CHOREOGRAPHY ON THE SEA: DECISION MAKING, SYNCHRONY AND
FORMATIONS IN GROUPS OF LONG-FINNED PILOT WHALES

by

Elizabeth M. J. Zwamborn

Submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
August 2024

Dalhousie University is located in Mi'kma'ki, the
ancestral and unceded territory of the Mi'kmaq.
We are all Treaty people.

To my family, whose unwavering support has been my anchor, and to the pilot whales, who continue to inspire me and deepen our understanding of the world beneath the waves.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The goal of my thesis is to improve our understanding of the group lives of social cetaceans through the quantitative exploration of collective decision making, synchrony and formations in long-finned pilot whales (hereafter also referred to as 'pilot whales'; *Globicephala melas*) off Cape Breton Island, Nova Scotia, Canada. Pilot whales live in stable, long-term (likely matrilineal) groups termed "social units" that ephemerally associate with each other, providing a good model for investigating group life in cetaceans. Furthermore, pilot whales frequently mass strand for reasons that are unclear, and knowledge of their natural social behaviour may help us to understand and perhaps mitigate these events. I began with a systematic review of decision making across both terrestrial and aquatic mammals, where I contributed a modified framework to the study of decision making by non-humans and highlighted the scarcity of studies on cetaceans. I then looked at collective decision making in long-finned pilot whales during group dives using frame-by-frame analysis of aerial footage and discovered that dive initiators were significantly more likely to be females in flanking positions. The leadership of these individuals may function akin to flanking horse riders in cattle drives, maintaining cohesion within the group. Using this same aerial footage, I then went on to explore within-group synchrony in breathing and how it varies across social contexts, discovering an increase in synchrony shortly before collective dives and in larger groups. This apparent pre-dive anticipation represents the first evidence of pre-departure behaviour in cetaceans and likely serves multiple purposes: enhancing group cohesion and preparing members for the energetically demanding dive. Finally, I explored group formations in pilot whales by extracting the positions of individuals whales from overhead aerial images, calculating measures of group spatial formation. The formations of pilot whales varied across behavioural states, as well as in the lead up to collective dives, and across group sizes. Overall, my findings elucidate the complex interplay between collective decision making, synchrony, and formations in the day-to-day group life of pilot whales and should help us understand and mitigate mass stranding events.

LIST OF ABBREVIATIONS USED

%	Percent
DFO	Department of Fisheries and Oceans
e.g.	example
et al.	and others
GLM	generalized linear regression models
GLMM	generalized linear mixed models
i.e.	that is
km	kilometre
m	metre
min	minute
n	sample size
N	number of quantitative measures
η_p^2	partial eta-squared
p	p-value
PCA	principal component analysis
s	seconds
S	supplemental
$sp.$	species
SD	standard deviation
vs.	versus

ACKNOWLEDGEMENTS

First and foremost, I'd like to express my gratitude to my supervisor, Hal Whitehead. Hal, your endless patience and guidance during my time in the lab is what got me through this Ph.D. thesis. I dove headfirst into more long-finned pilot whale research, which I knew would be a challenge, and you supported me throughout. Without the amazing opportunities in your lab (both my master and doctoral theses), I would not have experienced an incredible decade of living on the east coast, found my niche working with the long-finned pilot whales or crossed paths with my fiancé. For all this, and more, I am extremely grateful!

I also owe a huge thank you to the Frasers (Oshan Whale Watch), who have been a second family to me throughout this degree – and graciously let us use their vessel for after-hours research surveys when other plans fell through. Cheryl, your witty humour and eagerness to help us document local marine life has been a source of inspiration for me. Your love of pilot whales and knowledge of individuals rivals my own! Cisco, thanks for your willingness to take us out early mornings. You always extended a warm welcome and a place on the boat, no matter who I showed up with! Sharon, your conversation and wonderful meals have been very much appreciated. Thanks also to Ray and Sherry for the many great conversations during my time in the bay.

Additionally, I would like to express my thanks for my committee members. Dara Orbach, your enthusiasm and advice have been invaluable. Thank you for always being eager to review my work, even when it was not the most convenient timing. Shelley Adamo, I appreciate your willingness to review and be part of this work. Lauren Brent, I'm incredibly grateful you could serve as the external for my defence. And Marty Leonard, thank you for your interest in my project and for being such an encouraging preliminary exam external. Your feedback certainly helped strengthen my literature review and research chapters.

