanton, M. a, Patterson, E.M., Bienenstock, E.J., Singh, L.O., 2012. Social networks reveal cultural behaviour in tool-using dolphins. Nat. Commun. 3, 980. https://doi.org/10.1038/ncomms1983

Marcel, A., Daura-jorge, F.G., Firme, D., Simões-lopes, P.C., Nicholas, S., Volkmer, P., Castilho, D., 2019. Artisanal fishers' perceptions of the ecosystem services derived from a dolphin-human cooperative fishing interaction in southern Brazil. Ocean Coastal Mangmt. 173, 148–156. https://doi.org/10.1016/j.ocecoaman.2019.03.003

Marcoux, M., Rendell, L., Whitehead, H., 2007. Indications of fitness differences among vocal clans of sperm whales. Behav. Ecol. Sociobiol. 61, 1093–1098. https://doi.org/10.1007/s00265-006-0342-6

May, R.M., 1976. Simple mathematical models with very complicated dynamics. Nature 10, 459–67. https://doi.org/10.1038/261459a0

McComb, K., Moss, C., Durant, S.M., Baker, L., Sayialel, S., 2001. Matriarchs as repositories of social knowledge in African elephants. Science 292, 491–4. https://doi.org/10.1126/science.1057895

Mcgregor, P.K., Peake, T.M., Gilbert, G., 2000. Communication behaviour and conservation, in: Gosling, L.., Sutherland, W.J. (Eds.), Behaviour and Conservation. Cambridge University Press, pp. 261–280.

McMillan, M.E., 2016. I Am the State: Power, Politics, and the Cult of Personality, in: From the First World War to the Arab Spring. Palgrave Macmillan, New York, pp. 167–184. https://doi.org/10.1057/9781137522023_18

Mercader, J., Barton, H., Gillespie, J., Boesch, C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. Proc. Nation Acad. Sci. 104, 3043–3048. https://doi.org/https://doi.org/10.1073/pnas.060790910

Mesoudi, A., 2021. Cultural selection and biased transformation: two dynamics of cultural evolution. Phil. Trans. R. Soc. B 376, 20200053. https://doi.org/10.1098/rstb.2020.0053

Mesoudi, A., Chang, L., Dall, S.R.X., Thornton, A., 2016. The Evolution of Individual and Cultural Variation in Social Learning. Trends Ecol. Evol. 31, 215–225. https://doi.org/10.1016/j.tree.2015.12.012

Meyburg, B.-U., Bergmanis, U., Langgemach, T., Graszynski, K., Hinz, A., Börner, I., Meyburg, C., Vansteelant, W.M.G., 2017. Orientation of native versus translocated juvenile lesser spotted eagles (*Clanga pomarina*) on the first autumn migration. J. Exp. Biol. 220, 2765–2776. https://doi.org/10.1242/jeb.148932

Morin, O., Miton, H., 2018. Detecting wholesale copying in cultural evolution. Evol. Hum. Behav. 39, 392–401. https://doi.org/10.1016/j.evolhumbehav.2018.03.004

Morin, P.A., Dizon, A.E., 2018. Genetics, Management, in: Würsig, B., Thewissen, J.G.M., Kovacs, K.M.B.T. (Eds.), Encyclopedia of Marine Mammals. Academic Press, pp. 410–416. https://doi.org/https://doi.org/10.1016/B978-0-12-804327-1.00137-0

Mueller, T., O’Hara, R.B., Converse, S J, Urbanek, R.P., Fagan, W.F., O’Hara, R.B., Converse, Sarah J., Urbanek, R.P., Fagan, W.F., 2013. Social learning of migratory performance. Science 341, 999–1002. https://doi.org/10.1126/science.1237139

