LIFETIME STABILITY, MATERNAL EFFECTS, AND FITNESS OUTCOMES OF SOCIO-ECOLOGICAL STRATEGIES IN WILD BOTTLENOSE DOLPHINS

A Dissertation
submitted to the Faculty of the
Graduate School of Arts and Sciences
of Georgetown University
in partial fulfillment of the requirements for the
degree of
Doctor of Philosophy
in Biology

By

Taylor Camille Evans, B.S.

Washington, D.C.
November 17, 2021
LIFETIME STABILITY, MATERNAL EFFECTS, AND FITNESS OUTCOMES OF SOCIO-ECOLOGICAL STRATEGIES IN WILD BOTTLENOSE DOLPHINS

Taylor Camille Evans, B.S.

Thesis Advisor: Janet Mann, Ph.D.

ABSTRACT

Individuals within a population differ in behavior along both social and ecological axes. These differences are proposed to be governed by niche theory at the individual level, but empirical evidence is sparse, especially over longer time scales. To understand the proximate and ultimate factors behind individual socio-ecological niches, we need to know how stable individual differences are on a lifetime scale, how these multivariate traits are structured and what transmission mechanisms can tie socio-ecological differences to fitness. In this dissertation, I leverage 32 years of data collected on wild bottlenose dolphins to explore individual differences in social and ecological behavior.

Chapter 1 investigates the longevity of social ‘personality’ across the lifetime of bottlenose dolphins. Multiple measurements of social behavior (time spent alone, in large groups, average # of associates and same-sex associates) were repeatable beginning in the calf period and lasting through old age. Multivariate analysis revealed that social measurements are correlated and can be treated as a behavioral syndrome akin to the human extroversion-introversion axis.

Chapter 2 explores individual ecological differences, their relationship with social traits and a subsequent socio-ecological spectrum. Home range size, habitat use preferences, and some foraging tactics were individually repeatable over decades. The correlation between individual
ecological behaviors and social traits exposed a socio-ecological syndrome, with sex differences dictating tradeoffs between time-intensive foraging tactics and social behaviors.

Chapter 3 addresses the sex-dependent maternal effects and potential fitness effects of individual socio-ecological strategy. Maternal strategy was a strong predictor of offspring strategy, especially for females. Males were more likely to differ from their mothers compared to females. And while most strategies were not associated with differing fitness payoffs, corroborating predictions from niche theory, females that use marine sponges as tools during foraging had a reduced mortality hazard.

This dissertation provides rare empirical evidence for the existence, persistence, and transmission through maternal effects of individual socio-ecological strategies and builds a framework to consider individual socio-ecology through a sex-specific evolutionary lens.
ACKNOWLEDGEMENTS

Many thanks to the humans and dolphins who made this dissertation possible. Science is a group endeavor, and without the invaluable support I have received this work would never have been possible.

Thanks first to Dr. Janet Mann, for your belief in me, the incredible training and opportunities you provided, and perhaps most of all for the many meandering chats about science and beyond, from the Latin origins of the word personality to cultural evolution. You have made me the scientist I am today and I am forever grateful.

Thank you to my committee members, Dr. Céline Frère, Dr. Gina Wimp, and Dr. Pete Marra. Your advice and feedback have shaped and improved this dissertation beyond measure. I appreciate all of the time you took to work through tough questions with me.

Thank you to all of the Shark Bay Dolphin Research members past and present who have contributed to one of the richest databases on any mammal, and to our collaborators in Australia who make this work possible.

Thanks to the Mann lab, for making me feel welcome from the first time I set foot on campus. The sense of community I found here got me through the toughest parts of this process, and I feel so lucky to have found lifelong friends along the way. Molly and Ellen, I don’t know how I would have gotten through this dissertation, or the pandemic, without you.

Thanks to all of my family and friends who have listened to far too much talk about dolphins. Most of all, thanks to Simon; there aren’t enough words to express my appreciation of your support and willingness to jump into new adventures together. I love you always.
# TABLE OF CONTENTS

**INTRODUCTION** .................................................................................................................. 1

**CHAPTER I. LIFETIME STABILITY OF SOCIAL TRAITS IN A LONG-LIVED MARINE MAMMAL** .................................................................................................................. 6

- Introduction ................................................................................................................................ 6
- Results ........................................................................................................................................... 11
  - *Repeatability* ............................................................................................................................ 11
  - *Correlation between social measurements* ............................................................................. 11
- Discussion .................................................................................................................................... 12
- Methods ....................................................................................................................................... 17
  - *Study site and population* ........................................................................................................ 17
  - *Behavioral data* ....................................................................................................................... 18
  - *Repeatability* .......................................................................................................................... 19
  - *Correlation of social measurements* ...................................................................................... 21
- Figures and Tables ...................................................................................................................... 23

**CHAPTER II. SOCIO-ECOLOGICAL STRATEGIES OVER THE LIFETIME OF INDIVIDUAL BOTTLENOSE DOLPHINS** .................................................................................. 28

- Introduction .................................................................................................................................. 28
- Results ......................................................................................................................................... 31
  - *Repeatability of ecological traits* ............................................................................................. 31
  - *Socio-ecological syndrome correlations* ................................................................................. 33
- Discussion ..................................................................................................................................... 33
Methods.................................................................................................................................38

Study population ............................................................................................................................38

Ecological measurements .............................................................................................................38

Statistical analyses .........................................................................................................................39

Figures and Tables ..........................................................................................................................41

CHAPTER III. SEX-DEPENDENT TRANSMISSION OF SOCIO-ECOLOGICAL STRATEGIES........45

Introduction........................................................................................................................................45

Results............................................................................................................................................49

Maternal correlations ......................................................................................................................49

Survival analyses .............................................................................................................................50

Discussion.......................................................................................................................................51

Methods..........................................................................................................................................55

Data collection.................................................................................................................................55

Statistical analyses..........................................................................................................................55

Figures and Tables ..........................................................................................................................59

CONCLUSION....................................................................................................................................73

APPENDIX A: Chapter I Supplemental Information ........................................................................76

APPENDIX B: Ethics ..........................................................................................................................80

APPENDIX C: Acknowledgements .................................................................................................81

REFERENCES ....................................................................................................................................82

Introduction.......................................................................................................................................82

Chapter I.........................................................................................................................................110
LIST OF FIGURES

Figure I.1. Repeatability values for time alone, time in small groups (<6 dolphins), in large groups (≥6 dolphins), average number of associates and same-sex associates, and proportion of sightings in socially active groups and foraging ................................................................. 24

Figure I.2. Biplot of individual PCA scores .................................................................................. 26

Figure II.1. Repeatability estimates for a. general space use and foraging activity metrics, and b. use of specific foraging types .......................................................................................................................... 41

Figure II.2. Correlogram of among individual correlations for repeatable socio-ecological metrics for a. females and b. males ............................................................................................................. 43

Figure III.1. Linear regressions with 95% confidence intervals and Kendall’s tau correlations between maternal and offspring measurements .................................................................................. 63

Figure III.2. A. Biplot of principal components analysis on all dolphins with ≥15 sightings. B. Scree plot of explained variance for each component .............................................................................................................. 66

Figure III.3. Linear regressions and Kendall’s tau correlation of maternal and offspring PCA scores for the three retained components ........................................................................................................ 68

Figure III.4. Socio-ecological clusters for a. females (n = 178) and b. males (n = 187) with at least 15 sightings as adults ......................................................................................................................... 69

Figure III.5 Boxplot of metrics describing socio-ecological strategies for a. females (n = 178) and b. males (n = 187) with at least 15 sightings as adults ........................................................................................................ 70

Figure III.6. Kaplan-Meier plots of survival probability with 95% confidence intervals stratified by socio-ecological cluster for a. females (n = 248) and males (n = 245) .......................................................... 71

Figure III.7. Kaplan-Meier curve for sponge-foraging females (n = 35) compared to the rest of the females in the dataset (n = 213) ........................................................................................................ 72
**LIST OF TABLES**

Table I.1. Definitions for levels of behavioral measurements, as used in this paper............. 23

Table I.2. Among-individual correlations for repeatable social measurements ..................... 25

Table I.3. Loadings of the social measurements onto the first principle component, both total population and split by sex ...................................................................................................................... 27

Table II.1. Among-individual correlations for repeatable ecological and social measurements 44

Table III.1. Comparison of correlation strength between female and male offspring and their mother. ............................................................................................................................................. 64

Table III.2. Loadings for the three retained principal components..............................................65
INTRODUCTION

Consistent individual differences in behavior, or behavioral phenotypes, are no longer considered noise around the mean (Sih, Bell, and Johnson 2004; Réale et al. 2007; Bolnick et al. 2003). Variation along both behavioral and ecological axes is rampant across taxa, with major implications for population dynamics and evolution (Wolf and Weissing 2012). Many of the hypotheses surrounding the maintenance and consequences of behavioral phenotypes rely on the assumption of lifetime stability across ontogeny. However, there is little evidence to substantiate this assumption, with most studies covering either a small amount of time (often a single year), a short-lived species, or a single developmental stage (Sinn, Gosling, and Moltschaniwskyj 2008; Bell, Hankison, and Laskowski 2009; Brommer and Class 2015).

Theoretical frameworks and indirect evidence suggest that social and ecological phenotypes are intertwined (Ramos-Fernández, Boyer, and Gómez 2006; Daura-Jorge et al. 2012; Machado et al. 2019). Niche theory applied at the individual level predicts that individuals maintain socio-ecological strategies based on competition and density related factors (Toscano et al. 2016; Webber and Vander Wal 2018), but thus far individual differences in social behavior and ecological niches have been largely considered separately (Dall et al. 2012). Considering social and ecological variation as a correlated spectrum of behavior characterized by tradeoffs between time intensive foraging and socializing will shed light on the larger implications of socio-ecology for individual and population level fitness, especially with regards to climate change (Webber and Vander Wal 2018).

In this dissertation I capitalize on 32 years of data from the Shark Bay Dolphin Research Project (SBDRP) database to frame individual socio-ecology through the lens of niche theory.
The bottlenose dolphins (*Tursiops aduncus*) in Shark Bay provide a unique opportunity to examine individual differences in socio-ecology. These dolphins are bisexually philopatric, allowing data collection to span the lifetime of both sexes (Tsai and Mann 2013). They are long lived (40+ years) with a long developmental period; calves nurse for an average of 4 years, and average age at first birth for females is 13 years (Karniski, Krzyszczyk, and Mann 2018; Mann 2019). Their social lives are characterized by extremely high levels of fission-fusion, group composition changes more than 5 times an hour and there is no discernible dominance or kin structure (Mann 2006; Tsai and Mann 2013; Galezo, Krzyszczyk, and Mann 2018). Social behavior is highly individually variable and tied to fitness (Frère et al. 2010; Stanton and Mann 2012). Males and females tend to socialize differently in accordance with their mating strategies, with males forming alliances with other males that increase access to mates (Connor, Smolker, and Richards 1992; Krützen et al. 2004), and females forming looser social networks with other females (Smolker et al. 1992; Gibson and Mann 2008a). Females tend to be more solitary and males more cliquish (Mann et al. 2012). The sexual segregation present in the population also appears to be driven by sex-specific preferences (Galezo, Krzyszczyk, and Mann 2018).

Shark Bay dolphins are also highly ecologically variable. There are more than 20 different documented foraging tactics used, and individuals will use different subsets of them (Mann and Sargeant 2003, Patterson and Mann 2015). Some tactics, especially the use of sponges as tools, require an extended period of learning and high time investment and are passed down from mother to daughter through social learning in a small subset of the population (Mann and Sargeant 2003; Mann et al. 2008), whereas others are more widespread throughout the population. Certain foraging tactics are associated with individual habitat use (Sargeant et al. 2003).
2007), emphasizing the need to incorporate both foraging behavior and space use when investigating ecological phenotypes. In addition, Shark Bay dolphins exhibit a wide variety of home range sizes and habitat compositions (Tsai and Mann 2013), which are also often shared between mother and daughters and to a lesser extent, sons. Females who use sponge tools to forage socialize less than other dolphins (Gibson and Mann 2008; Mann et al. 2008). Female spongers also associate with other females who share their foraging tactics more often than non-spongers (Mann et al. 2012). There is evidence that foraging tactics are at least partially passed down through social learning (Sargeant and Mann 2009). Culture and social learning appear to be especially important for cetaceans in general (Cantor and Whitehead 2013; Whitehead 2017; Cantor et al. 2020), suggesting a vertical social transmission mechanism linking social and ecological phenotypes.