To my lab family, you've been my rock! It's impossible to list all the ways you've helped me. A large part of what brought me back to this lab was the collection of people who

through seasons where pilot whales were scarce with humour and comradery, while enjoying the good times with unparalleled enthusiasm.

To my friends scattered across the globe, your support has been my lifeline. Janna Murie, thank you for being such a good friend from afar. Living a continent away wasn't easy, but we enjoyed our times together to the fullest! Christine Konrad, I am blessed to know you as both a former lab mate and a wonderful friend. It's so nice to be living on the same coast once again! Marie-Ève Clark, I fondly remember our evenings singing, adventures on *Balaena*, and many years as roommates. Angela MacDonald, I am so glad our paths crossed early during my doctoral degree. You are a kindred spirit and always encouraged me in the things I was pursuing.

A huge thank you to my family. Mom, Dad, Emily—without your relentless encouragement to chase my passions, none of this journey would have been possible. Quentin, the pilot whales brought us together and our love has weathered this last decade. I was so grateful to call you a friend, then partner in crime, and now fiancé. There is no one I'd rather do life with. Thanks for your encouragement and help with my research, especially all those hours you put into captaining in the earlier years and during the shoulder season.

Much of the inspiration and motivation for this thesis was driven by my experiences with long-finned pilot whales off Cape Breton Island, Nova Scotia, Canada. I have been so privileged to spend summers amongst these beautiful social cetaceans. Though they are slow to surrender their secrets, I am excited for encounters with familiar fins each summer and the discoveries of the future.

CHAPTER 1 – INTRODUCTION

> "I must go down to the seas again, to the lonely sea and the sky,
> And all I ask is a tall ship and a star to steer her by;
> And the wheel's kick and the wind's song and the white sail's shaking,
> And a grey mist on the sea's face, and a grey dawn breaking."
> ~ John Masefield

1.1 Life in Groups

Many animals live or gather in groups, though the structure and stability of these groups can vary significantly between species. Some animals, such as African elephants *Loxodonta africana* and wolves *Canis lupus*, form long-term groups that can span several years or even entire lifespans (Archie et al., 2006; Bekoff et al., 1984). On the other hand, other species may form temporary groups for a specific purpose (e.g. breeding or feeding). For example, many bird species come together in large flocks during migration, benefiting from collective navigation and increased aerodynamic efficiency, and then disband once the migration is complete (Berthold, 2001).

One of the primary advantages of group living is increased protection against predators (Majolo et al., 2008). More individuals generally result in a greater collective vigilance, allowing for more efficient detection of threats, which can lead to more timely and effective evasive actions (Sorato et al., 2012). Being part of a group also functions as an anti-predatory strategy as a greater number of individuals can cause confusion during an attack, making it hard for the predator to target a single individual, or even dilute the impact of the predator(s) on each individual (Jeschke & Tollrian, 2007).

Similarly, there are numerous social benefits to living in groups, including care for offspring by non-parental members of a group (called alloparental care or allocare), as well as reduced competition between groups. Allocare has been observed in many species, from sperm whales *Physeter macrocephalus* (Konrad et al., 2019) nursing and caring for other members of their social units to free-ranging golden lion tamarins *Leontopithecus rosalia* (Bales et al., 2000). Allocare not only benefits the offspring directly, but gives the parent(s) an opportunity to forage without needing to attend to their young (especially if food is in hard-to-reach places) and may also function by having

more experienced members of a group help newer mothers successfully raise their offspring (Riedman, 1982). In some species, larger group sizes have been observed to result in less between-group conflict (Shen et al., 2014).

Being part of a larger group can also facilitate more efficient foraging. In many species, information about food sources can be rapidly shared amongst group members, improving the foraging efficiency for all (Giraldeau & Caraco, 2000). This can be particularly crucial in environments where food resources are patchy or unpredictable (e.g. blue whales *Balaenoptera musculus* collectively monitoring prey patches; Ryan et al., 2022). Increased group sizes can also allow for specialized coordinated hunting strategies that lead to increased success when targeting larger prey species (e.g. wolves predating on American bison *Bison bison*; Macnulty et al., 2014).

