Social transmission of foraging behaviour in bottlenose dolphins and its interplay with climate change

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The candidate confirms that the work submitted is their own, except where work which has formed part of jointly authored publications has been included. The contribution of the candidate and the other authors to this work has been explicitly indicated below. The candidate confirms that appropriate credit has been given within the thesis where reference has been made to the work of others.

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ABSTRACT

Cultural behaviour, *i.e.*, that which is transmitted socially among conspecifics, is found in a variety of taxa, including cetaceans. Different methods have been used to detect social learning in animal populations. ‘Network-based diffusion analysis’ (NBDA), for example, provides a statistical framework with which the importance of social learning on the spread of a behaviour can be quantified. It infers social learning if the diffusion of behaviour follows the social network and therefore relies on accurate association data among individuals. Incomplete association data can lead to uncertainty over the strengths of connections among individuals. Restricting analyses to only include individuals above a certain threshold of sightings can minimize such uncertainty, but at the same time reduce power of NBDA to detect learning when linking individuals are removed from the network. Following my General Introduction, Chapter 2 of this thesis therefore provides a tool for researchers to select an appropriate threshold for the inclusion of individuals that maximizes the power of NBDA to detect social learning. In the study of the rise and spread of cultural behaviour, ecology and genetics are potentially confounding factors as they too can drive behavioural variation between individuals, communities and populations. I use a multi-network version of NBDA, which can account for these potential confounds by including networks reflecting association patterns, genetic relatedness and habitat use, in Chapters 3 and 4 to investigate the spread of two foraging strategies, ‘shelling’ and ‘sponging’, in a population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the western gulf of Shark Bay, Western Australia, between 2007 and 2018. Shelling (Chapter 3) appears to spread horizontally among associated individuals, which stands in stark contrast to the predominantly vertically transmitted foraging strategies, from mother to offspring, in Shark Bay dolphins and indeed toothed whales in general. My study provides the first quantitative evidence of horizontal transmission in any toothed whale species and suggests similarities in the cultural nature of cetaceans and great apes, which rely extensively on both vertical and horizontal social learning. Conversely, the findings presented in Chapter 4 suggest vertical social transmission of sponging from mother to primarily female offspring, confirming the results of previous research using different methods. Chapters 3 and 4 illustrate how long-term data sets on individual associations, habitat use and genetics, in combination with new statistical tools like NBDA, provide an ideal framework to assess the spread of behaviour in free-ranging animal populations. In Chapter 5, I investigate the impacts of a marine heatwave, which led to catastrophic losses of habitat-forming seagrass beds and mass mortalities of fish and invertebrates in Shark Bay, on the vital rates of the resident dolphin population. Long-term demographic data and capture-recapture analyses on data collected before and after the heatwave indicate immediate and on-going reductions in both survival and reproductive rates within the dolphin population, presumably due to the cascading effects of the heatwave on lower-trophic organisms combined with a lack of ecosystem recovery. Remarkably, survival rates of sponging dolphins appear less adversely impacted compared to those of non-spongers, suggesting that their foraging niche may have buffered them against more negative impacts. Whether or not culturally different communities within a population may respond differently to environmental change remains an exciting avenue of research in the future. Finally, I discuss the broader ramifications of this thesis in the General Discussion and suggest further directions in the study of cultural behaviour in bottlenose dolphins.

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A NOTE ON STYLE

Chapters 2-5 of this thesis have been written in manuscript form intended for publication. I am lead author on all data chapters, but I acknowledge contributions of co-authors by using terms ‘we’ and ‘our’ throughout those chapters. General Introduction and Discussion represent my sole work, and terms ‘I’ and ‘my’ are therefore used throughout.

While Chapters 2-4 follow classic manuscript format with introduction, methods, results and discussion, Chapter 5 has been written in short correspondence format with a 1000 word limit and a continuous main text as was required by the editorial team of *Current Biology* where the manuscript is currently in review after resubmission of a revised version. Detailed methods and results for Chapter 5 can be found in the Appendix of this thesis.

CHAPTER 1.
General Introduction

1.0. Animal culture?

1.0.1. Culture defined

The existence of animal culture and the methods for providing evidence for it in nature have been debated among researchers (e.g. Laland and Hoppitt, 2003; Laland and Janik, 2006, 2007; Krützen et al., 2007). Part of this debate stems from the lack of a universally accepted definition of the term ‘culture’. Galef, (1992), for example, restricted culture to cases where the transfer of information takes place exclusively through complex forms of social learning such as imitation or teaching, which are thought to be restricted to species with high cognitive abilities. Boyd and Richerson, (1995), on the other hand, used a rather broad approach and refer to culture if a behavioural trait is acquired through some form of social learning from conspecifics. Furthermore, a widely accepted definition by Whiten and van Schaik, (2007) stated that culture requires the possession of a series of traditions – defined as shared behaviour that persists over time and is acquired through socially aided learning (Fragaszy and Perry, 2003) [page 12] - in different behavioural contexts.

As my primary interest lies in the mechanisms underlying the spread of animal culture, I will, throughout this thesis, refer to culture according to Boyd and Richerson's, (1995) definition from above. Many might argue that such a broad definition is too inclusive and is far from what we intuitively perceive as 'culture' in our own species. However, such a definition allows the comparison of socially learned behaviours across taxa with different social systems and from different environments, which can help us understand the emergence and spread of culture (Whitehead and Rendell, 2014).

1.0.2. From innovation to culture

All cultural traditions begin with an innovation by an individual, which can include the discovery of novel information, the establishment of a new behaviour or the performance of an already established behaviour in a different context (Reader and Laland, 2001). Innovations are essentially products of independent learning (also called ‘asocial learning’), which requires sampling of the environment and subsequently finding an appropriate response, often involving trial and error learning. Innovations therefore allow organisms to cope with new conditions in changing environments (Kawai, 1965; Sol et al., 2005).

However, trial and error learning can potentially incur considerable costs for an individual, and these costs can vary. For example, individual learning can be time-consuming if the process requires extensive sampling of the environment or if many attempts are required to find an appropriate response to a challenge. Costs can also be severe if errors during the learning process increase the risk of mortality, as in predator avoidance or ingestion of potentially poisonous food. In such cases, it is more beneficial for an individual to use information already gathered by others, *i.e.*, to acquire information through social learning rather than independent sampling of the environment (Galef and Laland, 2005; Webster and Laland, 2008; Galef, 2009). Social learning is thus often, though not exclusively, found in contexts where costs associated with individual learning are potentially high. For instance, when deciding to remain in or leave a food patch, minnows (*Phoxinus phoxinus*) relied increasingly on social learning as predation risk increased, confirming a strategy to copy others when asocial learning is costly (Webster and Laland, 2008). Social learning is also found in lower-risk contexts such as hygiene or even play. In Japanese macaques (*Macaca fuscata* spp.), for example, louse egg-handling techniques while grooming for parasite elimination (Tanaka, 1998) and stone-handling techniques in a play context (Leca et al., 2007) were passed on through social learning. Most reports on social learning in animals, however, come from a foraging context. Information on what, how and where to eat have been found to be transmitted socially in various animal species, for example in orangutans (*Pongo pygmaeus wurmbii*) (Van Schaik and Knott, 2001; Jaeggi et al., 2010), black bears (*Ursus americanus*) (Mazur and Seher, 2008), and songbirds (family Paridae) (Aplin et al., 2012).

The acquisition of information from others is particularly important for young, dependent individuals. They have to acquire skills crucial for survival, including foraging techniques, knowledge about diet, predator avoidance, seeking shelter and social interactions with conspecifics. Using information from older, more experienced individuals may thereby increase the efficiency with which young individuals learn such skills. Learning from older generations is referred to either as ‘oblique social learning’ or, if it occurs specifically between parent and offspring, ‘vertical social learning’. This is particularly prevalent in social species with prolonged parental care (Roper, 1986), such as primates and cetaceans, where nursing and offspring-foraging overlap, providing numerous opportunities for social learning of behaviour (Mann and Sargeant, 2003; Jaeggi et al., 2010). In orangutans, for instance, offspring rely heavily on vertical social learning in a foraging context by following their mothers’ choice in how and what to eat (Jaeggi et al., 2010). Social learning can also occur between members of the same generation, which is referred to as ‘horizontal social learning’. For example, ‘moss-sponging’, an innovative technique to retrieve water from a hole, spread horizontally among free-ranging chimpanzees (*Pan troglodytes schweinfurthii*) (Hobaiter et al., 2014).

1.0.3. Identifying culture in natural populations

Besides a lack of agreement on the term ‘culture’, there have been debates on how best to identify cultural behaviour in animal populations. To be considered cultural, a behaviour must be transmitted socially among individuals, leading to behavioural variation among groups or social units (cultural hypothesis). However, critics have argued that there are alternative hypotheses to social transmission explaining the observed patterns of behavioural differences between groups (Laland and Hoppitt, 2003; Laland and Janik, 2006). The genetic hypothesis states that different groups may be genetically predisposed to behave in different ways (Laland and Hoppitt, 2003). The ecological hypothesis, on the other hand, states that the local ecological conditions may differ between groups, and that by adapting to their local environment, individuals within a group tend to adopt a similar behavioural repertoire, which differs from that of individuals in other groups (Laland and Hoppitt, 2003). Researchers interested in putative culture therefore have to establish whether genetics and ecology are sufficient to explain observed patterns in the data. In order to disentangle the three hypotheses (social learning, ecological factors, genetics) to explain behavioural differences between groups or social units, several methods have been developed, which I will discuss in the following section.

1.0.3.1. Method of exclusion

Among primatologists, a commonly used method for the detection of social learning was the ‘ethnographic method’ or ‘method of exclusion’ (Boesch, 1996; Whiten et al., 1999; van Schaik et al., 2003). The method of exclusion identifies patterns of variation in the behavioural repertoires of the population in question and infers social transmission as at least partly responsible for the behavioural pattern by excluding genetic and ecological factors as sufficient explanations in causing the behavioural variation (Hoppitt and Laland, 2013 [p. 132]) (Fig. 1.1a). Thereby, the *basic method of exclusion*, following the categorisation of Hoppitt and Laland, (2013), infers social learning by arguing that it is implausible that ecological or genetic differences could influence the behavioural variation and that hence, social learning must be responsible. Laland and Janik, (2006), however, criticized that it is impossible to consider all potential environmental and genetic factors that could be responsible for causing behavioural variation, and that therefore, social learning could never be inferred with certainty. Low power when assessing environmental and genetic factors could furthermore lead to false claims of social learning and therefore culture (Hoppitt and Laland, 2013). Since social learning, ecological and genetics factors are not necessarily mutually exclusive, but can be responsible for causing behavioural variation at the same time (Fig. 1.1b), both proponents (e.g. Krützen et al., 2007) and opponents (Laland and Janik, 2006, 2007) of the method of exclusion agreed that the development of new methods that allow the quantification of social learning are desirable.

The *advanced method of exclusion*, following the categorisation of Hoppitt and Laland, (2013), takes the question of animal culture a step further by fitting a null model in which ecological and genetic factors influence the behaviour in question. It infers social learning, if the alternative explanations are insufficient in explaining the observed behavioural patterns. For example, Langergraber et al., (2011) assessed influences of genetic dissimilarity on previously documented behavioural differences between nine chimpanzee groups (Whiten et al., 1999). They found that behavioural and genetic dissimilarity between groups were highly correlated and that therefore, genetic dissimilarity could not be entirely ruled out as playing a role in generating different behavioural repertoires between chimpanzee groups (Langergraber et al., 2011). In a similar approach, Krützen et al., (2011) used pairwise dissimilarity matrices reflecting differences in behaviour, genetics and environment, to assess their importance on behavioural variation in orangutans. Since behavioural variation was explained by neither genetic nor environmental differences, they inferred that it was a result of social transmission.

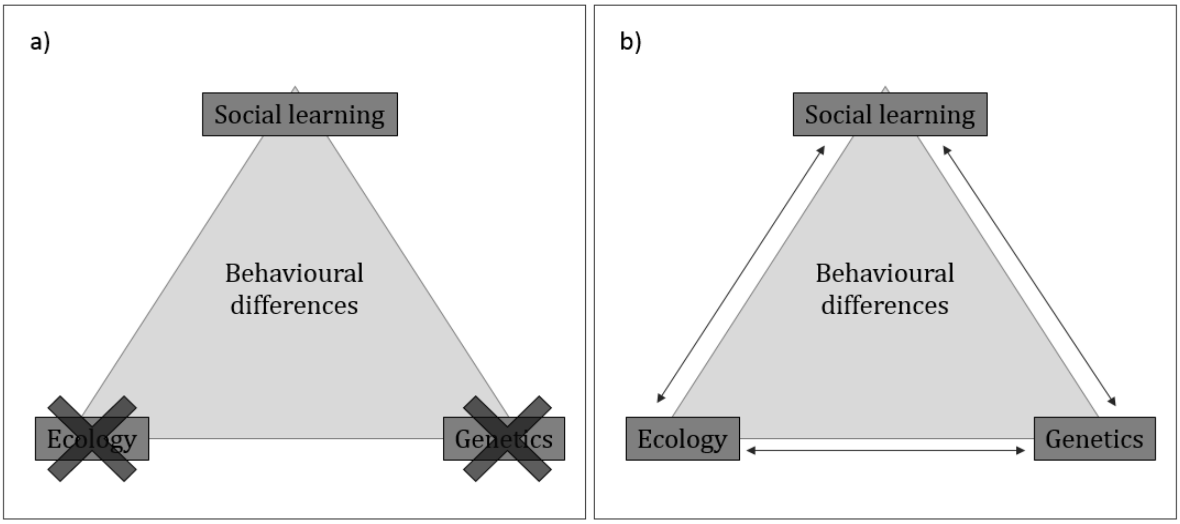

Figure 1.1: *Methods for detecting culture:* ***a)*** *The 'basic method of exclusion' identifies behavioural variation among populations as culture by ruling out genetic and environmental factors as being responsible for causing the behavioural differences.* ***b)*** *More recent approaches such as the 'advanced method of exclusion' or network-based approaches like 'network-based diffusion analysis' (NBDA) treat social learning, ecological factors and genetic predispositions as non-mutually exclusive.*

1.0.3.2. Option-bias method

Another approach which is based on a more subjective judgement of plausibility compared to the basic method of exclusion, the 'option-bias' method was introduced by Kendal et al., (2009). The method requires researchers to first assess the roles of genetic and ecological differences between populations. After accounting for these alternative factors, it is based on the assumption that social learning is expected to generate a greater within-population homogeneity in behaviour than would be expected in its absence, *i.e.*, when behaviour is generated through asocial learning (Kendal et al., 2009). Using a randomization approach, social learning is inferred if a particular behaviour occurs more often than expected by chance and asocial learning alone, and can therefore be inferred or refuted at the 5% level (Kendal et al., 2009). However, if there is genetic or ecological heterogeneity between populations, estimates of the probability of each option in each population are required, which can be difficult to obtain, particularly in free-ranging populations.

1.0.3.3. Network-based diffusion analysis (NBDA)

New, network-based analyses were developed in an attempt to resolve the animal cultures debate (e.g. Franz and Nunn, 2009; Hoppitt et al., 2010), in order to provide a framework by which social learning within a group or population could be quantified. These approaches posit that social transmission of a behaviour follows a social network. Usually, this network is taken to be the association pattern between individuals (Boogert et al., 2008), as closely associated individuals have more opportunity, and are therefore more likely to learn from each other (Coussi-Korbel and Fragaszy, 1995).

'Network-based diffusion analysis' (NBDA) has proven to be a powerful tool to detect and quantify social learning by comparing diffusion data, *i.e.*, the order in which or timing at which individuals acquire a behavioural trait, with a matrix that contains a measure of association among individuals (Hoppitt et al., 2010). Two variants of NBDA exist: The order of acquisition diffusion analysis (OADA) (Hoppitt et al., 2010) and the time of acquisition diffusion analysis (TADA) (Franz and Nunn, 2009), which both fit a model of social learning to the diffusion data based on maximum likelihood and test it against a model with no social transmission.

NBDA not only serves as a tool for the detection of social learning, but also allows the estimation of the strength of the social transmission effect. A social transmission parameter, s, is fitted to the data and estimates the rate of transmission per unit association with informed individuals relative to the average rate of asocial learning (Hoppitt et al., 2010; Box 1). In addition, individual-level variables (ILVs) can be included in the analysis, which have potential influence on an individual's learning rate, such as gender, rank or age. To date, these ILVs have been included in two different ways, either as *additive* or *multiplicative* models, which take different assumptions about the interaction of social learning and asocial variables (Hoppitt et al., 2010; Box 1). In the *additive* model, ILVs are modelled to only affect an individual's asocial learning rate, while in the *multiplicative* model, ILVs affect social and asocial learning rate to the same extent (Box 1). Alternatively, one could also fit an *unconstrained* model which allows the ILVs' effects on social and asocial learning to be estimated separately (Hoppitt and Laland, 2013).

Box 1.1: NBDA in detail (Hoppitt et al., 2010; Hoppitt and Laland, 2013):

NBDA can be generalized in the following form:

$$\lambda_i(t) = \lambda_0(t)\big(1 - z_i(t)\big)\left(s\sum_{j=1}^{N} a_{i,j} z_j(t) + 1 \right)$$

where $\lambda_i(t)$ denotes the rate of acquisition of individual *i* at time *t*, while $\lambda_0(t)$ is the baseline acquisition rate shared by all individuals. $z_i(t)$ and $z_j(t)$ represent the state of information of individuals *i* and *j* and take the value 1 for informed and 0 for uninformed individuals. Further, the social transmission parameter *s* estimates the strength of transmission as the rate of social transmission per unit association with informed individuals relative to the average rate of asocial learning (which is ensured by the term +1). For asocial models, the parameter *s* is set to 0. *N* denotes the number of individuals, $a_{i,j}$ represents the strength of association between individuals *i* and *j*. Social learning is inferred if a model where s>0 outperforms a model where s=0.

In the *additive* case, NBDA is defined as

$$\lambda_i(t) = \lambda_0(t)\big(1 - z_i(t)\big)\left(s\sum_{j=1}^{N} a_{i,j} z_j(t) + exp\left(\sum_{k=1}^{V} \beta_k\, x_{k,i}\right)\right)$$

and in the *multiplicative* case as

$$\lambda_i(t) = \lambda_0(t)\big(1 - z_i(t)\big)\left(s\sum_{j=1}^{N} a_{i,j} z_j(t) + 1 \right) exp\left(\sum_{k=1}^{V} \beta_k\, x_{k,i}\right)$$

where $x_{1,i} \dots x_{V,i}$ represent the *V* individual-level variables with potential effect on the asocial learning rate (in the *additive* models) or on both asocial and social learning rate (in the *multiplicative* model) and β_k is the coefficient giving the effect of variable *k* on the learning rate.

1.0.3.4. Applications of NBDA

NBDA can be used for two primary goals. It is i) a powerful tool to detect and quantify a social learning effect, as has been achieved in numerous studies on both captive and free-ranging populations across several taxa (Tab. 1.1); and ii) can be used to make inferences about the pathways of diffusion of information in a population and, for example, give insights into social learning strategies (Hoppitt, 2017).

Table 1.1: Application of NBDA (and similar approaches) to identify social transmission of behaviour in various animal species

Species	**Behaviour**	**Main results**	**Authors**	**Year**
Starlings (captive)	Foraging innovations	Reanalysing data (from Boogert et al., 2008) revealed social transmission of foraging innovations that had previously been missed.	(Hoppitt et al., 2010)	2010
Ring-tailed lemurs (wild)	Artificial extractive foraging task	Testing three different methods to detect social learning (inferential statistics, option-bias method, NBDA), only the option-bias method suggested a social learning effect in the diffusion of an artificial foraging task, whereas NBDA did not. The authors suggest that this was due primarily to low power and the data set not being appropriate for applying NBDA.	(Kendal et al., 2010)	2010
Songbirds (wild)	Discovery of food patches	The order of arrival at new food patches was predicted by social associations. Individuals at the centre of the social network were more likely to discover the food patches than those with limited social connections.	(Aplin et al., 2012)	2012
Three spine stickle-backs (captive)	Solving of a foraging task	Discovery of the foraging task was influenced by social network, but not the finding of a solution (untransmitted social effect). Individuals discovered a task sooner if a familiar individual had previously done so compared to if an unfamiliar individual had detected it.	(Atton et al., 2012; Atton et al., 2014)	2012/2014
Stickle-backs (captive)	Discovery of prey patches	Discovery of prey patches followed the social network in structured environments, but not in open environments.	(Webster et al., 2013)	2013
Humpback whales (wild)	Lobtail feeding	Lobtail feeding spread among associated individuals through horizontal social learning.	(Allen et al., 2013)	2013
Starlings (captive)	Solving two foraging tasks	Social learning increased the rate of acquisition of one foraging task solution by 6.67 times and acquiring one of the two tasks facilitated asocial acquisition of the other. The spread followed the perching rather than the foraging social network.	(Boogert et al., 2014)	2014
Chimpan-zees (wild)	Moss-sponging and leaf-sponge re-use	Diffusion patterns of ‘moss-sponging’, but not ‘leaf-sponge re-use’ (two behaviours for drinking water), were significantly better explained by social than individual learning. A	(Hobaiter et al., 2014)	2014/2017

		subsequent study shows that 'moss-sponging' persisted and that the secondary radiation of the behaviour followed the matrilines.	(Lamon et al., 2017)	
Songbirds (wild)	Novel foraging techniques	Experimentally introduced novel foraging techniques spread through social learning within the population. Individuals tended to adopt the most frequent local variant (= cultural conformity).	(Aplin et al., 2015)	2015
Chimpanzees (captive)	Extractive foraging tasks	Strategies to extract food spread socially through four captive groups of chimpanzees, with biases to copy high-ranking and expert individuals when uncertain or of low rank.	(Kendal et al., 2015)	2015
Songbirds (wild)	Artificial food patch	The authors applied NBDA to both inter- and intraspecific social networks, which both contributed to the spread of information.	(Farine et al., 2015a)	2015
Zebra finches	Foraging skills	Juvenile zebra finches, who, as nestlings were exposed to experimentally elevated stress hormone levels, changed learning strategies from learning from parents (vertical) to learning from unrelated adults (oblique).	(Farine et al., 2015b)	2015
Ravens (captive)	Artificial foraging task	The authors tested the relationships between social connections, observation and learning. NBDA revealed that the order of acquisition was best predicted by connections in the affiliative network (rather than aggressiveness or proximity) and by social rank and kinship.	(Kulahci et al., 2016)	2016
Songbirds (wild)	Selective feeding stations	By controlling which individuals could feed together, they manipulated the social structure of a community of songbirds. Discovery of new food patches followed the experimentally introduced social structure (context specific learning).	(Firth et al., 2016)	2016
Bees (captive)	Object manipulation	After some demonstrator bees were taught to pull a string to receive a food reward, the technique diffused through the population over several sets of learners ('generations').	(Alem et al., 2016)	2016
Guppy (captive)	Discovery of foraging sites	Groups with individuals all familiar with each other, all unfamiliar, or a mix of the two were analysed regarding network structure and the speed of diffusion of foraging	(Hasenjager and Dugatkin, 2016)	2016

		information. Even though speed and order of discovery of a food patch was socially influenced, there was little evidence for social transmission.		
Guppy (captive)	Approaching and solving a foraging task	Risk predation in guppies was manipulated and latency to approach and solve a task was recorded. In low-risk contexts, social transmission of the task solution occurred at higher rate. Furthermore, individuals in high-risk groups were more likely to investigate the task when associated with preferred social partners.	(Hasenjager and Dugatkin, 2017)	2017
Otters (captive)	Foraging tasks	One of two tested otter species was shown to be capable of social learning and presumably using a ’copy-when-young‘ strategy.	(Ladds et al., 2017)	2017
Amazon parrots (captive)	Two-action foraging box	Two groups (experimental and control) were exposed to a foraging experiment. The experimental group was more likely to interact with and open the box, but not more likely to use the demonstrated technique, which makes local or stimulus enhancement the most likely mechanism.	(Picard et al., 2017)	2017
Capuchin monkeys (wild)	Extractive foraging task	The authors did not use NBDA *per se*, but a Bayesian approach that is similar. They found that pay-off biased and age-biased social learning were primarily responsible for the diffusion of new techniques, with rare techniques receiving more attention and younger individuals.	(Barrett et al., 2017)	2017
Black-capped chickadees (wild)	Locating food patches	The rates of social learning were higher in high-ranked individuals and in rural over urban environments, while age, sex and explorative personality did not influence an individual’s rate of acquisition.	(Jones et al., 2017)	2017
Chimpanzees (captive)	Two-action puzzle box	Social transmission of successful manipulation of the puzzle box occurred only in a group with subordinate models, but not in the group with a dominant model.	(Watson et al., 2017)	2017
House sparrows (captive)	Discovery of hidden food patches	Discovery of the first but not the second food patch was predicted by social connections. Males discovered the food sooner than females, while age had no influence.	(Tóth et al., 2017)	2017

1.0.3.5. NBDA – case studies

Here, I will review several of the studies using NBDA, showing some of the characteristics and advantages of the method. I will first compare the power of NBDA to detect social learning to alternative methods; then show how NBDA can be used to identify social learning strategies in a population; and, finally, highlight some studies where NBDA has been modified from its original form.

In a study on the diffusion of foraging innovations in captive starlings (*Sturnus vulgaris*), the use of linear mixed models (LMM) and generalized linear mixed models (GLMM) revealed that object neophobia and rank were influencing the rate of the acquisition of a foraging task, but no social learning effect could be detected (Boogert et al., 2008). However, when reanalysing the same data, NBDA was able to detect a social transmission effect that had been previously missed (Hoppitt et al., 2010). This demonstrates the greater power of NBDA to detect a social learning effect compared to alternative methods, which helps to reduce rates of false negative results (Hoppitt and Laland, 2011). Conversely, in a study on free-ranging ring-tailed lemurs (*Lemur catta*), Kendal et al., (2010) applied both option-bias methods as well as NBDA to the diffusion of solutions to an artificial extractive foraging task to infer if the different solutions spread socially or not. Interestingly, results from the option-bias analysis suggested a social learning effect, while results from NBDA did not – indicating lower power of NBDA to detect social learning. From where does this apparent contradiction on the power of NBDA stem? Kendal et al., (2010) stated that such a result was not unsurprising, since the option-bias method worked at subgroup level and for specific option use (where social learning occurred), while NBDA considered the learning of the task in general at the group level. Furthermore, they hypothesized that the low power of NBDA may have been caused by small sample size (Franz and Nunn, 2010; Kendal et al., 2010; Hoppitt et al., 2010). In conclusion, NBDA can be a powerful tool to detect and quantify social learning, but power to detect learning has been shown to vary with sample size (*i.e.*, the number of learners), network structure, and uncertainty within the social network (Franz and Nunn, 2009; Franz and Nunn, 2010; Hoppitt et al., 2010).

NBDA is not only a useful tool to infer social learning, but can also give insight on underlying mechanisms such as social learning strategies, for example *when* or *who* it is beneficial to copy (Laland, 2004). In an experimental approach, for example, stress levels in zebra finches (*Taeniopygia guttata*) during early development were found to influence social learning strategies: While control juveniles learned foraging skills from their parents, juveniles exposed to elevated stress hormones as nestlings learned exclusively from unrelated adults (Farine et al., 2015b). Similarly, Aplin et al., (2015) used NBDA to investigate the spread of an experimentally introduced foraging technique in sub-populations of great tits (*Parus major*). Besides a rapid spread of the novel behaviour, they demonstrated a strong effect of conformity, *i.e.*, the tendency to disproportionally copy the most frequently used variant in the area (Aplin et al., 2015).

A further advantage of NBDA is its potential for modifications. Several studies have improved NBDA's power to detect social learning by adapting its form to their specific study design and available data. A study on a wild population of chimpanzees (*Pan troglodytes schweinfurthii*) in Budongo, Uganda, for example, addressed one limitation of NBDA, namely that it treats the social network as static, *i.e.*, that it has no time dimension and thus does not take into account that an observation can only influence the acquisition of a novel behaviour in the future, but not in the past (Hobaiter et al., 2014). In this particular study, the authors overcame this issue by using both a dynamic and a static network. Thereby, the dynamic network reflected an exact documentation of individuals that were present at the waterhole during the occurrence of two behaviours to drink water ('moss-sponging' and 'leaf-sponge re-use') (Hobaiter et al., 2014). Both the static and dynamic network model revealed that the diffusion of moss-sponging, but not leaf-sponge re-use, was significantly better explained by social transmission than independent learning (Hobaiter et al., 2014). Dynamic data, however, is often not available, in which case the original form of NBDA is preferred. A further study on songbirds investigated the influence of different networks (*i.e.*, intra-specific *versus* inter-specific) on arrival of these birds at new foraging sites (Farine et al., 2015a). Since the standard NBDA model cannot determine whether rates of learning differ between individuals within the network, the authors extended NBDA to include two different networks at the same time. They found that information about the location of the food patches diffused through both networks, but travelled faster between conspecifics compared to heterospecifics. Hence, NBDA can also serve as a tool to estimate strengths of transmission along different pathways.