Chapter 1 is an investigation into the longevity and multivariate nature of social phenotypes in the Shark Bay dolphins. Sociality has received less attention in the literature compared to other behavioral phenotypes, especially boldness, despite its impact on ecologically relevant factors such as dispersal (Cote and Clobert 2007), mating behavior (Johnson and Sih 2005), home range size and habitat use (Spiegel et al. 2017). I test the repeatability of several social metrics across maturation and several decades of adulthood, extending the length of behavioral phenotype studies. I then investigate the correlation structure of social metrics to determine whether social behavior is organized into a behavioral syndrome akin to human extraversion. Social behavior may also be influenced by the different life history pressures facing each sex, mate access for males, resource access for females, so I investigated whether repeatability and correlation of social metrics differed between males and females.
In Chapter 2, I examine the repeatability of ecological behavior over decades, as well as the correlation between individual ecological behavior and social phenotype. Some studies have found that foraging strategies can remain stable over long periods of time (Woo et al. 2008; Vander Zanden et al. 2010; van de Pol et al. 2010), but almost all studies of individual ecological variation focus on only a single metric, not necessarily an adequate measure of niche width (Sargeant 2007). Here I incorporate home range size, habitat preferences, and foraging tactic use to make a more complete assessment of ecological strategies. I also address sex differences, hypothesizing that females would show higher levels of repeatability in their foraging tactics and stronger correlations between ecological and social behaviors given the pressure on resource acquisition for raising calves.

Finally, in chapter 3, I begin to address how an individual develops a socio-ecological strategy, as well as the associated fitness consequences. Maternal effects are a prominent mechanism for the transmission of behavior (Wolf and Wade 2009; Bonduriansky and Day 2009; Russell and Lummaa 2009), and may be of particular importance for long-lived mammals with extended periods of maternal care and opportunity for social learning (Russell and Lummaa 2009; Mann 2019). I predicted that females would be more likely to mirror their mother’s strategy, given that they face more similar life history pressures than male offspring do. Males would then be more likely to diverge from their mother’s socio-ecological strategy. I also investigated fitness consequences of socio-ecological strategies, hypothesizing through niche theory that strategies serve to distribute competition, and thereby would not display large-scale differences in fitness, as measured by survival.
This dissertation adds rare empirical data to a framework of individual socio-ecological niches, improving our understanding of how individual differences are maintained within a population and their subsequent effects on individual fitness.
INTRODUCTION

For most animals, ontogeny involves dramatic changes beyond physiological maturation. Social environments expand and shift with independence, hormones rage and fade, and reproduction brings a new set of challenges. In the midst of this, individuals may display behavioral traits: consistent differences in behaviors across time and/or context. Here, we use the term behavioral trait, but this phenomenon has also been referred to as behavioral phenotypes or animal personality (Table 1). Behavioral traits are common across taxa (Sih, Bell, and Johnson 2004), heritable (Sinn, Apiolaza, and Moltschaniwskyj 2006; Dochtermann, Schwab, and Sih 2015), and influence population level dynamics such as niche partitioning (Hensley et al. 2012; Holtmann et al. 2017; Boyer et al. 2010), responses to environmental change (Schindler et al. 2010; Cockrem 2013; Villegas-Ríos et al. 2018), disease transmission (Boyer et al. 2010; Trnka et al. 2013; Bohn et al. 2017), and fitness (Ballew, Mittelbach, and Scribner 2017; Seyfarth, Silk, and Cheney 2012; Twiss et al. 2012). Traits can also be organized into correlated suites of behaviors, known as syndromes (Table 1). The degree of plasticity for many behaviors is widely debated, exacerbated by redundant terminology, but the widespread presence of behavioral traits precludes behavior from being considered a completely labile characteristic. The extent to which

---

behavioral traits and their syndromes persist throughout ontogeny is still poorly understood, and no obvious patterns have emerged in the literature. Studies have shown temporal stability on relatively short scales (Sinn, Gosling, and Moltschaniwskyj 2008), and behavioral traits may or may not last across extreme ontogenetic shifts such as metamorphosis (Monceau et al. 2017; Wilson and Krause 2012; Brodin 2009; Cabrera, Nilsson, and Griffen 2021). Long-lived, social mammals have protracted dependency periods, extensive behavioral repertoires, and can experience environmental change over multiple years and seasons, providing an opportunity to test the limits of behavioral stability. To this end, we examined the extent of stability in individual social behavior across decades, from infancy to late adulthood, in the Indo-Pacific bottlenose dolphin (Tursiops aduncus).

Behavioral traits are by definition stable over time, but the extent of temporal stability, either by raw number of years or percentage of an individual’s lifespan (Brommer and Class 2015), is not well defined. Most studies encompass only one year’s worth of testing (Bell, Hankison, and Laskowski 2009), and studies that do report data across years often cover only a minor portion of their subjects lifetime (Seyfarth, Silk, and Cheney 2012; López 2020; Yoshida, Meter, and Holekamp 2016; Kulahci, Ghazanfar, and Rubenstein 2018; Dingemanse et al. 2004). When behavioral stability has been measured over the majority of an animal’s lifetime, the focus is on species with short lifespans (Sinn, Gosling, and Moltschaniwskyj 2008; Polverino et al. 2016; Gyuris, Feró, and Barta 2012; Stanley, Mettke-Hofmann, and Preziosi 2017); such species typically experience little ecological, demographic, or social variation. Understanding the role of ontogeny is essential for identifying both causal mechanisms and age-specific selective pressures that lead to the maintenance of behavioral traits and syndromes (Stamps and Groothuis 2010;
A handful of studies have found that behavioral traits are stable through early maturation (Stanley, Mettke-Hofmann, and Preziosi 2017; Wuerz and Krüger 2015; Yoshida, Meter, and Holekamp 2016; Petelle et al. 2013; Urszán et al. 2015), hinting that behavior does persist across substantial ontogenetic change. But the majority of studies still include only one developmental stage, most often adult, (Suomi, Novak, and Well 1996) consigning us to a limited understanding of behavioral stability through ontogeny. By expanding the time span and developmental stages studied, we can better understand how behavioral traits are formed and maintained. Longitudinal studies of long-lived species require substantial human investment and resources, making datasets on behavioral traits across their life history stages quite rare.

In general, studies of behavioral traits and syndromes have focused on boldness and exploration, in ecological and/or social settings (Sih, Bell, and Johnson 2004; Réale et al. 2007). Social traits, typically defined by individual variation in gregariousness or social tolerance, have received comparatively less direct attention (Bell, Hankison, and Laskowski 2009) but are a rich area for study given that individual social style affects ecologically relevant factors such as dispersal (Cote and Clobert 2007), mating behavior (Johnson and Sih 2005), home range size and habitat use (Spiegel et al. 2017). Social traits have also been linked to reproductive success (Brent, Semple, Maclarnon, et al. 2014), but different types of social connectedness can have differential effects on survival (Ellis et al. 2019; Seyfarth, Silk, and Cheney 2012; Stanton and Mann 2012). How observed social behaviors can be used to define a social trait or syndrome is not simple. Many longitudinal studies of social behavior focus on the stability of dyadic relationships within highly stable groups rather than individual social styles (Seyfarth, Silk, and
A growing number of studies define social traits by network position (Aplin et al. 2015; Wilson et al. 2013; Formica et al. 2017), but this obscures individual preferences from the social environment. While some network metrics, such as degree, can be indicative of individual-level traits, most are aimed at describing the topology and higher-order properties of the network (Rankin et al. 2016). Social metrics measured at the individual level better describe individual social decisions, such as whether to join or leave a group. By incorporating several individually-measured social behaviors (such as group size preference) and examining their stability across time and correlation among individuals, we can better operationalize a “sociable” behavioral syndrome (Strickland and Frère 2018) along the lines of human social personality (e.g., extraversion, agreeableness).

The bottlenose dolphins of Shark Bay, Western Australia, provide a unique opportunity to examine social traits. Their life spans are very long (40+ years Karniski, Krzyszczyk, and Mann 2018) with an extended developmental period (average weaning age is 4 years, and average age at first birth is 13 years; Karniski, Krzyszczyk, and Mann 2018; Mann 2019; Stanton and Mann 2014). Shark Bay dolphins live in an open fission-fusion society; individual dolphins join and leave groups at will several times per hour, and can associate with any conspecifics they choose within their home range from an unbounded network (Frère et al. 2010a; Frère et al. 2010b; Tsai and Mann 2013; Galezo, Krzyszczyk, and Mann 2018). This flexibility makes group size preferences an informative metric. Societies classified as fission-fusion often retain structures or hierarchies which influence group membership, so associations are made based on factors other than individual social preference (such as rank, Smith, Memenis, and Holekamp
2007). Because Shark Bay bottlenose dolphins live in a large, open fission-fusion system with no clear social hierarchy, individual social decisions are not driven by rigid social structures; consequently individual traits can be better isolated. Additionally, social behavior in this population is both heterogeneous across individuals and tied to fitness (Frère et al. 2010a; Stanton and Mann 2012). Mating strategies drive male social behavior, with males forming long-term same-sex alliances to secure temporary access to cycling females (Connor, Smolker, and Richards 1992). Foraging ecology appears to influence female social behavior, varying from solitary to gregarious depending on the time demands of individual foraging tactics (Smolker et al. 1992; Gibson and Mann 2008; Mann et al. 2012).

Equipped with 32 years of longitudinal data, we measured the stability (i.e. repeatability, or proportion of variation due to the individual; Wolak, Fairbairn, and Paulsen 2012; Villemereuil, Gimenez, and Doligez 2013) of seven social measurements across maturation from calf to adulthood and into old age. We quantified time spent alone, time in small groups, time in large groups, raw number of associates, same-sex associates, time in socially active groups, and time foraging (individuals in this population forage alone so time foraging is a proxy for non-social activity budget) for nine age blocks. This allowed us to observe mean-level changes in these social behaviors across the lifespan. Then repeatability was calculated for each measurement. This was done for the entire population as well as split by sex to account for sex differences in social behavior. Finally, to address the fact that single measurements may be structured into a broader social syndrome, we tested the correlation between repeatable social measurements using multivariate analyses. By incorporating all ontogenetic stages and an
extended time period, we provide a robust framework for understanding the architecture of social traits outside of humans and the selective pressures which could be maintaining them.

RESULTS

Repeatability

Generalized linear mixed models for each of the seven traits measured revealed age and sex related patterns in social behavior (Fig. S1). In general, males were more gregarious than females, and sociability peaked around the juvenile and early adult period, with a decline in old age (Fig. S1). After extracting variance components and calculating repeatability estimates for each trait, four of the seven were highly repeatable for both sexes (time alone, time in large groups, number of associates and same-sex associates), indicating strong and stable individual traits. Time in small groups was highly repeatable for males but not females, and time foraging was repeatable for females but not males (Fig. 1). Time in socially active groups was not significantly repeatable at the individual level in any model.

Correlation between social measurements

A multivariate model of the highly repeatable traits showed that social traits correlated significantly at the among-individual level, forming a behavioral syndrome (Table 2). When split by sex, the models indicated that the traits that were repeatable for only one sex (foraging for
females, time in small groups for males) were also correlated with this syndrome, although in the male-only model time alone did not significantly correlate with the other traits except for time in large groups (Table 2). Principal components analyses including both sexes revealed that 76% of the variation in the four repeatable measurements could be condensed onto a single axis (Fig. 2), strongly suggesting an underlying “sociable” axis of behavior. All four repeatable measures loaded onto the first principal component (Table 3). When split by sex this axis still explained a substantial amount of variation (86% for females, 61% for males, Table 1). All four of the highly repeatable social measures were significantly correlated (p < 0.001, Fig. 3), with time alone negatively correlated to the other three and positive correlations between the rest.