However, living together also has its disadvantages. Species that live in groups often need to travel further and forage more often because food sources deplete at a much faster rate (Janson & Van Schaik, 1988). It has also been found that individuals in larger groups also spend more time bonding (e.g. grooming) and less time resting than members of smaller groups – so there is a social cost related to group size (Dunbar, 1992). Additionally, female fecundity is generally lower in groups, which is thought to be driven by intra-group resource competition (Majolo et al., 2008). Despite these costs, many species continue to spend time or live in groups, suggesting that the benefits often outweigh the disadvantages.

1.2 Collective Decision Making

Within groups, collective decision making is a process that contributes to survival and efficiency. These group-level decisions can be either unshared (e.g. leadership by one or several individuals) or shared (e.g. quorum or majority) (Conradt & Roper, 2005). It is thought that shared collective decisions allow group members to make choices that maximize the benefits for the group as a whole, rather than for individual members. Unshared decisions can also be beneficial if some individuals have more ecological knowledge than others, such as how to find food when resources are scarce (Brent et al., 2015). In more stable groups the decision making process may also be influenced by

social hierarchies, where dominant or more socially connected individuals play key roles in guiding the group's choices (Lusseau & Conradt, 2009; Sueur, 2011).

These collaborative decision making processes are often facilitated by distinctive communication systems within the group, such as sneezing within African wild dogs *Lycaon pictus*, moving calls in meerkats *Suricata suricatta* and individual positioning within the group indicating the choice of movement direction in barbary macaques *Macaca sylvanus* (Bousquet et al., 2011; Seltmann et al., 2013; Walker et al., 2017). However, for most species little is known about how collective decisions are made and how this varies across social and behavioural contexts (Zwamborn et al., 2023).

1.3 Synchronous Behaviour and Group Formations

Synchrony, or coordination on a temporal scale, is group-level behaviour that has both costs and benefits. On the beneficial side, synchrony can function to enhance social bonds and decrease the risk of predation within groups (Aguilar de Soto et al., 2020; Senigaglia et al., 2012). It can also lead to more efficient movements, such as the reduced energy expenditure observed when some bird species fly in synchrony (Badgerow & Hainsworth, 1981). Additionally, synchronous behaviours can improve the reproductive success of a species by ensuring that mating, nesting, and rearing of young occur when conditions are optimal (Santos et al., 2016).

However, maintaining synchrony also has its costs. High levels of coordination require constant communication and monitoring, which can be energetically taxing (Aivaz & Ruckstuhl, 2011). There is also the risk of increased visibility to predators when large groups move together synchronously, which can offset some of the protective benefits of the confusion effect or group vigilance (Majolo et al., 2008; Wrona & Jamieson Dixon, 1991). Furthermore, infectious disease transmission is facilitated within tightly synchronized groups, as close and constant proximity among individuals provides an ideal pathway for pathogens to spread (Loehle, 1995). Despite these drawbacks, synchrony is a commonly observed phenomenon in animals, suggesting that the benefits of occasional (or frequent) temporal coordination outweigh the potential costs in many circumstances.

Group formations are spatial configurations, which vary widely across different species. Spatial formations and temporal synchrony are often interdependent, though they are worth discussing as separate (yet related) aspects of group behaviour. One of the primary benefits of formations is enhanced defensive capabilities. For instance, fish moving in tightly spaced and coordinated schools can better evade predators through confusion effects, where the predator struggles to single out an individual spatially from the moving mass (Pitcher, 1993). Similarly, birds flying in a V-formation during migration are using both their temporal synchrony and spatial formation to conserve energy by exploiting the aerodynamic uplift generated by the bird in front, allowing them to travel longer distances with less fatigue (Weimerskirch et al., 2001).

However, these formations also come with inherent costs. In tightly knit formations, each animal must constantly adjust its speed, direction, and position relative to others, which can lead to increased metabolic costs (Zhang & Lauder, 2023). Furthermore, while group formations can provide protection from some predators, they can also make groups more visible and potentially attractive to others (Creel & Creel, 2002).

Differences in formations could also help or inhibit different types of communication, as well as help make certain behavioural activities more effective. For example, beaked whales that surface together after independently foraging usually are close enough that they can use visual and/or tactile communication, rather than longer range acoustic communication that might alert predators to their location (Aguilar de Soto et al., 2020; Alcázar-Treviño et al., 2021). Similarly, being spread out in rank formation may be better for surveying an area for food in contrast to tightly grouped individuals or those following each other and repeatedly surveying the same waters (Whitehead, 1989).