Dynamic (Hobaiter et al., 2014) and multi-network (Farine et al., 2015a) NBDA are just two of the extensions developed that show the potential of NBDA for modifications. Further adaptations of NBDA include NBDA in a Bayesian context (Whalen and Hoppitt, 2016), or spatial NBDA, which incorporates information on the spatial locations of individuals in the study population (Nightingale et al., 2015).

1.1. Cetacean culture

1.1.1. Why study cetacean culture?

Cetaceans are large-brained, long-lived animals who rely extensively on social learning (Whitehead and Rendell, 2014). The logistical difficulties of studying diving organisms in the marine environment, however, often lead to incomplete information, which makes studies on cultural phenomena challenging. Nevertheless, there is a growing body of research into cetacean culture, and compelling reasons why this is a topic worth pursuing.

First, cetaceans are large-brained animals known to be capable of behavioural innovations (Marino et al., 2007). Their capacity for innovation becomes apparent when considering, for example, the variety of foraging techniques that have emerged in different populations and species. Some bottlenose dolphins (*Tursiops truncatus*) in Laguna, Brazil, cooperate with local fishermen to catch mullet (Simões-Lopes et al., 1998), while others in the same population do not (Daura-Jorge et al., 2012). Other toothed cetaceans, including killer whales (*Orcinus orca*) and sperm whales (*Physeter microcephalus*), have figured out how to depredate fishing lines of their catch (Kock et al., 2006). Furthermore, dolphins in captivity have even been trained to 'innovate', *i.e.*, perform a completely novel behaviour not part of their established behavioural repertoire (Kuczaj II and Eskelinen, 2014).

Second, their social nature and complex societies combined with long lifespans provide countless opportunities for social learning. Despite differences in adult sociability between different species, all cetaceans are characterized by prolonged periods of maternal care, during which nursing and first foraging attempts by the calf overlap (Mann and Sargeant, 2003). During this period, calves acquire information on what to eat, how to eat, on social relationships with community members as well as unfamiliar individuals, predator avoidance and movement patterns – some of which is undoubtedly transferred through social learning (Whitehead and Rendell, 2014).

Finally, contrasting the similarities and differences of culture in cetaceans, which inhabit such a vastly different environment from our own, with that of great apes and humans can help us to understand the evolutionary roots of culture across markedly divergent societies (Whitehead and Rendell, 2014).

1.1.2. Cases of (putative) culture in cetaceans

There is growing evidence of cultural phenomena occurring in several cetacean species. Whitehead and Rendell, (2014) provide a detailed discussion of putative cultural behaviour in various cetacean species. The logistical difficulties of studying marine mammals can result in incomplete data sets, giving rise to uncertainty around whether particular behaviours actually qualify as culture. Even in data rich circumstances, it is often difficult to account for alternative explanations for behavioural differences between social groups, such as genetic or environmental factors. In table 1.2, I have compiled a (non-exhaustive) list of reports of (putative) cultural behaviour in cetaceans.

Here, I will outline a few cases of culture in humpback (*Megaptera novaeangliae*) and killer whales to illustrate how evidence for social learning can be obtained and what difficulties arise in determining whether a behaviour qualifies as culture, before examining cultural behaviour in Indo-Pacific bottlenose dolphins (*T. aduncus*) in more detail. Living in predominantly dark or opaque environments, it is not surprising that many cetaceans rely on sound as their primary means of navigation and communication. Sounds travels much further and faster through water than air, allowing individuals to communicate over vast distances. It is, perhaps, not surprising that many cultural phenomena in cetaceans occur in the acoustic domain. The highly structured and repetitive vocalizations, or 'songs', of male humpback whales, for example, have evolved as a vocal sexual display (Payne and McVay, 1971; Smith et al., 2008).

Their structure and transmission mechanisms have been studied in great detail for half a century. A song cycle is a repetition of so-called 'themes', which appear in a very distinctive, invariant order but which evolve over time. Males within a population conform to the most frequently used song type ('conformism'), while populations in different oceans (separated by continents) have unrelated songs (Cato, 1991). Noad et al., (2000) showed evidence for rapid horizontal social learning of humpback whale songs: those on the east coast of Australia were reported to have undergone radical song changes after being exposed to a handful of singers from the west coast, who appeared to have taken an unusual migratory route. Within only two years, the eastern songs were entirely replaced by the songs from the western population. Given the large distances (and dividing land mass) between the populations and the short time span for this complete change of songs, horizontal social learning seemed the only plausible explanation for this cultural 'revolution' of east coast humpback whale songs (Noad et al., 2000).

Further compelling evidence for horizontal social learning of humpback whale songs was delivered by Garland et al., (2011), who showed how the distinct song types in different humpback whale subpopulations have moved in an easterly direction, from eastern Australia to French Polynesia within only a couple of years. While an underlying genetic basis for song could not be excluded, the rapid speed at which these different song types diffused across populations made a genetic explanation for the observed diffusion unlikely. Similarly, an ecological explanation was unlikely, since whales using areas with entirely different ecology were using the same songs. Thus, humpback whale song represents a compelling case of cetacean culture.

Table 1.2: Transmission mechanisms of cultural behaviour in cetacean species

Species	**Behaviour**	**Domain**	**Mechanism**	**Authors**
Bottlenose dolphins	Sponge carrying	Foraging	Likely vertically socially learned influenced by distribution of sponges, and with cultural transmission shaping the genetic structure within the population.	(Krützen et al., 2005; Tyne et al., 2012; Kopps and Sherwin, 2012; Kopps et al., 2014)
Bottlenose dolphins	Human provisioning	Foraging	Social learning plausible	(Mann and Sargeant, 2003)
Bottlenose dolphin	Cooperative hunting with humans	Foraging	Social learning plausible	(Simões-Lopes et al., 1998; Cantor et al., 2018)
Bottlenose dolphins	Accepting food handouts from human provisioners	Foraging	Social learning plausible, influences of ecology likely: both associations with already provisioned dolphins and use of areas with high boat density predicted acquisition of behaviour.	(Donaldson et al., 2012)
Bottlenose dolphin	'Tail-walking'	Motor	Likely social learning, has disappeared from population	(Bossley et al., 2018)
Humpback whales	Radical song changes	Vocal	Horizontal social learning	(Noad et al., 2000)
Humpback whales	'Lobtail-feeding'	Foraging	Social learning with influence of ecological factors	(Allen et al., 2013)
Humpback whales	'Trap-feeding'	Foraging	Social learning plausible	(McMillan et al., 2018)
Killer whales	Intentional stranding	Foraging	Social learning, influence of mitochondrial genes difficult to exclude	(Lopez and Lopez, 1985; Guinet and Bouvier, 1995)
Killer whales	Vocal dialects	Vocal	Social learning, influence of mitochondrial genes difficult to exclude	(Yurk et al., 2002; Filatova et al., 2015)
Killer whales	Dead salmon carrying	Play?	Most likely social learning – has disappeared from the population	(Whitehead et al., 2004)
Sperm whales	Vocal clans	Vocal	Social learning plausible	(Rendell and Whitehead, 2003)

Further evidence for cultural transmission in humpback whales was found in a feeding-related context. Using NBDA, Allen et al., (2013) were able to show that a foraging technique named 'lobtail-feeding' spread through the population via horizontal social learning in combination with ecological factors - *i.e.*, a whale's proportion of time spent in a specific area. Furthermore, lobtail-feeding was more prevalent in years with higher annual abundance of sand lances, suggesting that lobtail-feeding targets specific prey. Lobtail-feeding therefore represents an example of how combinations of social learning, ecological (and genetic factors) can contribute to creating behavioural differences between social groups, and that they are not mutually exclusive.

In some cases of putative culture, genetic, ecological factors and social learning are not easy to tease apart, particularly when social units consist of highly related individuals, as is the case in highly matrilineal societies of killer whales, for example (Hoelzel et al., 1998). In Alaskan resident killer whales, individuals within different pods were found to share discrete vocal repertoires and, as usual in the matrilineal societies, these pods consist of closely related individuals belonging to the same matriline (Yurk et al., 2002; Filatova et al., 2015). Given the high degree of relatedness within pods, it appeared plausible that a genetic predisposition could be responsible for the emergence of vocal clans. Filatova et al., (2015), however, argued that, if call repertoire was genetically inherited from both parents, the offspring's repertoire would be expected to be an intermediate mixture of its parents' dialects. Offspring, however, were found to share the vocal repertoire of their maternal kin within their pods (Yurk et al., 2002; Filatova et al., 2015). A genetic explanation could still not be dismissed, since the call repertoire could also be encoded on the maternally inherited mitochondrial DNA or the maternal sex chromosome. The authors argued that the call types were too complex to be the result of genetic inheritance through mitochondrial or maternal sex chromosomes and thus, that the formation of vocal clans must have been the result of vertical social transmission (Yurk et al., 2002). Furthermore, the correlation between vocal repertoire and patterns of association was found to be stronger than that between vocal repertoire and genetic relatedness (Deecke et al., 2010). Captive studies also suggested that killer whales are, in fact, capable of imitating calls of unrelated tank mates (e.g. Crance et al., 2014). While I agree that it appears unlikely that a complex vocal repertoire could be somehow genetically encoded on the mitochondrial DNA, the killer whale case provides an excellent example of the difficulties that can arise when trying to assess patterns of transmission when highly related individuals are also closely associated and live under the same ecological conditions.

1.1.3. Foraging strategies in the bottlenose dolphins in Shark Bay

1.1.3.1. Vertical cultural transmission of sponge carrying

The Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia, have been extensively studied for over 35 years (Connor and Smolker, 1985) and thus provide an excellent opportunity to investigate cetacean culture. They exhibit a remarkable variety of foraging strategies within a single population (e.g. Smolker et al., 1997; Connor et al., 2000; Sargeant et al., 2005), which female offspring appear to adopt from their mothers through vertical social learning (Mann and Sargeant, 2003; Krützen et al., 2005). Sponge carrying, or 'sponging', is the most thoroughly studied foraging strategy which involves a dolphin carrying a marine sponge on its rostrum and, it is inferred, probing the substrate for buried prey, such as small fish (Smolker et al., 1997). The sponge likely protects the dolphin's rostrum from the rough seafloor and, to date, represents the only reported case of tool use in bottlenose dolphins (Smolker et al., 1997; Krützen et al., 2005; Mann et al., 2008).

Using the ethnographic method, Krützen et al., (2005) inferred that sponging was vertically socially transmitted primarily from mother to female offspring. Sponging was heavily female biased and all spongers but one shared the same mitochondrial haplotype (Krützen et al., 2005). Spongers were also more closely related than expected by chance, suggesting common ancestry (Krützen et al., 2005). The authors considered 10 different scenarios of genetic inheritance (x-linked or autosomal), which were all inconsistent with the observed data: The lack of an equal sex-ratio in sponging was inconsistent with autosomal as well as x-linked inheritance of sponging as, in both cases, a higher proportion of male spongers would have been expected (Krützen et al., 2005). The authors thus concluded that sponging appeared to be transmitted socially rather than genetically from mother to female offspring (Krützen et al., 2005). Simulations supported the finding that social transmission was a more feasible mechanism explaining the spread of sponging compared to genetic inheritance (Kopps and Sherwin, 2012).

Sargeant et al. (2007), however, argued that sponging could potentially be explained by ecological factors, as sponging occurred primarily in deep-water channels. Tyne et al.'s (2012) findings supported the theory of an additional influence of ecological factors, as sponging was positively correlated with the distribution of conical sponges, more abundant in deeper waters. Nevertheless, non-sponging dolphins used the same habitat for foraging, suggesting that ecology alone could not fully account for the observed diffusion pattern of sponging (Krützen et al., 2005).

Although all evidence strongly supports social learning of sponging as a transmission mechanism, no attempt has thus far been made to quantitatively assess the relative importance of social learning, genetics and ecology in promoting the diffusion of sponging behaviour.

1.1.3.2. Shelling – another remarkable foraging strategy in Shark Bay

More recent observations suggest the existence of another foraging technique, referred to as 'shelling', in the Shark Bay bottlenose dolphin population (Allen et al., 2011). During shelling, an individual dolphin surfaces carrying a large shell in front of its melon by inserting its rostrum in the aperture of the shell (Allen et al., 2011). The shell, either one of the two giant gastropod species *Syrinx aruanus* and *Melo amphora*, is lifted above the water surface and shaken from one side to the other (Allen et al., 2011). Photographs indicated that the dolphins were attempting to access the prey items that were using the empty shell as shelter (Allen et al., 2011). Shelling had only been observed seven times between 1996 and 2009 in Shark Bay (Allen et al., 2011). Given the large distances between sightings in the eastern and western gulfs of Shark Bay, the authors suggested that shelling was independently innovated (Allen et al., 2011), since both sexes are philopatric and not known for movements over large distances (Krützen et al., 2004; Tsai and Mann, 2013). The transmission patterns of shelling, however, had not been investigated.

1.2. My PhD Chapters

1.2.1. Overview

Chapter 1 provides a general introduction to the topic of animal social learning, as well as culture in cetaceans, with a focus on bottlenose dolphins. The following four chapters (2-5) revolve around NBDA, as well as the two foraging strategies ‘shelling’ and ‘sponging’ in the bottlenose dolphin population in the western gulf of Shark Bay, Western Australia, using data collected between 2007 and 2018. The second chapter provides a methodological approach on how to deal with observational error when applying NBDA. Chapters 3 and 4 investigate the transmission mechanisms of ‘shelling’ and ‘sponging’, respectively, using a multi-network version of NBDA (Farine et al., 2015a). Chapter 5 investigates the impacts of a marine heatwave on the vital rates of the western Shark Bay dolphins, while assessing differences in survival and reproduction between sponging individuals and those that do not use sponges for foraging. Finally, Chapter 6 provides an overall discussion and synthesis of the thesis. Here I overview each of my data chapters (2-5).

1.2.2. Chapter 2 – Choosing a sensible cut-off point: Assessing the impact of uncertainty in a social network on the performance of NBDA

Chapter 2 proposes a methodological approach to help select an appropriate threshold for including individuals in an NBDA analysis, which maximises power to detect social learning when association data is incomplete. In many studies on social networks, there is a trade-off between including as many individuals as possible to have a complete record of connections, and having reliable data, since certainty about the strength of connections increases with the number of sightings. Chapter 2 presents a simulation approach with which power of NBDA to detect social learning can be assessed for different thresholds when dealing with incomplete association data.

1.2.3. Chapter 3 – Evidence for social transmission of a dolphin foraging technique within and between generations

In Chapter 3, I investigate how shelling behaviour spreads in the western gulf of Shark Bay. Using multi-network NBDA (Farine et al., 2015a), I assess the relative importance of social learning, as well as ecological and genetic factors in promoting the spread of the behaviour. Besides an association network, I include a network depicting dyadic home range overlap as a measure to which extent two individuals experience the same ecology. The influence of genetics is assessed with a network containing biparental relatedness estimates, *i.e.*, the percentage of genes shared by two individuals.

1.2.4. Chapter 4 – Network-based Diffusion Analysis shows vertical cultural transmission of sponge tool use within dolphin matrilines

Using the ethnographic method, Krützen et al., (2005) suggested sponging behaviour is transmitted vertically from mother to female offspring, though this approach has been criticized (Laland and Janik, 2006, 2007; Sargeant et al., 2007). With new methods available, I revise the transmission mechanisms of sponging in Chapter 4, using the multi-network NBDA approach described above (Farine et al., 2015a) to test for influences of social learning, ecology and genetics on the spread of sponging. For pathways of social learning, I furthermore assess the importance of vertical *versus* horizontal/oblique learning.

1.2.5. Chapter 5 – Long-term decline in survival and reproduction of dolphins following a marine heatwave

Chapter 5 deals with the impacts of habitat degradation following a marine heatwave on the survivorship and reproductive rates of the western gulf dolphin population. During an unprecedented marine heatwave in the Austral summer/autumn of 2011 along the western Australian coastline, water temperatures rose to 2-4° Celsius above long-term averages for more than two months (Wernberg et al., 2012). The heatwave occurred when strong Easterly winds forced large volumes of warm water southwards along the coast during a strong La Niña event (Feng et al., 2013; Pearce and Feng, 2013). The effect was heightened by an anomalously high air-sea heat flux entering the ocean (Feng et al., 2013). Numerous consequences of the heatwave along the coastline were reported, including fish and invertebrate die-offs (Pearce et al., 2011; Caputi et al., 2014), contractions of seagrass and kelp distribution

(Smale and Wernberg, 2013; Wernberg et al., 2016), coral bleaching (Depczynski et al., 2013), the ‘tropicalisation’ of entire communities (Hyndes et al., 2016), and lower breeding success in penguins (Cannell et al., 2012; Caputi et al., 2014).

The affected area included the iconic World Heritage Area of Shark Bay, a relatively shallow, subtropical embayment with the most diverse assemblage of seagrasses worldwide (Walker et al., 1988). An estimated 36% of the bay’s seagrass meadows were damaged in the 2011 heatwave (Arias-Ortiz et al., 2018), and mortality events of invertebrate and fish communities followed, as well as declines in the health status of herbivorous marine turtles (Fraser et al., 2014; Thomson et al., 2014). Furthermore, several fisheries were closed in 2012 due to low yields (Caputi et al., 2014).

Using long-term demographic data, I assess effects of the heatwave and subsequent habitat degradation on survival and reproduction of the resident dolphin population. I furthermore assess differences in survival and reproduction between individuals that use sponges as foraging tools and those that do not, to investigate if culturally different subgroups are affected adversely by extreme climatic events.

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CHAPTER 2.

Choosing a sensible cut-off point: Assessing the impact of uncertainty on the performance of NBDA

2.0. Abstract

‘Network-based diffusion analysis’ (NBDA) has become a widely used tool to detect and quantify social learning in animal populations. NBDA infers social learning if the spread of a novel behaviour follows the social network and hence relies on appropriate information on individuals’ network connections. Most studies on animal populations, however, lack a complete record of all associations, which creates uncertainty in the social network. To reduce this uncertainty, researchers often use a certain threshold of sightings for the inclusion of animals (which is often arbitrarily chosen), as observational error decreases with increasing numbers of observations. Dropping individuals with only few sightings, however, can lead to information loss in the network if connecting individuals are removed. Hence, there is a trade-off between including as many individuals as possible and having reliable data. We here provide a tool in R that assesses the sensitivity of NBDA to error in the social network given a certain threshold for the inclusion of individuals. It simulates a social learning process through a population and then tests the power of NBDA to reliably detect social learning after introducing observational error into the social network, which is repeated for different thresholds. Our tool can help researchers using NBDA to select a threshold - specific to their data set - that maximizes power to reliably quantify social learning in their study population.

2.1. Introduction

Cultural behaviour, broadly defined, is behaviour that is passed on among individuals through social learning (Boyd and Richerson, 1995). Therefore, if researchers are to understand the importance of cultural behaviour in nonhuman primates and other animals, they need to be able to infer when social learning is responsible for the spread of behaviour in natural settings. Recent years have seen the development of novel methods that quantify the importance of social learning on the spread of a behaviour in freely interacting groups of animals. A method that has gained increasing popularity is ‘network-based diffusion analysis’ (NBDA), a statistical tool which can quantify the effect of social learning among a group or population of animals (including humans) (Franz and Nunn, 2009; Hoppitt et al., 2010). NBDA has been used in numerous studies to detect and quantify social learning in both free-ranging as well as captive animal populations across many taxa, including birds (e.g. Aplin et al.

2012; Boogert et al. 2014), insects (Alem et al., 2016), primates (Kendal et al., 2010; Schnoell and Fichtel, 2012; Hobaiter et al., 2014) and cetaceans (Allen et al., 2013).

NBDA, first developed by Franz and Nunn (2009), infers social learning if the diffusion of a behaviour follows the social network, (*i.e.*, a representation of connections among individuals within a social group or population), as it is based on the assumption that more closely associated individuals are also more likely to learn from each other (Coussi-Korbel and Fragaszy, 1995). NBDA compares diffusion data with a matrix that contains a measure of association among individuals (Hoppitt et al., 2010), *i.e.*, a measure of how frequently two individuals are observed together or in proximity. Diffusion data can either be the order with which individuals acquire a behaviour ('order of acquisition diffusion analysis' – OADA) (Hoppitt et al., 2010) or it can be the time at which they acquire a behaviour ('time of acquisition diffusion analysis' – TADA) (Franz and Nunn, 2009; Hoppitt et al., 2010).

As both OADA and TADA track the spread of a novel behaviour through the social network, accurate data on individuals' network connections are desirable. Ideally, information on all individuals' network connections is captured at once (Hoppitt and Farine, 2017). However, for most studies on animal populations, especially free-ranging, this is not feasible, either due to sampling restrictions (time or space) or the inability to reliably identify all individuals, resulting in an incomplete record of all associations. Missing information can lead to imperfect relationships, which creates uncertainty about association strengths among individuals in the social network (Hoppitt and Farine, 2017) with potential negative impacts on the power of NBDA to reliably quantify the importance of social learning (Hoppitt, 2017).

Uncertainty decreases with the number of times an individual has been seen, and information on its connections with other individuals and estimates of association strengths between them gets more reliable. Several studies have outlined that collecting enough information on individuals' associations is key to construct an accurate social network (Lusseau et al., 2008; Franks et al., 2010; Farine and Strandburg-Peshkin, 2015; Silk et al., 2015). Thereby, the minimum number of observations for an accurate depiction of the social network depends on the level of social differentiation within the population, *i.e.*, how varied the social system is, with more data required for populations with low social differentiation (Whitehead, 2008). To minimize uncertainty, researchers often restrict their analysis by only including individuals above a certain threshold of sightings. A further argument for excluding animals with only few sightings when using NBDA, is when not all individuals can be observed at all times and the target behaviour is short or rare and hence easily missed by observers. In that case, a high cut-off point for the inclusion of animals can increase the certainty about an individual's information status, *i.e.*, to reliably distinguish if it is naïve or informed.

Franks et al., (2010) support the notion that sampling should in fact maximize the amount of data collected on known individuals, rather than maximizing the number of sampled individuals, as uncertainty in the social network is more problematic than missing individuals altogether. This is supported by Silk et al., (2015), who found that knowing even only 30% of individuals in a population can be enough to create informative social networks, as judged by network measures of connectivity at a node level. Both findings support having a large and conservative cut-off point for the inclusion of animals to reduce uncertainty in the network, if the aim is to make inferences about network structure.

However, it is less clear that a large, conservative cut-off point is appropriate when using NBDA. Dropping individuals with few sightings from a social network comes at the cost of information loss, if network connections between individuals are lost due to linking individuals being removed. For example, imagine that novel behaviour is transmitted from A to B to C, where A and C are not directly linked. If B is removed due to a lack of data, it would appear that C has acquired the behaviour by asocial learning and not by social learning. Even if the connections from A to B and B to C are inaccurately estimated, inclusion of B may nonetheless more accurately portray the transmission of information. Thus, missing network connections might result in lower power of NBDA to detect a social learning effect, and the recommendations of Franks et al., (2010) and Silk et al., (2015) may not stand for NBDA. Instead, having a lower threshold and including more individuals, while risking larger uncertainty in the network, may be preferable. Hence, there is a trade-off in the selection of a criterion for including individuals in the analysis between including as many as possible to have complete information on social network, and restricting inclusion of animals to reduce uncertainty (Bejder et al., 1998).

To resolve this issue, we provide a tool which can help researchers using NBDA to choose an appropriate threshold for the inclusion of individuals that maximizes the power of NBDA to reliably quantify social learning. For our simulations, we use OADA, which uses the order of acquisition as diffusion data. Our results still stand for TADA using continuous time data (Hoppitt et al., 2010); the log-likelihood function for continuous TADA is equivalent to the sum of the log-likelihood of the order of acquisition (used in OADA) and the log-likelihood for the time course of the diffusion independent of the identities of the learners. Thus, impacts of network inaccuracies on the power of OADA will similarly affect continuous TADA. Furthermore, results of the discrete time version of TADA (Franz and Nunn, 2009) converge on those of the continuous TADA for small time periods (Hoppitt et al., 2010) suggesting that it will be similarly affected. Therefore, we suggest that researchers use the same technique described here to determine which individuals to include in a TADA, by omitting the time data from the procedure to determine the cut-off point that maximises statistical power. Using a simulated data set, we simulate a learning process through the population and then assess the rate of false negatives (type 2 error) and false positives (type 1 error) of NBDA for different cut-off points after introducing noise into the social network. We furthermore assess if keeping individuals that learned (*i.e.*, informed individuals) regardless of the number of times they have been seen, improves the power to detect social learning and assess the rates of false positives (type 1 error).

NBDA can also be applied to interaction data instead of association data (Franz and Nunn, 2009; Hoppitt, 2017). In this paper we focus on the use of association networks since these have been most commonly utilised in NBDA - thus, the method we present is only directly applicable to association networks. However, the procedure could be modified to account for the sampling variation present in interaction data for differing observation periods across individuals.

2.2. Methods

All simulations and analyses were run using R Studio v1.1.423 (R Core Team 2015). The supplementary material* contains the R code to simulate observational data (SM1), the NBDA code (SM2) and the code for the simulations for assessing sensitivity of NBDA to observational error (SM3), the code for the application of the simulations to the simulated observational data (SM4), the simulated observational data (SM5) and resulting social network (SM6) and summary of results of all simulations (SM7-10), as well as a guide on how to use the codes (SM11) and further detail on the algorithm with which the observational data was simulated (SM12; Appendix SI Chapter 2; Tab. 2.1).

2.2.1. Input data set

In developing our methodology we assume that researchers possess association data in an observation by individual matrix (see Farine (2013) for transformation of data), where a number of observations are made, with each individual in the population being recorded as being present during that observation (1) or absent (0). We assume these data are formatted as a matrix with observations (rows) x individuals (columns). In order to test and illustrate the method developed, we simulated data of this form by developing an algorithm that resulted in a reasonable level of underlying social structure, which is necessary for NBDA to reliably detect social learning. We provide details of this algorithm in the supplementary material (SM12; Appendix SI Chapter 2).

In our simulated data set we obtained a group by individual matrix with 60 individuals and 331 observations (SM5). Group size varied from 1 to a maximum of 10 individuals with a mean of 1.92 individuals per observation.

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* all supplementary material available under https://doi.org/10.1007/s10329-018-0693-4
SM12 additionally available in the Appendix (SI chapter 2) of this thesis

Table 2.1: Structure of online resources

Supplementary Materials	File name	Content
SM 1	Simulating data set	R code to simulate observational data for 60 individuals
SM2	Sensitivity functions	R code for simulations on the sensitivity of NBDA to observational error for different cut-off points
SM3	NBDA code 1.2.15.	R code NBDA
SM4	Application to simulated data set	R code where we apply our simulations (SM3) the to the simulated observational data (SM5)
SM5	Simulated observational data	CSV file with simulated observational data
SM6	Social network	CSV file with association matrix resulting from simulated data set
SM7-10	sensitivity summary	CSV files with summary of results of simulations applied to our simulated data set
SM11	How to use the code	Word document with guide on how to apply the sensitivity functions and specify the necessary parameters
SM12	Appendix	Word document that describes the algorithm we used to simulate observational data

From the simulated data set, we created a social network using the simple ratio association index (for details see below; R package 'asnipe'; OR6) for illustrative purposes (Cairns and Schwager, 1987; Farine, 2013; R Core Team, 2015). Illustration of the social network (Fig. 2.1) was created using the Force Atlas 2 algorithm in Gephi (Bastian et al., 2009).

To this end, the algorithm we use to generate our illustrative data set arbitrarily assumes a network with high modularity and that 33% of individuals account for most of the observations in the association data. However, these are not assumptions of the procedure presented here, which accounts for modularity in the social network as well as the pattern of variability in the number of times individuals are observed in the specific data set being analysed.