DISCUSSION

This study is the first evidence of social traits exhibiting stability on the scale of decades outside of humans, advancing our understanding of behavioral repeatability. In the Shark Bay dolphins, time spent alone, time spent in large groups, average number of associates, and average number of same-sex associates showed high levels of individual repeatability for both sexes. Time spent foraging was highly repeatable for females but not males, while time in small groups was repeatable for males but not females. Time in socially active groups, presumably a direct measure of sociality, was not repeatable for either sex, emphasizing the need for careful choosing of metrics. Furthermore, repeatable traits formed a strong social behavioral syndrome, emphasizing the correlative nature of social behavior. However, the pattern and magnitude of correlation within the syndrome differed between sexes.
The repeatability values for these dolphins were remarkably high compared to other behavioral trait studies (Bell, Hankison, and Laskowski 2009). This is counterintuitive given the dynamic nature of their social system, which lacks a clear kinship (Frère et al. 2010b) and dominance structure (Mann 2006) and is characterized by extreme fission-fusion dynamics where group size and composition changes >5 times per hour (Galezo, Krzyszczyk, and Mann 2018). However, we argue that the very nature of fission-fusion dynamics may in fact allow for individual preferences in social behavior to become more pronounced, resulting in individuals displaying stronger long-term stability in social trait differences. Other studies of fission-fusion societies have noted that individual variation in sociability over shorter time periods can only be partially explained by factors such as home-range overlap and kinship (Yoshida, Meter, and Holekamp 2016; Carter et al. 2013; Murphy, Mumby, and Henley 2020), corroborating this argument. Alternatively, fission-fusion dynamics may require individual stability. Dolphins form long-term social bonds, and are able to remember each other’s signature whistles for decades (Bruck 2013). Given the hundreds of individual social contacts that dolphins have in their lifetimes, stable social traits might be critical for formation and maintenance of varied relationships. Extreme fission-fusion social dynamics may well depend on stability and predictability of these interactions. In other words, it is necessary to know what to expect from your conspecifics when navigating interactions among flexible group contexts. Stability might be a fundamental feature of understanding sociality and relational complexity (Lukas and Clutton-Brock 2018).

The repeatable social traits we measured correlated to form a social syndrome. This underscores the idea that various social metrics and behaviors stem from the same underlying
variation. Too much independence has likely been assigned to different social behaviors, and caution is warranted when multiple measures of sociality are used. To our knowledge, this is the first demonstration of a stable social syndrome, challenging the perception of social behaviors as context-specific (Schradin 2013). The social behavioral syndrome constitutes a stable framework for the expression of social traits, akin to the extraversion-introversion axis of social expression in humans. Within this stable framework however, group composition, size, and context frequently change, patterns that require some flexibility. Future work could incorporate network dynamics to better parameterize how much social plasticity dolphins might demonstrate.

The behavioral syndrome strength and structure varied by sex. It is well documented that males and females have different pressures across life history stages (Kappeler and van Schaik 2002), but we provide new evidence that these sex differences can influence how behavioral traits covary. For females, all repeatable metrics measured, including social and foraging behavior, were very tightly correlated. This is consistent with our previous findings that female social behavior is largely driven by individual foraging strategy, a pattern exemplified by sponge-tool-using females in the population, who forage more and socialize less than other females (Mann et al. 2012). For males on the other hand, syndrome correlations were substantial but lower compared to females, and time spent alone did not correlate with the other traits of the syndrome except for time in large groups. This follows the pattern of male behavior showing lower repeatability values in general. During infancy, males, constrained by maternal behavior and her social network (Gibson and Mann 2008b), are expected to diverge more from their mothers post-weaning as their life history pressures shift towards alliance formation and reproduction (Stanton and Mann 2012). Male sociality is driven by mating strategy, supported by
the addition of time in small groups as a repeatable trait for males (but not females), as alliance membership generally falls in the range of small groups (2-6). Given that alliance membership is likely an arbiter of reproductive success for males, they show less social variation than females, leading to a weaker (but still defined) behavioral syndrome. In order to successfully navigate and maintain an alliance, males must spend a larger portion of their time in groups, generating a trade-off in time spent foraging (usually a solitary activity). Accordingly, males are less likely to specialize or engage in time-intensive foraging tactics, leading to less variation between males and the resulting lack of repeatability found. The time males do spend alone, which was only correlated (negatively) with time in large groups, could be driven by other aspects of male behavior and within-alliance dynamics.

The lifetime stability of this social syndrome can only be rivaled in timescale by human studies. Human personality (the human-centric version of a behavioral syndrome, Table 1) exhibits temporal stability over long periods (Roberts and DelVecchio 2000; Terracciano, Costa, and McCrae 2006). However there is evidence that it may be most significant only in the adult period (Costa, McCrae, and Löckenhoff 2019) and that stability may wane over the many decades of a human lifespan (Harris et al. 2016). Outside of humans, longitudinal datasets are rare and sex-biased dispersal (Trochet et al. 2016) limits the examination of sex differences in behavioral traits. Other mammalian studies have found stability in sociability, but these patterns are often conflated or intertwined with dominance structure (Murphy, Mumby, and Henley 2020; Turner, Bills, and Holekamp 2018; Brent, Semple, MacLarnon, et al. 2014; Koski 2011) (but see Seyfarth, Silk, and Cheney 2012). Our study is a unique contribution to the literature as it is the first non-human study to cover all life history stages as well as both sexes.
The strength and duration of social trait repeatability found in the Shark Bay dolphins and its organization into a syndrome offers new insight into the formation and maintenance of behavioral traits. Maternal effects are strongly implicated, given that social dynamics in the calf period were stable well into adulthood. Young animals often inhabit very different niches from adults, and their behavior may differ as a result (Groothuis and Trillmich 2011). However, social traits in the Shark Bay dolphins exhibited stability at the individual level across ontogenetic change. As these patterns are maternally inherited, i.e., calf social traits are strongly influenced by the mother, just as ecological traits are (Mann and Sargeant 2003), mothers play a foundational role in the trajectory of their offspring, especially daughters, but also for sons (Stanton and Mann 2012). It has also been theorized that increased sociality at the species level is a driver of stability in behavioral traits (von Merten, Zwolak, and Rychlik 2017), aligning with the extremely high repeatability values found in these very social dolphins. But more comparative studies are needed to parse this theory fully.

We provide rare empirical evidence that social behavioral traits are stable throughout an individual’s lifetime, a common but unverified assumption in the literature (Réale et al. 2007; 2010; Hall et al. 2015; M. Wolf and Weissing 2010; Dingemanse and Wolf 2010). We push the limits of longitudinal studies on behavioral traits, extending number of years measured, percentage of lifespan covered, and length of lifespan involved. Our study suggests that a stable social syndrome shepherds the individual dolphin through significant physiological and social changes as they move from dependency to adulthood. Dolphins, long suspected of having personality (Highfill and Kuczaj 2007; Kuczaj II, Highfill, and Byerly 2012; López 2020), do indeed show the hallmarks of life-long social traits, perhaps more so than humans.
METHODS

Study site and population

This study drew from 67,851 dolphin observations collected through the Shark Bay Dolphin Research Project (SBDRP) between 1988 and 2019. Researchers with the SBDRP have collected behavioral, demographic, genetic, and ecological data on >1800 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia since 1984. The study site covers roughly 500km² in the eastern gulf of Shark Bay, offshore from Monkey Mia (25°47’S, 113°43’E). The population is residential and bisexually philopatric (Tsai and Mann 2013), allowing data collection to span individual lifetimes for both sexes. Individuals are identified using photo-identification of dorsal fin shape and damage, pigmentation, and other obvious scars (i.e. shark bites or tooth rakes; Janet Mann et al. 2000; Bichell et al. 2018). The sex of each dolphin included in this study was determined by views of the genital area or by association with a calf, and/or with genetics (Smolker et al. 1992; Krützen et al. 2002, 20002). All calves in this study had a known mother based on association. Age was determined by known birth dates (Mann et al. 2000), size, or degree of ventral speckling (Krzyszczyk and Mann 2012). Based on these ages, dolphins were classified as either calves, juveniles, or adults at time of observation. The calf stage was defined as birth until weaning, as determined by the midpoint between last sighting in infant position or at least 80% of time spent with the mother, and when the association between mother and calf declined below 50% (Mann et al. 2000). Adult stage was defined as older than 10 years, as 9 is the earliest an individual has become pregnant (an outlier)
and the average age of first birth is 13 (Mann 2019), and juvenile as the ages between weaning and adulthood. To account for the extreme length of adulthood compared to calf and juvenile periods, the adult period was split into 5 year blocks from age 10 up until age 50. Only two dolphins had sufficient data past age 50, so this time period was excluded.

Behavioral data

Behavioral data were collected from boat-based observational surveys. Surveys are a 5-minute scan sample conducted when dolphins are sighted to determine group composition and predominant group activity (i.e. travel, rest, social, forage, other as in Karniski et al. 2015). Individuals were included in a group according to the 10m chain rule, where any dolphins within 10m of one another were considered a single group (Smolker et al. 1992). To be included in the study, individuals were required to be sighted in at least 15 surveys (as this is where social measurements tend to stabilize; Stanton 2011) in three consecutive time blocks. If individuals were sighted multiple times in a day, only the last survey in which it was sighted was included in order to reduce spatial and temporal autocorrelation (Tsai and Mann 2013). In order to account for uneven sampling, we drew a random subsample of 15 surveys per individual’s life history stage and calculated seven social measurements. This was repeated 1000x to create an average value per measurement for each individual. Social measurements included proportion of surveys alone (including mothers with dependent calves), to capture how often an individual decided to associate with other dolphins or not. Group size preferences when with others were then calculated as time spent in small groups (2 – 5 individuals, based on the average group size of 5
found in the dataset), and large groups (greater than the average group size of 5). Additionally, we calculated the average number of unique associates (i.e., dolphins sighted with each focal dolphin). This population has high levels of sexual segregation, with females primarily avoiding adult males (Galezo, Krzyszczyk, and Mann 2018). This segregation may obscure individual preferences in number of associates when both sexes are counted, therefore we also calculated the average number of same-sex associates. Finally, we calculated the proportion of surveys in socially active groups (where ≥50% of the group is exhibiting social behaviors), as well as proportion of surveys foraging, as this population generally forages alone.

*Repeatability*

In order to maximize sample size, this study utilized an unbalanced design for longitudinal data (Singer et al. 2003). The lifespan was divided into nine time blocks: calf, juvenile, and adulthood, broken into five year blocks from 10 years up until age 50 (there were only two dolphins with sufficient surveys past age 50). 179 dolphins met the data requirements (15 or more sightings in at least 3 consecutive time blocks) to be included, 89 females and 90 males. This dataset included 40,523 individual dolphin observations (mean per individual = 377, min 59, max 906). In order to assess the stability of individual social measurements, we measured the repeatability of each social measurement, or the proportion of variation attributed to among-individual difference. This is calculated as the intraclass correlation coefficient (ICC, Bell, Hankison, and Laskowski 2009). Following de Villemereuil et al. (2013), we fit generalized linear mixed models with dolphin identity (ID) as a random factor, allowing us to partition the
variance due to the individual and estimate the repeatability. The models also included age class and individual sex as fixed factors to account for differences in social behavior present based on these categories. Models were run with a Bayesian framework using the MCMCglmm package (Hadfield 2010) in R (version 4.0.2; R Core Team 2020). The models were assigned a Gaussian error distribution, and all measurements except associates and same-sex associates were square-root transformed to improve normality. Fixed effects were given uninformative priors, and the random effect (dolphin I.D.) was given a weakly informative inverse gamma prior. Models were run for 100000 iterations with a thinning interval of 10 and a burn-in period of 3000 iterations. Model convergence was checked by visually examining trace plots, autocorrelation, and the effective sample size. Fixed effects were considered significant if the associated credible intervals of the posterior distribution did not cross zero. The ICC for each measurement was then calculated by extracting the variance components of the models and calculating the proportion of variance due to the individual component. Social measurements are inherently non-independent, so it is critical to use a null model to assess the significance of repeatability (Aplin et al. 2015; Strickland and Frère 2018). To accomplish this, we randomized the identity associated with each observation and recalculated the social measurements and their repeatability due to chance. Observed repeatability values were then considered to be high if their 95% credible interval did not overlap the range generated by the null model.

*Correlation of social measurements*
Since different social measurements may be measuring the same underlying variation, we used a multivariate model to examine the correlation of repeatable traits at the among-individual level following Houslay and Wilson (2017). The same model structure as before was used, but with all four repeatable metrics included as a multivariate trait. Models were run for 200000 iterations with a thinning interval of 100 and a burn-in period of 10000 iterations. Model convergence was again checked by visually examining trace plots, autocorrelation, and the effective sample size. Posterior distributions of the variance components were then used to assess correlation of the social metrics at the between-individual level. If the 95% credible intervals for a correlation did not cross zero, that correlation was considered significant. This process was done for the population as a whole as well as split by sex.