1.4 Group Dynamics of Long-finned Pilot Whales

Long-finned pilot whales (*Globicephala melas*) are large oceanic dolphin species found in the North Atlantic and Southern Oceans (Bernard & Reilly, 1999). They prey predominately on squid and some smaller fish species, which they generally hunt

independently as opposed to collectively (Jákupsstovu, 2002). As with other cetaceans, their food sources are temporally and spatially patchy (Martin et al. 2002; Jákupsstovu, 2002). Adult pilot whales are thought to have few predators, with only several documented killer whale predation events (Jefferson et al., 1991).

Pilot whales form small, stable long-term groups termed "social units" that are thought to be matrilineal in nature, though the strictness of these associations is not fully understood (Amos et al., 1993; Augusto et al., 2017b; Ottensmeyer & Whitehead, 2003). These social units often are found to ephemerally associate with others, forming temporary groups of up to several hundred individuals (Jankowski, 2007; Ottensmeyer & Whitehead, 2003). Pilot whales are socially complex, showing behaviours such as tight group synchrony that is suggested to strengthen social bonds and minimize predation risk (Augusto et al., 2017a; Senigaglia et al., 2012). What is not yet understood is how this species makes collective decisions, how synchrony functions on a group level, and how individuals spatially arrange themselves while carrying out daily activities (such as foraging, travelling, resting and socializing).

Long-finned pilot whales are unique in many ways, displaying some enigmatic life history traits. This species disappeared from the North Pacific (around the 8th to 12th century CE) despite being highly successful in other temperate oceans (e.g. high biomass and numbers; Buckland et al., 1993; Hay, 1982; Payne & Heinemann, 1993). Long-finned pilot whales also display apparent bisexual philopatry, where sons and daughters stay with their mothers long-term, yet they do not have a post-menopausal lifespan as is found in similarly matrilineal species such as killer whales and short-finned pilot whales (Betty et al., 2023; Brent et al., 2015). Interestingly, they also display male-biased alloparental care, with many of these carers being from other social units than that of the calf being cared for (Augusto et al., 2017a). Long-finned pilot whales have a large acoustic repertoire, including repeated call sequences where baroque-like embellishments are added and removed to subsequent vocalizations (Zwamborn & Whitehead, 2017b, 2017a). The reasons for many of these unique and often confounding observations remain a mystery.

Mass strandings are a particularly puzzling aspect of pilot whale group behaviour. While long-finned pilot whales are the most frequently mass-stranded species of

cetacean, the reasons behind mass strandings are not well understood (Moore et al., 2018). Several hypotheses have been proposed, including errors in navigation, the pod following a sick leader ashore, geomagnetic anomalies and anthropogenic disturbances, such as noise from naval exercises or seismic surveys that could potentially disorient the whales and lead to strandings for a species with strong social cohesion (Jepson et al., 2003; Parsons et al., 2008; Moore et al. 2018). Understanding more about decisions, synchrony and formations in free-ranging long-finned pilot whales can help us determine what abnormal behaviours look like and could lead to early intervention and stranding mitigation in situations where this species is observed prior to beaching.

1.5 Research Context

The Cape Breton Pilot Whale Project represents a long-term study focused on the behaviours, social structures, and communication of long-finned pilot whales off the coast of Cape Breton Island, Nova Scotia, Canada. Initiated in 1998 by members of the Whitehead Lab, the project utilizes a combination of photo-identification, acoustic recordings, and behavioural observations to monitor and study these cetaceans. Some of the project's key findings relate to the documentation of complex and stable social structures of these pilot whales, characterized by long-lasting associations within social units (Augusto et al., 2017b; Ottensmeyer & Whitehead, 2003). These social bonds also facilitate cooperative behaviours such as alloparental care, where other pilot whales (both within and outside of these social units) participate in the care and protection of the young (Augusto et al., 2017a).

Acoustically, the project has shed light on the communication of pilot whales, a species which utilizes a diverse array of both simple and complex vocalizations (Nemiroff & Whitehead, 2009; Zwamborn & Whitehead, 2017b). These vocalizations play a crucial role in maintaining group cohesion in the murky, often visibility-limited waters of their natural habitat (Zwamborn & Whitehead, 2017a).