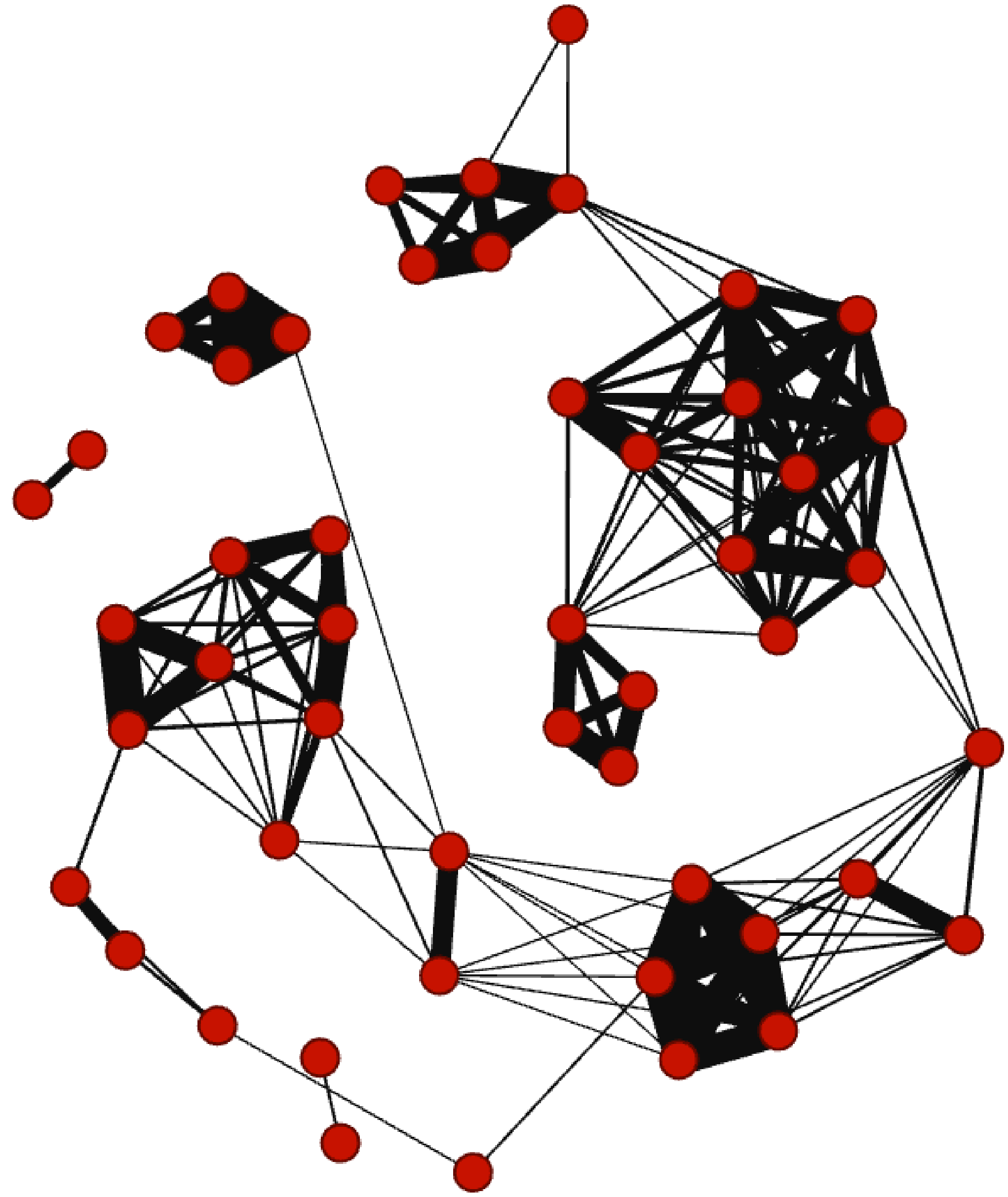

Figure 2.1: *Weighted and undirected social network of a simulated data set with 60 individuals and 331 observations: Individuals (=nodes) are represented with red circles, associations between them (=edges) with black lines. The closer together nodes are and the thicker the edges, the stronger the association is between them.*

2.2.2. Process overview

We developed a process that enables researchers to choose a justified cut-off point for the amount of association data (number of observations) that is required for inclusion of an individual into an NBDA (Fig. 2.2). This process consists of two steps: First, we simulated a social learning process, which we then analysed using NBDA after introducing noise into the social network while applying different cut-off points for the inclusion of individuals to see which yielded the highest statistical power, *i.e.*, the highest percentage of models where social learning correctly outperformed the null model with asocial learning, *i.e.,* having lower AICc. Secondly, we repeated the process of simulating a diffusion that was a result of only asocial learning to see which cut-off points yielded an appropriate false positive error rate, *i.e.*, where social models erroneously outperformed asocial learning models. We illustrate this process by applying both steps to the simulated data set described above.

Power of NBDA to detect social learning will inevitably decline if linking individuals within diffusion pathways are removed. Therefore, to investigate how retaining learners (*i.e.*, only excluding non-learners) influences power of NBDA to detect social learning, we then repeated the two steps, this time retaining all individuals who learned the behaviour regardless of how many times they had been observed.

2.2.3. Assessing statistical power of NBDA for different cut-off points after introducing observational error

Here we propose a procedure for assessing the performance of NBDA, using different cut-off points, for a given data set. We first simulated a learning process through the population assuming learning follows the NBDA model. We then analysed the resulting diffusion data using different cut-off points, and assessed the performance of NBDA to detect social learning in each case after introducing noise, *i.e.*, observational error, into the social network.

As a first step, we created an association network from the simulated observational data. Association strengths (a_{ab}) are usually estimated based on how many times two individuals (a and b) have been observed together as well as the number of times they have been seen apart (for guidance on choosing an appropriate association index, see Cairns and Schwager (1987); Hoppitt and Farine (2017)). We used the ‘simple ratio association index’ (hereafter ‘SRI’; Cairns and Schwager, 1987), which is defined as

$$SRI = \frac{x}{y_a + y_b + y_{ab} + x}$$

where x is the number of sampling periods individuals a and b were observed associated, y_a is the number of sampling periods with just a identified, y_b is the number of sampling periods with just individual b identified, and y_{ab} is the number of sampling periods where both individuals a and b were identified but not in association.

As a next step, we modelled a diffusion (the documented spread of a novel behaviour pattern) using the resulting social network from the simulated data (N=60, 331 observations): In a first round, one individual was randomly chosen to learn. In each subsequent round, we calculated the total association with informed individuals for each individual. Following the NBDA model (Hoppitt et al., 2010) we then calculated an individual’s learning rate Ri as

$$Ri = s * \sum_{j=1}^{n} a_{ij} + 1$$

where s denotes the social learning parameter, which estimates the strength of social learning per unit association with informed individuals relative to the average rate of asocial learning; and $\sum_{j=1}^{n} aij$ the total association of individual *j* with informed individuals. Here, *s* represents the strength of social learning relative to asocial learning and must be set by the user. The ultimate aim of this process is to determine which cut-off point has most power to detect social learning. If *s* is set too high then all simulations will have high power, whereas if *s* is set too low all simulations will have low power. The user must find a value of *s* (by trial and error) that results in a range of statistical power, in order to determine which cut-off point is most likely to detect social learning if it is occurring. For this simulation, we set *s*=8, which corresponds to an 8-fold increase of the social learning rate per unit association with informed individuals compared to an individual's asocial learning rate. The probability that each individual was next to learn is then given as:

$$\frac{Ri}{\sum_j Rj}$$

This process was repeated until 20 individuals had acquired the behaviour (this represents an arbitrarily chosen number of learners - in practise this would be matched to the actual number observed to learn in the population).

As a third step, we used a Bayesian approach to simulate a social network that introduced a level of error for each dyad that depended on the number of times each dyad had been seen together and the number of times they had been seen apart. Thereby, the more often members of a dyad had been seen, the closer their simulated association strength was to the real value. Similarly, if a dyad had only been seen a handful of times, the simulated values would be more varying (more noise) and potentially further away from the real value. Since the value of a_{ij} is a proportion (proportion of times i and j are expected to be seen together), knowledge about a_{ij}, given the data available, can be modelled as a Beta distribution (known as the 'conjugate' prior distribution for a proportion, meaning that they are part of the same probability distribution family) with parameters *a* and *b*:

$$a_{ij} \sim Beta(a, b)$$

When we have no data, we set *a* = *b* = 1, which gives a uniform distribution for a_{ij}- *i.e.*, we accept that a_{ij} is equally likely to take any value from 0 to 1. After we collect data, we update our prior distribution for a_{ij} to yield a posterior distribution, giving our updated knowledge about a_{ij}.

After collecting data of *n* independent observations the posterior distribution for a_{ij}, given x, is given by

$$a_{ij}|data{\sim}Beta(a+x,b+n-x)$$

where x represents the number of successes (*i.e.*, number of times two individuals have been seen together) and $n-x$ the number of failures (*i.e.*, number of times two individuals have been seen apart). The smaller *n* is, the wider the Beta distribution will be, reflecting our increased uncertainty in the value of a_{ij}. This conjugate method of updating our knowledge about a proportion based on independent Bernoulli trials is a standard and accepted method in Bayesian statistics. Therefore, this method of calculating the level of uncertainty is appropriate for the common situation where association data is used to calculate the SRI with observations sufficiently spaced out that they can be considered independent. Researchers could, in principle, substitute an alternative appropriate expression for error for other indices (e.g. Hoppitt and Farine 2017).

Hence, from the sightings record, we created a matrix containing the number of times each dyad had been observed together (successes). A second matrix contained the cumulative number of times each member of a dyad had been observed without the other individual in the dyad (failures). We provide a function that extracts said matrices from the observation record (SM3). Making no assumptions about the distribution of the association strengths within the social network, we used an uninformative (uniform) prior $Beta(1,1)$. We then simulated association strengths a_{ij} using

$$a_{ij}|data{\sim}Beta(1+x,1+n-x)$$

The resulting association matrix represented a social network with noise and was used to test for statistical power of NBDA for different cut-off points. For our simulated data, we used cut-off points of N = {1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 13, 14, 15, 16, 17, 18, 19, 21, 22, 24, 26, 27}. In each case all individuals with fewer sightings than N were dropped from the social network. Note that the user has the option to keep individuals who learned and only drop non-learners (as described at the bottom of the method section).

The fourth step was to test the performance of NBDA to correctly identify social learning. We ran the OADA (‘order of acquisition diffusion analysis’; Hoppitt et al., 2010) variant using the simple ratio association matrix (simulated – with observational error) and the simulated order of acquisition that was obtained using the error free network.

From the OADA model, we extracted the estimates for the social learning parameter *s*, the p-value of the likelihood ratio test, the AICc (Akaike information criterion corrected for small sample size;

Burnham and Anderson, 2002) values for the social models as well as the models where *s* was constrained to zero, *i.e.*, the asocial models. To select a model over an alternative model, differences in AICc values (delta AICc) need to cross a certain threshold (defaulted to 2 in our simulation; can be set by user; Burnham and Anderson, 2002). We hence calculated the delta AICc value between social and asocial models. Note that a more stringent threshold in AICc difference would reduce the percentage of models where one model outperforms the other, but would affect all cut-off points to the same extent. Therefore, the threshold at which power of NBDA is maximized, is unlikely to change even with a more stringent criteria for delta AICc. We furthermore recorded if the true value of *s* was within the 95% confidence interval (C.I.) for set *s* (*i.e.*, within 1.92 units on the log likelihood scale) and if outside of the confidence interval, we determined if *s* was an under- or overestimate. The whole process was repeated 10,000 times for each cut-off point.

As a last step, we calculated the percentage of models where the delta AICc value was above the set threshold of 2, *i.e.*, where one model (social or asocial) was outperforming the alternative model. From those models, we calculated i) the mean and standard deviation for the estimates of *s* for each cut-off point; ii) the percentage of models where social models performed better than asocial models - giving the power of NBDA to detect social learning; iii) the percentage of models where the true value of *s* fell within the 95% C.I. for *s* (this should be ~95% if the model is performing well); and iv) the percentage of models that over- or underestimated the value of *s*, *i.e.*, were above the upper limit of the 95% C.I. or below the lower limit respectively (this should be approximately even if NBDA is performing well).

To investigate in how far NBDA's power to reliably detect social learning is impacted by the removal of linking individuals within a transmission pathway, we then repeated the entire process, but this time retaining all individuals who had learned, irrespective of how many times they had been sighted, *i.e.*, only excluding individuals that did not learn. We provide the option to retain all learners in our code.

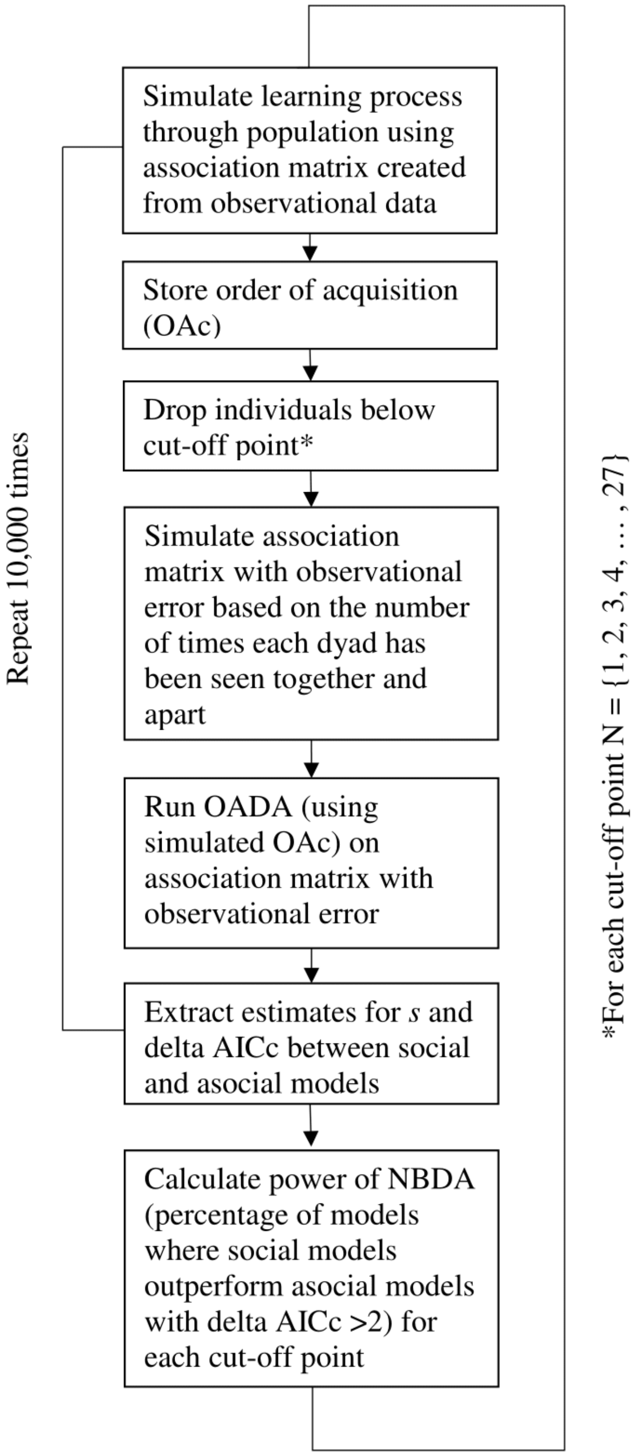

Figure 2.2: *Flow diagram of simulation assessing the sensitivity of NBDA after introducing noise into the social network. * The user has an option to keep individuals who learned in the simulation, even though they would not make the cut-off.*

2.2.4. Assessing the false positives error rate in NBDA for different cut-off points

In order to assess the rate of false positives, *i.e.*, where NBDA identifies a social learning effect where there is in fact none, we repeated the procedure described above, but this time constraining $s = 0$, which corresponds to learning asocially, *i.e.*, through independent innovations. We assessed the rate of false positives for both models where individuals were dropped regardless of their information status as well as models where learners were retained regardless of how many times they had been sighted.

2.3. Results

2.3.1. Assessing statistical power of NBDA for different cut-off points

In an NBDA, social learning is inferred if the AICc for the model including social learning is lower than for a model without social learning. Therefore, the percentage of occasions that social learning models outcompete asocial learning models gives a measure of statistical power for each cut-off point, when $s>0$.

For models where all individuals were dropped with sightings below the cut-off point (regardless of information status), statistical power was highest at a cut-off point of 4 with 83.96% power (Fig. 2.3a, OR7). Averaged estimates for *s* were consistently higher than set in the simulation ($s=8$), ranging from 307.68 to 784.11 (SM7). Estimates for *s* followed an upwards trend as the cut-off point increased (SM7) - we explain why this occurs in the Discussion, below. In 96.51% to 100% of models - depending on the cut-off point - the true value of *s* (8) fell within the 95% C.I. (Fig. 2.3a, OR7), suggesting that the 95% C.I. for *s* can be trusted as being appropriate for all cut-off points, if $s>0$.

For models, where learners were kept regardless of how many times they were observed, power to correctly detect social learning was highest at cut-off point 6 with 92.95% power (Fig. 2.3b, OR8). Averaged estimates for *s* ranged between 267.23 and 383.64, and in between 95.59% and 99.19% of models – depending on the cut-off point – the true value of *s* (8) fell within the 95% C.I (Fig. 2.3b, OR8). For all cut-off points, retaining learners increased the power to detect social learning compared to when learners were dropped.

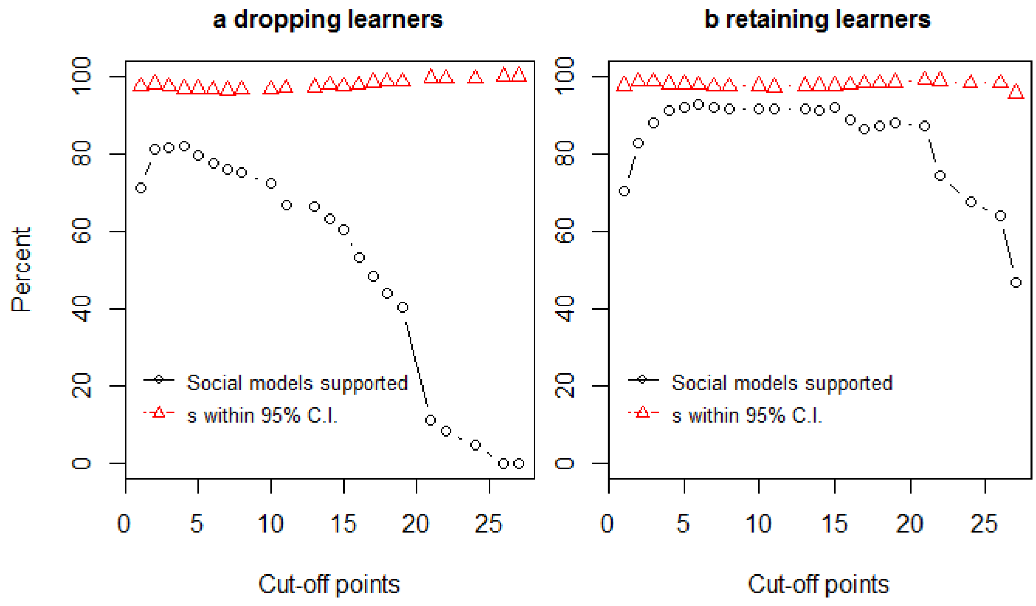

Figure 2.3: *Power of NBDA to correctly identify social learning after introducing noise into a social network (black circles) and percentage of models where estimates for the social learning parameter s fell within the 95% C.I. of the set s (=8) for a given cut-off point (red triangles) for **a)** models where all individuals were dropped below the cut-off point and **b)** models where learners were retained regardless of how many times they had been observed.*

2.3.2. Assessing the false positives error rate in NBDA for different cut-off points

For models where all individuals were dropped below the cut-off regardless of their information status, the percentage of models where social learning was incorrectly outperforming asocial models when *s*=0 (false positives) ranged between 0% and 2.23% (Fig. 2.4a, OR9). Therefore, for these data, the false positive error rate was always below that commonly accepted (5%) ('commonly' refers to all statistics that consider a p-value of <0.05 as statistically significant). In this case a researcher could safely choose whichever cut-off point gave the highest statistical power. Averaged estimates for *s* were again consistently higher than set in the simulation (*s* = 0), ranging from 23.18 to 488.5 and exponentially increasing with an increasing cut-off point (Fig. 2.4a, OR9). The true value of *s* (0) fell within the 95% C.I. of the estimated set *s* in 97.37%-100% of the models depending on the cut-off point (Fig. 2.4a, OR9), further supporting the fact that, for this data, all cut-off points can be trusted.

For models where informed individuals (learners) were retained, the percentage of models where social models incorrectly outperformed asocial models (for *s*=0) ranged between 2.37% and 35.14%, and was for most cut-off points above the commonly accepted 5% (Fig. 2.4b, OR10). Averaged estimates for *s* ranged between 38.23 and 245.28 and the true value of s (=0) fell within the 95% C.I. of the estimated *s* in 64.83%-97.2% of models (Fig. 2.4b, OR10).

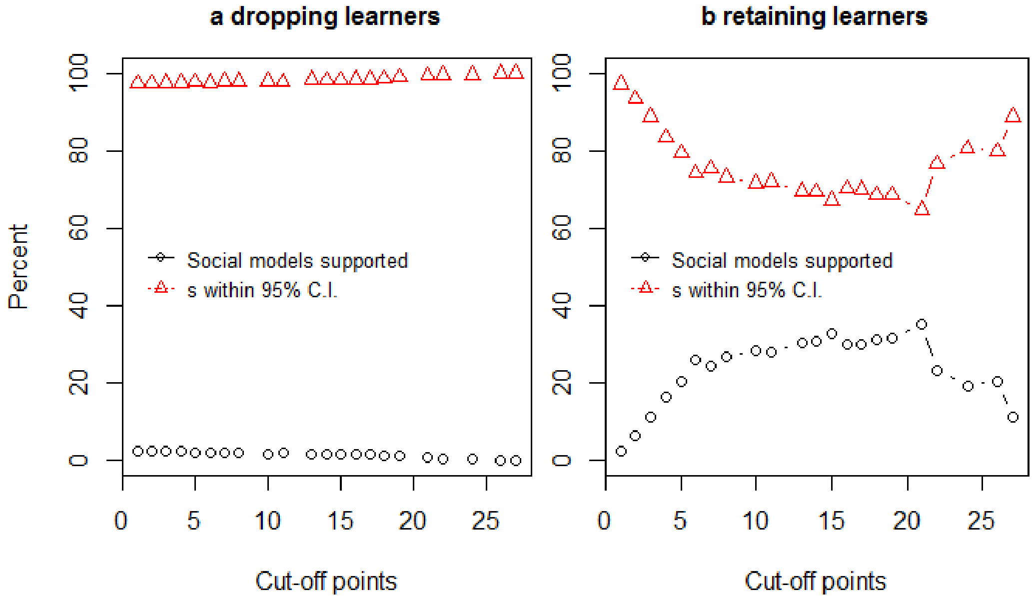

Figure 2.4: *Percentage of models where NBDA incorrectly identifies social learning after introducing noise into a social network (black circles) and percentage of models where estimates for the social learning parameter s fell within the 95% C.I. of the set s (=0) for a given cut-off point (red triangles) for* ***a)*** *models where all individuals were dropped below the cut-off point and* ***b)*** *models where learners were retained regardless of how many times they had been observed.*

2.4. Discussion

We present a method for choosing a cut-off point for the inclusion of individuals that maximizes power of NBDA to detect learning, based on the number of times they are observed in the construction of the social (association) network. Above, we illustrated this process by applying it to a simulated data set. Below, we discuss how the results obtained could be used to select an appropriate cut-off point for this data set. There is no reason to think that the cut-off point identified for our simulated data would be applicable in general - the appropriate cut-off point will depend on the properties of the data set in question. Nonetheless, the same logic could be used to choose a cut-off point for real data sets.

After simulating a learning process through a social network, we used a Bayesian approach to simulate a social network that introduced a level of error for each dyad depending on the number of times each dyad had been seen together and apart. The diffusion data and the social network with observational error were then analysed using NBDA to find an appropriate cut-off point for the data set.

The same approach could be used to estimate the impacts of noise in a social network for real NBDA data, where the social network is constructed from association data. We provide a function that allows the extraction of one matrix with the number of times each dyad has been seen together and a second matrix with the number of times they have been seen apart, which can then be used to simulate an association network including noise. Alternatively, users can provide their own matrices for the simulation. The approach presented here is for an NBDA that assumes a static association network that is essentially unchanging over time. NBDA itself can be extended to allow the use of a dynamic instead of a static network (Hobaiter et al., 2014), but further work is needed to determine cut-off points under such circumstances.

The simulations presented then allow researchers to test a) the statistical power and b) the false positive error rate of NDBA under different cut-off points. In our simulated data set – for models where all individuals were dropped below the cut-off point regardless of their information status - false positive error rates were appropriate across the range of cut-off points. Furthermore, for both *s*=0 and *s*=8, the true value of *s* was within the 95% C.I. approximately 95% of the time. This suggests that the validity of NBDA could be trusted for any cut-off point, and so the cut-off point should be chosen to maximise statistical power. Our results correspond broadly with Hoppitt's (2017) finding that error in the network does not increase false positives in NBDA but can act to make the analysis more conservative in detecting social learning (see also Whalen and Hoppitt 2016). However, it is uncertain if invariability of false error rate to cut-off point choice is a general feature of NBDA, so we encourage researchers to always run the simulations on their own data set before accepting a cut-off point.

In our simulated data set, power of OADA was maximized at a cut-off point of 4 sightings, which would result in the inclusion of 41 out of the 60 individuals (=68%). Silk et al.'s, (2015) finding that having data on as little as 30% of the population allows to create an informative social network, does not prove to be true for NBDA using our simulated data, as power to detect social learning dropped to only 60% with 20 individuals being included (which corresponds to a 30% threshold). Thus, we show that Silk et al.’s, (2015) threshold is not generally appropriate for NBDA (and was not suggested for this purpose). Instead, the threshold where power of OADA is maximized is likely to vary depending on the specific data set – the number of individuals in the population, the length of diffusion, association strengths among individuals and the social differentiation of the population, *i.e.*, how varied the social system is (Franz and Nunn, 2009; Hoppitt et al., 2010). Hence, we recommend using our proposed methods to ensure a threshold for the inclusion of animals that is specific to the data set, and discourage the use of arbitrarily chosen thresholds when using NBDA.

For models where all informed individuals were kept regardless of how many times they had been seen, power of NBDA to detect social learning was highest at a cut-off point of 6. Furthermore, power to detect social learning was higher compared to when learners were dropped. Dropping individuals will intuitively reduce power to detect social learning when linking individuals are being removed (as explained in the Introduction). However, false positive rates (when s=0) for most cut-off points were high when all learners were retained (and above the commonly accepted 5%) for all but one cut-off and over 25% for the cut-off point of 6 which yielded highest statistical power. Hence, even though keeping learners may improve the statistical power to detect social learning, it may also substantially increase the risk of false positive results. Therefore, the option to keep all informed individuals in the simulation should only be made use of after ensuring that the rate of false positives falls below the 5% threshold for the chosen cut-off point. For our simulated data set, we would conclude that we should drop learners both in the simulation as well as the actual NBDA analysis if they do not make the cut-off point, since risking a 25% chance of a false positive result would make a positive result untrustworthy. We suspect that it may prove to be a general pattern that retaining all learners results in an unacceptable false positive error rate.

In order to run the simulation to assess statistical power researchers must choose a value of *s*. In a sense, this choice is arbitrary, since, allowing for sampling error, power will peak at approximately the same point for all *s*>0. However, if *s* is set too high, then statistical power will appear level at 100%, if *s* is set too low, statistical power will appear level at 0%. Therefore, some trial and error may be required to find a useful value for *s*. A value of 10 for s may be a good starting point, which can then be adjusted upwards or downwards depending on the percentages of power obtained.

In all simulations on the sensitivity of NBDA (with *s*=8 and *s*=0, both with dropping and keeping learners), average estimates for the social learning parameter *s* across simulations were considerably higher than the true values set, even though when learners were dropped. Nevertheless, in ~95% of cases the true value of *s* fell within the 95% C.I. as would be expected if OADA was performing well. Hoppitt (2017) found the same effect in OADA. The bias arises because in cases where the diffusion follows the network very closely, the likelihood of the data increases and plateaus as *s* increases to infinity. Thus the optimisation algorithm used to fit the model converges on an arbitrarily large value for the estimate of *s*, which biases the average value of estimates of *s* upwards. In such cases there is also no upper limit for the 95% C.I. of *s*. Therefore, this is not a reason to generally distrust estimates of *s* obtained from an OADA. Instead, one should mistrust the estimated value of *s* if it appears unrealistically high and there is no upper limit for its 95% C.I. In such cases one can still take the lower bound of the 95% C.I. as providing a lower plausible limit on the strength of learning. The upper bound of infinity is merely indicating that it is plausible that everyone in the population who learned the behaviour while connected to an informed individual, did so by social learning. Overall, the results obtained here and by Hoppitt (2017) indicate the best way to interpret OADA is to consider the 95% C.I. as a plausible range of values for *s*, as opposed to focussing on the value of the maximum likelihood estimate for *s*. Given this is a sensible strategy for interpreting the outputs of any statistical model, this is unlikely to represent a severe limitation of OADA.

In the current form, our simulations do not take potential influences of individual-level variables on social and asocial learning rates into account, which can in theory be included in an NBDA model (Hoppitt et al., 2010). Our simulations could in principle be extended to allow for differences in learning rate among individuals (e.g. between sexes). However, there seems no obvious reason why such differences would impact significantly on the optimal threshold for inclusion in the NBDA. The position of individuals in the network, and how this relates to the number of times they were observed is likely to be the dominant influence on this threshold.

NBDA has gained increasing popularity to detect social learning in both captive and free-living populations of various species. It has proven to be a useful tool to detect and quantify social learning in animal (and human) populations (e.g. Kendal et al. 2010; Hoppitt et al. 2010; Aplin et al. 2012; Allen et al. 2013; Alem et al. 2016). We show that previously proposed thresholds for the inclusion of animals for building networks may not be applicable to studies using NBDA (Lusseau et al., 2008; Franks et al., 2010; Whitehead, 2008). Hence, we strongly encourage researchers to use our simulation to choose a cut-off point that maximizes power of NBDA that is specific to their data set, and discourage the use of arbitrarily chosen thresholds in order to minimize the risk of false negative and positive results.