We also used an exploratory principal components analysis and Kendall’s tau correlation to visualize and quantify broader phenotypic-level correlation structure between the highly repeatable measures (Supplemental info). To better characterize large-scale variation and avoid the pitfalls of repeated measurements in principle component analyses, a larger dataset was used for the PCA. Dolphins were included if they met data requirements (15+ surveys) for at least two adult age blocks (eliminating variation due to early ontogeny), and a single adult measurement was then calculated using their adult sightings for the four significantly repeatable social metrics. This avoided variance due to early ontogeny, and increased the sample size for this analysis to better visualize patterns of variance between the sexes. The expanded dataset included 218 dolphins, 112 female, 106 male. Bartlett’s test of sphericity indicated that the correlation matrix of the variables was significantly different from the identity matrix (p < 0.001), and thus appropriate for dimensionality reduction. Keyser-Meyer-Olkin tests returned an overall measure
of sampling adequacy of 0.71 (individual MSAs for each variable ranged from 0.64-0.76). PCA scores were calculated using the psych (Revelle and Revelle 2015) package, and correlations with the corrplot (Wei et al. 2017) package, both in R (R Core Team 2020).
Table I.1. Definitions for levels of behavioral measurements, as used in this paper.

<table>
<thead>
<tr>
<th>Term</th>
<th>Definition</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Behavioral trait</td>
<td>Differences at the between-individual level in a single behavior that are consistent (repeatable) across time and/or context. Often termed ‘animal personality’ in the literature.</td>
<td>Sih et al. 2004</td>
</tr>
<tr>
<td>Behavioral syndrome</td>
<td>A suite of behavioral traits that are correlated at the between-individual level. Use of a multivariate approach allows partitioning of between-individual correlations from phenotypic and among-individual correlations.</td>
<td>Sih et al. 2004, Thys et al. 2017</td>
</tr>
<tr>
<td>Personality</td>
<td>The endogenous (but not immune to environmental influences) temperament or disposition of an individual, or the individual’s characteristic patterns of thoughts, feelings, and actions. Personality is largely measured through self and peer ratings, and is most analogous to behavioral syndromes. Here personality is used exclusively to describe human-focused studies.</td>
<td>McCrae &amp; John 1992, McCrae &amp; Costa 1999, McCrae et al. 2000</td>
</tr>
<tr>
<td>Behavioral phenotypes</td>
<td>An individually expressed behavior or behavioral strategy, not necessarily repeatable (e.g., alternative mating strategies such as singer or satellite males).</td>
<td>Dominey 1984</td>
</tr>
</tbody>
</table>
Figure I.1. Repeatability values for time alone, time in small groups (<6 dolphins), in large groups (≥6 dolphins), average number of associates and same-sex associates, and proportion of sightings in socially active groups and foraging. Values are shown for the entire cohort as well as split by sex. Dashed bars represent the expected repeatability from the null model. Repeatability was considered significant if the 95% CI did not overlap the expected null range.
Table I.2. **Among-individual correlations for repeatable social measurements.** 95% credible intervals for each estimate are in italics. Bolded numbers indicate significant correlation, as determined by CIs that do not cross zero. For the female and male specific analyses, the trait which was only repeatable for that sex was included.

<table>
<thead>
<tr>
<th></th>
<th>Alone</th>
<th>Large</th>
<th>Associates</th>
<th>Same-Sex Associates</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A. All dolphins</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alone</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large</td>
<td>-0.84</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-0.89, -0.77)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Associates</td>
<td>-0.52</td>
<td>0.69</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-0.66, -0.37)</td>
<td>(0.59, 0.79)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Same-Sex</td>
<td>-0.49</td>
<td>0.71</td>
<td>0.85</td>
<td>-</td>
</tr>
<tr>
<td>Associates</td>
<td>(-0.64, -0.33)</td>
<td>(0.60, 0.81)</td>
<td>(0.80, 0.91)</td>
<td></td>
</tr>
<tr>
<td><strong>B. Females</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alone</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large</td>
<td>-0.91</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-0.96, -0.87)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Associates</td>
<td>-0.74</td>
<td>0.74</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-0.85, -0.62)</td>
<td>(0.63, 0.85)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Same-Sex</td>
<td>-0.85</td>
<td>0.87</td>
<td>0.84</td>
<td>-</td>
</tr>
<tr>
<td>Associates</td>
<td>(-0.93, -0.77)</td>
<td>(0.79, 0.93)</td>
<td>(0.75, 0.91)</td>
<td></td>
</tr>
<tr>
<td>Foraging</td>
<td>0.82</td>
<td>-0.85</td>
<td>-0.62</td>
<td>-0.76</td>
</tr>
<tr>
<td></td>
<td>(0.73, 0.91)</td>
<td>(-0.92, -0.77)</td>
<td>(-0.78, -0.44)</td>
<td>(-0.87, -0.62)</td>
</tr>
<tr>
<td><strong>C. Males</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alone</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Large</td>
<td>-0.63</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-0.80, -0.46)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Associates</td>
<td>-0.02</td>
<td>0.52</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(-0.27, 0.29)</td>
<td>(0.30, 0.72)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Same-Sex</td>
<td>0.14</td>
<td>0.36</td>
<td>0.85</td>
<td>-</td>
</tr>
<tr>
<td>Associates</td>
<td>(-0.14, 0.40)</td>
<td>(0.12, 0.62)</td>
<td>(0.77, 0.92)</td>
<td></td>
</tr>
<tr>
<td>Small Groups</td>
<td>0.01</td>
<td>-0.64</td>
<td>-0.76</td>
<td>-0.67</td>
</tr>
<tr>
<td></td>
<td>(-0.26, 0.30)</td>
<td>(-0.81, -0.47)</td>
<td>(-0.89, -0.62)</td>
<td>(-0.85, -0.50)</td>
</tr>
</tbody>
</table>
Only social measures that were highly repeatable were included (time alone, in large groups ≥ 6 dolphins, average number of associates and same-sex associates). Females exhibited more variation along PC1, the axis explaining most of the observed variation.
Table I.3. Loadings of the social measurements onto the first principle component, both total population and split by sex. All measures were present on PC1, but time alone loaded heavily onto PC2 as well (all = 0.68, females = 0.77, males = 0.80). For all individuals, PC2 explained 16.58% of variation, for females 7.36%, but for males 30.42%.

<table>
<thead>
<tr>
<th></th>
<th>PC1: All</th>
<th>PC1: Female</th>
<th>PC1: Male</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alone</td>
<td>-0.47</td>
<td>-0.48</td>
<td>-0.25</td>
</tr>
<tr>
<td>Large</td>
<td>0.53</td>
<td>0.51</td>
<td>0.55</td>
</tr>
<tr>
<td>Associates</td>
<td>0.50</td>
<td>0.50</td>
<td>0.59</td>
</tr>
<tr>
<td>Same-Sex associates</td>
<td>0.50</td>
<td>0.50</td>
<td>0.53</td>
</tr>
<tr>
<td>Total % of variation</td>
<td>75.98</td>
<td>86.10</td>
<td>61.18</td>
</tr>
</tbody>
</table>
CHAPTER II

Socio-ecological strategies over the lifetime of individual bottlenose dolphins

INTRODUCTION

Individuals within a population are not uniform in their resource use. Instead, populations are often composed of individual specialists which utilize only part of the population niche width through individual differences in diet specialization, space use, and habitat choice (Bolnick et al. 2003). Ecological niche theory applied at the individual level posits that density (of both conspecifics and resources) and competition can explain the formation and maintenance of individual ecological specialization (Araújo, Bolnick, and Layman 2011). However this theory is founded on the assumption of long-term repeatability of individual niches, something not widely tested in the literature. In other words, the raw materials for selection on individual traits, such as resource use, depend on the stability of those relative differences through time. Understanding these processes is vital during our current period of rapid environmental change. A handful of studies have found that individuals maintain foraging strategies over prolonged periods (Vander Zanden et al. 2010; van de Pol et al. 2010; Woo et al. 2008), mainly in marine species which return to predictable roosting or breeding sites. But more comprehensive data over the majority of an individual’s lifetime are needed to establish individual ecological niches as a lifelong trait.

2 Authorship for paper: Taylor Evans, Vivienne Foroughirad, Ewa Krzyszczyk, Céline Frère, Janet Mann
The choice of metrics to define a niche is another under-studied facet of individual ecology. Individual niches are most often assessed with a single metric, despite the fact that focusing on a single measure of specialization (e.g. the use of a rare foraging tactic) is not necessarily an informative measure of individual niche width (Sargeant 2007). For example, two individuals could occupy the same habitat, but specialize on different prey within their ranges. Alternatively, similar foraging styles or behaviors (such as dive depth or duration) could be used to target different prey. Stable isotope analysis has provided valuable data on diet specialization (Vander Zanden et al. 2010), but such analyses alone cannot separate diet from habitat variables, or account for behavior in determining drivers of dietary differences. A multivariate approach can identify ecological strategies not easily recognized by a single metric, providing a more complete understanding of a population’s interaction with its environment (Toscano et al. 2016; Ingram, Costa-Pereira, and Araújo 2018; Schwarz et al. 2021).

Individuals also exhibit variation in social traits (Aplin et al. 2015; Seyfarth, Silk, and Cheney 2014), and evidence is building that social and ecological specializations are intricately connected. Foraging competition and niche construction can influence social structure (Ramos-Fernández, Boyer, and Gómez 2006; Janson 2000), especially in cetaceans (Baird, Abrams, and Dill 1992; Daura-Jorge et al. 2012; Mann et al. 2012; Ansmann et al. 2015). In two bottlenose dolphin species, high individual foraging specialization leads to homophily in social associations (Mann et al. 2012; Machado et al. 2019) emphasizing the influence of foraging tactics on population-level social structure, and the potential for individuals to have stable ‘socio-ecological strategies’. Foraging innovations can be socially learned and/or culturally transmitted (Estes et al. 2003; Mann and Sargeant 2003), further linking sociality and ecology. But the direct
consequences and pressures guiding socio-ecological niche formation at an individual level remain unclear, as social behavior and ecological niches have largely been considered separately (Dall et al. 2012). Niche theory provides a framework to consider the covariance between social and ecological specializations and the larger implications for individual and population level fitness, particularly in the face of climate change (Webber and Vander Wal 2018). And despite the robust theoretical development, empirical study of individual socio-ecological traits is in its infancy.

The bottlenose dolphins of Shark Bay, Western Australia exhibit characteristics suggestive of socio-ecological strategies. They display more than 20 different documented foraging tactics, and individuals use different subsets of them (Patterson and Mann 2015). Some tactics require an extended period of learning, high time investment, and are passed down from mother to daughter through social learning in a small subset of the population (Mann and Sargeant 2003; Mann et al. 2008), whereas other tactics are more widespread throughout the population. Certain foraging tactics are associated with individual habitat use (Sargeant et al. 2007), and prey abundance and composition are different across habitat types (Heithaus 2004; Patterson and Mann 2011), emphasizing the need to use both foraging behavior and space use when investigating ecological phenotypes. In addition to a range of foraging breadth and specialization, Shark Bay dolphins exhibit a wide variety of home range sizes and habitat compositions, which are also often shared between mother and weaned offspring (Tsai and Mann 2013). Social traits are stable over their long lifetimes, and correlate into a behavioral syndrome (Evans et al. 2021). Sex differences play a substantial role in both social and ecological behavior, suggesting that the different pressures facing each sex (resource access for females, female
access for males; Kappeler and van Schaik 2002) likely steer individual socio-ecological strategies.

Despite the prevailing evidence, the multivariate composition of individual ecological niches and their intersection with social traits has not been empirically demonstrated. We drew on a database of 32 years of behavioral and demographic data to evaluate the composition of individual ecological niches and their potential correlation with social traits into socio-ecological strategies. We calculated the stability on a lifetime scale of home range size, habitat preferences, foraging activity budget, level of foraging tactic specialization, breadth of foraging tactics used and tendency to use the most common tactics. Based on socioecological theory (Kappeler and van Schaik 2002) and previous evidence for vertical social transmission, our hypothesis is that social and ecological behaviors would correlate into socio-ecological strategies, which are maintained in the population because of (1) high stability through an individual’s lifetime; and (2) social inheritance of strategies, particularly from mother to daughter. We predicted that both sexes would show repeatability in social and ecological behaviors, but females would show stronger repeatability than males due to pressure around resource acquisition, whereas males would be less individually differentiated due to alliance dynamics. More specifically, we predicted that females would show higher levels of stability in their foraging tactics than males as well as stronger correlations between social and ecological traits. Multivariate models were used to investigate the correlation between stable ecological variables and social traits at the between-individual level. This detailed, multivariate approach to socio-ecological behavior sheds light on the trade-offs, selective pressures, and potential adaptive consequences linked to individual specialization.
RESULTS

*Repeatability of ecological traits*

Home range size and habitat preferences (across shallow, channel and deep open habitat) were highly repeatable for both males and females (Figure 1a). Males overall maintained larger home ranges than females (pMCMC < 0.001, 95% CI 9.50-21.98). The number of unique foraging tactics used were repeatable for females but not males (Fig. 1a), whereas percent of foraging activity spent on an individual’s most dominant tactic was not repeatable for either sex (Fig. 1a).