1.6 Summary of Thesis Chapters and Objectives

The goal of my thesis is to characterize the group dynamics of long-finned pilot whales by examining how this species uses collective decision making as well as coordination – on both a temporal (synchrony) and spatial (formations) scale – using aerial footage of groups coupled with behavioural data. Firstly, I reviewed what is known of decision making in mammals and how it relates to what is known of how aquatic mammals (e.g. cetaceans, pinnipeds, etc.) make collective decisions (Chapter 2). Secondly, I looked at whether the timing of individual dives during the group dives of long-finned pilot whales suggested unshared (leadership) or shared (majority) decision making, whether dive initiators were more often represented by a specific age-sex class and whether they initiated the dive from different positions within the group (Chapter 3). Following this I investigated how group synchrony (Chapter 4) and formations (Chapter 5) in pilot whales varied leading up to collective deep dives, as well as across group behavioural state and group size. Finally, I conclude by summarizing what we have learned about group-level decision making and social interactions in long-finned pilot whales (Chapter 6) in the context of theoretical hypotheses, reflect on the challenges of this research and suggest further studies that will help us learn more about group-living in this species.

CHAPTER 2 – COLLECTIVE DECISION MAKING IN AQUATIC MAMMALS[1]

> "Alone we can do so little; together we can do so much"
> ~ Helen Keller

2.1 Abstract

Collective decision making is an essential part of day-to-day life for group-living animals. These decisions can be unshared (e.g. leadership) or shared (e.g. consensus). Aquatic mammals face particular challenges when making collective decisions, including a three-dimensional habitat that can make group coordination and collective navigation a challenge. We systematically reviewed literature on decision making in non-human mammals by examining the types of collective decisions observed and hypotheses used to structure analyses. Most of the current literature was centred around terrestrial species, particularly within primates and artiodactyls. There are no collective decision making studies on aquatic mammal species outside of cetaceans. Both unshared and shared decision making has been reported in whales and dolphins, with leadership found in killer whales *Orcinus orca* and bottlenose dolphins *Tursiops* sp. and consensus decisions in sperm whales *Physeter macrocephalus*. Five recommendations for decision making research include: 1) clearly delineating the temporal components of decision making; 2) standardising research to allow for comparisons; 3) considering both shared and unshared decision making; 4) analyzing decision making across behavioural contexts; and 5) avoiding anthropomorphic terminology. Future studies of collective decision making will help us better understand how non-human mammals overcome environmental and contextual challenges – particularly in the case of aquatic species such as cetaceans, which face challenges related to their aquatic environment and exhibit phenomena such as mass strandings.

2.2 Introduction

Animals that spend time in groups must align individual and collective decisions about where to forage, when to travel, and how to escape predators. It can be argued that collective decision making itself is inherent to the definition of what a group is (Wilson 2000): "any set of organisms, belonging to the same species, that remain together for a period of time while interacting with one another to a greater degree than with other conspecifics." In contrast, an aggregation may be defined as individuals attracted to the same area at the same time for non-social reasons such as abundant food or adequate shelter (Plötz et al., 1991; Heyman et al., 2001).

Within the current literature on collective decision making, decisions are often classified as either unshared or shared according to the framework set out by Conradt and Roper (2005). When decisions are unshared there can be either a single leader (fully unshared) or a few leaders (partially shared), which may or may not be consistent over time (Conradt & Roper 2005). A leadership event can be defined in terms of time (e.g. the first individual(s) to initiate a behavioural change; Krueger et al. 2014) or space (e.g. the individual(s) physically positioned in front of a group leading movement; Lewis et al. 2011). There are many examples of unshared decisions in wild animal populations, such as the leadership of southern resident killer whale *Orcinus orca* matriarchs during times of food scarcity (Brent et al. 2015), distributed leadership in group recruitment of pavement ants *Tetramorium caespitum* (Collignon et al. 2014), and unshared leadership seen during chacma baboon *Papio ursinus* morning departures from their sleeping sites (Stueckle & Zinner 2008).

Conversely, collective decisions can be made in a shared manner with a majority decision made by group members or by reaching a required threshold – such as a quorum in human societies (Conradt & Roper 2005). Some examples include meerkat *Suricata suricatta* quorum-like decisions of when to return to their sleeping sites (Gall et al. 2017), as well as the sneezing of African wild dogs *Lycaon pictus* as a voting-like mechanism for decisions on movement (Walker et al. 2017). Sometimes a consensus cannot be reached, resulting in inaction or even group fission. Societies with fission-fusion

dynamics may avoid conflict, as has been hypothesized in American bison *Bison bison* (Merkle et al. 2015), if individuals can leave a group when they do not agree with the decisions made by others. Fission decisions have been classified as 'combined' decisions because animals make their choices individually, such as whether to stay or leave a given group, in comparison to 'consensus' decisions, which are generally undertaken by spatially cohesive groups that must make decisions about cooperative actions such as travel (Conradt & Roper 2005).