Nelms, S., Alfaro-Shigueto, J., Arnould, J., Avila, I., Bengtson Nash, S., Campbell, E., Carter, M., Collins, T., Currey, R., Domit, C., Franco-Trecu, V., Fuentes, M., Gilman, E., Harcourt, R., Hines, E., Hoelzel, A., Hooker, S., Johnston, D., Kelkar, N., Kiszka, J., Laidre, K., Mangel, J., Marsh, H., Maxwell, S., Onoufriou, A., Palacios, D., Pierce, G., Ponnampalam, L., Porter, L., Russell, D., Stockin, K., Sutaria, D., Wambiji, N., Weir, C., Wilson, B., Godley, B., 2021. Marine mammal conservation: over the horizon. Endanger. Species Res. 44, 291–325. https://doi.org/10.3354/esr01115

Nicol-Harper, A., Claire, H., David, D., Markus, P., Jakub, M., David, B., Townley, S., Ezard, T., 2018. Inferring transient dynamics of human populations from matrix non- normality. Popul. Ecol. 60, 185–196. https://doi.org/10.1007/s10144-018-0620-y

Pace, D.S., Arcangeli, A., Mussi, B., Vivaldi, C., Ledon, C., Lagorio, S., Giacomini, G., Pavan, G., Ardizzone, G., 2018. Habitat suitability modeling in different sperm whale social groups. J. Wildl. Manage. 82. https://doi.org/10.1002/jwmg.21453

Paxton, K.L., Sebastián-González, E., Hite, J.M., Crampton, L.H., Kuhn, D., Hart, P.J., 2019. Loss of cultural song diversity and the convergence of songs in a declining Hawaiian forest bird community. R. Soc. Open Sci. 6, 190719. https://doi.org/10.1098/rsos.190719

Petts, J., Niemeyer, S., 2004. Health risk communication and amplification: learning from the MMR vaccination controversy. Heal. Risk Soc. 6. https://doi.org/https://doi.org/10.1080/13698570410001678284

Record, N.R., 2021. The Intertwined Futures of Whales and Humans. Oceanography 34, 16–18. https://doi.org/10.2307/27051385

Rendell, L., Boyd, R., Cownden, D., Enquist, M., Eriksson, K., Feldman, M.W., Fogarty, L., Ghirlanda, S., Lillicrap, T., Laland, K.N., 2010. Why copy others? insights from the social learning strategies tournament. Science 328, 208–13. https://doi.org/10.1126/science.1184719

Rendell, L., Cantor, M., Gero, S., Whitehead, H., Mann, J., 2019. Causes and consequences of female centrality in cetacean societies. Philos. Trans. R. Soc. B Biol. Sci. 374. https://doi.org/10.1098/rstb.2018.0066

Rendell, L., Fogarty, L., Hoppitt, W.J.E., Morgan, T.J.H., Webster, M.M., Laland, K.N., 2011. Cognitive culture: theoretical and empirical insights into social learning strategies. Trends Cogn. Sci. 15, 68–76. https://doi.org/10.1016/j.tics.2010.12.002

Rendell, L., Mesnick, S.L., Dalebout, M.L., Burtenshaw, J., Whitehead, H., 2012. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? Behav. Genet. 42, 332–343. https://doi.org/10.1007/s10519-011-9513-y

Rendell, L.E., Whitehead, H., 2003. Vocal clans in sperm whales (*Physeter* *macrocephalus*). Proc. Biol. Sci. 270, 225–31. https://doi.org/10.1098/rspb.2002.2239

Richerson, P.J., Boyd, R., 2005. Not by Genes Alone: How Culture Transformed Human Evolution. University of Chicago Press. https://doi.org/10.1111/j.1467-9744.2009.01005.x

Riebel, K., Lachlan, R.F., Slater, P.J.B., 2015. Learning and cultural transmission in chaffinch song. Adv. Study Behav. 47, 181–227. https://doi.org/10.1016/bs.asb.2015.01.001

Riesch, R., Barrett-Lennard, L.G., Ellis, G.M., Ford, J.K.B., Deecke, V.B., 2012. Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? Biol. J. Linn. Soc. 106, 1–17. https://doi.org/10.1111/j.1095-8312.2012.01872.x