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CHAPTER 3.
Evidence for social transmission of a dolphin foraging technique within and between generations

3.0. Abstract

Cultural behaviour, *i.e.*, that which is socially learned, is found in a variety of animal taxa. Social learning is particularly important for young individuals during the transition to independency. Vertical social learning between parent and offspring is therefore commonly found, particularly in species with prolonged parental care. Conversely, horizontal learning among generations, particularly adults, is thought to primarily occur in species with extensive cultural repertoires, such as great apes. Here we investigate the spread of a unique foraging strategy, 'shelling', in a population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, between 2007 and 2018. Using 'network-based diffusion analysis' (NBDA), we show that shelling behaviour spreads through horizontal social learning, standing in stark contrast to the predominantly vertically transmitted foraging behaviours in this population and toothed whales in general. Our study - establishing horizontal cultural transmission of a foraging tactic in toothed whales in a quantitative manner - suggests similarities in the nature of cultural transmission between great apes and cetaceans.

3.1. Introduction

Cultural behaviour, *i.e.*, behaviour that is transmitted among conspecifics through social learning (Boyd and Richerson, 1995), is found in a variety of animal taxa, including insects (e.g. Alem et al., 2016), reptiles (e.g. Kis et al., 2015), birds (e.g. Farine et al., 2015), primates (e.g. Hobaiter et al., 2014) and cetaceans (e.g. Krützen et al., 2005; Krützen et al., 2014). Social learning can greatly increase the efficiency with which formerly naïve individuals acquire new skills. It is, therefore, particularly important for young, dependent individuals having to acquire knowledge crucial for survival, such as how to forage, avoid predators, find shelter or interact with conspecifics (Galef and Laland, 2005).

Vertical social learning (*i.e.*, social transmission from parent to offspring (Cavalli-Sforza and Feldman, 1981)), is usually adaptive because the parental generation is likely to be more skilled than maturing individuals. Information transfer between generations is therefore commonly found throughout the animal kingdom, particularly in species with prolonged parental care (e.g. Mann and Sargeant, 2003; Jaeggi et al., 2010). For example, in vervet monkeys (*Chlorocebus aethiops*) similarities in food cleaning techniques within matrilines suggested vertical social transmission between mother and offspring (van de Waal et al., 2012).

Learning can also occur among members of the same generation, *i.e.*, through horizontal social learning (Cavalli-Sforza and Feldman, 1981). Horizontal learning has, for example, been demonstrated among free-ranging populations in several animal species such as vervet monkeys (Van De Waal et al., 2013), American crows (*Corvus brachyrhynchos*) (Cornell et al., 2012, both vertical and horizontal) and songbirds (Farine et al., 2015). It has been suggested that learning horizontally (particularly among adults) may be biased towards species with extensive cultural repertoires (Van Schaik, 2010). In great apes, for example, who exhibit a wide range of cultural behaviour (e.g. Whiten et al., 1999; van Schaik et al., 2003; Lamon et al., 2017), learning was found to occur both vertically as well as horizontally (Whiten, 2017). For instance, immature Bornean orangutans were found to consistently follow their mothers' choice in what and how to eat (Jaeggi et al., 2010), thereby strictly relying on vertical acquisition of information. Meanwhile, 'moss-sponging', a technique to retrieve water from a hole, was found to spread horizontally among associated individuals in a group of chimpanzees (Hobaiter et al., 2014). Since horizontal learning tends to homogenize behaviour within a social unit (Kendal et al., 2009), behavioural variation in great apes is usually best documented between populations (Whiten et al., 1999; Van Schaik and Knott, 2001; Krützen, 2012).

Conversely, in cetaceans, who are also known to rely extensively on social acquisition of behaviour or information (Rendell and Whitehead, 2001), behavioural variation is mostly found within populations due to primarily vertical transmission pathways from mother to offspring (e.g. Yurk et al., 2002; Mann and Sargeant, 2003; Krützen et al., 2005). Horizontal social learning, on the other hand, seems relatively rare and has thus far been described in few species, e.g. bottlenose dolphins (Donaldson et al., 2012; Bossley et al., 2018), killer whales (Whitehead et al., 2004) and humpback whales (McMillan et al., 2018), but quantitatively assessed in only the humpback whale (lobtail feeding - Allen et al., 2013; songs - Noad et al., 2000; Garland et al., 2011).

Behavioural transmission patterns have been extensively studied in the Indo-Pacific bottlenose dolphin population (*Tursiops aduncus*) of Shark Bay, Western Australia. Foraging techniques in this population appear to be almost exclusively passed on through vertical social transmission from mother to primarily female offspring (e.g. Mann and Sargeant, 2003; Krützen et al., 2005). Such strict reliance on vertical transmission has reportedly led to matriline-specific foraging techniques and patterns of haplotype similarity among individuals engaging in the same technique, since the mitochondrial haplotype is maternally inherited (genetically) (Kopps et al., 2014). Horizontal learning of any foraging strategy in this population has yet to be demonstrated.

During ‘shelling’, a novel behaviour described in the Shark Bay dolphin population, dolphins surface carrying empty shells of the two giant gastropod species (*Melo amphora* or *Syrinx aruanus*), shaking them vigorously above the surface (Allen et al., 2011). Photos and observations indicated that shelling behaviour serves the purpose of extracting prey that have sought refuge inside the empty shell, and therefore represents a further foraging behaviour in the Shark Bay population (Allen et al., 2011). Transmission pathways, including a potential role of social learning of shelling, have thus far not been investigated. Here, we use ‘network-based diffusion analysis’ (NBDA) (Franz & Nunn 2009; Hoppitt et al. 2010), which infers social transmission if the diffusion follows the social network, on an extensive data set to investigate the diffusion of shelling in this population.

There are, however, other, non-mutually exclusive factors that can influence behavioural variation, namely ecology and genetics, which could plausibly result in patterns that superficially resemble social learning (Laland and Hoppitt, 2003). For example, dolphins that have strong social connections may also be subject to similar local ecology by sharing similar habitats. If an ecological factor drives the adoption of shelling, then a pattern could result that resembles social transmission.

To avoid such issues, we used a multi-network approach of NBDA (Farine et al., 2015), with three networks modelling the effect of social transmission, shared ecological factors and genetic similarity. This allowed us to establish which network, or combination of networks, best predicted the pathways of diffusion, and quantify the effects of each network whilst statistically controlling for the others.

3.2. Methods

3.2.1. Field methods

We collected data between 2007 and 2018 during boat-based surveys off the township of Useless Loop in the western gulf of Shark Bay, Western Australia (Fig. 3.1), using standardized behavioural sampling methods. On approach to each dolphin group, observers took a GPS location within 30 m of the initial sighting, and determined group composition using individual photo-identification (Würsig and Jefferson, 1990). All individuals within 10 m of any other dolphin (10 m chain rule) during the first five mins of each encounter were considered part of the same group (Smolker et al., 1992). All occurrences of shelling behaviour were noted, including the identity of the individual performing the behaviour. Given the distinctiveness of the behaviour and its obvious function, any individual observed performing the behaviour at least once was considered a ‘sheller’. We also obtained small tissue samples on an opportunistic basis using a biopsy system developed specifically for cetaceans (Krützen et al., 2002).

3.2.2. Determining biparental relatedness and matrilineal membership

We wished to control for the possibility that genetically related individuals might be similarly predisposed to learn shelling, and therefore obtained a dyadic measure of biparental relatedness to include as a network in the analysis. We also wanted to allow for the possibility that shelling might be vertically socially transmitted to some degree. Previous work on bottlenose dolphins provides evidence that foraging skills tend to be socially learned from the mother (Mann and Sargeant, 2003; Krützen et al., 2005). As these foraging techniques are matrilineally transmitted, they show an association with mitochondrial haplotype (henceforth 'haplotype'), which is also maternally inherited. Thus, inclusion of haplotype as a factor in the analysis models the potential effects of vertical transmission down the matriline.

Sampled individuals (N = 295) were genetically sexed (Gilson et al., 1998) and genotyped based on 27 microsatellite markers (Appendix SI Chapter 3, Tab. A3.1). To assign dolphins to defined haplotypes (Krützen et al., 2004), we sequenced a 468 bp-long fragment of the mtDNA (D-Loop). We then calculated dyadic biparental relatedness for individuals with no more than three loci missing (N = 293) using COANCESTRY 1.0.1.7 (Wang, 2011). To determine which of the seven proposed relatedness estimators performed best, we simulated 1,000 genotypes based on the allele frequency distribution in the population (Appendix SI Chapter 3, Tab. A3.2). Subsequently, we simulated 100 dyads each for half siblings (relatedness (r) = 0.25), parent-offspring (r = 0.5), full siblings (r = 0.5), first cousins (r = 0.125), and unrelated individuals (r = 0). The estimator TrioML showed lowest variance (Appendix SI Chapter 3, Tab. A3.3) and highest correlation with the true data (Appendix SI Chapter 3, Tab. A3.4) and was subsequently chosen as the best performing estimator for this study population. Using the empirical data, we calculated relatedness for each dyad within the population using TrioML. For dyads where no genetic information was available, we used the population average relatedness of 0.043. Error rates were determined based on 29 individuals that had been genotyped more than once (Appendix SI Chapter 3, Tab. A3.1).

3.2.3. Inclusion of individuals

When using NBDA, there is a trade-off between sample size and data quality: dropping individuals with only a few sightings can increase certainty about the strength of connections within the social network but, at the same time, impact the power of NBDA to detect social learning if connecting individuals are removed (Wild and Hoppitt, 2018; Chapter 2). We therefore used a simulation approach to choose a cut-off point that maximizes the power of NBDA to reliably detect social learning (Wild and Hoppitt, 2018; Chapter 2). For computational reasons, we only considered individuals with at least 5 sightings (N = 538 individuals). We ran the simulations with parameters s = 14 (selected by trial and error) and set the number of learners at 18 (which corresponds to the actual number of shellers at a cut-off point of five sightings in the empirical data set), and tested for the power of NBDA to detect social learning for cut-offs of 5-20 sightings. The parameter *s* estimates the strength of social transmission per unit of association with informed individuals relative to the rate of asocial learning (Hoppitt et al., 2010). A cut-off point of 11 yielded highest statistical power, with an acceptable level of false positives (= 1.3% at 5% significance level).

3.2.4. Association strengths

Dyadic association strengths were calculated considering individuals that were part of the group within the first five mins of each encounter and with at least 11 observations, but disregarding sightings of the same group (or a subset thereof) within two hours of the initial encounter. We calculated association strengths using the 'simple ratio index' (SRI), which ranges from 0 (never seen together) to 1 (always seen together) (Cairns and Schwager, 1987), using R package 'asnipe' (Farine, 2013).

3.2.5. Calculating home range overlaps

Diffusion of a foraging skill, like shelling, might follow an association network simply because individuals who spend a lot of time together also experience the same environments. Thereby, being subject to the same ecological conditions, individuals would tend to asocially learn the same foraging skills. If this were the case, we would expect a network of similarity in environmental usage to be a better predictor of the pattern of diffusion, since individuals who do not spend time together but utilise the same environments would be similarly predisposed to learn the skill. Therefore, unless environmental usage and the social network are highly correlated, one could distinguish these two alternatives and/or quantify the relative influence of each. We used dyadic home range overlap as a proxy for the extent to which two individuals experience the same ecological conditions. For each individual with at least 11 sightings, a home range was defined using 95% kernel density estimates (R package adehabitatHR (Calenge, 2015); Epanechnikov kernel). When calculating kernel densities, the choice of the smoothing factor greatly influences the accuracy of the estimated home range and should therefore be carefully considered (Jones et al., 1996). The commonly used smoothing factor *href* (reference bandwidth), which is defined as

$$href = \sigma * n^{-1/6}$$

$$\text{where } \sigma = 0.5(\sigma_x + \sigma_y).$$

assumes that the true distribution of observations follows a normal distribution (Silverman, 1986). If this assumption is violated, *href* tends to over-smooth and therefore overestimate home ranges (Seaman et al., 1998; Fig. 3.1). Nevertheless, it is often preferred over alternative methods, such as least-square cross validation (LSCV), which makes no assumption about the true distribution but tends to under-smooth and cannot be estimated in many cases (Calenge, 2015). Visual inspection, which can aid in finding an appropriate smoothing factor (Jones et al., 1996), of 12 different dolphin home ranges revealed that *href* tended to over-smooth home ranges, particularly in cases where relocations were far apart, but under-smooth for home ranges with only a few relocations that were close together. We therefore selected a subjective smoothing parameter by setting a lower limit of 1,000 and an upper limit of 4,000 for *href*, and then calculated a new smoothing factor for each individual as

$$h = 0.5(href) + 1500$$

where 1000 ≤ href ≤ 4000

which appeared to accurately reflect the twelve inspected home ranges given the number and distribution of the sightings.

In order to remove land from the estimated kernel densities (the land boundaries in our study area were too complex to implement the ‘boundary’ parameter provided in adehabitatHR (Calenge, 2015)), each individual’s utilisation distribution was multiplied with a grid (100 m resolution) with values of 1 for grid cells on water and 0 for grid cells on land. We then re-weighted each grid cell within an individual’s home range to ensure that, overall, the kernel density added up to 1 again (Fig. 3.1). We then calculated dyadic home range overlap (95%) using the method UDOI (adehabitatHR (Calenge, 2015)), considered most accurate when quantifying space-use sharing (Fieberg and Kochanny, 2005).

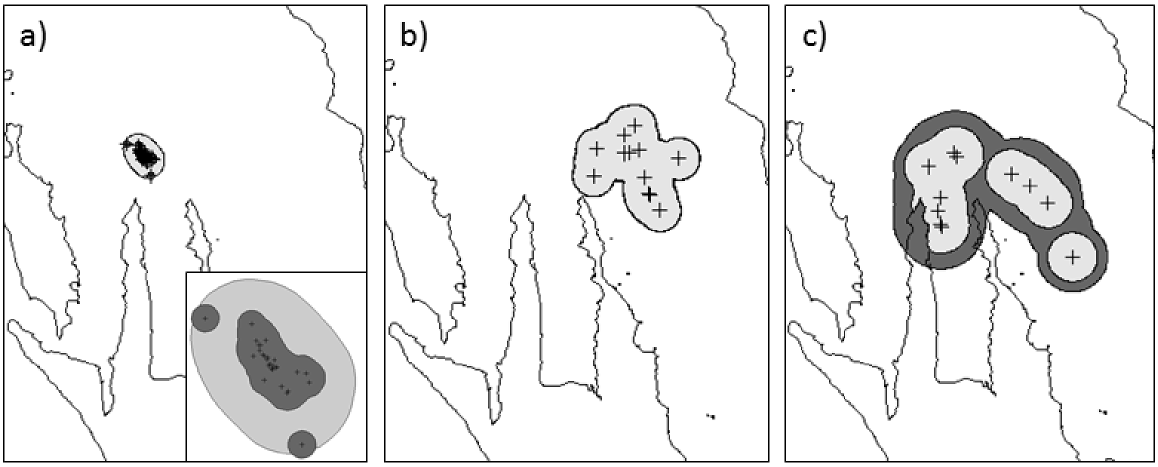

Figure 3.1: *Contours (95%) of home ranges with reference bandwidth (href; dark grey) and customized smoothing factor after land removal (light grey) for* ***a)*** *a home range with small smoothing factor (href: 632; custom: 2000; 29 sightings);* ***b)*** *a home range with an average smoothing factor (href: 3181; custom: 3090; 12 sightings); and* ***c)*** *a home range with large smoothing factor (href: 5703; custom: 3500; 11 sightings).*

3.2.6. NBDA: networks and individual-level-variables

Analyses were run using the NBDA package v0.6.1 (Hoppitt et al., 2018). We then applied multi-network NBDA (Farine et al., 2015) to our data to assess the importance of social learning on the spread of shelling, while accounting for the importance of ecological factors (measured as dyadic home range overlap) as well as a potential genetic predisposition (measured as dyadic biparental relatedness). We applied the 'order of acquisition diffusion analysis' (OADA), while additionally including several individual-level variables (ILVs) with potential influence on an individual's rate of acquisition, namely: an individual's gender (-0.5 for females, 0.5 for males, 0 for unknown sex); the number of times each individual had been seen (to control for spurious effects of frequently sighted individuals being more likely to be observed with shells); the average water depth of each individual's sightings (as a proxy for habitat use); the average group size; and maternal relatedness as a factor (reduced to 3 levels: haplotypes E, D and other; Appendix SI Chapter 3). Gender was determined genetically or, for adult females, by the presence of a dependent calf.

The main effects each ILV had, and its interaction with the effects of the network(s) were modelled independently (the 'unconstrained' model (Hoppitt and Laland, 2013); Appendix SI Chapter 3). We fitted OADA to the data with social transmission ($s > 0$) and without social transmission ($s = 0$) and with all possible combinations of the three networks and the eight ILVs on asocial and social effects (Appendix SI Chapter 3). Support for each model was calculated using the Akaike Information Criterion corrected for sample size (AICc) (Burnham and Anderson, 2002). This allowed us to derive the support for each combination of networks, and for each ILV (separately for main effects and network interaction). Model averaging methods were used to provide a more stabilized inference about the strength of the transmission parameter for the three different networks and the influence of ILVs on the social and asocial acquisition of shelling (Burnham and Anderson, 2002). The calculation of the profile likelihood intervals for the transmission parameter s conditional on the best model with social transmission allowed a measure of certainty of the estimate of the strength of transmission (Appendix SI Chapter 3).

3.2.7. Correlations between sea surface temperatures and shelling

Since the number of observations of shelling showed a pattern of peaks and troughs, we further tested the influence of sea surface temperatures (SST) on the number of shelling events in each field season (considering all shelling events during each encounter, *i.e.*, not restricted to the first five mins of each encounter – but excluding events occurring during designated focal follows). Daily SST data were downloaded from the National Oceanic and Atmospheric Administration's Advanced Very High-Resolution Radiometer Optimally Interpolated Sea Surface Temperature (Reynolds et al., 2007) (grid cell: -

26.125/113.375 WSG84) and averaged across each month. We then selected the highest monthly temperature each season (usually in Feb or Mar) and tested its correlation with the number of shelling events (Poisson GLM). We controlled for varying effort between different field seasons by including the number of shellers seen each season (again considering all observations, *i.e.*, not restricted to the first five mins) as a model offset.

3.3. Results

Over 5,300 dolphin groups were encountered in the western gulf of Shark Bay between 2007 and 2018 (Fig. 3.1), with over 1,000 different dolphins identified. A total of 42 shelling events were documented in that period (Fig. 3.1; Fig. 3.2), performed by 19 identified individuals. With a cut-off point of 11 observations (see methods), a total of 310 individuals remained for analyses, of which 15 were shellers (six females; nine males).

Results of OADA analyses revealed most support for models including only the social network ($\sum w_i = 0.771$; Fig. 3.3). Models with asocial learning or other network combinations received little support ($\sum w_i < 0.1$; Fig. 3.3).

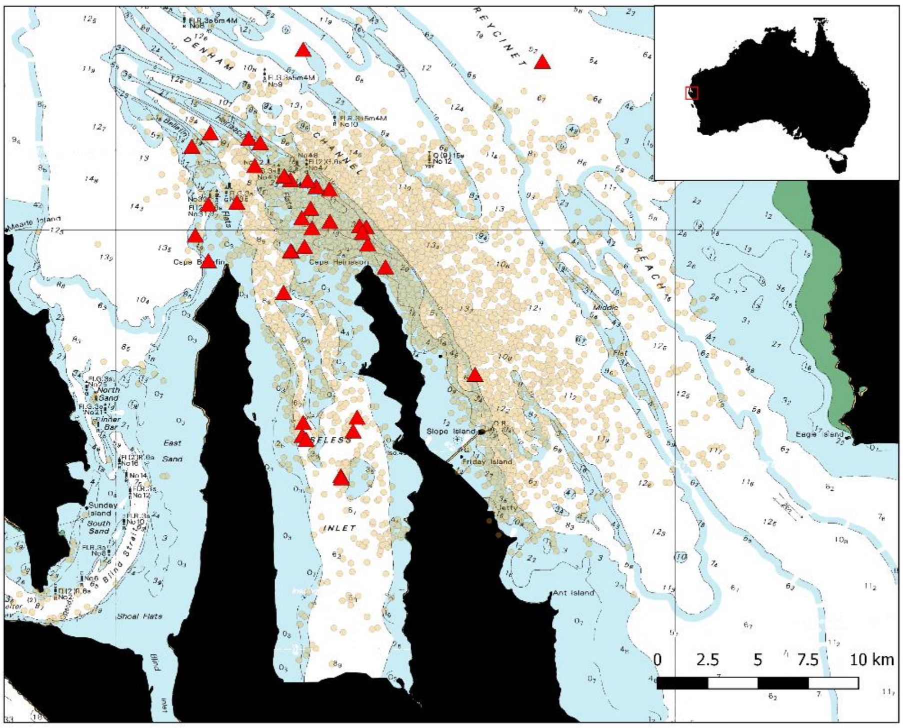

__Figure 3.2:__ Locations of all dolphin group encounters (orange dots) and 42 documented shelling events (red triangles) in the western gulf of Shark Bay, Western Australia, between 2007 and 2018.

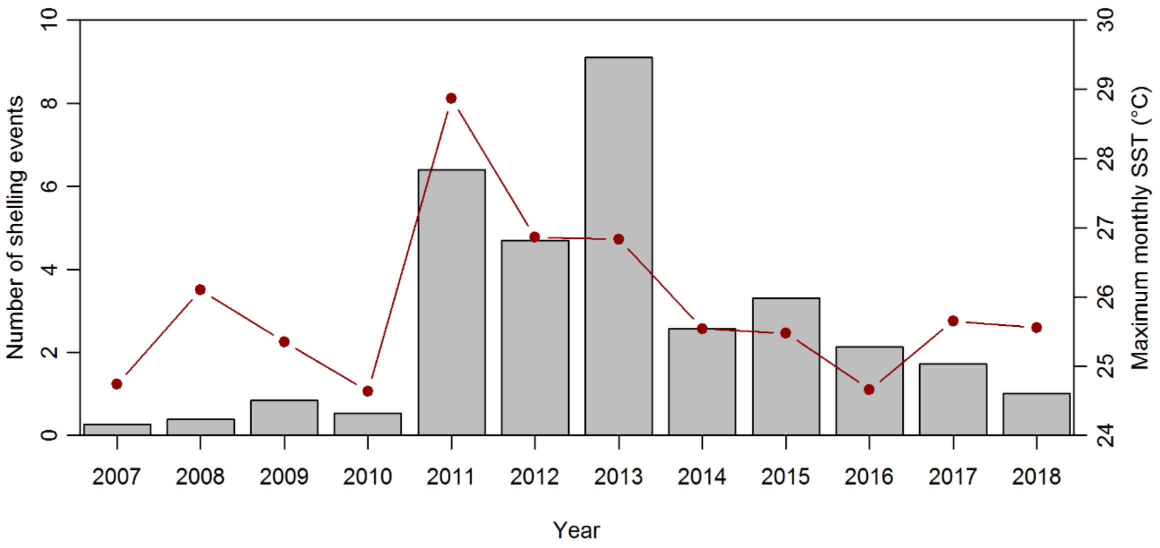

Figure 3.3: *Number of shelling events (grey bars; controlled for the number of shellers seen each field season) and maximum monthly sea surface temperatures (SST) (in red) in western Shark Bay between 2007 and 2018.*

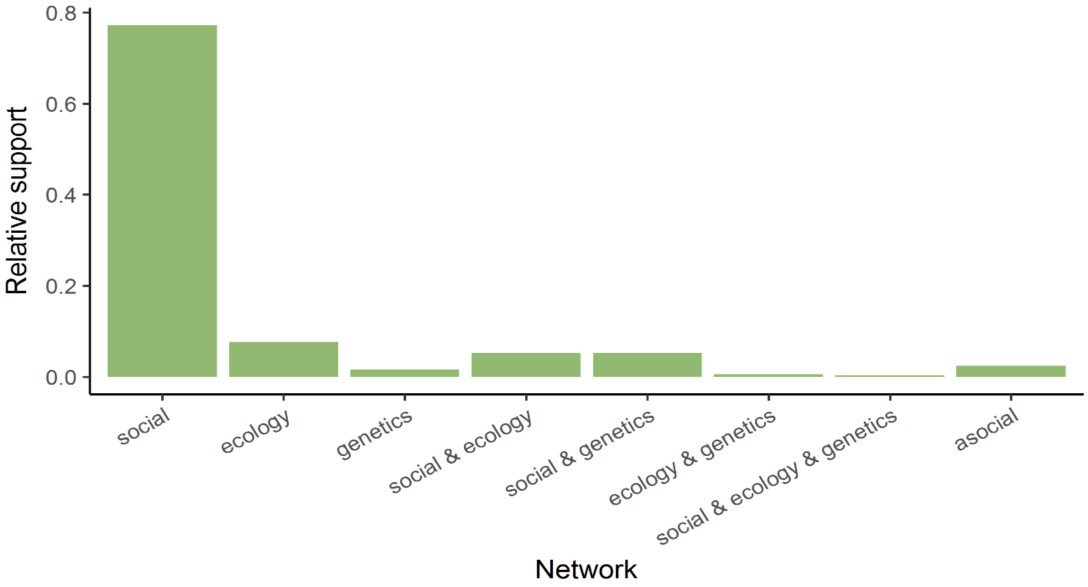

Figure 3.4: *Relative support for different network combinations resulting from multi-network NBDA.*

The best performing model included social transmission via the social network, affected negatively by average group size, with haplotype affecting the rate of asocial learning. An individual's horizontal social transmission rate per unit network connection (*s*) was found to decrease by a factor of 2.0 [95% C.I. 1.18-3.91] per associate ($\sum w_i$=0.629), which corresponds to the back-transformed parameter estimate for the average group size obtained from the best performing model. This may be because dolphins that tended to spend time in larger groups will have their attention divided among more associates, and thus learn at a lower rate per unit of association. None of the other ILVs (gender, number of sightings, av. water depth, haplotype) had an influence on an individual's horizontal social learning rate (all $\sum w_i$<0.5; Appendix SI Chapter 3). For an individual with average group size, s was estimated to be 15.6 [95% C.I. 2.06-145], indicating a 15.6-fold increase in learning rate per unit connection relative to the baseline level of learning (set to be the learning rate for individuals with haplotype E). This corresponds to an estimated 57% [95% C.I. 41-74] of dolphins learning shelling by horizontal social transmission. The estimated strength of social transmission stayed the same even if the ecological network or relatedness network were added to the best model.

There was strong support for a difference in learning rates among dolphins with different haplotypes ($\sum w_i$=0.973). Dolphins with haplotype D were an estimated 47.1x [95% C.I. 5.6-303] faster to learn than those with haplotype E, whilst dolphins with haplotype E were an estimated 1.5x10^9x [95% C.I. 3.1-Inf] faster to learn than those of other haplotypes. These inferences are largely influenced by the fact that *hitherto* only dolphins of haplotypes E and D have learned shelling while having no social network connections to shellers (3 individuals). Given the limited sample size, the large estimates of the size of this effect are unlikely to be accurate, however, the 95% confidence intervals provide a reasonable lower limit for the effect.

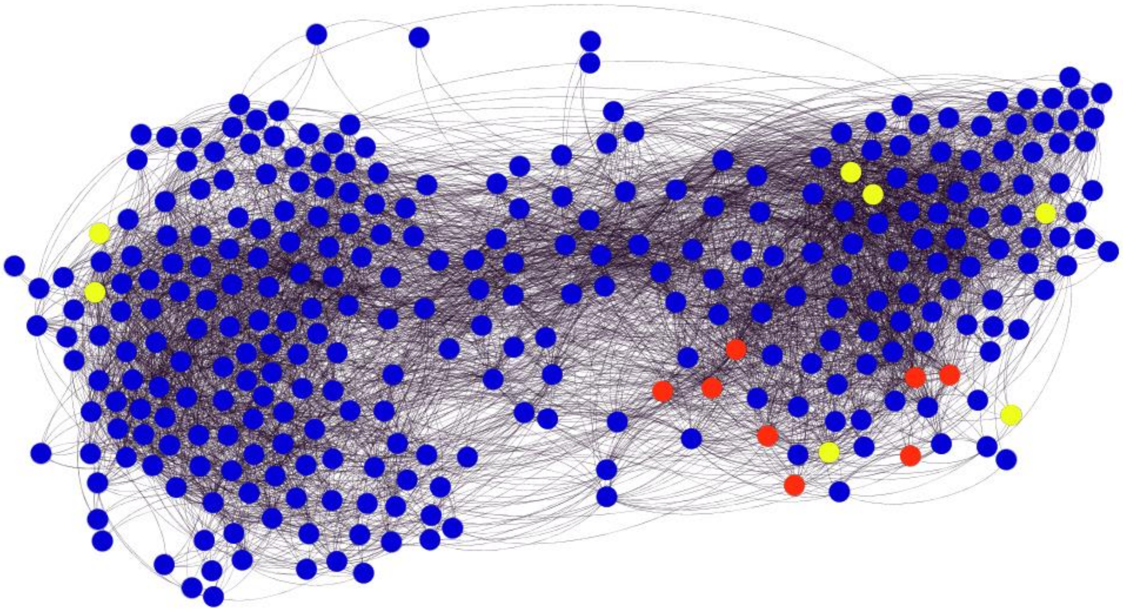

Figure 3.5: *Social network (undirected, and displayed as unweighted) of 310 bottlenose dolphins in the western gulf of Shark Bay (Force Atlas 2 algorithm (Jacomy et al., 2014) in Gephi (Bastian et al., 2009)). Blue nodes depict individuals who have never been observed carrying shells; red nodes depict individuals who are likely (>50%) to have learned shelling socially, while yellow nodes represent individuals who have learned shelling asocially (<50%). Nodes that are closer together are also more closely associated (spring-embedded network).*

The number of shelling events documented each year was significantly correlated with the maximum monthly SST (Poisson GLM; effect size=33.29%; 95% C.I. = [6.25%; 59.01%]; z=2.486; p=0.01), with more shelling events occurring in years with higher SST (Fig. 3.2).