Decision making processes found in mammals are complex and diverse. Many mammalian species are at least partially group living, with examples ranging from extremely stable matrilines to solitary individuals that congregate occasionally under particular conditions to forage (Bigg et al. 1990, Nowacek et al. 2011). Mammals are often individually identifiable and make particularly interesting subjects for research in collective decision making due to an abundance of dedicated long-term studies where the temporal consistency of leadership can be studied (Krueger et al. 2014, Brent et al. 2015). There have been several reviews of mammalian decision making (see Appendix A). Published literature has assessed focused subjects, such as leadership in mammalian societies (Smith et al. 2016, 2020) and collective movement decisions in non-human primates (Fischer & Zinner 2011, King & Sueur 2011), but none has looked at collective decision making across mammals more broadly.

Collective decisions in aquatic environments can lead to additional challenges for both the mammals reaching these decisions and the researchers studying them. Visibility is often low or non-existent and the environment is frequently used in a much more three-dimensional way (e.g. deep diving) in comparison to terrestrial species (Norris & Schilt 1988, Hindell et al. 2002). One taxon of aquatic mammals, cetaceans, includes species that live in groups and frequently make collective deep dives. During these coordinated dives, they are subject to extreme pressures and go to places where they cannot simply return from in a quick manner without serious consequences (e.g. decompression sickness; Fernández et al. 2017). Certain cetacean species are known for commonly mass strandings (Moore et al. 2018). In species such as killer whales and sperm whales *Physeter macrocephalus*, the groups are highly mobile, tight-knit and long-term (Bigg et al. 1990, Christal et al. 1998). How does the different use of space in an aquatic

environment impact how they make collective decisions? How are we to understand the best response or intervention during mass strandings, when we do not understand how the species involved make such collective decisions? Part of the difficulty of examining decision making in aquatic mammals, including cetaceans, is the challenge of collecting continuous observations for species that spend the majority of their time underwater. Recent advances in technology, such as drones (Hartman et al. 2020), have allowed scientists to acquire the data needed to investigate questions about decision making further.

In this review we consider what is known of collective decision making for terrestrial non-human mammalian species and compare this to what has been learned about collective decision making in cetacean species (the only group of aquatic mammals for which collective decision making has been studied). Our goal is to suggest new research directions in this developing field for both aquatic and terrestrial mammals. Our recommendations will allow for more focused and comparable studies in future, at both population and species levels.

We ask the following questions:

1) Which collective decision making processes are used by mammals?
2) What hypotheses have been tested in studies of collective decision making in mammals?
3) How can our knowledge of the collective decision making processes in mammals be used to direct and advance our understanding of collective decision making processes in aquatic mammal species?

2.3 Methods

We used a systematic database search to gather literature on available collective decision making in non-human mammalian species, and then ran a second search targeting decision making literature in cetacean species. The databases Web of Science, Biological Abstracts, ProQuest and Scopus were searched. Identical terms were used for each database during the respective searches (see Appendix B). Only peer-reviewed