Robinson, K.P., Sim, T.M.C., Culloch, R.M., Bean, T.S., Aguilar, I.C., Eisfeld, S.M., Filan, M., Haskins, G.N., Williams, G., Pierce, G.J., 2017. Female reproductive success and calf survival in a North Sea coastal bottlenose dolphin (Tursiops truncatus) population. PLoS One 12, 1–16. https://doi.org/10.1371/journal.pone.0185000

Rogers, L.A., Salomon, A.K., Connors, B., Krkošek, M., 2018. Collapse, Tipping Points, and Spatial Demographic Structure Arising from the Adopted Migrant Life History. Am. Nat. 192, 49–61. https://doi.org/10.1086/697488

Rutz, C., Hays, G.C., 2009. New frontiers in biologging science. Biol. Lett. 5, 289–292. https://doi.org/10.1098/rsbl.2009.0089

Rutz, C., Klump, B.C., Komarczyk, L., Leighton, R., Kramer, J., Wischnewski, S., Sugasawa, S., Morrissey, M.B., James, R., St Clair, J.J.H., Switzer, R.A., Masuda, B.M., 2016. Discovery of species-wide tool use in the Hawaiian crow. Nature 537, 403–407. https://doi.org/10.1038/nature19103

Rutz, C., Loretto, M.C., Bates, A.E., Davidson, S.C., Duarte, C.M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R.B., Ropert-Coudert, Y., Tucker, M.A., Wikelski, M., Cagnacci, F., 2020. COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. Nat. Ecol. Evol. 4, 1156–1159. https://doi.org/10.1038/s41559-020-

1237-z

Ryan, S.J., 2006. The role of culture in conservation planning for small or endangered populations. Conserv. Biol. 20, 1321–1324. https://doi.org/10.1111/j.1523-1739.2006.00347.x

Sandercock, B., Beissinger, S., 2002. Estimating rates of population change for a neotropical parrot with ratio, mark-recapture and matrix methods. J. Appl. Stat. 29, 589–607. doi.org/10.1080/02664760120108818

Sargeant, B.L., Mann, J., 2009. Developmental evidence for foraging traditions in wild bottlenose dolphins. Anim. Behav. 78, 715–721. https://doi.org/10.1016/j.anbehav.2009.05.037

Schakner, Z.A., Lunsford, C., Straley, J., Eguchi, T., Mesnick, S.L., 2014. Using models of social transmission to examine the spread of longline depredation behavior among sperm whales in the Gulf of Alaska. PLoS One 9, e109079. https://doi.org/10.1371/journal.pone.0109079

Schumaker, N.H., Ernst, T., White, D., Baker, J., Haggerty, P., 2004. Projecting wildlife responses to alternative future landscapes in Oregon’s Willamette Basib. Ecol. Appl. 14, 381–400. https://doi.org/10.1890/02-5010

Schuppli, C., van Schaik, C.P., 2019. Animal cultures: how we’ve only seen the tip of the iceberg. Evol. Hum. Sci. 1, 1–13. https://doi.org/10.1017/ehs.2019.1

Shannon, G., Slotow, R., Durant, S.M., Sayialel, K.N., Poole, J., Moss, C., McComb, K., 2013. Effects of social disruption in elephants persist decades after culling. Front. Zool. 10, 62. https://doi.org/10.1186/1742-9994-10-62

Sheppard, C.E., Marshall, H.H., Inger, R., Thompson, F.J., Vitikainen, E.I.K., Barker, S., Nichols, H.J., Wells, D.A., McDonald, R.A., Cant, M.A., 2018. Decoupling of Genetic and Cultural Inheritance in a Wild Mammal. Curr. Biol. 28, 1846–1850. https://doi.org/10.1016/j.cub.2018.05.001

Singh, J.S., 2002. The biodiversity crisis: a multifacedted review. Curr. Sci. 82, 638–647.