3.4. Discussion

Shelling represents the first quantitatively assessed evidence of a horizontally learned foraging behaviour in Shark Bay dolphins or, indeed, any toothed whale species, and the second in any cetacean (following Allen et al., 2013). Overall, the multi-network NBDA indicates that the pathway of diffusion of shelling is consistent with the scenario in which dolphins with haplotype D and some with haplotype E learn independently of the social network (either by independent learning or perhaps by vertical social transmission) and other dolphins of haplotypes E and H learn from their peers by horizontal social transmission. Horizontal social transmission is supported because the pattern of diffusion follows the connections of the social (association) network, suggesting dolphins learn shelling if they spend time with other shellers.

It is possible that such a statistical pattern could arise due to the influence of another confounding variable that influences learning of shelling and is correlated with the social network. However, our analysis suggests that the most plausible confounds are unlikely to account for the data: when patterns of home range overlap and relatedness are statistically controlled for, the effect of the social network remains.

Another alternative explanation is that dolphins learn shelling from their mothers before weaning (*cf*. sponging (Krützen et al., 2005)), or at least observation of their mothers' shelling predisposes them to learn the behaviour pattern later in life. This could result in a spurious horizontal social transmission effect if dolphins from the same matrilines tend to associate. Our record of parentage and of shelling status is not sufficiently complete to allow us to model this transmission pathway directly. However, by including mitochondrial haplotype as a factor in the analysis, we are able to control for it - since vertical transmission from mother to offspring would result in a correlation of shelling with haplotype. Our analysis shows that haplotype does not sufficiently explain the pathway of diffusion, and when controlling for it, there is still a sizable effect of the social network.

Whilst the influence of mitochondrial haplotype was included primarily as a statistical control, the propensity of dolphins with haplotypes D and E to exhibit shelling could be taken as evidence for a vertical (maternal) component to social transmission. Profile likelihood intervals suggest that in fact, such a pattern is unlikely to have arisen by chance alone. However, given small sample sizes, the importance of a potential role of vertical learning and size of potential effects of haplotypes cannot be estimated reliably at this stage.

Given the high support for transmission along the association network, there is evidence for a strong horizontal transmission effect. Vertical social learning has been established as the primary transmission mechanism for most foraging behaviours in Shark Bay's bottlenose dolphins (e.g. Mann and Sargeant, 2003; Sargeant et al., 2005; Krützen et al., 2005) and cetacean behaviour in general (e.g. Simões-Lopes et al., 1998; Boran and Heimlich, 1999; Yurk et al., 2002). The pattern of vertical social learning from mother to female offspring within Shark Bay dolphins has reportedly led to haplotype similarity (both eastern and western gulf of Shark Bay) and higher genetic relatedness (eastern gulf of Shark Bay) among individuals engaging in the same technique (Krützen et al., 2005; Kopps et al., 2014). The low support for transmission of shelling along the relatedness network and the fact that individuals from three different matrilines engaged in shelling appears to be consistent with a strong horizontal component of social learning.

Shelling can only occur where dead shells (and appropriate prey) are available and is therefore directly dependent on the distribution and abundance of *Melo amphora* and *Syrinx aruanus*. Shelling appeared to have occurred more frequently in the field seasons 2011 and 2012, following a marine heatwave in early 2011, which caused catastrophic seagrass die-off (Thomson et al., 2014; Arias-Ortiz et al., 2018), and mass mortalities of fish and invertebrates followed (Pearce et al., 2011). Given the increase in shelling events immediately following the marine heatwave, we assume that high water temperatures may also have had negative effects on large gastropods, leading to increased abundance of dead shells and thus more opportunity for shelling behaviour. In fact, our analyses revealed that shelling occurred significantly more often in years with higher SSTs, which suggests temperature sensitivity in *M. amphora* and *S. aruanus*.

The 2011 heatwave caused catastrophic seagrass die-off and subsequent ecological disturbance across trophic levels in Shark Bay (Cheung et al., 2012; Thomson et al., 2014; Arias-Ortiz et al., 2018). In fact, long-term declines in dolphin survival and female reproduction following the heatwave suggest protracted habitat degradation and delays in prey stock recovery (Chapter 5). Theory predicts that stable environments should favour cultural conservatism, *i.e.*, reliance on already established information obtained from older generations, since it is tested, experience-based and therefore most likely adapted to current ecological conditions (Whitehead et al., 2004). Rapid environmental change, however, should thus favour cultural progressivism, as such information can become out-dated, promoting the acquisition of innovative behaviour from conspecifics in order to rapidly adapt to novel ecological conditions (Whitehead et al., 2004). It has been suggested that species with the capacity for horizontal transmission may be better able to survive (Whitehead et al., 2004). It remains unclear though, if and to what extent horizontal social transmission among shelling dolphins was a response to ecological perturbation, or if it had any impact on survival, since this has not been formally tested. Given the predicted increase in extreme weather events due to anthropogenic climate breakdown (Oliver et al., 2018), selection may favour a shift from the extensive cultural conservatism to more progressive behaviour.

Our findings of horizontal social transmission of shelling support previous (anecdotal or descriptive, but long-suspected) cases of plausible horizontal transmission in toothed whales (Whitehead et al., 2004; Donaldson et al., 2012; Bossley et al., 2018). For example, some bottlenose dolphins accepted food handouts from recreational boaters. Both the use of areas with high boat density and association rates with already conditioned individuals predicted whether dolphins became conditioned to accepting handouts themselves, suggesting a combination of ecological factors and horizontal social learning driving the spread of the behaviour (Donaldson et al., 2012; Krützen, 2012). Two cultural ‘fads’ (*i.e.*, non-adaptive behaviours) were further suggestive of horizontal transmission in cetaceans: ‘dead salmon-carrying’ in a subset of killer whales (Whitehead et al., 2004); and ‘tail-walking’ in a community of bottlenose dolphins (Bossley et al., 2018).

While young individuals of many animal species rely heavily on social information, the benefits of learning socially are thought to decrease as maturing individuals become more skilled (Van Schaik, 2010). However, species with extensive cultural repertoires, like great apes, tend to exhibit both vertical and horizontal behavioural transmission (Van Schaik, 2010; Hobaiter et al., 2014). The horizontal social transmission of shelling among adult dolphins thus sets an important milestone in assessing pathways of transmission in dolphins, and suggests that the cultural nature between great apes and dolphins may not be so different. Indeed, despite living in markedly disparate environments (terrestrial and aquatic), great apes and dolphins show striking similarities in cognitive abilities, life history characteristics and social systems. They are long-lived, large-brained mammals with high capacities for innovation (Reader and Laland, 2001; Marino, 2007). Furthermore, many dolphin species live in fission-fusion societies (e.g. Connor et al., 2000) similar to those found in chimpanzees (Nishida, 1968). These societies are characterised by extensive social tolerance, which provides many opportunities for social interactions, thought to be a predictor of social learning rates in a species (Van Schaik et al., 2003; Van Schaik, 2010).

Shelling represents the first quantitative evidence of horizontal social transmission in any toothed whale species, where alternative pathways of transmission (genetic and ecological) have been statistically controlled for. Our results provide further evidence supporting suggestions of similarities in the cultural nature between great apes and cetaceans (e.g. Rendell and Whitehead, 2001; Krützen et al., 2005; Allen et al., 2013). Furthermore, relying on social information as adults through horizontal learning can be advantageous in fast changing environments (Rendell and Whitehead, 2001; Whitehead et al., 2004), and may help buffer against the effects of ecological disturbances and habitat degradation associated with global climate breakdown.

3.5. Ethics

Permits for the use of animals for scientific purposes were granted by the Dept. of Biodiversity, Conservation and Attractions. The animal ethics committees of the University of Western Australia, Murdoch University and the University of Zurich provided approvals for the ethical treatment of animals in scientific research.

3.6. Acknowledgements

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CHAPTER 4.
Network-based Diffusion Analysis shows vertical cultural transmission of sponge tool use within dolphin matrilines

4.0. Abstract

Behavioural differences among social groups, communities or populations can arise from differing ecological conditions, genetic predispositions or be the result of social learning. These potential drivers have been treated as mutually exclusive in the past, and social learning has typically been inferred as being responsible for the spread of behaviour by the exclusion of ecological and genetic factors. This 'ethnographic' method was used to infer that 'sponging', a foraging behaviour involving tool use in the bottlenose dolphin (*Tursiops aduncus*) population in Shark Bay, Western Australia, was socially transmitted. However, critics have argued that the method can never fully account for alternative factors, and that social learning, ecology and genetics are not mutually exclusive in causing behavioural variation. Here, we use a multi-network version of 'network-based diffusion analysis' (NBDA) to quantify the importance of social learning on the diffusion of sponging in the western gulf of Shark Bay, while also accounting for ecological and genetic similarity. Our results provide compelling support for previous findings that sponging is vertically socially transmitted from mother to (primarily female) offspring. Further, this research provides an example of the utility of social network analysis in elucidating the explanatory mechanisms behind the transmission of behaviour in wild animal populations.

4.1. Introduction

Various mechanisms can be responsible for causing behavioural differences between social groups or populations (Boyd and Richerson, 1995). The cultural hypothesis states that behavioural variation between groups is the result of social transmission of different behavioural innovations. The ecological hypothesis, on the other hand, proposes that behavioural variation may be the result of geographic variation, and that differences between groups can be attributed to differing ecological conditions. Finally, the genetic hypothesis assumes that different groups are genetically predisposed to behave in different ways (Boyd and Richerson, 1995; Laland and Hoppitt, 2003).

The last few decades have seen increasing interest in animal cultural phenomena (e.g. Boesch, 1996; Madden, 2008; Wich et al., 2012), *i.e.*, behaviours that are socially transmitted among conspecifics (Boyd and Richerson, 1995). As a result, various methods have been used to identify social learning in animal populations. For example, the *method of exclusion* or *ethnographic method* identifies patterns of variation in the behavioural repertoires of the population in question and infers social transmission as at least partly responsible for the behavioural pattern by excluding genetic and ecological factors as sufficient explanations (Hoppitt and Laland, 2013) [p. 132]. The method of exclusion has been commonly used among primatologist in the past, for example to identify cultural behaviour in orangutans (van Schaik et al., 2003) or chimpanzees (Whiten et al., 1999).

The method of exclusion has also been used to assess patterns of transmission of 'sponging', a foraging behaviour involving tool use in a population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia (Smolker et al., 1997; Krützen et al., 2005). This behaviour involves dolphins carrying conical sponges as protective 'gloves' on their rostra when foraging for prey buried in the substrate (Smolker et al., 1997). Sponging was found to be female-biased with only a few males regularly engaging in sponging behaviour, with almost all sponging dolphins possessing the same mitochondrial haplotype, *i.e.*, belonging to the same matriline (Krützen et al., 2005; Kopps et al., 2014a). As the deep-water channels where sponging occurs were used by both spongers and non-spongers, a purely ecological explanation seemed unlikely (Krützen et al., 2005). By considering 10 different pathways of genetic inheritance (x-linked and autosomal), Krützen et al., (2005) inferred that sponging was vertically socially transmitted from mother to female offspring.

The method of exclusion has been criticised, however, with considerable debate over its utility among its proponents and opponents ensuing (Laland and Janik, 2006; Krützen et al., 2007; Laland and Janik, 2007). Laland and Janik, (2006) argued that it is impossible to take all plausible explanations for the spread of behaviour into account, and therefore that social learning can never be inferred with absolute certainty. This, in turn, would lead to increased rates of false positive results (Hoppitt and Laland, 2013). Furthermore, they argued that social learning, ecology and genetics are not necessarily mutually exclusive but can be responsible for causing behavioural variation at the same time (Laland and Janik, 2006; Laland and Janik, 2007; Sargeant et al., 2007).

Therefore, in a more quantitative approach, Krützen et al., (2011) inferred social learning to be responsible for causing behavioural variation among orangutans by assessing the relative importance of ecology, genetics and social learning on orangutan behavioural variation using dissimilarity matrices, which contained measures of behavioural, geographic and genetic dissimilarity among each dyad. Langergraber et al., (2011) used a similar approach, showing that genetic dissimilarity among chimpanzee groups could not be ruled out as an important factor generating previously documented behavioural variation.

In a further attempt to resolve the animal cultures debate, new methods have been developed with which to quantify the importance of social learning on the spread of novel behaviour. In particular, ‘network-based diffusion analysis’ (henceforth NBDA) (Franz and Nunn, 2009; Hoppitt et al., 2010), has been used increasingly in recent years to detect and quantify social learning in both captive and free-ranging animal populations (e.g. Allen et al., 2013; Hobaiter et al., 2014; Farine et al., 2015). NBDA infers social transmission if the spread of a behaviour follows the social network, assuming that more closely associated individuals have more opportunities to learn from each other (Coussi-Korbel and Fragaszy, 1995; Hoppitt et al., 2010). Multi-network NBDA allows the inclusion of several different networks to quantify the relative importance of transmission along different pathways (Farine et al., 2015).

Here, we apply new methods to assess the transmission mechanisms of sponging in the dolphin population of Shark Bay, Western Australia. Using multi-network NBDA, we quantify the relative importance of social learning (distinguishing between vertical and horizontal/oblique pathways), ecological factors and genetic relatedness on the spread of this tool using behaviour.

4.2. Methods

4.2.1. Field methods

We collected association and behavioural data during boat-based surveys using standardised sampling methods for cetaceans between 2007 and 2018 in the western gulf of Shark Bay, Western Australia. On approach of each dolphin group (≥1 individuals), we took a GPS location within 30m of the initial sighting. Group composition during the first five mins was determined using standard photo-identification techniques (Würsig and Jefferson, 1990), and individuals were considered part of the same group according to the 10m-chain-rule, *i.e.*, if within 10m of any other group member during the first five minutes of an encounter (Smolker et al., 1992). Predominant group behaviour was recorded during the first five minutes as foraging, travelling, socializing or resting. All occurrences of sponging (*i.e.*, not restricted to the first five mins) were recorded, including the identity of the dolphin carrying the sponge. An individual was deemed a ‘sponger’ once it had been seen carrying a sponge on at least two independent occasions. Small biopsy samples were taken on an opportunistic basis using a system designed specifically for sampling cetaceans (Krützen et al., 2002).

4.2.2. Genetic methods

4.2.2.1. Estimating pairwise biparental relatedness and determining matriline membership

In order to test if genetically similar individuals shared a predisposition to develop sponging behaviour, we wanted to obtain a measure of genetic biparental relatedness for each dyad. Since critics had argued that a predisposition for sponging could, in theory, be a result of differences in energy budgets due to genetic variation in mitochondrial efficiency (Laland and Janik, 2006) - although this was refuted both theoretically (Krützen et al., 2007) and empirically (Bacher et al., 2010) - we also statistically controlled for a correlation between matriline membership and sponging behaviour.

Individuals for which biopsies were available (N=295) were genetically sexed (Gilson et al., 1998) and genotypes determined based on 27 microsatellite markers (Appendix SI Chapter 4, Tab. A4.1) (Shinohara et al., 1997; Krützen et al., 2001; Nater et al., 2009). We sequenced a 468 bp-long mtDNA fragment (D-Loop) to assign dolphins to predefined haplotypes, *i.e.*, to determine their genetic maternal lineage (Krützen et al., 2004). Using COANCESTRY 1.0.1.7 (Wang, 2011), we calculated dyadic biparental relatedness based on genotypes for individuals with no more than three microsatellite loci missing (N=293). To select the best performing relatedness estimator, we simulated 1,000 genotypes based on the empiric allele frequency in the population (Appendix SI Chapter 4, Tab. A4.2). Subsequently, we simulated 100 dyads each for half sibling (relatedness (r) = 0.25), parent-offspring (r = 0.5), full siblings (r = 0.5), first cousins (r = 0.125) and unrelated individuals (r = 0). The estimator TrioML was chosen as the most accurate estimator, showing lowest variance and highest correlation with the true data (Appendix SI Chapter 4, Tab. A4.3; Tab. A4.4). We then calculated dyadic biparental relatedness among individuals using TrioML. For dyads where no genetic information was available, the population average relatedness of 0.043 was used. We obtained error rates for each locus based on 29 individuals that had been genotyped more than once (Appendix SI Chapter 4, Tab. A4.1).

4.2.2.2. *Maternity analyses*

To test for influences of vertical social learning, we created a network reflecting the mother-offspring relationship based on field observations of 278 mother-offspring pairs. In addition, we ran maternity analyses in CERVUS 3.0.7 (Kalinowski et al., 2007) for individuals with haplotype E and H (since 42 spongers with known haplotype in our empirical data set carried haplotype E, and one sponger carried haplotype H) and with no more than three microsatellite loci missing.

First, in order to obtain critical values of likelihood ratios used for parentage analysis on empirical data, a maternity simulation was run for individuals with haplotypes E and H separately. As the mitochondrial haplotype is maternally inherited, candidate mother and offspring always carry the same haplotype. To determine the number of candidate mothers for all offspring in the E and H data set, respectively, we created a home range with all GPS locations of observations of individuals carrying haplotypes E and H, respectively (for details on calculating home ranges see below). We then calculated home range overlap of all individuals who were either female or of unknown sex (*i.e.*, excluding genetically known males) who had any overlap with the E or H home range, respectively. This resulted in 355 candidate mothers for the haplotype E data set and 343 candidate mothers for the H data set, both of which are likely a conservative over-estimate (since some individuals of unknown sex will be male). Other input parameters were set as following: the proportion of sampled individuals (calculated as the proportion of sampled females out of the total number of candidate mothers) was set to 0.44 (for both E and H), while the allele frequency (Appendix SI Chapter 4; Tab. A4.1.), the proportion of loci typed (=0.995) and the proportion of loci mistyped (=0.0038) were obtained from empirical data – the latter stemming from 29 individuals who had been genotyped more than once.

The simulations (run for 1,000 offspring) were then used to run the maternity analyses on empirical data. To match mother-offspring pairs reliably, we only considered matches with 'logarithm of the odds' (LOD) scores significantly higher (at 5% level) than the critical value obtained from simulations (Kalinowski et al., 2007) and with dyadic relatedness estimates between 0.4265 and 0.6308, which corresponded to the range of relatedness estimates between known mother-offspring pairs. Furthermore, we only matched mother-offspring pairs where approximate birth date of both candidates (based on speckle levels (Krzyszczyk and Mann, 2012), body size and time of first offspring for females) was known and at least 10 years apart (Wallen et al., 2016).

4.2.3. Network constructions & NBDA

To test for the relative importance of social learning, ecological factors and genetics in promoting the spread of sponging, we ran multi-network NBDA (Farine et al., 2015) using four different networks. All network constructions and data analysis were conducted in R studio v1.1.423 (R Core Team, 2015), using the NBDA package v0.6.1 (Hoppitt et al., 2018). The first network (social) tested for learning between mother and offspring with entries of 1 between mother and known offspring pairs and all other connections set to 0. The second network (social) allowed for horizontal/oblique (henceforth 'horizontal') learning using dyadic association strengths (Simple Ratio Index (Cairns and Schwager, 1987)) among all individuals but excluding mother-offspring associations, which were set to 0. Association strengths among individuals were calculated using only association data recorded during the first five mins of each survey. Restriction to the use of just the first five minutes of each observation ensured that association measures were comparable across all surveys. Resights (=same or a subset of the original group within two hours) were excluded. Association matrices were created using R package 'asnipe' (Farine, 2013). The third network (ecological) contained a proxy of the environmental similarity experienced by individuals, *i.e.*, dyadic home range overlap. We created a home range using individual GPS locations based on 95% (Epanechnikov) kernel density estimates ('adehabitatHR' (Calenge, 2015)) with a customized smoothing factor, as detailed in Chapter 3. Dyadic home range overlap (95%) was calculated using the method UDOI ('adehabitatHR') (Calenge, 2015), which has been suggested as most appropriate when quantifying space-use sharing (Fieberg and Kochanny, 2005). Finally, the fourth network (genetics) contained measures of biparental genetic relatedness among individuals.

Since NBDA infers social learning if a behaviour follows the social network, there is a trade-off between sample size and data quality. Only considering individuals above a certain threshold of sightings (*i.e.*, dropping individuals with only few sightings) can increase certainty about the strengths of connections within the network, but at the same time decrease power of NBDA to reliably detect social learning, if linking individuals are removed (Wild and Hoppitt, 2018; Chapter 2). A simulation approach (Wild and Hoppitt, 2018; Chapter 2) revealed highest power to detect social learning at a cut-off point of 7 sightings (Appendix SI Chapter 4).

Since exact dates of acquisition of sponging were not known, we applied the 'order-of acquisition diffusion analysis' (OADA) (Hoppitt et al., 2010). In OADA, social learning is inferred if the order with which individuals learn the behaviour follows the social network. Unlike the alternative time of acquisition diffusion analysis (TADA), OADA does not make any assumptions about the baseline rate of acquisition, which may have fluctuated over time as changing prey availability and environmental conditions made sponging more or less likely to be learned, across the population. For several individuals, the order of acquisition of sponging was unknown, as they were likely already spongers when first encountered. In an NBDA model, such individuals can be taken to be 'informed' at the start of the diffusion (termed 'demonstrators') - thus they can potentially transmit behaviour to others, but their own acquisition of the behaviour is not used to fit the model (Hoppitt et al., 2010). We considered all individuals as demonstrators who had been seen carrying a sponge within the first two encounters where predominant group behaviour was foraging. We argue that an individual's information state can be determined with reasonable certainty after two sightings, given spongers carry sponges 96% of the time when foraging (Mann et al., 2008). Furthermore, for nine individuals who acquired sponging after 2007, maternity data was unavailable. These nine individuals were excluded as learners using the filteredNBDAdata function provided in the NBDA package v0.6.1 (Hoppitt et al., 2018)

For all possible combinations of the four networks described above, we applied the 'order-of acquisition diffusion analysis' (OADA) (Hoppitt et al., 2010), while additionally including several individual-level variables (ILVs) with potential influence on an individual's social and asocial rate of acquisition, namely: an individual's gender; the average water depth of each individual's sightings (as a proxy for habitat use since sponging occurs in deep water channels (Sargeant et al., 2007)); as well as the average group size (since sponging was demonstrated to be a solitary activity (Mann et al., 2008)) and mitochondrial haplotype. Since all spongers but one carried haplotype E, we included haplotype as a two-level factor with either haplotype E or 'other' (B, D, F, H, K, unknown). Gender was determined genetically and/or by the presence of a dependent calf for females.

The strength of transmission along a network (*s* parameter) is estimated relative to a baseline rate of asocial learning. Continuous variables were standardized to a mean of 0 and the baseline rate of asocial learning was set to the mean of all continuous variables and a mid-point between male and female and haplotype E, in order to obtain a more stable parameterization.

We fitted OADA with and without transmission along the networks and with all possible combinations of networks and ILVs (Hoppitt et al., 2010). Thereby, ILVs were allowed to influence both social and asocial learning rate independently ('unconstrained' models (Hoppitt and Laland, 2013; Appendix SI Chapter 4), resulting in 4096 different models. Unfitted models (300) were removed, as these were all models with a large number of parameters and, therefore, likely over-parametrised. Support for each model was calculated based on the Akaike Information Criterion corrected for sample size (AICc) (Burnham and Anderson, 2002). To provide a more stabilized inference about strength of transmission for the different networks and the influence of ILVs, model averaging methods were employed (Burnham and Anderson, 2002). The calculation of the profile likelihood intervals for the transmission parameter *s* conditional on the best performing model with social transmission allowed a measure of reliability of the estimate of the strength of transmission (Appendix SI Chapter 4). We obtained an estimate of the proportion of individuals having learned socially in the best performing model using the oadaPropSolveByST function provided in the NBDA package v0.6.1 (Hoppitt et al., 2018).

4.3. Results

Between 2007 and 2018, over 5,300 dolphin groups were encountered in the western gulf of Shark Bay and >1,000 different dolphins identified (Fig. 4.1a). Sponging was observed on 825 occasions and restricted to the deep-water channels within the study area (Fig. 4.1b). A total of 76 individuals were identified as spongers, of which 49 were confirmed female, 14 male and 13 of unknown sex. We matched a further 16 mother-calf pairs to 278 already known (see Methods).

After removal of individuals with fewer than seven sightings, as well as eight offspring that were either dependent calves at the time of analyses or had died before weaning, 415 individuals remained of which 62 were spongers (18 learners [of which 9 were filtered out], 44 as demonstrators). All spongers with maternity data available were born to sponging mothers. All spongers with genetic data available carried haplotype E, with one exception: a male sponger with haplotype H.

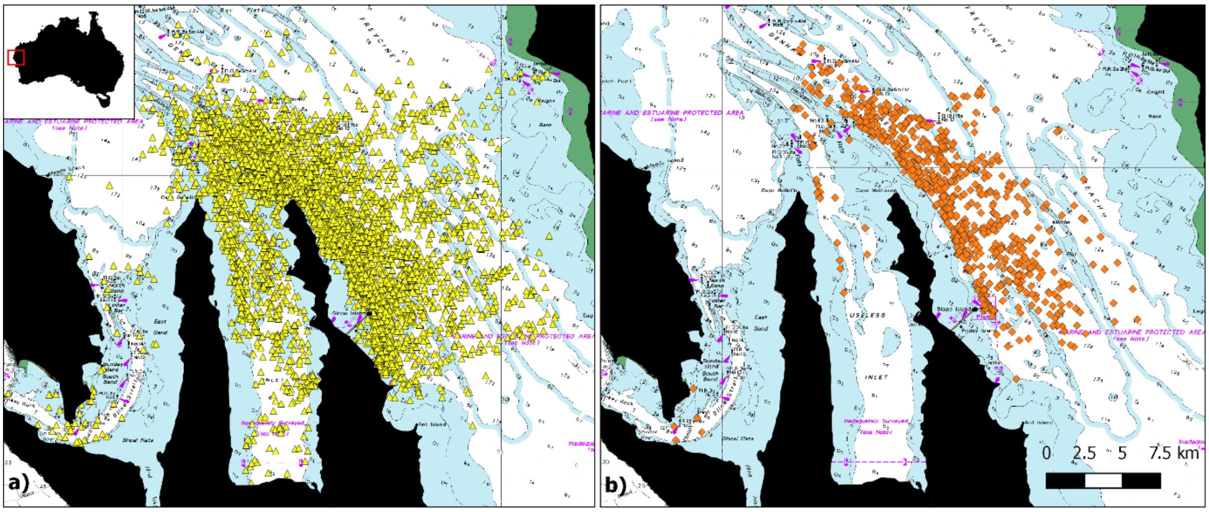

Figure 4.1: *Locations of a) dolphin groups encountered in the western gulf of Shark Bay between 2007 and 2018; and b) observations of sponging behaviour, which was restricted to deep (>10m) water channels (white areas).*

Multi-network NBDA revealed most support for models with transmission along the vertical social network ($\sum w_i$=0.986), while asocial learning, and transmission along the horizontal, environmental or genetic network (or any combination of the four networks) received little support ($\sum w_i < 0.1$) (Fig. 4.2). In the best performing model, which included vertical social transmission and gender influencing social learning, an individual's learning rate of sponging increased by a factor of 126 (95% C.I. [9.5; 2897]) when being female ($\sum w_i$=0.975), while average group size, average water depth or haplotype had no influence on an individual's social or asocial learning rate (all $\sum w_i$<0.5). In the best model 100% were estimated to have learned sponging socially from their mothers (95% C.I. [98.9; 100]).