Out of the top 6 foraging tactics seen in the population, only tool use with marine sponges (i.e., sponging) and foraging in seagrass showed high levels of repeatability for both males and females (Figure 1b). Females only were repeatable in their use of mill foraging (rapid and irregular surfacing, often changing direction) and foraging in seagrass. Snacking (chasing fish while belly-up at the surface) was not repeatable for females or males (Fig. 1b), even though males were more likely to exhibit this behavior (pMCMC = 0.02, 95% CI: 0.003, 0.05). Leap and porpoise foraging (rapid surfacing with all or most of body clearing the surface) was not repeatable for either sex (Fig. 1b) but showed a decline in the oldest age category (pMCMC < 0.001, 95% CI: -0.03, -0.04).
Socio-ecological syndrome correlations

Multivariate models combining the highly repeatable ecological traits and highly repeatable social traits revealed a socio-ecological syndrome (Table 1). In general, dolphins who spent more time in deep open habitat had larger home ranges and were more gregarious, whereas dolphins who spent more time in shallow habitat had smaller home ranges and were less gregarious. Sponging seems to drive a specific strategy within channel habitat, with sponging female dolphins being less gregarious and spending more time foraging. Sex differences appear to influence some correlations, with shallow habitat preferences interacting with social traits more heavily for males than females (Fig. 2). Conversely, while sponging interacted (negatively) heavily with female gregariousness, it did not interact with male gregariousness.

DISCUSSION

Several (but not all) ecological traits were stable over the adult lifetime of bottlenose dolphins. This stability persisted despite ontogenetic, demographic, seasonal, and reproductive shifts over decades of an animal’s lifetime, supporting the existence and relative permanence of individual ecological niches. Furthermore, robust correlations between ecological and social traits corroborate hypotheses predicting covariance of social and ecological traits along a socio-ecological spectrum (Webber and Vander Wal 2018). Individual differences in home range size and habitat use patterns established in the calf period were stable well into adulthood. In addition, time dedicated to three habitat specific foraging tactics (foraging in seagrass, mill
foraging, and sponge tool use) were established by the juvenile period and continued throughout adulthood. In fact, one of the sponge-tool users has been sponging regularly for at least 37 years.

Individuals could be broadly allocated to three socio-ecological categories within the population: (1) a preference for deep water, large home range and more social contact; (2) a preference for shallow habitat, smaller home ranges, high use of foraging in seagrass and mill foraging, and fewer social contacts; and (3) a strategy driven by a specific foraging tactic, with sponge-tool using female dolphins spending much of their time in the channel habitat, alone, with fewer associates in their network. Each strategy entails distinct tradeoffs that are sex-specific given greater selection pressure on females for prey resources, and on males for access to females. For example, seagrass habitats have more prey biomass but more tiger sharks, their primary predator (Heithaus and Dill 2002; Heithaus and Dill 2006). This tradeoff would be more acute for females given the vulnerability of calves. This does not mean that there are reproductive benefits for females to engage in one strategy over another. Niche theory generally predicts that these tradeoffs result in roughly equal reproductive outcomes (MacArthur 1984), a pattern we found for female habitat use (Mann et al. 2008; Strickland et al. 2021). The tradeoffs for males are not yet known given the difficulties in documenting male reproductive success (Krützen et al. 2004).

While our results substantiate a behavioral syndrome of ecology and sociality at the individual level, the extent of repeatability and correlation structure of socio-ecological niches were not uniform between females and males. Sex differences in socio-ecological strategies suggest that the different pressures facing each sex guide the formation of individual socio-ecological strategies. Both sexes had individually distinct habitat use, home range size, and
social preferences. But a repeatable use of foraging tactics and an ensuing correlation between foraging tactics, home range size, and sociality was only observed for females, with the exception of sponge foraging. Sponge foraging was repeatable for both sexes, aligning with previous research showing sponge foraging is a difficult, time-intensive skill passed down from mother to offspring over generations (Mann et al. 2008). And while sponging has a large effect on female sociality, this effect was not pronounced for males. Males tend to use tactics that are common across the population, and with this less constrained niche can dedicate more time to social tactics necessary for navigating relationships within and between alliances. This is consistent with Bizzozzero et al. (2019) who found male spongers foraged more than other males but did not sacrifice social activity.

Foraging tactics overall did not have a straightforward relationship with sociality, reiterating the need for multiple metrics when defining a niche. Some tactics, such as sponge-foraging, take up much of a female’s activity budget (Mann et al. 2008), leaving less time for grouping. This may be why males sponge forage much less than females (Mann and Patterson 2013), but forage more than other males (Bizzozzero et al. 2019). The use of some tactics may be predicated by physical ability, as suggested by a decline in leap and porpoise foraging in older dolphins. Tactics that take less skill, such as snacking, were exhibited more often by males. Snacking is often the first independent foraging tactic exhibited by calves, so presumably entails less skill than other tactics (Mann and Sargeant 2003). Given that males rarely exhibit some of the most demanding foraging tactics, such as beaching (Sargeant et al. 2005) and sponging (Mann et al. 2008), suggests they are less likely to invest in such tactics – and consequently, are less likely to adopt some maternal ecological traits.
The dramatic socio-ecological variation exhibited by this population occurs sympatrically in a highly socially connected population, unlike other systems outside of humans. In killer whales, one of the most well studied cases of ecological ‘types’, ecological specialization often involves social cooperation, as seen in the co-operative hunting of large whales, or wave-washing for pinniped prey (Pitman and Durban 2012; Pitman et al. 2015). And while killer whale ‘ecotypes’ can have overlapping ranges, different types do not tend to interact and social groups are relatively rigid (Bruyn, Tosh, and Terauds 2013). Sea otters are well known for their individual tool-use preferences and foraging specializations, but lack persistent social bonds and their ecological niches appear to be driven by density-dependent factors (Estes et al. 2003; Tinker, Bentall, and Estes 2008; Newsome et al. 2015; Fujii, Ralls, and Tinker 2017; Lodé et al. 2021). Sympatric ecotypes have not been reported for terrestrial mammals, but have been reported for several fish species (e.g., whitefish, cod; Bernatchez, Chouinard, and Lu 1999; Campbell and Bernatchez 2004; Grabowski et al. 2011) suggesting that marine environments sometimes favor divergence. And while killer whale ecotypes might differ socially (gregarious fish-eating killer whales vs. small groups of mammal-eating killer whales, Baird and Whitehead 2000), social bonds between ecotypes have not been documented elsewhere. Shark Bay dolphins have hundreds of available associates and interact regularly with those that use different strategies, which suggests considerable social and ecological complexity in this system. Extreme fission-fusion dynamics and the fact that most foraging is solitary (Galezo, Krzyszczyk, and Mann 2018) may allow for more individual variation in niche construction within a population. Bisexual philopatry combined with the lack of migration likely intensifies the pressure to diversify behavior, both socially and ecologically. The residential nature of population leads to
sustained pressure on prey, who develop counterstrategies, creating greater selective pressure on specialization and learning. This is combined with the difficulty of navigating an unstructured network and varied relationships that last for decades, a system that favors high relational social complexity (Lukas and Clutton-Brock 2018)

This work can also be connected to theories on brain size evolution, as many delphinid species, including bottlenose dolphins, exceed all non-human primates in relative brain size (Marino 1998; 2006; Montgomery et al. 2013). Ecological and social theories on brain size evolution are hotly debated with a rapprochement in the cultural intelligence hypothesis, which predicts that increased opportunity for social learning should increase individual skills (van Schaik and Burkart 2011). Our results are consistent with this hypothesis, in that Shark Bay dolphins, especially females, exhibit extreme social tolerance (Scott et al. 2005, Mann, Sargeant, and Minor 2007), and the calf, especially daughters, socially inherits the maternal network, with lengthy exposure to her ecological niche. However, sex-specific life history pressures interact with maternal inheritance to determine how an individual creates a socio-ecological niche.

While the benefits of prolonged learning and niche specialization allow for a complex residential network of relationships in a stable environment, even flexible species known for their plasticity may be slow to respond to environmental change. This was evident during a recent seagrass die-off caused by an extreme marine heatwave, disproportionately impacting individuals that specialize in seagrass habitat (Mann et al. 2021). In the face of extreme habitat loss, dolphins did not shift to other habitats, highlighting the limits of plasticity and calling into question predictions that long-lived species will be able to adjust behavior in response to climate change (Huey et al. 2012; Beever et al. 2017; Buchholz et al. 2019). As such, understanding the
stability of socio-ecological strategies has obvious and vital implications for adaptive responses of wildlife populations to the vagaries of climate change.

METHODS

Study population

This study utilized observational, boat-based survey data collected by the Shark Bay Dolphin Research project (SBDRP) between 1988-2019. The study area covers roughly 500km² in the eastern gulf of Shark Bay, Western Australia offshore from Monkey Mia (25° 47’S, 113° 43’E). Behavioral, demographic, genetic, and ecological data on >1800 individually identified Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) have been collected by members of the SBDRP since 1984. Both males and females are residential (Tsai and Mann 2013), enabling lifespan data collection for both sexes.

Ecological measurements

Several measurements of ecological behavior were calculated using sighting records for 160 dolphins, 73 female, 87 male, who met our data requirements of at least 15 sightings during routine surveys within at least three life history periods (calf, juvenile, and 5 year blocks through adulthood). Using GPS points recorded for each sighting, home range sizes were calculated using 90% kernel density estimates with the package adehabitatHR (Calenge 2011). Habitat
preferences were calculated as the proportion of a dolphin’s sightings recorded in each of the three main habitats found in the study area (shallow sand and seagrass, channels, and deep open habitat) using habitat types assigned visually during surveys, supplemented with remote sensing data (Patterson 2012). Foraging activity budget was calculated as the percentage of sightings assigned as predominantly foraging behavior. The dominant foraging tactic (a measure of specialization) was calculated as the percentage of the foraging activity budget taken up by the most used foraging tactic. Foraging breadth was the number of distinct foraging tactics each animal was observed using. Finally, to estimate the repeatability of the use of specific tactics, we calculated the time spent by each dolphin on the six most prevalent foraging tactics in the population (mill foraging, leap and porpoise foraging, tail/peduncle dive foraging, snacking, foraging in seagrass, and sponge foraging). Calves were excluded from foraging measures as their foraging rates are low and they are provisioned by their mother. To address different sample sizes across individuals, a random sample of 15 sighting was drawn for each life stage to calculate each metric, and then resampled for a total of 100 estimates. The mean of these estimates was taken for each metric for each individual.

Statistical analyses

Repeatability for each metric was calculated using procedures outlined by de Villemereuil, Gimenez, and Doligez (2013) using the MCMCglmm package in R (Hadfield 2010). The significance of repeatability was assessed using a null distribution generated by randomizing the dolphin identification and recalculating the metrics without the individual
component. If repeatability estimates did not overlap the null distribution they were considered significant. The correlation between repeatable ecological metrics and with previously reported repeatable social traits (time alone, time in large groups, # of associates and same-sex associates, Evans et al. 2021) at the between-individual level was assessed using multivariate MCMCglmm model procedures outlined by Houslay and Wilson (2017). Model convergence was checked by visual examination of traceplots and assessment of autocorrelation. All analyses were performed in R version 4.0.2 (R Core Team 2020).
Figure II.1. Repeatability estimates for a. general space use and foraging activity metrics, and b. use of specific foraging types. Values are shown for the entire cohort as well as split by
sex. Dashed bars represent the expected repeatability from the null model. Repeatability was considered significant if the 95% CI did not overlap the expected null range.
Figure II.2. Correlogram of among individual correlations for repeatable socio-ecological metrics for a. females and b. males. Darker blue indicates a stronger positive correlation while darker red indicates a stronger negative correlation. All correlations are Kendall’s tau.
Table II.1. Among-individual correlations for repeatable ecological and social measurements. 95% credible intervals for each estimate are in italics. Bolded numbers indicate significant correlations, as determined by CIs that do not cross zero. For sex-specific analyses, the traits which were only repeatable for that sex were included.