Slagsvold, T., Wiebe, K.L., 2007. Learning the ecological niche. Proc. R. Soc. B

Biol. Sci. 274, 19–23. https://doi.org/10.1098/rspb.2006.3663

Somers, M.J., Graf, J.A., Szykman, M., Slotow, R., Gusset, M., 2008. Dynamics of a small re-introduced population of wild dogs over 25 years: Allee effects and the implications of sociality for endangered species’ recovery. Oecologia 158, 239–47. https://doi.org/10.1007/s00442-008-1134-7

Stephens, P.A., Sutherland, W.J., Freckleton, R.P., 1999. What is the Allee effect ? Oikos 87, 185–190. https://doi.org/DOI: 10.2307/3547011

Stoinski, T.S., Beck, B.B., Bloomsmith, M.A., Maple, T.L., 2003. A behavioral comparison of captive-born, reintroduced golden lion tamarins and their wild-born offspring. Behaviour 140, 137–160. https://doi.org/10.1163/156853903321671479

Stott, I., Townley, S., Hodgson, D.J., 2011. A framework for studying transient dynamics of population projection matrix models. Ecol. Lett. 14, 959–970. https://doi.org/10.1111/j.1461-0248.2011.01659.x

Strogatz, S., 2015. Nonlinear Dynamics and Chaos: with applications to Physics, Biology, Chemistry and Engineering (2nd ed.). CRC Press.

Sutherland, W., 1998. The importance of behavioural studies in conservation biology. Anim. Behav. 56, 801–809. https://doi.org/10.1006/anbe.1998.0896

Switzer, P. V., 1993. Site fidelity in predictable and unpredictable habitats. Evol. Ecol. 7, 533–555. https://doi.org/10.1007/BF01237820

Tainter, J.A., 1988. The collapse of complex societies. Cambridge University Press.

Tavares, S.B., Whitehead, H., Doniol-Valcroze, T., 2022. Assessing social structure: a data-driven approach to define associations between individuals. Mamm. Biol. https://doi.org/https://doi.org/10.1007/s42991-022-00231-9

Taylor, B.L., Martinez, M., Gerrodette, T., Barlow, J., Hrovat, Y.N., 2007. Lessons from monitoring trends in abundance of marine mammas. Mar. Mammal Sci. 23, 157–175. https://doi.org/doi: 10.1111/j.1748-

7692.2006.00092.x

Teitelbaum, C.S., Converse, S.J., Mueller, T., 2018. The importance of early life experience and animal cultures in reintroductions. Conserv. Lett. 1–7. https://doi.org/10.1111/conl.12599

Tetley, M.J., Braulik, G., Landredi, C., Minton, G., Panigada, S., Politi, E., Zanardelli, M., Notarbartolo-di-Sciara, G., Hoyt, E., 2022. The important marine mammal area network: a tool for systematic spatial planning in response to the marine mammal habitat crisis. Front. Mar. Sci. 9. https://doi.org/doi.org/10.3389/fmars.2022.841789

Thornton, A., Malapert, A., 2009. Experimental evidence for social transmission of food acquisition techniques in wild meerkats. Anim. Behav. 78, 255–264. https://doi.org/doi.org/10.1016/j.anbehav.2009.04.021

Tim Tinker, M., Guimarães, P.R., Novak, M., Marquitti, F.M.D., Bodkin, J.L., Staedler, M., Bentall, G., Estes, J.A., 2012. Structure and mechanism of diet specialisation: Testing models of individual variation in resource use with sea otters. Ecol. Lett. 15, 475–483. https://doi.org/10.1111/j.1461-0248.2012.01760.x

Trouwborst, A., Blackmore, A., Boitani, L., Bowman, M., Caddell, R., Chapron, G., Cliquet, A.N., Couzens, E.D., Epstein, Y., Fernández-galiano, E., Fleurke, F.M., Gardner, R., Hunter, L., Jacobsen, K.I.M., Krofel, M., Lewis, M., López-bao, J.V., Macdonald, D., Redpath, S., Wandesforde-smith, G., Linnell, J.D.C., 2017. International Wildlife Law : Understanding and Enhancing Its Role in Conservation. Bioscience 67, 784–790. https://doi.org/10.1093/biosci/bix086