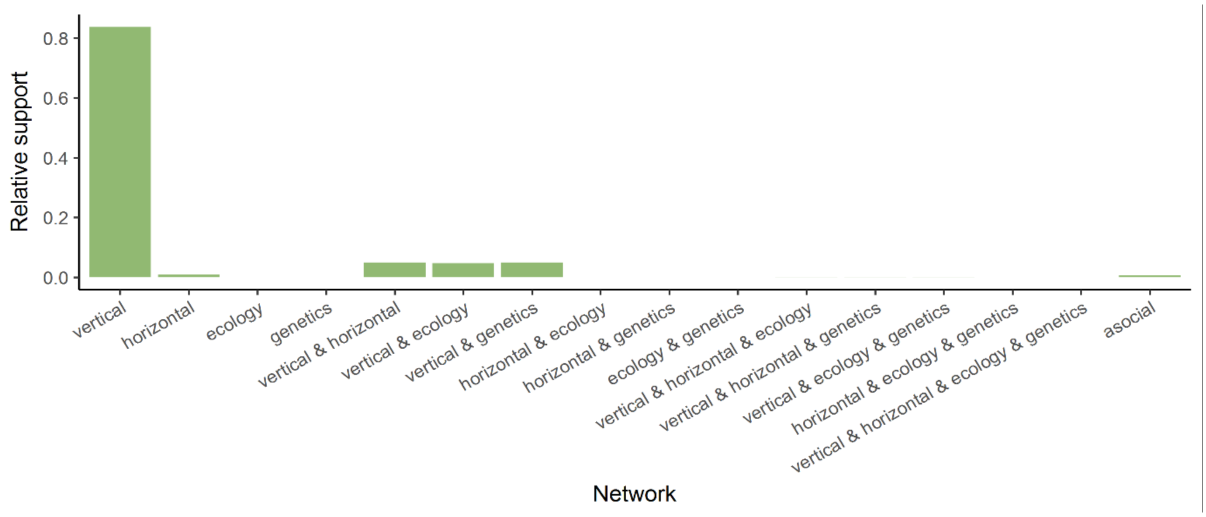

Figure 4.2: *Multi-network NBDA reveals most support for transmission of sponging along the vertical social network, while transmission along the horizontal network, ecological and relatedness network receive little support.*

4.4. Discussion

Using over 10 years of data on dolphin associations, habitat use and genetics, multi-network NBDA revealed overwhelming support for social transmission along the vertical mother-offspring network, with little or no support along the horizontal association network, the ecological or genetic networks. These results suggest a strong role of vertical social learning of sponging from mother to offspring, as has been described in previous work using different methods (Mann and Sargeant, 2003; Krützen et al., 2005; Kopps and Sherwin, 2012).

Previous findings suggested that the distribution of conical sponges, which are more abundant in deeper water, restricts sponging to deep water channels in Shark Bay (Sargeant et al., 2007; Tyne et al., 2012; Kopps et al., 2014b). Locations of sponging sightings in our more extensive data set confirm these results. However, despite the restriction of sponging to the deep-water habitat, our analysis suggests that environmental factors only play a minor role once vertical social learning has been taken into account.

Low support for transmission due to genetic similarity among individuals confirms previous findings that sponging individuals in the western gulf are not more closely related than expected by chance (Kopps et al., 2014a). This stands in contrast to findings from the eastern gulf, where spongers show higher relatedness compared to population average, suggesting recent common coancestry (Krützen et al., 2005).

We also confirm a previously documented female sex-bias (Mann and Sargeant, 2003; Mann et al., 2008; Kopps et al., 2014b). It has been suggested that the female sex-bias is due to differing sex-specific reproductive strategies between males and females (Mann et al., 2008). After weaning, male dolphins have to focus on forming multi-male alliances to coerce and consort oestrous females (Connor et al., 1992; Connor and Krützen, 2015), which requires significant investment in social relationships and is therefore incompatible with a time-consuming, solitary and difficult-to-master activity like sponging (Mann et al., 2008; Mann et al., 2012; Patterson et al., 2015). Meanwhile, female offspring are expected to primarily invest in feeding related activities such as developing foraging skills to maximize food intake (Gibson and Mann, 2008). Thereby, since female offspring preferentially associate with their mothers after weaning, and thus use similar habitat, selection should favour similar foraging strategies (Mann and Sargeant, 2003). Alternatively, Zefferman, (2016) proposed that the female sex-bias could be the result of a maternal teaching strategy, arguing that teaching a daughter would result in higher long-term fitness for a female: a potential advantage of sponging for a son would last only one generation, while a daughter can pass on the behaviour to subsequent generations which all gain potential benefits associated with sponging.

Nevertheless, 22% of spongers with known sex in the western gulf were males, which corresponded to previously suggested proportions of male offspring learning sponging from their mothers in the eastern gulf (Mann et al. 2008; but see Mann and Patterson 2013). Sponging males in the western gulf were found to be closely associated, often even part of the same reproductive alliance (Bizzozzero et al., unpublished data). The preference of forming alliances with males that engage in the same specialized foraging technique (*i.e.*, homophilic tendencies) may help to reduce the costs associated with sponging (Mann et al., 2008; Mann et al., 2012), since all males within the alliance use similar habitat and have similar activity budgets (Bizzozzero et al., unpublished data).

All but one of the western gulf spongers with genetic data available carried haplotype E. The single male sponger carrying haplotype H was only seen with a sponge twice out of 25 observations. Haplotype similarity among spongers had previously been described for both the eastern and western gulfs of Shark Bay (Krützen et al., 2005; Kopps et al., 2014a, respectively), although sponging haplotypes differ between the gulfs. Laland & Janik (2006) had argued that, strictly speaking, mitochondrial genes could be responsible for the spread of sponging. However, Bacher et al. (2010) showed that the non-coding HVRI (hypervariable region I) of the mitochondrial DNA was a predictor of sponging, and that the mitochondrial coding genes were not: there was no evidence of selection in the investigated genes. In our analysis, carrying the haplotype E did not influence an individual's rate of acquisition of sponging, presumably because only 50% of the individuals with this haplotype in our data set were actually spongers. Our results thus support the notion that spongers sharing the same haplotype is not due to a genetic inheritance of sponging but, rather, a result of the simultaneous transmission of a vertically transmitted behaviour and the maternally inherited mitochondrial DNA, a phenomenon referred to as 'cultural hitchhiking' (Kopps et al., 2014a).

To conclude, multi-network NBDA provides a useful tool to quantify the effects of social learning on a behaviour while explicitly accounting for the influence of ecological and genetic factors. Applying NBDA to sponging behaviour in the dolphins of western Shark Bay, we show a strong effect of vertical social learning in the spread of sponging, which, as such, had not been previously quantified. A long-term data set on individuals' associations, habitat use and genetics, in combination with new statistical tools like NBDA provides an ideal framework to assess patterns of transmission of behaviour in free-ranging wild animal populations.

4.5. Ethics

Permits for the use of animals for scientific purposes were granted by the Dept. of Biodiversity, Conservation and Attractions. The animal ethics committees of the University of Western Australia, Murdoch University and the University of Zurich provided approvals for the ethical treatment of animals in scientific research.

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CHAPTER 5.
Long-term decline in survival and reproduction of dolphins following a marine heatwave

5.0. Main text*

One of many challenges in the conservation of biodiversity is the recent trend and predicted increase in the frequency and duration of extreme climatic events (Oliver et al., 2018). The Shark Bay World Heritage Area, Western Australia, endured an unprecedented marine heatwave in 2011. Catastrophic losses of habitat-forming seagrass meadows throughout the bay followed (Arias-Ortiz et al., 2018), along with mass mortalities of invertebrate and fish communities (Pearce et al., 2011). Our long-term demographic data on Shark Bay's iconic population of resident Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) revealed a significant decline in female reproductive rates subsequent to the heatwave. Moreover, capture-recapture analyses indicated 5.9% and 12.2% post-heatwave declines in the survival of dolphins that use tools to forage and those that do not, respectively. This implies that the tool-using dolphins may have been somewhat buffered against the cascading effects of habitat loss following the heatwave by having access to a less severely affected foraging niche (Krützen et al., 2014). Overall, however, lower survival levels have persisted post-heatwave, suggesting that habitat loss following extreme weather events may have prolonged negative impacts on even behaviourally flexible predators feeding at the highest trophic level.

In the Austral summer/autumn of 2011, the coastal waters of Western Australia experienced an unprecedented marine heatwave, with water temperatures rising to 2-4° Celsius above long-term averages for more than two months (Wernberg et al., 2012). In the shallow, subtropical embayment of Shark Bay, an estimated 36% of seagrass meadows were damaged (Arias-Ortiz et al., 2018). Wide-ranging effects associated with the heatwave were documented across lower trophic levels, while those on long-lived or large vertebrates remained more elusive. We investigated the vital rates, *i.e.,* survival and reproduction, of dolphins in the western gulf of Shark Bay, using long-term demographic and behavioural data collected between 2007 and 2017 (Fig. 5.1a; Appendix SI Chapter 5).

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* Chapter 5 has been written in short correspondence format (1000 word limit, continuous main text) and has been accepted for publication in *Current Biology*. Detailed descriptions of methods and results can be found in the Appendix (SI Chapter 5).

We assessed changes in apparent survival of dolphins over time using capture-recapture analyses (Pollock, 1982) (Fig. 5.1a; Appendix SI Chapter 5). Using Akaike weights as approximate model probabilities, there was evidence of a considerable decrease in survival after the heatwave. We suggest that this was likely linked to the well-documented and sizeable losses of prey during the heatwave (Pearce et al., 2011). We also found that, on average, survival remained lower in the seven years after the heatwave compared to before. Again, having most support from the Akaike weights, we suggest that this result is best interpreted as evidence that dolphin mortality was impacted over a protracted period, rather than a single peak following the temperature anomaly, which had much lower support by AIC. As such, the catastrophic reduction in seagrass coverage (Arias-Ortiz et al., 2018), which shows little sign of recovery (Nowicki et al., 2017), appears to be responsible for preventing fish stock recovery, since well-established seagrass meadows represent important breeding grounds and refuge habitat for numerous species (Heithaus, 2004).

We also tested for potential differences in survival between dolphins occupying different habitats, and those that use marine sponges as foraging tools (‘spongers’) versus those that do not (‘non-spongers’) (Krützen et al., 2014). Interestingly, the best performing models based on Akaike weights included an interaction term of the heatwave and individual foraging strategy: while there was an overall decline in dolphin survival post-heatwave, survival of spongers was not as adversely impacted as that of non-spongers (5.9% versus 12.2% decline in survival from pre- to post-heatwave, respectively; Fig. 5.1b; Appendix SI Chapter 5). Sponge use is restricted to deeper channel habitats with no seagrass cover. While both spongers and non-spongers use these channels for foraging, sponge use allows access to a foraging niche which dolphins without the tool-using know-how cannot access (Krützen et al., 2014), implying that the spongers’ foraging niche may have been less severely impacted by the heatwave and subsequent seagrass losses (Fig. 5.1b).

A significantly greater number of calves per female per year was detected pre-heatwave compared to post-heatwave (Poisson GLM; z = -2.579; effect size = 31.6%; 95% C.I. = [7.5%, 55.7%]; p < 0.010; Fig. 5.1c), while no significant differences were found when comparing reproductive success for females from different habitat types (Poisson GLM; z = 1.468; effect size = 18.17%; 95% C.I. = [-6.0%; 42.6%]; p = 0.142), or using different foraging techniques (spongers, non-spongers; Poisson GLM; z = -0.673; effect size = -9.6%; 95% C.I. = [-38.5%; 17.8%]; p = 0.501). This suggests that spongers’ access to a different foraging niche may have led to less severe effects on survival, but not reproduction. Reduced reproductive success as a consequence of significant ecological changes is not surprising, since a decline in food availability is expected to affect the most vulnerable members of a population, *i.e.,* young individuals and those with high nutritional demands, such as pregnant or lactating females (Trites and Donnelly, 2003).

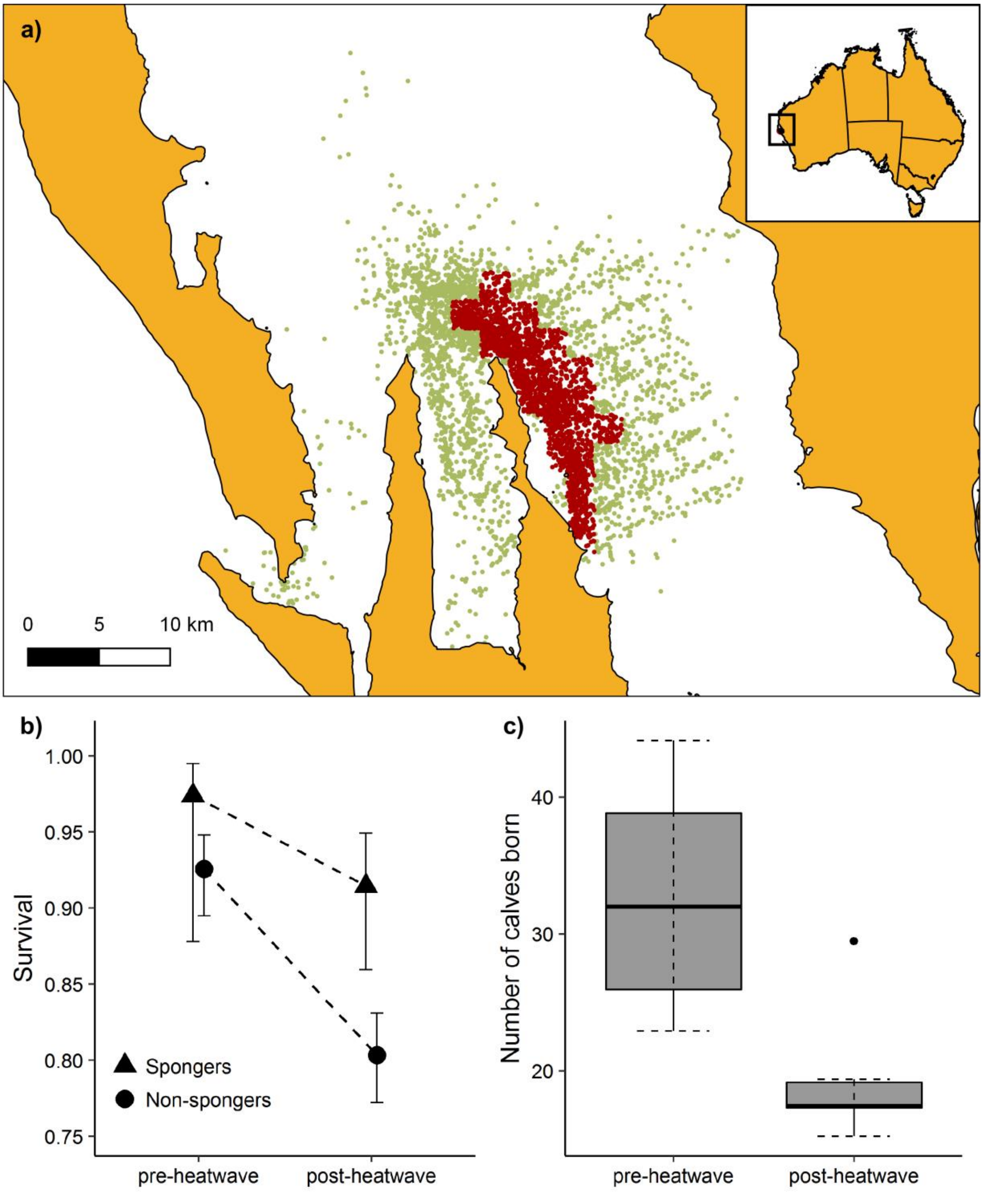

Figure 5.1: *Dolphin vital rates before and after the 2011 marine heatwave in western Shark Bay.* ***a)*** *The study area in the western gulf of Shark Bay, Western Australia, encompassing approximately 1,500 km^2. Over 5,000 dolphin group encounters have been documented between 2007 and 2017 (all dots). To account for unequal survey effort in each field season, the study area was overlaid with a grid of 2 km x 2 km cells. Only encounters within grid cells covered in all seasons ('core' study area) were considered for capture-recapture analyses (dark red dots).* ***b)*** *While both spongers and non-spongers experienced a decline in survival from pre- to post-heatwave, spongers were less affected than non-spongers (5.9% decline versus 12.2% decline, respectively).* ***c)*** *The number of calves detected (controlled for number of known mothers observed each field season) was significantly higher pre- compared to post-heatwave, suggesting that female dolphin reproductive success was also negatively impacted by habitat degradation and prey species loss following the heatwave. (Note that the pre-heatwave data set encompassed only four years, while that post-heatwave was seven).*

There are several plausible explanations for this reduced reproductive success: First, lower prey availability is likely to have forced female dolphins to spend more time foraging, leading to reduced vigilance and, ultimately, greater shark predation on calves. Second, reduced food availability can lead to either increased rates of abortion during pregnancy or increased neonate mortality, when both the mother's and the offspring's nutritional needs cannot be sustained (Trites and Donnelly, 2003). Both abortions and increased mortality of young calves would effectively appear as lower reproductive success in the demographic data. Third, suppressed ovulation or delayed sexual maturity may have occurred when females did not reach a certain threshold of body weight (Boyd et al., 1999). Indeed, along with juvenile survival, fertility is the vital rate most sensitive to changes in resource availability in marine mammals (King et al., 2015).

Western Australia's 2011 marine heatwave negatively impacted habitat-forming and lower-trophic level organisms (Pearce et al., 2011; Wernberg et al., 2012; Arias-Ortiz et al., 2018), and our results suggest a cascading effect on a behaviourally flexible, top-order predator. Long-lived taxa, such as some birds, great apes and cetaceans, are likely to experience changing ecological conditions throughout their lifetimes and, hence, may display behavioural plasticity in adapting to such changes (e.g. Krützen et al., 2011). However, our findings suggest that the ecological consequences of extreme weather events may be too sudden or disruptive for even highly adaptable, cognitively advanced animals to respond, leading to long-term negative impacts on their population viability. Such impacts may persist if ecosystems fail to recover. Furthermore, our study adds to prior research illustrating that extreme events can drive biodiversity patterns and cause shifts in community structure toward more depauperate states (Wernberg et al., 2012; Cheung et al., 2012). These findings raise concerns over the long-term viability of the dolphin population, given that marine heatwaves are occurring with greater frequency and duration in association with anthropogenic climate change (Oliver et al., 2018).

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CHAPTER 6.
General Discussion

6.1. Chapter overview

All four PhD chapters revolved around network-based diffusion analysis (NBDA) and the two foraging strategies, 'shelling' and 'sponging', in the bottlenose dolphin population in Shark Bay, Western Australia. The first of my data chapters (Chapter 2) provided a tool in R to help researchers select an appropriate threshold for the inclusion of individuals in an NBDA when dealing with incomplete association data. Chapter 3 inferred that shelling was horizontally socially transmitted among associated individuals using a multi-network version of NBDA (Farine et al., 2015a), which assessed the importance of social learning while accounting for the influences of ecology and genetics on the spread of the behaviour. In Chapter 4, multi-network NBDA revealed vertical social transmission of sponging from mother to (primarily) female offspring, confirming previously established pathways with new methods (Krützen et al., 2005; Kopps and Sherwin, 2012). Finally, Chapter 5 showed how dolphin vital rates, *i.e.*, reproduction and survival, were negatively affected following a catastrophic marine heatwave in 2011 along the west coast of Australia (Pearce and Feng, 2013; Thomson et al., 2014; Arias-Ortiz et al., 2018), with less adverse effects on sponging individuals compared to individuals without the tool using knowledge.

6.2. NBDA – a powerful and flexible tool to detect and quantify social learning

The last few decades have seen increased interest in questions revolving around animal culture. The development of novel methods like NBDA (Franz and Nunn, 2009; Hoppitt et al., 2010) have brought quantitative statistical tools with which social learning can be detected and quantified in both captive and free-ranging animal populations (e.g. Allen et al., 2013; Watson et al., 2017), and have therefore considerably advanced the field of animal social learning. NBDA has been used not only in its original form to quantify social learning *per se*, but also, for example, to detect social learning strategies (Farine et al., 2015b), and to assess differences in learning between and within species (e.g. Farine et al., 2015a). NBDA's flexibility and potential to be modified from its original form and adapted to improve power to detect learning makes it a valuable and popular tool in studies on animal culture.

The second of my chapters contributes to NBDA's power to detect social learning when dealing with incomplete association data and the resulting uncertainty in social networks. It provides a tool for researchers using NBDA to select a threshold for including individuals when dealing with data on free-ranging populations where not all individuals can be observed at all times. In fact, I have been able to successfully implement the developed simulation approach to the data used in Chapters 3 and 4 to find an appropriate cut-off point for the inclusion of dolphins into the respective data sets that maximized power to detect social learning.

Multi-network NBDA allows the inclusion of several different networks to investigate the spread of a behaviour along different pathways (Farine et al., 2015a). Originally, the multi-network version was used to quantify learning between and within species in populations of wild songbirds (Farine et al., 2015a). In this thesis, I have used multi-network NBDA to assess transmission patterns of shelling (Chapter 3) and sponging (Chapter 4) to quantify the influence of social learning, ecological and genetic factors on their spread. As such, multi-network NBDA takes a further step towards solving the animal cultures debate (Laland and Janik, 2006; Krützen et al., 2007; Laland and Janik, 2007), since it permits not only the quantification of social learning, but also the assessment of the influence of ecology and genetics at the same time, building upon and providing an alternative to repertoire-based methods (Madden et al., 2004; Krützen et al., 2011; Rendell et al., 2012).

6.3. Does shelling qualify as tool use?

Tool use is defined as ‘the conditional external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself when the user holds or carries the tool during or just before use and is responsible for the proper and effective orientation of the tool’ (Mann and Patterson, 2013) based on (Shumaker et al., 2011 [page 5]). Even though tool use is scarce in animals, it is found across several taxa including birds (e.g. Bird and Emery, 2009; Uomini and Hunt, 2017), primates (e.g. Ottoni and Mannu, 2001; Biro et al., 2003), cetaceans (e.g. Krützen et al., 2005; Fujii et al., 2015) and even cephalopods (Finn et al., 2009). In cetaceans, the most famous case of tool use is undoubtedly the use of sponges as foraging tools by bottlenose dolphins in Shark Bay (Smolker et al., 1997; Krützen et al., 2005). The same population of dolphins engages in shelling (Chapter 3), during which dolphins lift empty shells above the surface to gain access to prey items hiding therein (Allen et al., 2011). When shelling, the dolphins use the shell (an unattached environmental object) to expose the prey item to gravity by lifting the shell out of the water (change of the position of another organism, when the user holds the tool) in order to facilitate prey capture and consumption. Therefore, I argue that shelling qualifies as tool use following the Mann and Patterson, (2013) definition, and is therefore the second report of tool use within the Shark Bay dolphin population and in bottlenose dolphins in general.

6.4. Changing climate and behavioural responses

Global climate change is predicted to lead to an increase in the frequency and duration of extreme weather events (Easterling et al., 2000). In a marine environment, such events can include unusual fluctuations in water temperatures, heavy rainfalls, droughts, changes in ocean currents and changes in the frequency of extremes in the El Niño Southern Oscillation cycle (Wu et al., 2012; Cai et al., 2014; Cai et al., 2015). The resulting environmental changes have impacts on marine mammals (and other species) living within the affected ecosystems. Thereby, environmental change can affect a population either directly, for example through rising sea levels or changes in water temperature, or indirectly, such as through changes in the availability of prey or shelter (Learmonth et al., 2006). Combined, both direct and indirect effects can have impacts on community structure, abundance, migration patterns or susceptibility to diseases. These can, in turn, influence reproduction and mortality and hence are important factors in determining if a population persists in the new environment or goes extinct (Learmonth et al., 2006). When faced with environmental changes, individuals may be able to mitigate environmental challenges either by migration to a more suitable habitat or by staying in the affected environment and adapting behaviourally (Learmonth et al., 2006). Behavioural adaptations can, for example, include increases in foraging rates (e.g. Bearzi et al., 1999), temporal shifts of seasonal migration (e.g. Ramp et al., 2015), or changes in reproductive behaviour such as delayed sexual maturity (e.g. Read and Gaskin, 1990; Boyd et al., 1999). If neither migration nor behavioural adaptations are sufficient to buffer environmental changes (if they are too sudden, for example), mortality will increase and, in extreme cases, extirpation or local extinction may occur. In an example of this, an unusual cold-water event combined with two other environmental stressors led to a mass mortality event in a dolphin population in the Gulf of Mexico (Carmichael et al., 2012).

The 2011 marine heatwave in Shark Bay caused a catastrophic die-off of habitat forming seagrass meadows (Thomson et al., 2014; Arias-Ortiz et al., 2018) and mass mortalities in fish and invertebrate communities (Caputi et al., 2014), likely affecting prey availability for the dolphin population. Findings from Chapter 3 suggest that some potential behavioural adaptations may have occurred. First, increased rates of shelling behaviour in years with higher sea surface temperatures suggest that shelling could be a behavioural response to the greater numbers of dead giant gastropod shells available following the 2011 marine heatwave. Second, horizontal social transmission of shelling among adults (rather than the sole reliance on vertically learned foraging strategies during dependency) may represent an adaptation to reduced prey availability through a change in social learning strategies: While stable environments favour conservative behaviour, ecological changes warrant more innovative behaviour to counter-act ecological pressures (Heyes and Galef Jr, 1996; Rendell and Whitehead, 2001;

Whitehead et al., 2004). Horizontal social learning can facilitate the rapid spread of novel adaptive behaviour (Whitehead et al., 2004; Aplin, 2016). Shark Bay dolphins, similar to other toothed whales, are known to be culturally conservative (Rendell and Whitehead, 2001; Whitehead et al., 2004; Barrett-Lennard, 2011), *i.e.*, to heavily rely on the transmission of information and behaviour from mother to offspring (e.g. Yurk et al., 2002; Mann and Sargeant, 2003). I therefore hypothesize that reductions in prey availability after the heatwave may have increased dolphins' willingness to copy novel foraging behaviour from others, *i.e.*, causing a switch in social learning strategies from exclusively using foraging techniques learned from mothers during dependency to also copying novel adaptive behaviour from associates. A switch in social learning strategies due to raised stress levels has been observed in zebra finches (*Taeniopygia guttata*), for example. While juvenile zebra finches would normally adopt foraging skills from their parents (vertically), finches whose stress levels were artificially increased during development learned exclusively from unrelated adults (Farine et al., 2015b). However, in how far the 2011 marine heatwave was responsible for a reliance on horizontal social learning of shelling is difficult to assess without experimental evidence and suitable control data. Given previous anecdotal evidence of horizontal social learning in dolphins (Donaldson et al., 2012; Bossley et al., 2018), such a transmission mechanism appears well within dolphins' capacities, despite being rarely observed.

It is plausible that, when previously learned strategies no longer pay off, behaviourally flexible species, like dolphins, although normally conservative, could adopt novel adaptive behaviours from associates (Whitehead et al., 2004). Nevertheless, Chapter 5 reports long-lasting reductions in survival rates in the Shark Bay dolphin population after the 2011 marine heatwave, suggesting that potential behavioural responses have not been enough to buffer the rapid environmental changes. Mass mortalities in fish and invertebrate communities during and immediately following the heatwave (Pearce et al., 2011; Thomson et al., 2014; Arias-Ortiz et al., 2018) reduced prey availability for higher trophic levels, and the on-going lower survival rates in the dolphin population are likely to reflect a lack of recovery in these stocks. The massive losses of seagrass coverage, combined with slow recovery of the ecologically important seagrass *Amphibolis antarctica* (Nowicki et al., 2017), is thereby most likely preventing prey stock recovery, as seagrass meadows represent important breeding grounds and refuge habitat (Francour, 1997; Heithaus, 2004). Changes in survival have been linked to reduced prey availability in other delphinids. In several killer whale populations, for example, the limited availability of Chinook salmon (*Oncorhynchus tshawytscha*) appeared to have been an important driver of increased mortality (Ford et al., 2010). Further, massive declines in the encounter rates of common dolphins (*Delphinus delphis*) and other high-order predators in the Ionian Sea have been attributed to prey depletion caused by over-fishing (Bearzi et al., 2006).

Chapter 5 further reports a long-term reduction in reproductive rates among female dolphins, which is not surprising since a decline in food availability is expected to primarily affect the most vulnerable members of a population, *i.e.,* young individuals, and those with increased nutritional needs, such as pregnant or lactating females (Trites and Donnelly, 2003). I proposed three, perhaps non-mutually exclusive, plausible explanations for the lower reproductive rates detected in the dolphin population post-heatwave (Chapter 5): i) higher shark predation on dolphin calves due to reduced vigilance of females (Smith et al., 2018); ii) increased rates of abortions or neonate mortality (Trites and Donnelly, 2003); or iii) suppressed ovulation or delayed sexual maturity in female dolphins (Boyd et al., 1999). Increased mortality of very young individuals as a result of environmental stressors was documented in the Gulf of Mexico, where the Deepwater Horizon spill, combined with an unusual influx of cold water, resulted in unusually high mortality of young bottlenose dolphins, twice the rate recorded in a comparable period prior to the events (Carmichael et al., 2012).

Lowered reproductive rates in times of food scarcity have been reported in other marine mammals (Lockyer, 1986; Read and Gaskin, 1990; Boyd, 1996; Boyd et al., 1999). In harbour porpoises (*Phocoena phocoena*), for example, growth rate and age of sexual maturity were found to be related to prey availability (Read and Gaskin, 1990), and, in Antarctic fur seals (*Arctocephalus gazella*), pregnancy duration was longer and reproduction occurred later in life in times of decreased food abundance (Boyd, 1996). Hence, female dolphin ovulation in Shark Bay may have been suppressed in order to conserve energy in response to reduced prey availability. In this case, reduced reproduction may present an adaptation to a new ecosystem in which food is not as abundant.