### A. All dolphins

<table>
<thead>
<tr>
<th></th>
<th>Home Range</th>
<th>Alone</th>
<th>Large</th>
<th>Associates</th>
<th>SS Assoc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Home Range</td>
<td>---</td>
<td>-0.32</td>
<td>0.43</td>
<td>0.59</td>
<td>0.52</td>
</tr>
<tr>
<td>Channel</td>
<td>-0.09</td>
<td>0.48</td>
<td>-0.41</td>
<td>-0.05</td>
<td>-0.01</td>
</tr>
<tr>
<td>Deep</td>
<td>0.59</td>
<td>-0.41</td>
<td>0.46</td>
<td>0.28</td>
<td>0.18</td>
</tr>
<tr>
<td>Shallow</td>
<td>-0.55</td>
<td>-0.04</td>
<td>-0.08</td>
<td>-0.25</td>
<td>-0.18</td>
</tr>
<tr>
<td>Sponging</td>
<td>-0.11</td>
<td>0.65</td>
<td>-0.58</td>
<td>-0.38</td>
<td>-0.32</td>
</tr>
<tr>
<td>Seagrass Forage</td>
<td>-0.48</td>
<td>0.00</td>
<td>-0.19</td>
<td>-0.25</td>
<td>-0.22</td>
</tr>
</tbody>
</table>

### B. Females

<table>
<thead>
<tr>
<th></th>
<th>Home Range</th>
<th>Alone</th>
<th>Large</th>
<th>Associates</th>
<th>SS Assoc.</th>
<th>Foraging</th>
<th># Tactics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Home Range</td>
<td>---</td>
<td>-0.32</td>
<td>0.32</td>
<td>0.64</td>
<td>0.50</td>
<td>-0.12</td>
<td>-0.33</td>
</tr>
<tr>
<td>Channel</td>
<td>-0.13</td>
<td>0.43</td>
<td>-0.41</td>
<td>-0.14</td>
<td>-0.36</td>
<td>0.24</td>
<td>-0.15</td>
</tr>
<tr>
<td>Deep</td>
<td>0.52</td>
<td>-0.31</td>
<td>0.32</td>
<td>0.36</td>
<td>0.26</td>
<td>-0.17</td>
<td>-0.47</td>
</tr>
<tr>
<td>Shallow</td>
<td>-0.40</td>
<td>-0.11</td>
<td>0.09</td>
<td>-0.22</td>
<td>0.09</td>
<td>0.07</td>
<td>0.63</td>
</tr>
<tr>
<td>Sponging</td>
<td>-0.27</td>
<td>0.84</td>
<td>-0.89</td>
<td>-0.61</td>
<td>-0.83</td>
<td>0.10</td>
<td>-0.48</td>
</tr>
<tr>
<td>Seagrass Forage</td>
<td>-0.31</td>
<td>-0.22</td>
<td>0.12</td>
<td>0.12</td>
<td>0.15</td>
<td>-0.14</td>
<td>0.16, 0.73</td>
</tr>
</tbody>
</table>

### C. Males

<table>
<thead>
<tr>
<th></th>
<th>Home Range</th>
<th>Alone</th>
<th>Large</th>
<th>Associates</th>
<th>SS Assoc.</th>
<th>Small</th>
</tr>
</thead>
<tbody>
<tr>
<td>Home Range</td>
<td>---</td>
<td>-0.32</td>
<td>0.59</td>
<td>0.39</td>
<td>0.42</td>
<td>-0.47</td>
</tr>
<tr>
<td>Channel</td>
<td>-0.10</td>
<td>0.56</td>
<td>-0.39</td>
<td>0.13</td>
<td>0.42</td>
<td>-0.03</td>
</tr>
<tr>
<td>Deep</td>
<td>0.67</td>
<td>-0.54</td>
<td>0.67</td>
<td>0.12</td>
<td>0.02</td>
<td>-0.32</td>
</tr>
<tr>
<td>Shallow</td>
<td>-0.71</td>
<td>0.06</td>
<td>-0.39</td>
<td>-0.29</td>
<td>-0.47</td>
<td>0.42</td>
</tr>
<tr>
<td>Sponging</td>
<td>-0.02</td>
<td>0.61</td>
<td>-0.31</td>
<td>-0.03</td>
<td>0.12</td>
<td>-0.16</td>
</tr>
<tr>
<td>Seagrass Forage</td>
<td>-0.65</td>
<td>0.05</td>
<td>-0.48</td>
<td>-0.39</td>
<td>-0.48</td>
<td>0.53</td>
</tr>
</tbody>
</table>
CHAPTER III

Sex-dependent vertical transmission of socio-ecological strategies

INTRODUCTION

Evidence is accumulating for the long-term persistence of individual social and ecological traits (Vander Zanden et al. 2010; van de Pol et al. 2010; Parthasarathy et al. 2019; Wuerz and Krüger 2015), that combine into broader socio-ecological strategies (Chapter 2). Although both social and ecological variation exhibit demonstrable impacts on population dynamics (Bezamat et al. 2019; Boyer et al. 2010; Sacks et al. 2008), how this variation is maintained through generations is not known. Understanding the evolutionary significance of socio-ecological strategies requires quantifying individual variation, its proximate source, and its fitness consequences.

Concerning its source, maternal effects, or the influence of a mother’s phenotype on her offspring (Bernardo 1996; J. B. Wolf and Wade 2009), are a substantial mechanism of behavior transmission. Maternal effects can be a source of inter-individual variation and thereby natural selective processes (Moore, Whiteman, and Martin 2019). Vertical transmission of behaviors from mother to offspring is prevalent across taxa (Bonduriansky and Day 2009), and may be particularly pertinent for long-lived mammals with extended maternal care and ample opportunity for social learning, such as primates (including humans; Russell and Lummaa 2009)

3 Authorship for paper: Taylor Evans, Molly McEntee, Vivienne Foroughirad, Ewa Krzyszczyk, Céline Frère, Janet Mann
and delphinids (Mann 2019, Rendell et al. 2019). Maternal effects on socio-ecological strategy have not been empirically investigated, although some behavioral phenotypes, such as foraging traditions, are vertically transmitted (Estes et al. 2003; Mann and Sargeant 2003). In hierarchical societies, social rank is often socially inherited from the mother (Dloniak, French, and Holekamp 2006; Ilany, Holekamp, and Akçay 2020; East et al. 2009) but little is known about other social traits. Maternal effects are evident in the juvenile period (Moore, Whiteman, and Martin 2019), but few studies extend into adulthood, despite the changes in niche that come with maturation. One exception is the banded mongoose, which maintains a socially learned adult dietary niche for their lifetimes, albeit this niche is not just learned from the mother (Sheppard et al. 2018). Given the potential lifetime stability of individual socio-ecological traits, maternal effects can have dramatic implications for ecological and evolutionary processes.

The long-term persistence of individual differences implies adaptive significance, making maternal effects a likely mediator of fitness via socio-ecological strategies. Viewed through the lens of niche theory, these individual differences may alleviate direct competition and distribute fitness across a population (Laland, Matthews, and Feldman 2016). Consequently, fitness advantages for a particular socio-ecological strategy are not expected as the relative benefits may be frequency dependent. This is hinted at by the tool-using dolphins in Shark Bay, who are few in number and highly specialized but do not have significantly higher calving success compared to the population at large (Mann et al. 2008). Similarly, habitat preference is not linked to female calving success (Strickland et al. 2021). Instead, the strength of maternal effects and associated fitness consequences may be differentiated by sex. Females and males face distinct life history pressures, resource acquisition and access to mating opportunities respectively (Kappeler and
van Schaik 2002). Therefore, it may be more advantageous for female offspring to follow their mother’s example and for males to diverge, especially from highly specialized ecological behavior. Ample theoretical literature links the socio-ecological environment to fitness (Webber and Vander Wal 2018), but empirical data on ontogeny and subsequent fitness consequences of socio-ecological strategies are sparse.

The dolphins living in Shark Bay, Western Australia provide a unique opportunity to investigate potential vertical transmission and fitness consequences of behavioral specializations. This population is monitored by the Shark Bay Dolphin Research Project, a longitudinal project that has collected behavioral, genetic, ecological and demographic data since 1984 on >1800 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). Shark Bay dolphins exhibit bisexual philopatry (Tsai and Mann 2013), a rarity for mammals (Trochet et al. 2016) allowing data collection to span the entire lifetime for both sexes. They exhibit extreme fission-fusion dynamics where group size and composition changes >5 times per hour (Galezo, Krzyszczyk, and Mann 2018). The flexibility in decision-making afforded by fission-fusion dynamics is theorized to link social and ecological traits to fitness (Webber and Vander Wal 2018), making such a dynamic society a strong candidate for investigation of individual differences and their consequences. The Shark Bay dolphins are also characterized by extensive individual variation, both in foraging (over 20 different foraging tactics have been described; Mann and Sargeant 2003, Patterson and Mann 2015) and in sociality (Gibson and Mann 2008a). They exhibit lifetime stability in social traits (Evans et al. 2021) and sociality correlates with some ecological specializations (Mann et al. 2012, Chapter 2). For certain foraging strategies, especially sponging, a case of tool-use where individuals use basket sponges to root out bottom-dwelling
fish from deep channels, foraging skills are passed from mother to offspring with a strong female bias (Mann et al. 2012; Mann and Sargeant 2003). Preliminary evidence shows that use of specific habitat types are vertically transmitted (Strickland et al. 2021; Mann et al. 2021). Calves have an extended period of dependency (an average of 4 years extending up to 8, Mann 2019; Karniski, Krzyszczyk, and Mann 2018) where they associate extensively with their mothers, providing opportunities for vertical transmission of behavior. The adult period begins at age 10, generally 3-8 years after maternal care has ended, allowing us to extend the known reach (in years and lifespan) of maternal effects. Males and females have divergent life history pressures, with females likely driven by ecological specialization and resource acquisition (Mann et al. 2012; Frère et al. 2010), and males by mate access through cooperative alliances (Krützen et al. 2004). This sex difference in life history may then dictate how advantageous a particular socio-ecological strategy is, leading to a sex-bias in how much an offspring mirrors its mother.

This study is the first to directly investigate the connection between maternal effects, socio-ecological strategies, and fitness. Rather than exclude genetic effects completely, divergence between the sexes would suggest that maternal genetic inheritance is not the sole inheritance mechanism. Furthermore, previous work found much stronger social environment effects than genetic effects in female social behavior (Frère et al. 2010) and genetic inheritance of ecological behavior seems unlikely (Krützen et al. 2005). We utilized the extensive SBDRP database to examine whether socio-ecological strategies are vertically transmitted from mother to offspring. We calculated the correlation between an individual’s adult socio-ecological strategy and that of their mother based on metrics known to be stable individual traits (time spent alone, time in large groups, number of associates and same-sex associates, home range size, and habitat...
use preferences) in order to determine how strongly maternal strategy predicts offspring strategy. The strength of maternal effects was predicted to be sex dependent, given the divergent life history pressures facing females and males. Differences in fitness (as measured by survival) were hypothesized to be more likely found within socio-ecological strategies, than between them, mediated by the sex-dependent dissonance in advantageous behavior between mother and offspring.

RESULTS

Maternal correlations

For females, all social metrics (time alone, time in large groups, # of associates, # same-sex associates) and ecological metrics (home range size, habitat use preferences, and use of sponge tools) correlated between mothers and their adult offspring (p < 0.05, Figure 1). For male offspring, time in large groups and # of same-sex associates were not correlated with maternal measurements (p > 0.05, Figure 1). Time alone and # of associates were weakly correlated (p = 0.4, Figure 5) and all ecological measurements were strongly correlated (p < 0.01, Figure 5). Fisher’s z and Zou’s confidence intervals (Zou 2007) calculated between male and female correlations showed that correlations were stronger between females and their mothers than between males and their mothers for all social metrics as well as for time spent in channel habitat and time spent sponge foraging (Table 1). Correlations were not different between female and
male offspring for home range size, time spent in deep open habitat or time spent in shallow habitat (Table 1).

Nine metrics could be reduced to three principal components (Table 2, Figure 2, Figure 3). Linear regressions and Kendall’s tau show that maternal PCA scores for each component were strongly correlated with offspring scores (Figure 3), and again, the correlation between mothers and adult daughters was stronger than for sons. Similarly, a glmm using euclidean distances calculated between maternal and offspring PCA scores revealed that males, more than females, differ from their mothers in socio-ecological metrics ($p_{mcmc} < 0.001$, 95% CI 0.84 – 1.9).