Tulloch, V.J.D., Plagányi, É.E., Brown, C., Richardson, A.J., Matear, R., 2019. Future recovery of baleen whales is imperiled by climate change. Glob. Chang. Biol. 25, 1263–1281. https://doi.org/10.1111/gcb.14573

UN, 2015. United Nations Department of Economic and Social Affairs, Population Division. Population 2030: demographic challenges and opprotunities for sustainable development planning (ST/ESA/SER.A/389).

UNESCO, 2016. What is Intangible Cultural Heritage? [WWW Document]. URL http://www.unesco.org/culture/ich/en/what-is-intangible-heritage-00003 (accessed 2.24.16).

UNFPA, 2011. The World at Seven Billion [WWW Document]. UNFPA - United Nations Fund Popul. Act. URL http://www.unfpa.org/sites/default/files/resource-pdf/7B_fact_sheets_en.pdf (accessed 2.24.16).

Van De Waal, E., Borgeaud, C., Whiten, A., 2013. Potent social learning and conformity shape a wild primate’s foraging decisions. Science 340, 483–485. https://doi.org/10.1126/science.1232769

van Schaik, C.P., 2009. Geographic variation in the behaviour of wild great apes: Is it really cultural?, in: Laland, K.N., Galef, B.G. (Eds.), The Question of Animal Culture. Harvard University Press, Cambridge, MA, pp. 70–98.

Vélez-Espino, L.A., Ford, J.K.B., Araujo, H.A., Ellis, G., Parken, C.K., Sharma, R., 2015. Relative importance of chinook salmon abundance on resident killer whale population growth and viability. Aquat. Conserv. Mar. Freshw. Ecosyst. 25, 756–780. https://doi.org/10.1002/aqc.2494

Wade, P.R., Angliss, R., 1997. Guidelines for assessing marine mammal stocks: Report of the GAMMS Workshop, NOAA Technical Memorandum NMFS.

Wade, P.R., Reeves, R.R., Mesnick, S.L., 2012. Social and Behavioural Factors in Cetacean Responses to Overexploitation: Are Odontocetes Less “Resilient” Than Mysticetes? J. Mar. Biol. 2012, 567276. https://doi.org/10.1155/2012/567276

Ward, A.J.W., Duff, A.J., Horsfall, J.S., Currie, S., 2008. Scents and scents-ability: Pollution disrupts chemical social recognition and shoaling in fish. Proc. R. Soc. B Biol. Sci. 275, 101–105. https://doi.org/10.1098/rspb.2007.1283

Warner, R.R., 1988. Traditionality of mating-site preferences in a coral reef fish. Nature 335, 719–721. https://doi.org/10.1038/335719a0

West, J.B., Bowen, G.J., Cerling, T.E., Ehleringer, J.R., 2006. Stable isotopes as one of nature’s ecological recorders. Trends Ecol. Evol. 21, 408–414.

https://doi.org/10.1016/j.tree.2006.04.002

Whitehead, H., 2017. Gene–culture coevolution in whales and dolphins. Proc. Natl. Acad. Sci. 114, 7814–7821. https://doi.org/10.1073/pnas.1620736114

Whitehead, H., 2010. Conserving and managing animals that learn socially and share cultures. Learn. Behav. 38, 329–336. https://doi.org/10.3758/LB.38.3.329

Whitehead, H., 2003. Sperm Whales: Social Evolution in the Ocean. University of Chicago Press.