Both survival and reproduction are important vital rates determining a population's viability. For K-selected species, such as cetaceans, adult survival has been shown to be more important for a population's viability compared to reproduction (Heppell et al., 2000; Crone, 2001; Oli and Dobson, 2003). However, a comparison of two bottlenose dolphin populations in Western Australia found that differences in viability between the Shark Bay and Bunbury populations were best explained by differences in reproduction, rather than adult survival (Manlik et al., 2016). Therefore, while lower survival after the heatwave may have impacted viability in the Shark Bay population to some extent, reduced reproductive rates are, arguably, more problematic for the future viability of this population.

Long-lasting reduced rates of survival and reproduction are eventually going to affect population structure, including association patterns and, potentially, the formation and maintenance of male alliances (Connor et al., 1992; Connor and Krützen, 2015). Male alliances in Shark Bay dolphins serve the purpose of gaining access to oestrous females and defending them against theft by other alliances

(Connor and Krützen, 2015). Alliances are formed in the years after weaning, preferentially with already familiar males of similar age (Gerber et al., in review). Continued reduced reproductive rates, however, may decrease the pool of available allies, forcing young males into suboptimal choices in the formation of alliances. This may mean allying with males with larger age differences, or forming smaller alliances, when successful alliance formation is critical to gaining paternities (Connor and Krützen, 2015; Gerber et al., in review).

6.5. Maintenance of sponging

Krützen et al., (2005) originally inferred vertical social transmission of sponging using the ethnographic method. I used multi-network NBDA in Chapter 4 to show that there is indeed a strong social learning component in promoting the spread of sponging, while ecological and genetic influences were considerably less important. I further confirmed previously suggested vertical pathways of social transmission of sponging from mother to primarily female offspring (Krützen et al., 2005; Mann et al., 2012).

Mathematical modelling has shown that a behavioural trait socially inherited from only one cultural parent is unlikely to be maintained in a population since, in the absence of a fitness benefit of the behaviour, cultural drift, *i.e.*, random fluctuations in the number of individuals performing a behaviour, is likely to eliminate the behaviour (Enquist et al., 2010). Such cultural 'fads', behaviour that appears and disappears again, have been found in killer whales, for example, who started to carry dead salmon (Rendell and Whitehead, 2001), and in bottlenose dolphins, where 'tail-walking' spread among members of the population before disappearing again (Bossley et al., 2018). Kopps and Sherwin, (2012) argued that sponging could be maintained even in the absence of a fitness benefit in the population under some restrictions, specifically, if virtually all daughters acquired sponging from their mothers. Large estimates of the strength of social transmission from mother to female offspring (Chapter 4) indeed suggested that nearly all female offspring of spongers adopt sponging themselves, and hence, sponging could in theory be maintained in the population even in the absence of a fitness benefit. In fact, Mann et al., (2008) could not find any significant differences in reproductive success between sponging and non-sponging females. Results from Chapter 5 confirm that reproductive rates were negatively impacted to the same extent for all females, regardless of foraging specialization. However, while survival rates of all dolphins decreased after the heatwave, spongers were less negatively affected compared to non-spongers, suggesting that sponge tool use, by enabling access to a different foraging niche (Krützen et al., 2014) that may have escaped the effects of the heatwave, may provide a fitness benefit compared to foraging without tools. This may help maintain sponging in the population, even if not all female offspring adopt the behaviour.

6.6. Future research

Multi-network NBDA tracks the spread of a behaviour through different networks. When behaviour is socially transmitted among associated individuals, an individual's likelihood of learning the behaviour increases with the number of informed individuals with whom it associates, since it is more likely to be exposed to the behaviour. An individual's likelihood of being next to learn therefore changes with each acquisition event. Conversely, if a behaviour is purely ecologically driven, an individual's rate of learning is, theoretically, independent of the number of informed individuals with whom it shares a home range and stays constant throughout all acquisition events. Similarly, if individuals were genetically predisposed to behave in a certain way (and there was no effect of social learning), their likelihood of performing the behaviour would remain constant, since they either carry the genetic variant or they do not. In the multi-network NBDA model, however, which tracks the spread of the behaviour with the ecological or genetic network, the likelihood of an individual being next to learn changes with the number of informed individuals that share the same habitat or are closely related. As such, future research should focus on extending the framework of NBDA to include ecological and genetic similarity among individuals as covariates, while testing if the spread of behaviour follows the association networks.

Both shelling and sponging behaviour can only occur where appropriate tools (*i.e.*, empty shells and sponges, respectively) are available. To adequately quantify the influence of ecological factors on the spread of shelling and sponging it is thus desirable to include the number of shells and sponges occurring in each dolphin's home range as covariates in the NBDA models. While prior work has identified ecological characteristics that influence sponge distribution within Shark Bay (Tyne et al., 2012), knowledge of the distribution of shells is not available as yet. Work from other Australian locations shows that both gastropods occur on soft, sandy or muddy substrates, up to 30m and 10m depth for *S. aruanus* and *M. amphora*, respectively (Poutiers, 1998; Slack-Smith and Bryce, 2004). *S. aruanus* is known to feed on polychaete worms, *M. amphora* on sea hares and other molluscs (Coleman, 1975; Taylor and Glover, 2003). Benthic habitat sampling and subsequent habitat suitability modelling may provide insight into the biotic and abiotic factors influencing the abundance and distribution of these giant gastropods within Shark Bay so that, ultimately, shell abundance may be incorporated into future analyses on the spread of shelling behaviour.

Extreme weather events can have long-lasting negative effects on ecosystems and their inhabitants, (e.g. Thomson et al., 2014; Chapter 5). In order to assess the impacts of such events, it is crucial to have ecological and demographic data available from both before and after the event (Smith, 2006). Given the unpredictability of such climatic events, long-term projects are invaluable for research into the impacts of climate change. Research has shown that the below-ground biomass of the seagrass was lowered after the 2011 heatwave, which reduces resilience to disturbances (Fraser et al., 2014). Hence, future extreme heatwaves may have severe consequences on the ecosystem, including higher trophic level predators like bottlenose dolphins. Continued demographic assessments will help to assess the impacts of future ecological disturbances and inform on potential conservation measures.

6.7. Conclusion

Extreme climatic events are occurring with increased frequency (Easterling et al., 2000; Oliver et al., 2018), leading to rapid and potentially long-lasting ecological changes, particularly where habitat forming species are reduced and fail to recover (Thomson et al., 2014; Nowicki et al., 2017). Both effects of and potential responses to such events are difficult to measure in the absence of experimental controls, but can be inferred from observational data collected before and after the impact. Following the 2011 marine heatwave in Shark Bay, three observations are suggestive of behavioural adaptations by dolphins as a response to the environmental stress: i) significantly more shelling behaviour in years with higher sea surface temperatures (Chapter 3); ii) horizontal social transmission of shelling behaviour (Chapter 3); and iii) reduced reproductive rates in female dolphins after the heatwave (Chapter 5). The extent to which they represent responses to the heatwave and subsequent environmental changes, however, requires further investigation. Post-heatwave reductions in survival (Chapter 5) suggest that, though some behavioural responses may have occurred, they were not sufficient to buffer environmental impacts. Sponging individuals were less adversely affected than non-sponging individuals (Chapter 5), so culturally different subpopulations may face different conservation threats, *i.e.*, they may respond to the same threat in different ways (Whitehead et al., 2004). Overall, however, the population experienced long-term reductions in vital rates which may further affect population structure and social dynamics, including association patterns and, potentially, the maintenance of male reproductive alliances (Connor and Krützen, 2015).

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APPENDIX

A2. SI CHAPTER 2

A2.1 Generation of simulated association data

We first simulated a data set with 60 animals. The goal here was simply to generate a typical set of data to test the proposed method developed. The form of the data is similar to the data typically collected by researchers aiming to construct social networks based on association data (for transformation of data formats see Farine, (2013)). We generated a binary data matrix: where each row represents an observation or group, whereas each column represents an individual, with 1 denoting presence in that observation and 0 denoting absence. To generate data of this form, we first simulated how many times each individual was seen using Poisson distributions with 5 different means (25 individuals with a mean of 1, 15 individuals with a mean of 5, 10 individuals with a mean of 20 and 5 individuals each with a mean of 20 and 30 respectively), in random order. This was done as a method to represent heterogeneity in the sampling observation/detection of individuals.

We first simulated the presence/absence of the first individual A in 600 observations by randomly attributing a 1 (presence) to the observations with a probability of n/600 (n = number of sightings for individual A) and 0 (absence) otherwise. For the next, randomly chosen, individual (e.g. individual B), we first chose an associate (*i.e.*, an animal whose sightings had already been assigned), which in the first round was only individual A. We then determined if the two individuals were associated (with a probability of 0.7 of them being associated). If A and B were chosen to be associates, we simulated the strength of association between them using a uniform distribution ranging between 0.5 and 1 (e.g. 0.7). For each observation in which the A was present, we simulated B's presence using their association strength (*i.e.*, 0.7) as a probability of B being present in the same observation. For observations in which A was absent, we determined B's presence as follows: First, we first extracted B's simulated number of sightings (from the Poisson distribution). From that number, we then subtracted both the number of times B had already been seen without A as well as the number of times we would expect A and B to be seen in association (number of sightings for A times the association strength of A and B (*i.e.*, 0.7)). This resulted in an estimate of the remaining number of observations where we expected B to be seen without A. We then divided this number by the remaining number of observations where no other individual was present, which resulted in a probability of B's presence in the observations where A was absent. To reduce noise, we multiplied that probability of B's presence – in absence of A – by 0.001 in all observations where another individual (other than A) was already present. This step prevented B being associated with random individuals. For observations where no other individual was present yet (and A was absent), we multiplied the probability of B's presence by 0.999. After all of B's sightings had been assigned, we chose a new individual from the 58 remaining and randomly selected an associate (*i.e.*, for the second round either A or B) and followed the process as described above. We repeated this process until observations for all 60 individuals had been assigned. We then removed observations where no individual had been assigned, which resulted in 331 remaining observations (SM5).

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A3. SI CHAPTER 3

A3.1. Genetic simulations – Input data and summary statistics

Biopsy sampled individuals were genotyped based on 27 microsatellite markers (Tab. A3.1). We obtained allele frequencies for each locus (Tab. A3.1 and A3.2), missing and error rates (Tab. A3.1) from empirical data and used them as input parameters for simulations in COANCESTRY (Wang, 2011). We chose the estimator with the lowest variance (Tab. A3.3) and the highest correlation with the true value (Tab. A3.4) as the most appropriate estimator for the study population (TrioML).

Table A3.1: Microsatellite markers used to assign genotypes, including error and missing rate

Locus	Missing rate	Error rate	Reference
E12	0.003	0.000	(Nater et al., 2009)
MK6	0.003	0.000	(Krützen et al., 2001)
Tur4_105	0.000	0.000	(Nater et al., 2009)
Tur4_108	0.000	0.000	(Nater et al., 2009)
Tur4_111	0.017	0.000	(Nater et al., 2009)
Tur4_117	0.000	0.034	(Nater et al., 2009)
Tur4_128	0.007	0.000	(Nater et al., 2009)
Tur4_66	0.000	0.000	(Nater et al., 2009)
Tur4_98	0.000	0.000	(Nater et al., 2009)
D22	0.003	0.000	(Shinohara et al., 1997)
D8	0.047	0.000	(Nater et al., 2009)
F10	0.007	0.000	(Nater et al., 2009)
Tur4_138	0.000	0.000	(Nater et al., 2009)
Tur4_141	0.000	0.000	(Nater et al., 2009)
Tur4_87	0.000	0.034	(Nater et al., 2009)
Tur4_91	0.000	0.000	(Nater et al., 2009)
Tur4_162	0.000	0.000	(Nater et al., 2009)
MK9	0.007	0.000	(Krützen et al., 2001)
MK5	0.000	0.000	(Krützen et al., 2001)
Tur4_132	0.000	0.000	(Nater et al., 2009)
KWM12	0.000	0.000	(Hoelzel et al., 1998)
EV37	0.041	0.000	(Valsecchi and Amos, 1996)
Tur4_80	0.000	0.000	(Nater et al., 2009)
MK3	0.007	0.000	(Krützen et al., 2001)
Tur4_142	0.000	0.034	(Nater et al., 2009)
Tur4_153	0.000	0.000	(Nater et al., 2009)
MK8	0.007	0.000	(Krützen et al., 2001)

Table A3.2: Allele frequencies in the western gulf Indo-Pacific bottlenose dolphin population

Locus																
E12	Alleles	260	276	280	264	272	256									
	Frq	0.1854	0.2007	0.051	0.1412	0.3793	0.0425									
MK6	Alleles	154	166	156	174	182	184	172	160	176	152	188	168	180	190	186
	Frq	0.0969	0.0289	0.1156	0.0969	0.017	0.0714	0.1497	0.0697	0.1259	0.1803	0.0374	0.0034	0.0017	0.0017	0.0034
Tur4_105	Alleles	391	367	395	399	387	403									
	Frq	0.1746	0.5458	0.1153	0.0915	0.039	0.0339									
Tur4_108	Alleles	270	258													
	Frq	0.7271	0.2729													
Tur4_111	Alleles	299	303	307	287	295										
	Frq	0.1052	0.7776	0.0672	0.0448	0.0052										
Tur4_117	Alleles	183	179	187	175											
	Frq	0.5915	0.3288	0.0661	0.0136											
Tur4_128	Alleles	303	307	295	299	311										
	Frq	0.5973	0.2031	0.1229	0.0751	0.0017										
Tur4_66	Alleles	201	193	197	205	189										
	Frq	0.7932	0.1644	0.0102	0.0237	0.0085										
Tur4_98	Alleles	192	196													
	Frq	0.4051	0.5949													
D22	Alleles	116	118	110	120											
	Frq	0.4031	0.4677	0.0731	0.0561											
D8	Alleles	326	342	322												
	Frq	0.4751	0.306	0.2189												
F10	Alleles	386	390	382	378											
	Frq	0.3549	0.07	0.43	0.1451											

Tur4_138	Alleles	223	215	207	219	227	211									
	Frq	0.2746	0.4102	0.0644	0.0915	0.1576	0.0017									
Tur4_141	Alleles	238	250	242	282	246	278	254	234	230	218					
	Frq	0.0576	0.2746	0.2542	0.0458	0.1288	0.0254	0.1119	0.061	0.0136	0.0271					
Tur4_87	Alleles	186	178	190	182	194										
	Frq	0.6492	0.1305	0.178	0.0237	0.0186										
Tur4_91	Alleles	227	207	223	231	235	215	211	219							
	Frq	0.3932	0.239	0.0373	0.2085	0.0373	0.0254	0.0237	0.0356							
Tur4_162	Alleles	407	411	403												
	Frq	0.3542	0.5797	0.0661												
MK9	Alleles	168	174	172	170	176	178									
	Frq	0.4352	0.1177	0.2133	0.2116	0.0205	0.0017									
MK5	Alleles	205	213	211	215	219										
	Frq	0.1288	0.3356	0.2949	0.2322	0.0085										
Tur4_132	Alleles	330	334	326												
	Frq	0.9136	0.078	0.0085												
KWM12	Alleles	166	170	174	186	156	164	168	182	190	184	160	188	178	162	161
	Frq	0.3576	0.1729	0.1763	0.0881	0.0712	0.0153	0.0136	0.039	0.0034	0.0475	0.0017	0.0017	0.0017	0.0085	0.0017
EV37	Alleles	204	210	216	202	220	212	194	222	218	224	206	208			
	Frq	0.3339	0.3145	0.0901	0.0495	0.0389	0.0689	0.0477	0.03	0.0159	0.0053	0.0018	0.0035			
Tur4_80	Alleles	311	323	291	315	319	303	327								
	Frq	0.0458	0.3356	0.1305	0.2525	0.1831	0.0305	0.022								
MK3	Alleles	161	163	157	165	167	147	169								
	Frq	0.099	0.3567	0.0956	0.3891	0.0256	0.0034	0.0307								
Tur4_142	Alleles	330	342	334	338											
	Frq	0.1458	0.0492	0.1559	0.6492											

Tur4_153	Alleles	215	219							
	Frq	0.7271	0.2729							
Tur4_MK8	Alleles	103	109	111	107	113	105	87	115	97
	Frq	0.1451	0.0939	0.4471	0.244	0.0119	0.0222	0.0256	0.0068	0.0034

Table A3.3: Summary statistics of seven relatedness estimators resulting from simulations in COANCESTRY

n=600	**TrioML**	Wang	LynchLi	LynchRd	Ritland	QuellerGt	DyadML	TrueValue
Mean	0.267	0.268	0.265	0.269	0.278	0.262	0.289	0.271
Variance	**0.038**	0.046	0.047	0.052	0.095	0.046	0.039	0.033
MSE	0.010	0.015	0.015	0.019	0.060	0.015	0.011	

Table A3.4: Correlation matrix of seven relatedness estimators and the simulated true value.

Correlation Coef	**TrioML**	Wang	LynchLi	LynchRd	Ritland	QuellerGt	DyadML	TrueValue
TrioML	1							
Wang	0.927	1						
LynchLi	0.927	0.969	1					
LynchRd	0.884	0.840	0.841	1				
Ritland	0.666	0.560	0.610	0.820	1			
QuellerGt	0.923	0.930	0.962	0.844	0.635	1		
DyadML	0.995	0.938	0.936	0.894	0.669	0.932	1	
TrueValue	**0.860**	0.820	0.822	0.790	0.610	0.820	0.859	1

A3.2. Modelling vertical transmission using mitochondrial haplotype

We wished to allow for the possibility that shelling might be vertically socially transmitted to some degree. Previous work on bottlenose dolphins provides evidence that foraging skills tend to be socially learned from the mother (Mann and Sargeant, 2003; Krützen et al., 2005). Foraging skills learned in this way show an association with mitochondrial haplotype (henceforth ‘haplotype’) which is also maternally inherited. Thus, inclusion of haplotype as a factor in the analysis models the potential effects of vertical transmission down the matriline. It is important to include haplotype in the analysis for two reasons: a) individuals with the same haplotype might tend to associate, thus if the effects of haplotype are ignored, vertical social transmission might result in a spurious horizontal transmission effect; and b) it allows us to examine at the relative effects of horizontal and vertical social transmission.

Haplotypes A, B, D, E, H, F, I and K were identified in the population. However, including ‘haplotype’ as an 8-level factor is not feasible given the number of acquisition events observed, since it would result in model overfitting. The factor would also be heavily penalized by AICc. We would also not expect all levels of haplotype to differ in their propensity to learn shelling, rather we would expect one or a few haplotypes to show an enhanced propensity to learning shelling due to its presence in the associated matriline. Here our aim is to allow for any confounding effects of vertical transmission.

Consequently, we reduced the levels of ‘haplotype’ to better reflect the potential effects of vertical transmission. It seems clear that Haplotypes E and D had the strongest association with shelling, possibly followed by H. Therefore, we tried three versions of the variable, and ran the full set of NBDA models that included haplotype with each, allowing us to obtain the relative support for each version:

Table A3.5: Support for the haplotype variable with different number of levels

Number of levels	Levels	Support
5	Haplotype E, Haplotype D, Haplotype H, Haplotype F, Haplotypes A,B,I,K	0.4%
4	Haplotype E, Haplotype D, Haplotype H, Haplotypes A,B,I,K,F	8.1%
3	Haplotype E, Haplotype D, Haplotypes A,B,I,K,F,H	88.8%

We therefore based our inferences on analyses using the 3-level version of haplotype. We used Haplotype E as the reference/baseline level since this resulted in a more stable parameterization of the model, and more easily interpreted estimates for *s* (social learning) parameters.

A3.3. Applying network-based diffusion analysis

Analyses were run using the NBDA package v0.6.1 (Hoppitt et al., 2018). We used the multi-network variant of NBDA (Farine et al. 2015), to accommodate our three networks (social association, home range overlap and genetic relatedness). We used the order of acquisition diffusion analysis (OADA) variant of NBDA, which is sensitive only to the order in which individual learned and not the exact times of learning, and makes fewer assumptions (Hoppitt et al., 2010). We included several individual-level variables (ILVs) with potential influence on an individual’s rate of acquisition, namely: an individual’s gender (-0.5 for females, 0.5 for males, 0 for unknown sex); the number of times each individual had been seen (to control for spurious effects of frequently sighted individuals being more likely to be observed with shells); the average water depth of each individual’s sightings (as a proxy for habitat use); the average group size; and mitochondrial haplotype as a factor (reduced to 3 levels: E, D and other; see above).

The parameter *s* (the relative rate of social transmission through each network per unit connection) is estimated relative to a baseline rate of asocial learning. Continuous variables were standardized to have a mean of 0, such that *s* is estimated relative to the asocial learning rate for an individual with mean values for all such variables. The baseline asocial learning rate was set to the midpoint of males and females, and for Haplotype E (which was found to give the most stable parameterization).

Previous studies using NBDA with the inclusion of individual-level variables have selected between an 'additive' model in which the ILVs affect only the rate of asocial learning, and a 'multiplicative' model in which the ILVs all affect both asocial learning and social transmission in the same way. In most published cases so far, either the additive or multiplicative data has been strongly favoured by the data, justifying the use of that model for inference, e.g. (Hasenjager and Dugatkin, 2016; Ladds et al., 2017). In cases where support has been equivocal, the key results have been found to be robust to selection of the additive or multiplicative model. However, we found that different networks were favoured by the additive model (social association network) and multiplicative model (ecological home range overlap). Whilst the additive model was favoured, the difference in support was not large enough for us to be confident in the result.

We therefore used an approach suggested by (Hoppitt and Laland, 2013) and fit a more general 'unconstrained' model in which the effects of each ILV on asocial and social learning are estimated as independent parameters. Thus, we allow for the fact that a) some variables might influence social learning without forcing the model to assume that all variables do so; and b) variables might have a different effect on asocial and social learning.

Here note that the ILV 'haplotype' is intended to model the effects of vertical social transmission (see above). In the standard terminology of NBDA, this ILV is modelled as potentially having an effect on 'asocial' learning and an effect on social transmission. However, note that in this case the first so-called 'asocial' effect is intended to model vertical social transmission.

We fit models with every combination of ILVs affecting social and asocial learning, and every combination of the three networks resulting in 7,200 different models. 123 models could not be fitted and were dropped from the analysis - these were models with a large number of parameters. This is not surprising since we would expect some combinations of variables to result in over-parameterised models given the low number of acquisition events. Such models, if they could be fitted are highly unlikely to yield a favourable AICc and therefore dropping these models is unlikely to affect our conclusions.

Support for each model was calculated using the Akaike Information Criterion corrected for sample size (AICc) (Burnham and Anderson, 2002). This allowed us to derive the support for each combination of networks, and for each ILV (effects on asocial and social learning). We found that standard errors could not be reliably obtained, probably because too many of the key parameters had a highly asymmetrical profile likelihood. For example, for the effect of social transmission we have more information about the lower bound of the effect than about the upper bound. This also makes standards errors a misleading measure of precision, as standard errors may be large due to the uncertainty about the upper bound, obscuring the high degree of confidence in the lower bound. This prevents use of a full model-averaged approach in which one presents unconditional standard errors as a measure of precision (Burnham and Anderson, 2002). Instead we derive 95% confidence intervals using profile likelihood techniques (Morgan, 2008) based on the best predictive model.

A3.4. Influence of ILVs on social and asocial learning of shelling

Analyses suggested a decrease in horizontal learning of shelling with increasing group size, and individuals with haplotype E and D were more likely to acquire shelling independent of the horizontal social network (Tab. 3.6). None of the other ILVs were associated with shelling behaviour (Tab. A3.6).

Table A3.6: Support for ILVs and model averaged estimates

ILV	Gender	Number of sightings	Average water depth	Average group size	Haplotype
Relative support for effect on social learning	0.136	0.108	0.119	**0.629**	0.025
Model averaged estimate* (back-transformed)	-	-	-	x1.99 per associate	-
Profile likelihood confidence interval conditional on the best model	-	-	-	[1.18-3.91] per associate	-
Relative support for effect on asocial learning	0.199	0.097	0.444	0.093	**0.973**
Model averaged estimate* (back-transformed)	-	-	-	-	E/others: 1.46E9 D/E: 41.7
Profile likelihood confidence interval conditional on the best model	-	-	-	-	E/others: [3.1-Inf] D/E: [5.6-303]

* Model averaged estimates are weighted medians across the set of values. In OADA extreme values can badly skew weighted means, even in models with a very small model weighting. Thus, we used weighted medians as a more robust estimate.

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A4. SI CHAPTER 4

A4.1. Genetic simulations – input data and summary statistics

Biopsied individuals were genotyped based on 27 microsatellite markers (Tab. A4.1). We obtained allele frequency for each locus (Tab. A4.1 and A4.2), missing and error rates (Tab. A4.1) from empiric data and used them as input parameters for simulations in COANCESTRY (Wang, 2011). We chose the estimator with the lowest variance (Tab. A4.3) and the highest correlation with the true value (Tab. A4.4) as the most appropriate estimator for the study population (TrioML).