Survival analyses

PAM (partitioning around medoids) clustering indicated six socio-ecological clusters best described female strategies, while 3 clusters fit best for males (Fig. 4) For females, there were two clusters associated with each of the three main habitat types, and for males one cluster associated with each habitat (Fig. 5). We used these cluster categorizations to determine if socio-ecological strategy had fitness consequences, measured by mortality hazard (Fig. 6). Cox proportional hazard models for male socio-ecological clusters showed that the cluster characterized by more time in shallow water was at higher mortality risk than the other two clusters (Figure 6). For females, the cluster characterized by sponge foraging showed lower mortality risk in comparison to the other clusters (Figure 6). When the same model was run comparing sponge-foraging females to all other females, there was still a significant decrease in
mortality risk (Figure 7). There were no other discernible differences in mortality risk between female clusters. A euclidean distance between mother and offspring PCA scores was not a predictor of survival for either sex, (p > 0.1). Another cox hazards model including the interaction between cluster and distance from mother also did not predict survival for either sex (p > 0.05).

DISCUSSION

Our results established a strong correlation between maternal socio-ecology and adult offspring socio-ecology. This influence persisted for decades, extending the known reach of maternal effects on individual niches. Maternal and offspring correlation was preserved even when metrics were condensed onto PCA components. We posit vertical transmission as a driving force in the formation of socio-ecological specializations, with adult individuals, especially daughters, closely mirroring their mother’s socio-ecological behavior long after dependency. This provides the necessary evidence to treat individual socio-ecological niches as traits under selection pressure.

As predicted, the strength of maternal effects differed by sex, with females being more likely to emulate their mother’s behavior than males. This was especially evident for social behavior, suggesting that the social demands of alliance formation overtake maternal effects. For females, maternal kinship is an important basis for social networks (Foroughirad et al. in review), leading to strong correlations between mother and daughter social traits. However, there was still a modest correlation between male offspring and mother for time spent alone and total
number of associates; maternal influence on male social traits is evident. Maternal effects were comparable between males and females for ecological measurements, even though adult males have comparatively larger home ranges than females (Chapter 2). And while females do associate with their mothers more after weaning than males do (Tsai and Mann 2013; Krzyszczyk et al. 2017), the amount of time is low for both sexes and the difference is not enough to fully explain the differences in maternal effects, especially since foraging is a solitary activity. Additionally, time in temporary separations and weaning age does not differ between female and male calves (Karniski, Krzyszczyk, and Mann 2018; Gibson and Mann 2008; Stanton et al. 2011), so there is no obvious sex difference in the opportunity for vertical transmission. That said, mothers adjust their diving behavior more for daughters than sons (Miketa et al. 2018), suggesting that mothers might facilitate social learning of foraging tactics for daughters more than sons. Possibly mothers provide the baseline from which males deviate to a certain extent, but maternal influence persists. Females, who by their own existence have a successful mother to emulate, have little reason to deviate from behaviors learned during 30,000+ hours of dependency.

Population density has been at the center of hypotheses surrounding individual socio-ecological specialization (Fortin, Morris, and McLoughlin 2008; Webber and Vander Wal 2018). It has been proposed that high social centrality, i.e. the number of connections an individual has within its social network, is more beneficial at low population density (Fortin, Morris, and McLoughlin 2008). However, our results suggest that sex specific life history pressures dictate the costs and benefits underlying individual tradeoffs between social and ecological behavior. Fission-fusion dynamics may loosen density dependence, as social behavior is not constrained by
group membership. Males in this population rely on tight social bonds with other males to gain access to cycling females, whereas females have looser social bonds that are not tied to their pressure of resource acquisition, as foraging is a solitary activity. The different selective pressures for each sex may mean that social activity and associations have more fitness benefits for males than females. This too is hinted at by our previous work showing that male survival in the juvenile period was linked to social dynamics during the calf period (Stanton and Mann 2012).

Survival analyses did not unambiguously affirm assumptions of distributed fitness based on niche theory; there were no differences in survival between most of the female clusters. We also did not find differences in survival based on maternal effects within clusters, suggesting that individual fitness variation is influenced by environmental or other factors we did not test. However, the cluster characterized by sponge foraging did have increased survival. Sponge foraging females seem to have a highly derived niche compared to the rest of the population, on the extreme end of the socio-ecological spectrum. They spend most of their time alone and foraging in the channels, with few associates. The increased survival rate could have several possible explanations. These dolphins exploit different fish from the rest of the population, which are perhaps more reliably abundant year-round than fish found in other habitats (Patterson and Mann 2011). The channel habitat where sponging takes place may also provide some protection from shark predation, as shark predation risk is highest in shallow water (Heithaus & Dill 2002). But despite the apparent benefit to survival, spongers are a small percentage of the population. There is no difference in calving success between sponging and non-sponging females (Mann et al. 2008), and males are less likely to take up sponging (Mann and Patterson...
Within female spongers, performance does not peak until their mid-20s (Patterson, Krzyszczyk, and Mann 2016). This time investment combined with the geographical limitations of the channels where sponges are used may limit the number of sponger dolphins the area can support. In other words, the most ‘successful’ socio-ecological strategy for females may be more strictly frequency dependent.

For males, the cluster characterized by a high percentage of time in shallow habitat had increased mortality risk. This may be indicative of a high-risk high-reward strategy. Shark predation is highest in shallow habitat (Heithaus and Dill 2002). And shallow habitat, especially when covered in seagrass, reduces sound transmission (Quintana-Rizzo, Mann, and Wells 2006), making communication and detection more difficult. Males in shallow habitat spend more time in small groups (Chapter 2), perhaps allowing them to escape detection (and thereby competition) by larger male alliances. Early evidence that at least some of the most successful males in the population spent more time than expected by chance in shallow water (Krützen et al. 2004, unpublished data) corroborates the idea of a tradeoff between mortality risk and mating opportunities.

Taken cumulatively, this study establishes a framework of feedback between sex-dependent life history pressures, maternal vertical transmission of socio-ecological strategies, and fitness. It also raises the importance of considering the relationship between sex differences, socio-ecological strategy, and different components of fitness (Clutton-Brock 1988, Stearns 1992). Our results contrast with previous work in the Shark Bay population finding no differences in fitness as measured by calving success across habitat types (Strickland et al. 2021), perhaps due to our incorporation of a multivariate niche structure. Similarly, foraging
specializations (as measured by isotopic niche) in males of two fur seal species do not correlate with fitness differences (Kernaléguen et al. 2016), but in this case only one sex and one ecological measure were incorporated. Outside of marine mammals, studies in terrestrial ungulates have found that use of particular habitat types has differential effects on fitness, both between sexes and fitness components (Kruuk et al. 1999, Regan et al. 2016), and there are sex-differentiated fitness consequences of individual foraging strategies in seabirds (Patrick and Weimerskirch 2014, Van De Pol et al. 2010). With this study, we demonstrate that incorporating sex differences allows for a fuller understanding of the interplay between socio-ecological strategies and fitness, and this framework will aid in connecting individual strategies to larger population dynamics.

METHODS

This study drew from 61,336 individual sighting records collected by the Shark Bay Dolphin Research Project between 1988 – 2019. The study based out of Monkey Mia in Western Australia (25° 47’S, 113° 43’E) has collected behavioral, demographic, genetic, and ecological data on >1800 individually identified dolphins since 1984. Sightings are obtained through observational boat-based surveys, which are 5 min snapshots of predominant activity, location, and group membership (Karniski et al. 2015).

We included 173 dolphins with sufficient sighting records as adults (at least 15 sightings) as well as mothers with similarly sufficient sighting records. Nine socio-ecological metrics known to be repeatable (time spent alone, time in large groups (≥6 dolphins), number of unique
associates and number of same-sex associates, home range size, use of channel, shallow, and deep open habitat, and time spent sponge foraging) were calculated for each individual as an adult according to procedures outlined in Evans et al. 2021 and Chapter 2. The same metrics were then calculated for their mother. Kendall’s tau as well as linear regressions were then calculated for females and males separately to assess the correlation between offspring and mother socio-ecology. The differences in correlation strength between female and male offspring were measured using Fisher’s z and Zou’s confidence intervals, calculated using the cocor package (Diedenhofen and Musch 2015).

There were 494 individuals who met the requirements of 15 or more sightings post-weaning. Their socio-ecological metrics were also calculated and subsequently used in a principal components analysis. This sample included the original set of offspring and mothers as well as a larger swath of the population. PC scores for the three retained axes were then extracted for the 173 adult dolphins and their known mothers. Subsequent Kendall’s tau and linear regressions were calculated to verify that maternal PC scores were correlated with offspring scores. A three-dimensional Euclidean distance between mother and offspring PC scores for individuals with an included mother was calculated as a measure of similarity between mother and offspring socio-ecological strategy. Using the MCMCglmm package (Hadfield 2010), an mcmcmglmm model with sex as a fixed factor was run to assess whether sex was a predictor for distance from mother. With the same larger dataset, PAM clustering (partitioning around medoids) using the cluster package (Maechler et al. 2013) was used to assign socio-ecological clusters to the population, split by sex. Boxplots of socio-ecological metrics split by cluster were used to describe behavior associated with each cluster.
To assess how socio-ecological strategy is connected to survival, cox proportional hazard models tailored to right-censored data were run with cluster assignment and distance from mother as predictors. All models were split by sex, and were constructed with the survival package (Therneau and Lumley 2014). Models were also run with the interaction between cluster and distance from mother. All analyses were run in R (version 4.0.2; R Core Team 2020).
FIGURES AND TABLES

a.

b.
e.

![Graph showing the relationship between offspring home range size and maternal home range size. The x-axis represents maternal home range size, and the y-axis represents offspring home range size. The graph includes data points for both female and male offspring, distinguished by color. The correlation coefficient for female offspring is R = 0.48, p < 0.01, and for male offspring is R = 0.52, p < 0.01.]

f.

![Graph showing the relationship between offspring channel use and maternal channel use. The x-axis represents maternal channel use, and the y-axis represents offspring channel use. The graph includes data points for both female and male offspring, distinguished by color. The correlation coefficient for female offspring is R = 0.62, p < 0.01, and for male offspring is R = 0.68, p < 0.01.]
g.

h.
i. Figure III.1. Linear regressions with 95% confidence intervals and Kendall’s tau correlations between maternal and offspring measurements for a. time alone, b. time in large groups, c. # associates, d. # same-sex associates, e. home range size, f. time in channel habitat, g. time in deep open habitat, h. time in shallow habitat, i. time spent sponge foraging. N = 173 dolphins, 96 female 77 male. (Note, sponging is a rare tactic so most dolphins are concentrated at 0% time spent sponge foraging)
<table>
<thead>
<tr>
<th>Metric</th>
<th>Fisher's Z</th>
<th>p value</th>
<th>Zou's confidence interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alone</td>
<td>3.79</td>
<td>&lt; 0.001</td>
<td>0.1975, 0.6598</td>
</tr>
<tr>
<td>Large</td>
<td>4.87</td>
<td>&lt;0.001</td>
<td>0.3318, 0.8138</td>
</tr>
<tr>
<td>Assoc.</td>
<td>2.86</td>
<td>0.004</td>
<td>0.1076, 0.5965</td>
</tr>
<tr>
<td>SS.Assoc</td>
<td>4.71</td>
<td>&lt;0.001</td>
<td>0.3503, 0.8571</td>
</tr>
<tr>
<td>Home Range</td>
<td>0.76</td>
<td>0.45</td>
<td>-0.0964, 0.2333</td>
</tr>
<tr>
<td>Channel</td>
<td>3.98</td>
<td>&lt;0.001</td>
<td>0.0620, 0.2343</td>
</tr>
<tr>
<td>DeepOpen</td>
<td>-1.94</td>
<td>0.052</td>
<td>-0.0803, 0.0004</td>
</tr>
<tr>
<td>Shallow</td>
<td>1.91</td>
<td>0.056</td>
<td>-0.0015, 0.1582</td>
</tr>
<tr>
<td>Sponge</td>
<td>4.04</td>
<td>&lt;0.001</td>
<td>0.1148, 0.4012</td>
</tr>
<tr>
<td>Forage</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table III.1.** Comparison of correlation strength between female and male offspring and their mother.
Table III.2. Loadings for the three retained principal components. The highest loading for each variable is in bold.
Figure III.2. A. Biplot of principal components analysis on all dolphins with ≥15 sightings.