Whitehead, H., Antunes, R., Gero, S., Wong, S.N.P., Engelhaupt, D., Rendell, L., 2012. Multilevel Societies of Female Sperm Whales (*Physeter macrocephalus*) in the Atlantic and Pacific: Why Are They So Different? Int. J. Primatol. 33, 1142–1164. https://doi.org/10.1007/s10764-012-9598-z

Whitehead, H., Ford, J.K.B., 2018. Consequences of culturally-driven ecological specialization : Killer whales and beyond. J. Theor. Biol. 456, 279–294. https://doi.org/10.1016/j.jtbi.2018.08.015

Whitehead, H., Laland, K.N., Rendell, L., Thorogood, R., Whiten, A., 2019. The reach of gene–culture coevolution in animals. Nat. Commun. 3, 2405 https://doi.org/10.1038/s41467-019-10293-y

Whitehead, H., Lusseau, D., 2012. Animal social networks as substrate for cultural behavioural diversity. J. Theor. Biol. 294, 19–28. https://doi.org/10.1016/j.jtbi.2011.10.025

Whitehead, H., Rendell, L., 2015. The cultural lives of whales and dolphins. The University of Chicago Press, Chicago.

Whitehead, H., Rendell, L., Osborne, R.W., Würsig, B., 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. Biol. Conserv. 120, 427–437. https://doi.org/10.1016/j.biocon.2004.03.017

Whitehead, H., Richerson, P.J., 2009. The evolution of conformist social learning can cause population collapse in realistically variable environments. Evol. Hum. Behav. 30, 261–273.

https://doi.org/10.1016/j.evolhumbehav.2009.02.003

Whitehead, H.A.L., Rendell, L., 2004. Movements, habitat use and feeding success of cultural clans of South Pacific sperm whales. J. Anim. Ecol. 73, 190–196. https://doi.org/10.1111/j.1365-2656.2004.00798.x

Whiten, A., 2021. The burgeoning reach of animal culture. Science 372, 6537. https://doi.org/10.1126/science.abe6514

Whiten, A., 2019. Cultural Evolution in Animals. Annu. Rev. Ecol. Evol. Syst. 50, 27–48. https://doi.org/10.1146/annurev-ecolsys-110218-025040

Whiten, A., 2017a. A second inheritance system: the extension of biology through culture. Interface Focus 7, 20160142. https://doi.org/10.1098/rsfs.2016.0142

Whiten, A., 2017b. Culture extends the scope of evolutionary biology in the great apes. Proc. Natl. Acad. Sci. 114, 7790–7797. https://doi.org/10.1073/pnas.1620733114

Whiten, A., 2005. The second inheritance system of chimpanzees and humans. Nature 437, 52–5. https://doi.org/10.1038/nature04023

Whiten, A., Goodall, J., McGrew, W.C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C.E., Wrangham, R.W., Boesch, C., 1999. Cultures in chimpanzees. Nature 399, 682–5. https://doi.org/10.1038/21415

Whiten, A., Spiteri, A., Horner, V., Bonnie, K.E., Lambeth, S.P., Schapiro, S.J., de Waal, F.B.M., 2007. Transmission of Multiple Traditions within and between Chimpanzee Groups. Curr. Biol. 17, 1038–1043. https://doi.org/10.1016/j.cub.2007.05.031

Wild, S., Allen, S.J., Kru, M., King, S.L., Gerber, L., Hoppitt, W.J.E., Wild, S., 2019a. Multi-network-based diffusion analysis reveals vertical cultural transmission of sponge tool use within dolphin matrilines. Biol. Lett. 15 20190227. https://doi.org/10.1098/rsbl.2019.0227

Wild, S., Krützen, M., Rankin, R.W., Hoppitt, W.J.E., Gerber, L., Allen, S.J., 2019b. Long-term decline in survival and reproduction of dolphins following a marine heatwave. Curr. Biol. 29, R239–R240.

https://doi.org/10.1016/j.cub.2019.02.047

Williams, R., Lusseau, D., 2006. A killer whale social network is vulnerable to targeted removals. Biol. Lett. 2, 497–500. https://doi.org/10.1098/rsbl.2006.0510

Yamey, G., Gonsalves, G., 2020. Donald Trump: A political determinant of covid-19. BMJ 369, m1643. https://doi.org/10.1136/bmj.m1643