Table A4.1: Microsatellite markers used to assign genotypes including error and missing rates

Locus	Missing rate	Error rate	Reference
E12	0.003	0.000	(Nater et al., 2009)
MK6	0.003	0.000	(Krützen et al., 2001)
Tur4_105	0.000	0.000	(Nater et al., 2009)
Tur4_108	0.000	0.000	(Nater et al., 2009)
Tur4_111	0.017	0.000	(Nater et al., 2009)
Tur4_117	0.000	0.034	(Nater et al., 2009)
Tur4_128	0.007	0.000	(Nater et al., 2009)
Tur4_66	0.000	0.000	(Nater et al., 2009)
Tur4_98	0.000	0.000	(Nater et al., 2009)
D22	0.003	0.000	(Shinohara et al., 1997)
D8	0.047	0.000	(Nater et al., 2009)
F10	0.007	0.000	(Nater et al., 2009)
Tur4_138	0.000	0.000	(Nater et al., 2009)
Tur4_141	0.000	0.000	(Nater et al., 2009)
Tur4_87	0.000	0.034	(Nater et al., 2009)
Tur4_91	0.000	0.000	(Nater et al., 2009)
Tur4_162	0.000	0.000	(Nater et al., 2009)
MK9	0.007	0.000	(Krützen et al., 2001)
MK5	0.000	0.000	(Krützen et al., 2001)
Tur4_132	0.000	0.000	(Nater et al., 2009)
KWM12	0.000	0.000	(Hoelzel et al., 1998)
EV37	0.041	0.000	(Valsecchi and Amos, 1996)
Tur4_80	0.000	0.000	(Nater et al., 2009)
MK3	0.007	0.000	(Krützen et al., 2001)
Tur4_142	0.000	0.034	(Nater et al., 2009)
Tur4_153	0.000	0.000	(Nater et al., 2009)
MK8	0.007	0.000	(Krützen et al., 2001)

Table A4.2: Allele frequencies in the western gulf bottlenose dolphin population

Marker																
E12	Alleles	260	276	280	264	272	256									
	Frq	0.1854	0.2007	0.051	0.1412	0.3793	0.0425									
MK6	Alleles	154	166	156	174	182	184	172	160	176	152	188	168	180	190	186
	Frq	0.0969	0.0289	0.1156	0.0969	0.017	0.0714	0.1497	0.0697	0.1259	0.1803	0.0374	0.0034	0.0017	0.0017	0.0034
Tur4_105	Alleles	391	367	395	399	387	403									
	Frq	0.1746	0.5458	0.1153	0.0915	0.039	0.0339									
Tur4_108	Alleles	270	258													
	Frq	0.7271	0.2729													
Tur4_111	Alleles	299	303	307	287	295										
	Frq	0.1052	0.7776	0.0672	0.0448	0.0052										
Tur4_117	Alleles	183	179	187	175											
	Frq	0.5915	0.3288	0.0661	0.0136											
Tur4_128	Alleles	303	307	295	299	311										
	Frq	0.5973	0.2031	0.1229	0.0751	0.0017										
Tur4_66	Alleles	201	193	197	205	189										
	Frq	0.7932	0.1644	0.0102	0.0237	0.0085										
Tur4_98	Alleles	192	196													
	Frq	0.4051	0.5949													
D22	Alleles	116	118	110	120											
	Frq	0.4031	0.4677	0.0731	0.0561											
D8	Alleles	326	342	322												
	Frq	0.4751	0.306	0.2189												
F10	Alleles	386	390	382	378											
	Frq	0.3549	0.07	0.43	0.1451											

Tur4_138	Alleles	223	215	207	219	227	211									
	Frq	0.2746	0.4102	0.0644	0.0915	0.1576	0.0017									
Tur4_141	Alleles	238	250	242	282	246	278	254	234	230	218					
	Frq	0.0576	0.2746	0.2542	0.0458	0.1288	0.0254	0.1119	0.061	0.0136	0.0271					
Tur4_87	Alleles	186	178	190	182	194										
	Frq	0.6492	0.1305	0.178	0.0237	0.0186										
Tur4_91	Alleles	227	207	223	231	235	215	211	219							
	Frq	0.3932	0.239	0.0373	0.2085	0.0373	0.0254	0.0237	0.0356							
Tur4_162	Alleles	407	411	403												
	Frq	0.3542	0.5797	0.0661												
MK9	Alleles	168	174	172	170	176	178									
	Frq	0.4352	0.1177	0.2133	0.2116	0.0205	0.0017									
MK5	Alleles	205	213	211	215	219										
	Frq	0.1288	0.3356	0.2949	0.2322	0.0085										
Tur4_132	Alleles	330	334	326												
	Frq	0.9136	0.078	0.0085												
KWM12	Alleles	166	170	174	186	156	164	168	182	190	184	160	188	178	162	161
	Frq	0.3576	0.1729	0.1763	0.0881	0.0712	0.0153	0.0136	0.039	0.0034	0.0475	0.0017	0.0017	0.0017	0.0085	0.0017
EV37	Alleles	204	210	216	202	220	212	194	222	218	224	206	208			
	Frq	0.3339	0.3145	0.0901	0.0495	0.0389	0.0689	0.0477	0.03	0.0159	0.0053	0.0018	0.0035			
Tur4_80	Alleles	311	323	291	315	319	303	327								
	Frq	0.0458	0.3356	0.1305	0.2525	0.1831	0.0305	0.022								
MK3	Alleles	161	163	157	165	167	147	169								
	Frq	0.099	0.3567	0.0956	0.3891	0.0256	0.0034	0.0307								
Tur4_142	Alleles	330	342	334	338											
	Frq	0.1458	0.0492	0.1559	0.6492											

Tur4_153	Alleles	215	219							
	Frq	0.7271	0.2729							
Tur4_MK8	Alleles	103	109	111	107	113	105	87	115	97
	Frq	0.1451	0.0939	0.4471	0.244	0.0119	0.0222	0.0256	0.0068	0.0034

Table A4.3: Summary statistics of seven relatedness estimators resulting from simulations in COANCESTRY

n=600	TrioML	Wang	LynchLi	LynchRd	Ritland	QuellerGt	DyadML	TrueValue
Mean	0.267	0.268	0.265	0.269	0.278	0.262	0.289	0.271
Variance	**0.038**	0.046	0.047	0.052	0.095	0.046	0.039	0.033
MSE	0.010	0.015	0.015	0.019	0.060	0.015	0.011	

Table A4.4: Correlation matrix of seven relatedness estimators and the simulated true value

Correlation Coef	**TrioML**	Wang	LynchLi	LynchRd	Ritland	QuellerGt	DyadML	TrueValue
TrioML	1							
Wang	0.927	1						
LynchLi	0.927	0.969	1					
LynchRd	0.884	0.834	0.841	1				
Ritland	0.666	0.595	0.610	0.820	1			
QuellerGt	0.923	0.930	0.962	0.844	0.635	1		
DyadML	0.99	0.938	0.936	0.894	0.669	0.932	1	
TrueValue	**0.860**	0.820	0.822	0.790	0.610	0.821	0.859	1

A4.2. Selecting a threshold for including individuals to maximize power of NBDA

Since NBDA infers social learning if a behaviour follows the social network, there is a trade-off between sample size and data quality. Only considering individuals above a certain threshold of sightings (*i.e.*, dropping individuals with only few sightings) can increase certainty about the strengths of connections within the network, but at the same time decrease power of NBDA to reliably detect social learning, if linking individuals are removed (Wild and Hoppitt, 2018; Chapter 2). To select a threshold that maximises power of NBDA to detect social learning, we ran a simulation approach (Wild and Hoppitt, 2018; Chapter 2), – for computational reasons only considering individuals that had been seen at least five times (N=538 individuals). A social learning process is simulated though the population assuming learning follows the NBDA model. The resulting order of acquisition is then used in an NBDA which uses a social network with introduced observational error that varies with the number of times each dyad has been seen together or apart. Low numbers of sightings may result in greater error, while a large number of sightings results in a value that is closer to the real strength of association between individuals. Power of NBDA is then calculated as the percentage of models where social learning correctly outperforms asocial models. We ran the simulations with parameters *s* = 20 (selected through trial and error), number of learners = 9 and tested for cut-off points of 5-20 sightings. Thereby, the social learning parameter *s* estimates the strength of social transmission per unit of association with informed individuals relative to the rate of asocial learning (Hoppitt et al., 2010). The number of individuals that learned sponging between 2007 and 2018 in our empirical data set was 18. However, for nine individuals maternity data was unavailable and they were therefore excluded from the NBDA analysis as learners (see manuscript), which is why we set the number of learners in the simulation to nine instead of 18. A threshold of seven sightings resulted in highest statistical power, with an acceptable (though slightly conservative) level of a false positive error rate (1.2%), in models where *s* was set to 0. The simulation approach is set up to simulate learning among associated individuals and does not take different pathways into account. Therefore, the threshold of seven is thought to maximize the power of NBDA to detect horizontal social learning in the sponging data set.

A4.3. Applying NBDA

Previous studies using NBDA with the inclusion of individual-level variables (ILVs) have selected between an 'additive' model in which the ILVs affect only the rate of asocial learning, and a 'multiplicative' model in which the ILVs all affect both asocial learning and social transmission in the same way. Here, we used an approach suggested by (Hoppitt and Laland, 2013) and fit a more general 'unconstrained' model in which the effects of each ILV on asocial and social learning are estimated as independent parameters. Thus, we allow for the fact that a) some variables might influence social learning without forcing the model to assume that all variables do so; and b) variables might have a different effect on asocial and social learning.

We found that standard errors for transmission parameters *s* and for the ILVs could not be reliably obtained, because of highly asymmetrical profile likelihood. This also makes standard errors a misleading measure of precision. Therefore, we derived 95% confidence intervals for parameters using profile likelihood techniques (Morgan, 2008) based on the best predictive model.

A4.4. Influence of ILVs on social and asocial learning rates

Results suggested an increase in vertical social learning of sponging when being female. None of the other ILVs were associated with the learning rate of sponging (socially or asocially) (Tab. A4.5).

Table A4.5: Support for ILVs and model averaged estimates

ILV	Gender	Average water depth	Average group size	Haplotype
Relative support for effect on social learning	**0.975**	0.167	0.110	0.069
Model averaged estimate* (log-scale)	4.84	-	-	-
Profile likelihood confidence interval conditional on the best model	[-7.97, 2.24]	-	-	-
Relative support for effect on asocial learning	0.056	0.017	0.060	0.056
Model averaged estimate	-	-	-	-
Profile likelihood confidence interval conditional on the best model	-	-	-	-

* Model averaged estimates are weighted medians across the set of values. In OADA, extreme values can badly skew weighted means, even in models with a very small model weighting. Thus, we use weighted medians as a more robust estimate.

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A5. SI CHAPTER 5

A5.1. Field methods

Boat-based surveys were conducted between April and October from 2007 to 2017 in the western gulf of Shark Bay, Western Australia, based at our long-term research site at the township of Useless Loop. The broader study area stretches over approximately 1,500 km^2 (Fig. A5.1). Weather-dependent sampling (daylight hours, low wind, no rain, Beaufort sea state ≤3) was carried out on either predetermined, systematic transects or on a less structured basis within the boundaries of the study area (see below). On sighting, each dolphin group was approached for the purposes of recording GPS location and water depth, conducting individual photo-identification and observing behaviour over a minimum of five minutes (hereafter termed a 'survey'). Individuals were identified based on the markings on and shape of their dorsal fins using standard photo-ID techniques (Würsig and Jefferson, 1990). Group composition was recorded based on the 10 m chain rule (Smolker et al., 1992). Foraging behaviour was recorded (as sponging or otherwise), and an individual was considered a 'sponger' after having been seen foraging with a sponge on at least two different days (Mann et al., 2008). Date of birth for 266 calves was estimated based on body size, presence of foetal lines (Mann and Smuts, 1999) and time since the last encounter of the mother in absence of a calf. For 118 calves, birth dates were estimated with an accuracy of two years, for 148 calves accuracy was one year or less.

A5.2. Demographic analyses

Photographic capture-recapture data was used to estimate apparent survival (the product of true survival and permanent emigration), while controlling for temporary migration patterns and capture and recapture probabilities, using Pollock's closed robust design (PCRD) (Pollock, 1982). The PCRD is a hierarchical sampling strategy that includes repeated sampling of a population under 'closure' (*i.e.,* no births or deaths, called 'secondary periods'), which are nested within broadly spaced 'primary periods'. The sampling structure increases the effective capture-probability of animals that are difficult to detect and facilitates estimation of temporary emigration processes (Pollock, 1982; Kendall and Nichols, 1995; Kendall et al., 1997). The population is assumed 'closed' within primary periods and open between primary periods (Pollock, 1982). Consideration of temporary migration is especially important for populations with wide-ranging individuals, such as dolphins. In the case of Shark Bay dolphins, temporary migration can be viewed as movements in and out of the study area, given the well documented, strong philopatric tendencies of both sexes in this population (Krützen et al., 2004; Tsai and Mann, 2013; Allen et al., 2016).

Ideally, capture-recapture analyses are based on data collected along systematic transects designed to ensure consistent coverage of the study area. Since the Dolphin Innovation Project is long-term and multi-strategy, with foci on behaviour, social structure, genetics, ecology, and communication, systematic transects have not been conducted in all field seasons. In seasons in which transect-based sampling was not conducted, either particular areas or subsets of dolphins were targeted according to different scientific questions, or broad coverage of the study area was attempted in order to continue contributing to the long-term demographic data. To account for unequal survey effort across field seasons, we overlaid the study area with a 2 x 2 km grid and only included surveys within grid cells that had been covered in all field seasons (core study area) (Fig. A5.1a). To test for robustness of the model estimates, analyses were repeated with a more inclusive data set based on visual inspection (Fig. A5.1b), with more grid cells included in the Northern (shallower) part of the study area, where seagrass loss has been most severe (Arias-Ortiz et al., 2018) and survey effort had been intensified after 2008 (results on robustness follow the main results).

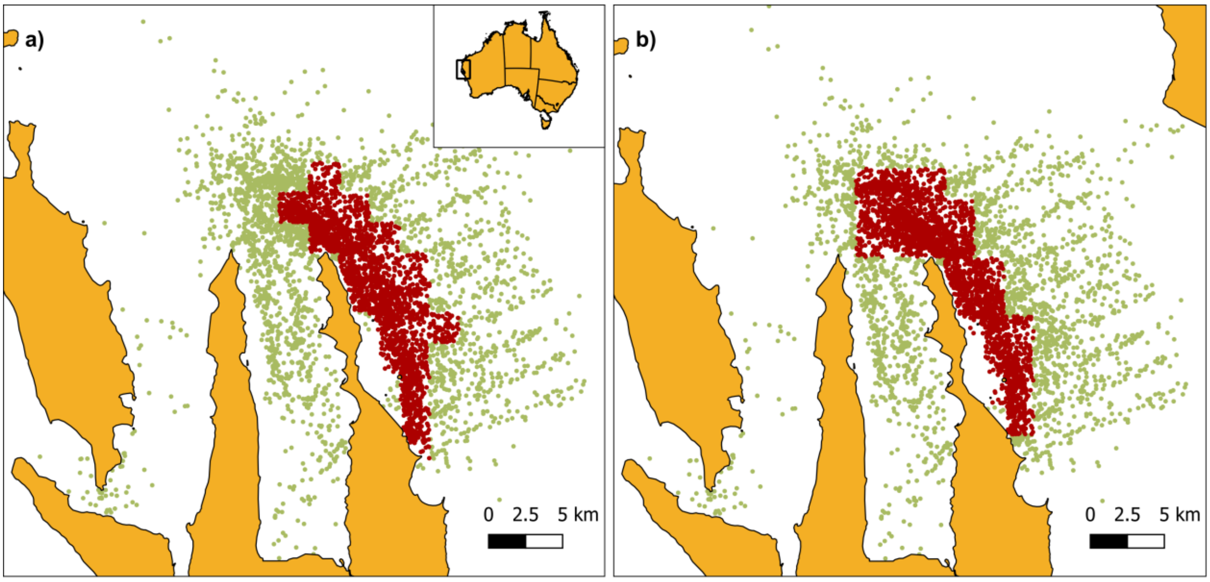

Figure A5.1: *The study area in the western gulf of Shark Bay, Western Australia, encompasses approximately 1,500 km*^{2}*. Over 5,000 dolphin group encounters have been documented between 2007 and 2017 (all dots).To account for unequal survey effort in each field season, the study area was overlaid with a grid of 2 km x 2 km cells. Capture-recapture analyses were run on data sets with two different levels of inclusiveness:* ***a)*** *the core study area consisting of grid cells that had been covered in all seasons; and* ***b)*** *a more inclusive area of mainly the Northern part of the study area where seagrass die-off had been most severe (Arias-Ortiz et al., 2018). Light green dots represent locations of all dolphin groups encountered between 2007 and 2017, whereas dark red dots represent the surveys that were included in the respective data set.*

For application of PCRD, several assumptions have to be fulfilled (Pollock, 1982; Pollock et al., 1990):

First, individuals have to possess unique markings and be correctly identified (Otis et al., 1978). Hence, many previous studies on the demographic characteristics of marine mammals, including survival or abundance, have excluded individuals with insufficient markings (e.g. Nicholson et al., 2012; Sprogis et al., 2016). This is usually the case for calves and juveniles, as they are born with 'clean' fins and only acquire marks throughout their lifetimes. However, we were interested primarily in survival rates across the population. We elected to keep all individuals in our data set, regardless of the distinctiveness of the fin, because calves and recently weaned juveniles are expected to be most vulnerable to environmental stressors (Trites and Donnelly, 2003). For identification, we also relied on more subtle features, such as small nicks, fin shape or scarring patterns for less distinctive individuals. Most individuals in the study population are very well known and have been photographed on numerous occasions, allowing matching based on more subtle marks, including temporary scarring. To verify correct identification of individuals, all photo-identification data were double checked by a second observer.

Second, populations are assumed to be closed within primary periods (*i.e.*, no births, deaths or permanent emigration), but open between primary periods (Pollock, 1982). We chose years as primary periods, assuming population closure over the duration of one field season (two-four months), because reproduction is moderately seasonal in Shark Bay, with most births occurring between September and January (Austral summer) (Connor et al., 1996; Mann et al., 2000).

Third, individuals are supposed to have equal probability of being captured within sampling periods. Unequal capture probability primarily influences abundance estimates, but is less likely to influence survival rates (Pollock, 1982), the main inference of our study. Nevertheless, we accounted for unequal capture probabilities by fitting full heterogeneity models, which allow for individual heterogeneity in both capture as well as recapture probabilities.

Fourth, all individuals have equal probability of survival. This assumption is likely to be violated in our data, given we included all individuals regardless of age, and calf mortality in the Shark Bay dolphins is known to be high, at 44% by the age of three years (Mann et al., 2000). However, we were primarily interested in survival estimates as a whole-population index, and document changes over time (especially pre- and post-heatwave). This is somewhat confounded with changes in the demographic composition of the marked population over time (e.g., if the proportion of low-survival juveniles changes *versus* the proportion of high-survival adults). However, we assumed such changes were essentially random and exhibited no trend over the study.

Fifth, secondary period sampling occasions are supposed to be instantaneous. To ensure coverage of the entire core study area described above, we used calendar months as secondary periods, resulting in eleven primary (2007-2017) and two to five secondary periods per primary period, depending on the duration of the field seasons. Since calendar months as secondary periods are relatively large, the assumption of instantaneous sampling is violated. This places downward pressure on capture probabilities (animals assumed to be in the study area during all secondary periods, but who have left, are scored as 'missed-captures'), and potentially larger survival estimates. So long as the magnitude of the violation is constant over the study period, then the relative change in survival will be unbiased. Alternatively, we deemed it more plausible that periods of intense changes in survival may result in more intense in-and-out movement of animals between secondary periods (and, therefore, more downward bias in capture probabilities and more upward bias in point-survival efforts). Therefore, this bias works to *reduce* our power to detect changes in survival.

Models were created fitting the parameters apparent survival rate (*S*), temporary migration rates (*Gamma'*, *Gamma''*), capture probability (*p*), recapture probability (*c*), and the parameter *pi*, which controls individual capture and recapture heterogeneity. *Gamma''* is defined as the probability of an individual becoming a temporary emigrant, given it was alive and observed in the study area during the previous primary period (Kendall et al., 1997). *Gamma'* describes the probability of an individual being a temporary emigrant given it was already a temporary emigrant in the previous primary sampling period (Kendall et al., 1997).

The models assumed that either survival was constant over time (denoted *(.)*), varied from year to year (denoted *(time)*), or varied only between the periods 'pre' (2007-2010) and 'post' (2011-2017) heatwave (denoted *(heat)*). We also included individual-level variables to investigate potential differences in survival among dolphins: *forage* allowed for a difference between spongers and non-spongers, *depth* for a difference between habitat types. For *depth*, we averaged the water depth of all sightings for each individual and assigned each individual to either *shallow* (<10 m) or *deep* (>10 m), since dolphins in the western gulf show strong natal habitat preferences for either shallow or deep water habitat (Kopps et al., 2014). Seagrass almost exclusively occupies depths of less than 12m in western Shark Bay (Tyne et al., 2012), which is why the two habitats may have been differentially affected by the heatwave. Where both *forage* and *depth* occurred in a model together, they were replaced with a single composite variable (*composite*) with three levels ('shallow all'; 'deep sponger'; 'deep non-sponger'), since, in our entire data set, only one sponger was found in shallow water. The variable 'composite' served for avoiding three-way interactions and, hence, over-complexity of models. We also allowed for interactions between each individual-level variable (*forage/depth/composite*) and time variables (*time/heat*) (Fig. A5.2).

To estimate temporary emigration out of the study area (resulting in individuals being unavailable for capture), three patterns were considered: i) no emigration (*Gamma′* and *Gamma′′* = 0); ii) random temporary emigration, where the probability of an individual being present within a primary period is independent of its presence in the previous sampling period (*Gamma′* = *Gamma′′*); and iii) Markovian emigration, where the presence of an individual within a primary period is dependent on whether it was present during the previous primary sampling period (*Gamma′* and *Gamma′′* independently estimated). Both *Gamma* parameters were either i) set to be constant (.), ii) allowed to vary with years (*time*), the heatwave covariate (*heat*), foraging strategy (*forage*), habitat preference (*depth*) or the variable grouping individuals into habitat/forage categories (*composite*), or iii) were set to 0 (for no emigration). We did not specify any interaction terms among the Gamma parameters (Rankin et al., 2016), in order to avoid over-complexity for the *Gamma′* parameter that is not easily identifiable (Fig. A5.2).

In a first set of models, both capture and recapture probabilities were either set to be constant *(.)*, or varying with years (*t = time*) or both with years and months (*ts = time.session*). As such, setting *pi* = 1 enforced no heterogeneity in individual capture or recapture probabilities. We further fitted full heterogeneity models, which allowed for individual heterogeneity in both capture as well as recapture probabilities (*het*, *het2*) while varying *pi* either with foraging strategy (*forage*), depth (*depth*), the composite variable (*composite*) or setting it to be constant (.). Thereby, '*het*' only allowed for individual heterogeneity in capture and recapture probability, while '*het2*' also allowed for variation between primary and secondary periods.

Models were fit using R package Rmark (White and Burnham, 1999; Laake and Rexstad, 2015) in all possible combinations of the parameters (as specified in Fig. A5.2), resulting in 7,548 different models. The Akaike's Information Criterion corrected for small sample size (AICc) (Hurvich and Tsai, 1989; Anderson et al., 1998) was used to estimate relative model support, the model with the lowest AICc having the most evidential support (Anderson et al., 1998; Burnham and Anderson, 2002). Eleven models that did not result in parameter estimates were refitted with new initial parameters from similar models.

Survival *Temporary emigration* *Individual capture/recapture probabilities*

$$\text{Encounter history} = \left\{\begin{matrix} S(.)\\ S(heat)\\ S(time)\\ S(forage)\\ S(depth)\\ S(split)\\ S(heat * forage)\\ S(time * forage)\\ S(heat * depth)\\ S(time * depth)\\ S(heat * composite)\\ S(time * composite) \end{matrix}\right\} * \left\{\begin{matrix} Gamma'(.) = Gamma''(.)^{*}\\ Gamma'(time) = Gamma''(time)^{*}\\ Gamma'(heat) = Gamma''(heat)^{*}\\ Gamma'(forage) = Gamma''(forage)^{*}\\ Gamma'(depth) = Gamma''(depth)^{*}\\ Gamma'(composite) = Gamma''(composite)^{*}\\ \begin{pmatrix} Gamma'(.)\\ Gamma'(time)\\ Gamma'(heat)\\ Gamma'(forage)\\ Gamma'(depth)\\ Gamma'(composite) \end{pmatrix} * \begin{pmatrix} Gamma''(.)\\ Gamma''(time)\\ Gamma''(heat)\\ Gamma''(forage)\\ Gamma''(depth)\\ Gamma''(composite) \end{pmatrix}^{**}\\ Gamma' = Gamma'' = 0^{***} \end{matrix}\right\} * \left\{\begin{matrix} \begin{pmatrix} p(.)\\ p(t)\\ p(ts) \end{pmatrix} * \begin{pmatrix} c(.)\\ c(t)\\ c(ts \end{pmatrix} * (pi = 1)\\ (p(het) * c(het) * \begin{pmatrix} pi(.)\\ pi(forage)\\ pi(depth)\\ pi(composite) \end{pmatrix}\\ p(het2) * c(het2) \begin{pmatrix} pi(.)\\ pi(forage)\\ pi(depth)\\ pi(composite) \end{pmatrix} \end{matrix}\right\}$$

S	apparent survival between primary periods
Gamma''	probability of leaving the study area between primary periods
Gamma'	probability of staying outside the study area
p	individual capture probability
c	individual recapture probability
pi	mixture parameter, allowing for heterogeneity in *p* and *c*; *pi* = 1 enforces no heterogeneity

* Random temporary emigration (*Gamma'' = Gamma'*)

** Markovian temporary emigration (*Gamma''≠Gamma'*)

*** No temporary emigration (*Gamma'' = Gamma'* = 0)

Figure A5.2: *Set of Pollock's Closed Robust Design (PCRD) models considered to assess apparent survival rates in the bottlenose dolphin population in the western gulf of Shark Bay, while controlling for temporary emigration and differences in capture and recapture probabilities. The notation (.) indicates that a parameter was kept constant; (heat) indicates that the parameter was allowed to vary with a binary heatwave variable ('pre' for the years 2007-2010 and 'post' for years 2011-2017); (time) indicates that the parameter was allowed to vary with the primary period (years); (forage) indicates that the parameter was allowed to vary with an individual's foraging technique ('sponger' or 'non-sponger'; (depth) allowed a parameter to vary with a binary variable describing habitat preferences ('deep' or 'shallow'); (composite) allowed the parameter to vary with a variable grouping individuals into habitat and foraging preferences ('shallow all'; 'deep sponger'; 'deep non-sponger'); (ts) indicates that capture (p) and recapture (c) probabilities were allowed to vary by both primary (years) and secondary periods (months); (het) allowed for individual heterogeneity in capture and recapture probabilities (when pi≠1), while (het2) allowed for individual heterogeneity in capture and recapture probabilities plus allowed for them to vary by primary and secondary periods (when pi≠1).*

To assess changes in female reproductive rates, we used a Poisson Generalised Linear Model (GLM) to test for the number of calves born each year pre- and post-heatwave, while correcting (as an offset) for the number of females seen each season that were known to have had a least one calf between 2007 and 2017. To investigate differences in reproduction between dolphins from different habitat types and/or with different foraging techniques, we ran the models i) on all females pooled together; ii) with depth as a covariate (shallow, deep); iii) with foraging technique as a covariate (non-sponger, sponger); and iv) with the composite variable as a covariate with levels as described above (shallow all, deep non-sponger, deep sponger).

A5.3. Demographic results

Between 2007 and 2017, over 5,000 dolphin groups were encountered in the western gulf of Shark Bay and 1,013 different individuals identified. After removal of surveys outside the core study area (see Methods), 2,005 surveys including 482 different individuals remained for fitting capture-recapture models. Of these, 60 individuals were defined as spongers and 422 as non-spongers.

A5.4. Reduced survival after the heatwave

The top four models accounted for >95% of the posterior model probabilities. They shared several structural features: they included heatwave and foraging strategy as covariates for survival (either as *S(heat*forage)* or *S(heat*composite)*); they had time-varying random emigration; they included re/capture probabilities with temporal heterogeneity by primary and secondary periods, including habitat and/or foraging strategy dependent individual heterogeneity probabilities. Since *S(heat*composite)* and *S(heat*forage)* refer to slightly different groups of dolphins (see Methods), and the top two models (both with *S(heat*forage)*) reached a cumulative Akaike weight of >0.8, estimates for apparent survival were averaged across the first two models only.

The fundamental motivation of AIC is not hypothesis testing. Instead, the AIC provides support for estimates that are (approximately) best at minimizing expected estimation error. In our study, models including the heatwave covariate received most support. Therefore, best approximation of the shape of the survival time series is one in which there is a sudden break following the heatwave. It is important to note that in reality, the survival time series could of course have a more complex shape (such as a recovery in survival since the heatwave or other forms). Such forms, however, were not favoured as evidenced by the low Akaike weights of models with survival varying by years. Note that a very large sample size would increase power sufficiently to reliably estimate year-to-year changes in survival. The AICc, however, suggests that, given the current sample size, more complex forms could not be reliably estimated. If we use Akaike weights are approximate model probabilities (Link and Barker, 2006; Lukacs et al., 2007), then there is evidence of a persistent effect of the heatwave and subsequent habitat degradation.

Model averaged estimates indicate that apparent survival of spongers was less negatively affected than that of non-spongers (5.9% *versus* 12.2% decline in survival from pre- to post-heatwave, respectively). The difference in the effect of the heatwave on spongers and non-spongers was estimated to be 6.3%. Apparent survival, normally encompassing both true survival and permanent emigration, is here assumed to be a good approximation of true survival, because both sexes are highly philopatric and permanent emigration has not been documented in Shark Bay dolphins (Krützen et al., 2004; Nicholson et al., 2012).

A5.5. Assessing robustness of survival estimates

To account for unequal survey effort across seasons, we overlaid the study area with a 2x2 km grid and only included grid cells that had been covered in all seasons, *i.e.*, contained at least one survey each year (see methods and main results). The demarcation of the 'core study area' has an element of reasoned arbitrariness to it. Therefore, to ensure robustness of our results, we repeated all sets of models with a more inclusive data set (Fig. A5.1b), as well as shorter secondary periods (calendar months and half months) for the core study area. For half months, all encounters on the 1st until the 15th of each month were considered to be in the first half, while encounters between the 16th until the end of each month were considered to be in the second half of the month. With calendar months, the number of secondary periods varied between two and five for each primary period, whereas for half months the number of secondary periods within each primary period ranged between five and 10. Eight models not resulting in parameter estimates (inclusive data set) were rerun using initial parameters of similar models. The top 95% of models of each data set (based on their Akaike weights) were considered in the results.

For both the core (main results) and inclusive data set, the top 95% of models (based on Akaike weights) showed most support for survival varying with the heatwave covariate as well as individual foraging strategy (Akaike weight core: 0.806; Akaike weight inclusive: 0.896). Model averaged parameter estimates for apparent survival of the more inclusive data set confirmed findings of the core study area: estimates for apparent survival were within 0.3% of estimates presented in the main results, and reductions in survival from pre- to post-heatwave for non-spongers were 11.7% (from 92.6% to 80.9%) and 6.3% for spongers (from 97.4% to 91.1%). For smaller secondary periods (half months), models with survival varying with the composite variable received most support (Akaike weight: 0.991), which further confirmed differential impacts of the heatwave depending on an individual's foraging strategy. Reductions from pre- to post-heatwave were lowest for spongers in deep water (6.0% reduction from 97.4% to 91.4%), followed by non-spongers in deep water (10.8% reduction from 92.6% to 81.8%) and all shallow water individuals (13.4% reduction from 92.4% to 79.0%). This suggests that, despite unequal survey effort across different field seasons and the *ad libitum* data collection in some field seasons, results on differential impacts on spongers *versus* non-spongers are reliable. While models with half months as secondary period show differential survival for non-spongers from shallow and deep habitat, they confirm our main results, that i) survival estimates for all individuals declined post-heatwave, and ii) that spongers were less affected than non-spongers from both shallow and deep habitat.

Lower survival of shallow water individuals compared to deep water individuals (both spongers and non-spongers) further indicates that reductions in vital rates are most likely driven by losses of seagrass and a lack of recovery (Nowicki et al., 2017).

A5.6. Ethics

Permits for the use of animals for scientific purposes were granted by the Dept. of Biodiversity, Conservation and Attractions. The animal ethics committees of the University of Western Australia, Murdoch University and the University of Zurich provided approvals for the ethical treatment of animals in scientific research.

A5.7. References

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