B. Scree plot of explained variance for each component. N = 494 dolphins.
a.

b.
Figure III.3. Linear regressions and Kendall’s tau correlation of maternal and offspring PCA scores for the three retained components.
Figure III.4. Socio-ecological clusters for a. females (n = 178) and b. males (n = 187) with at least 15 sightings as adults.
Figure III.5 Boxplot of metrics describing socio-ecological strategies for a. females (n = 178) and b. males (n = 187) with at least 15 sightings as adults.
Figure III.6. Kaplan-Meier plots of survival probability with 95% confidence intervals stratified by socio-ecological cluster for a. females (n = 248) and males (n = 245).
Figure III.7. Kaplan-Meier curve for sponge-foraging females (n = 35) compared to the rest of the females in the dataset (n = 213).
CONCLUSION

This dissertation used extensive longitudinal data on individual dolphins to add empirical evidence to theoretical predictions surrounding repeatable individual differences. Longitudinal data, especially from long-lived, social mammals that have protracted dependency periods and can experience environmental change over multiple years and seasons, allows an increase in resolution over ontogeny. I expanded the time span and ontogenetic stages covered in the literature for both social and ecological behavioral phenotypes. This is the first data-driven study to assess socio-ecological strategies, and to investigate the maternal effects and fitness consequences associated with individual socio-ecology.

In Chapter 1 I showed that dolphins in Shark Bay exhibit strong social tendencies beginning in the calf period, and lasting through decades of adulthood, a length of time rivaled only by human studies of personality. The level of stability seen at first could seem surprising for a social system characterized by extreme flexibility, but I argue that such fission-fusion dynamics coupled with long term bonds requires social trait stability. Individuals need to be predictable to allow for relational complexity, as an unpredictable social partner is a liability. The social metrics that were repeatable correlated into a behavioral syndrome, akin to human extraversion. This is also the first study to show the structure of a behavioral syndrome varying by sex. Sex differences in life history pressures must be considered when discussing selection on individual differences.

In Chapter 2, I demonstrated that home range size and habitat preferences were very stable over the lifetime of bottlenose dolphins. This affirmed predictions of stability posited by niche theory at the individual level. Foraging tactics presented a more complicated situation,
with ubiquitous repeatability found only for the use of sponge tools, a rare and time-intensive tactic dominated by females. These ecological metrics were correlated with social traits, providing new evidence for a socio-ecological spectrum of behavior. And again, sex differences played a role in structuring individual socio-ecological strategies. This is the first empirical evidence of life history trade-offs leading to the formation of individual niches along a socio-ecological gradient.

Finally, given the strong evidence for individual socio-ecological strategies being a lifelong trait, in Chapter 3 I was able to be the first to investigate the role of maternal effects and fitness consequences in maintaining individual differences. As predicted, maternal socio-ecological strategy was a very strong predictor for offspring strategy, with the caveat that males are more likely to differ from their mothers than females, especially in social metrics. This corroborates the framework of sex-dependent life history pressures influencing individual socio-ecology. Surprisingly, when I looked at survival across socio-ecological clusters, sponge foraging females had increased survival, while males spending time in shallow habitat were at increased mortality risk. Female spongers are rare in the population, and do not have increased calving success; their survival benefit may be frequency dependent. For shallow water males, increased shark predation and/or male-male competition could account for the increased mortality, but access to females may be easier in shallow habitat, leading to a high-risk high-reward strategy.

The Shark Bay dolphins provide unique insight into the proximate and ultimate drivers of individual differences. Intriguingly, while individuals have distinct behavioral strategies, this variation develops despite social connections throughout the population. Conversely, similar
socio-ecological strategies occur in dolphins who are not direct associates. And while dolphins do in fact grow up to resemble their mothers, this effect is sex dependent, and only sometimes connected to fitness. This work sets the stage for future investigations on how individual differences influence population dynamics on a larger scale, especially as behavior is bound to be the interface between the individual and a changing environment.
Figure A.1. Time spent alone across the lifespan. Time was calculated as proportion of sightings alone (including dependent mother-calf pairs). Males spent significantly less time alone than females ($p_{MCMC} = -0.197$, 95% CI = -0.26--0.14). Calves and the two oldest adult categories spent more time alone than the other age categories ($p_{MCMC} = 0.095$, 95% CI = 0.05--0.15; $p_{MCMC} = CI$ 0.07, 0.01, 0.14; p.m = 0.13, CI = 0.01--0.23). Juveniles spent less time alone than other age categories ($p_{MCMC} = -0.06$, CI = -0.10--0.01).
Figure A.2 Time spent in large groups (6 or more dolphins) across the lifespan. Males spent more time in large groups than females ($p_{MCMC} = 0.11$, CI = 0.06-0.16). The two oldest adult categories spent less time in large groups than the rest of the age blocks ($p_{MCMC} = -0.07$, CI = -0.12—0.02; $p_{MCMC} = -0.11$, CI = -0.18—0.02).
Figure A.3. **Average number of associates across the lifespan.** There was no significant effect of sex on the number of associates per individual. Calves and juveniles had fewer associates than other age categories ($p_{MCMC} = -9.6$, CI = -13.35—5.53; $p_{MCMC} = -4.90$, CI = -8.54—1.11).

Figure A.4. **Average number of same-sex associates across the lifespan.** Males had more same-sex associates than females ($p_{MCMC} = 6.21$, CI = 3.71-8.92). Calves had fewer same-sex associates than other age categories ($p_{MCMC} = -3.34$, CI = -5.77—0.99).
Figure A.5. Phenotypic correlations (Kendall's tau) of the four repeatable social measurements (time alone, in large groups ≥ 6 dolphins, average number of associates and same-sex associates). All correlations were significant (p<0.001).

Table A1. Number time blocks per dolphin in study

<table>
<thead>
<tr>
<th>Number of time blocks</th>
<th>Number of dolphins</th>
</tr>
</thead>
<tbody>
<tr>
<td>3</td>
<td>70</td>
</tr>
<tr>
<td>4</td>
<td>57</td>
</tr>
<tr>
<td>5</td>
<td>26</td>
</tr>
<tr>
<td>6</td>
<td>19</td>
</tr>
<tr>
<td>7</td>
<td>7</td>
</tr>
</tbody>
</table>
**Table A2.** Dolphins per age category

<table>
<thead>
<tr>
<th>Age category</th>
<th>Number of dolphins</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calf (0 – weaning)</td>
<td>56 (36 female, 20 male)</td>
</tr>
<tr>
<td>Juvenile (weaning – 10 years)</td>
<td>78 (45 female, 33 male)</td>
</tr>
<tr>
<td>Adult 1 (10-15 years)</td>
<td>108 (57 female, 51 male)</td>
</tr>
<tr>
<td>Adult 2 (15-20 years)</td>
<td>134 (66 female, 68 male)</td>
</tr>
<tr>
<td>Adult 3 (20-25 years)</td>
<td>122 (56 female, 66 male)</td>
</tr>
<tr>
<td>Adult 4 (25-30 years)</td>
<td>107 (47 female, 60 male)</td>
</tr>
<tr>
<td>Adult 5 (30 – 35 years)</td>
<td>72 (30 female, 42 male)</td>
</tr>
<tr>
<td>Adult 6 (35 – 40 years)</td>
<td>40 (17 female, 23 male)</td>
</tr>
<tr>
<td>Adult 7 (45 – 50 years)</td>
<td>12 (6 female, 6 male)</td>
</tr>
<tr>
<td>Adult 8 (50+ years)</td>
<td>2 (2 female) excluded from analyses</td>
</tr>
</tbody>
</table>
APPENDIX B

Ethics

Research performed for this dissertation was conducted under Georgetown University Animal Care and Use permits: IACUC-13-069, 07-041, 10-023 and 2016-1235; and Department of Parks and Wildlife Permits (Western Australia): SF-009876, SF- 010347, SF-008076, SF009311, and SF007457.
APPENDIX C

Acknowledgements

I acknowledge the Malgana peoples, the traditional custodians of Gutharraguda and Irrabuga Mia where this research was conducted. Many thanks to colleagues and research assistants on the Shark Bay Dolphin Research Project; I am also grateful to the rangers and scientists at the Department of Biodiversity, Conservation and Attractions in W. Australia for logistical support. Special thanks to Monkey Mia Resort and Royal Automobile Club of Australia for field support. Funding support for this dissertation comes from NSF grants #0847922, 0820722, 9753044, 0316800, 0918308, 0941487, 1559380, 1755229 and ONR 10230702 to J.M.. T.E. received support from the Animal Behavior Society and Georgetown University.
REFERENCES

INTRODUCTION


83


Maechler, Martin, Peter Rousseeuw, Anja Struyf, Mia Hubert, Kurt Hornik, and Matthias Studer. 2013. “Package ‘Cluster.’” *Dosegljivo Na.*


Parthasarathy, Bharat, Chinmay Hemant Joshi, Sreethin Sreedharan Kalyadan, and Hema Somanathan. 2019. “Early Ontogenic Emergence of Personality and Its Long-Term


https://repository.library.georgetown.edu/handle/10822/557522.


CHAPTER I


https://doi.org/10.1111/eth.12651.


Hensley, Nicholai M., Taylor C. Cook, Mason Lang, Matthew B. Petelle, and Daniel T. Blumstein. 2012. “Personality and Habitat Segregation in Giant Sea Anemones...


Karniski, Caitlin, Eric M. Patterson, Ewa Krzyszczyk, Vivienne Foroughirad, Margaret A. Stanton, and Janet Mann. 2015. “A Comparison of Survey and Focal Follow Methods for


CHAPTER II


Brent, Lauren JN, Stuart Semple, Ann MacLarnon, Angelina Ruiz-Lambides, Janis Gonzalez-Martinez, and Michael L. Platt. 2014. “Personality Traits in Rhesus Macaques (Macaca

https://doi.org/10.1093/beheco/arn111.


https://doi.org/10.1016/j.anbehav.2019.02.005.


Cockrem, John F. 2013. “Corticosterone Responses and Personality in Birds: Individual Variation and the Ability to Cope with Environmental Changes Due to Climate Change.”


Maechler, Martin, Peter Rousseeuw, Anja Struyf, Mia Hubert, Kurt Hornik, and Matthias Studer. 2013. “Package ‘Cluster.’” *Dosegljivo Na.*


Parthasarathy, Bharat, Chinmay Hemant Joshi, Sreethin Sreedharan Kalyadan, and Hema Somanathan. 2019. “Early Ontogenic Emergence of Personality and Its Long-Term

Patterson, Eric M., Ewa Krzyszczyk, and Janet Mann. 2016. “Age-Specific Foraging
Performance and Reproduction in Tool-Using Wild Bottlenose Dolphins.” *Behavioral

Patterson, Eric M., and Janet Mann. 2011. “The Ecological Conditions That Favor Tool Use and

Patterson, Eric Michael. 2012. “Ecological and Life History Factors Influence Habitat and Tool
Use in Wild Bottlenose Dolphins (*Tursiops* Sp.).” *Georgetown University-Graduate
School of Arts & Sciences*. Thesis, Georgetown University.
https://repository.library.georgetown.edu/handle/10822/557522.

Petelle, Matthew B., Dakota E. McCoy, Vanessa Alejandro, Julien G. A. Martin, and Daniel T.

and Prey Handling by Pack Ice Killer Whales (*Orcinus Orca*), Type B, in Antarctic

Pitman, Robert L., John A. Totterdell, Holly Fearnbach, Lisa T. Ballance, John W. Durban, and
Whale Predation on Humpback Whale Calves off Western Australia.” *Marine Mammal


CHAPTER III


Maechler, Martin, Peter Rousseeuw, Anja Struyf, Mia Hubert, Kurt Hornik, and Matthias Studer. 2013. “Package ‘Cluster.’” *Dosegljivo Na.*


Quintana-Rizzo, Ester, David A. Mann, and Randall S. Wells. 2006. “Estimated Communication Range of Social Sounds Used by Bottlenose Dolphins (*Tursiops Truncatus*).” *The

https://doi.org/10.1121/1.2226559.


Comprehensive Approach to Foraging Strategies of a Tropical Marine Predator.”


Silk, Joan B., Susan C. Alberts, and Jeanne Altmann. 2006. “Social Relationships among Adult Female Baboons (Papio Cynocephalus) II. Variation in the Quality and Stability of Social


https://doi.org/10.1111/1365-2656.13513.


https://doi.org/10.1111/eth.12133.