articles, books, and theses published up until March 2020 were kept. All citations were uploaded to a systematic review manager (Covidence Systematic Review Software 2021) for analysis. Duplicate literature was removed. Two qualified reviewers screened abstracts (see Figure 2.1 for flowchart) and excluded any studies that were not linked to collective decision making. There was a 94% proportionate agreement between the two reviewers in the selection of studies. A consensus was reached for the remaining literature via consultation and discussion between both reviewers. Both reviewers then evaluated the full text of each article. We excluded studies unrelated to collective decision making, such as research on individual decisions made in a non-group context. We also excluded any theses for which the relevant chapters had been published. Studies on both wild and captive animals were considered. However, as this review focuses on providing suggestions for furthering the field of decision making studies in free-ranging populations of mammals, particularly cetaceans, experimental studies were excluded. We used a quality assessment to exclude any studies that had inadequate data (see Table 2.1).
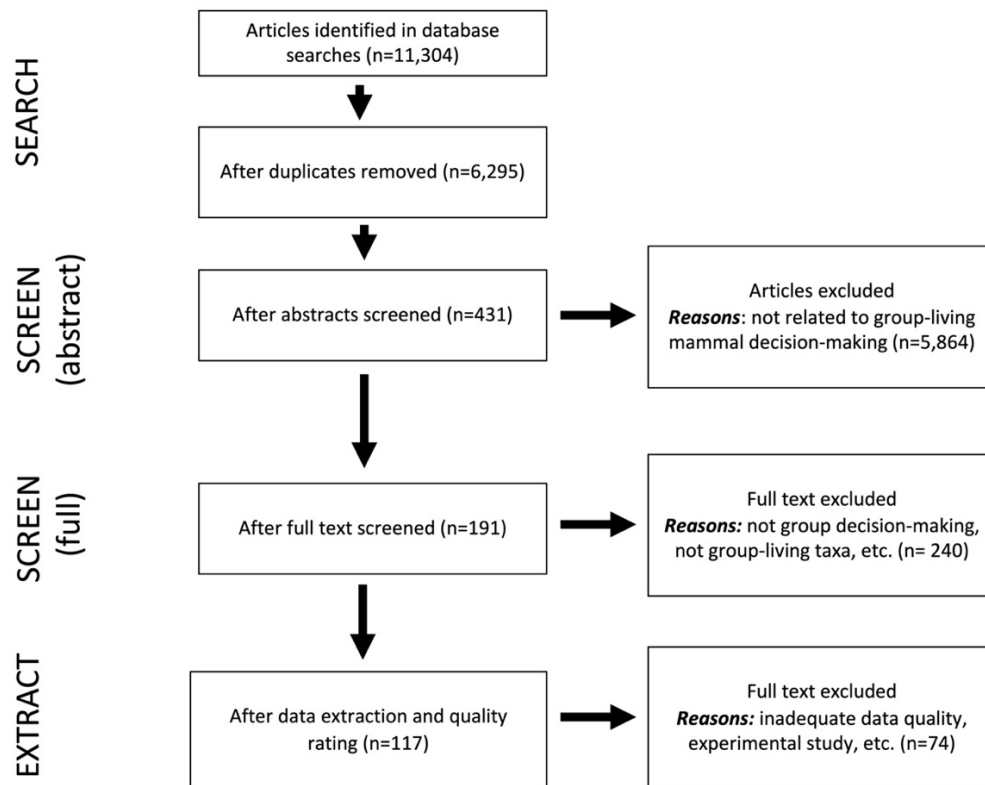
Figure 2.1 Flowchart for systematic review of collective decision making studies in mammal species

Table 2.1 Quality assessment domains for mammalian decision making systematic review

Quality Domain	Considerations
Methods	Are methods well-described and sufficient for inclusion? This ensures that only repeatable studies are included in this review.
Sample Size	Is the study based on an adequate sample size to draw the conclusions made? Inadequate sample sizes are more likely to result in inaccurate conclusions that are not representative.
Quantitative vs. qualitative?	Is the study of decision making purely observational or supported by quantitative analyses? How robust is the conclusion about collective decision making – is it well supported by quantitative data or just a statement made in a broader study?
Evolutionary Framework	Does the study discuss evolutionary reasons or a functional framework for the observed decision making? Is there an evolutionary explanation given for the conclusions of the study?
Study Design	Is the study experimental or non-experimental? Experimental studies do not always produce results that can be observed in nature because of the artificial environment they take place in.
Other Bias	Are there any other obvious biases resulting from the study design that should be considered when deciding whether or not to include this article in this review? Are there funding, professional, environmental, or other considerations that could bias the outcome of the study?

We then extracted for each study: (1) the decision making hypotheses used; (2) the type of decision making found (e.g. unshared, partially shared, shared, mixed, etc.); and (3) the evolutionary explanations proposed by the authors. Box 1 provides definitions for the types of decisions used in this review, based on Conradt and Roper (2005) with additional clarifications.

BOX 1: DECISION MAKING CLASSIFICATIONS

SHARED: equal contribution from all group members on a given decision (quorum – a majority, sub majority or super majority – or voting) (Conradt & Roper, 2005).

UNSHARED (single leader): A single individual who makes a given decision (Conradt & Roper, 2005). For addressing the temporal aspect of unshared decisions, leaders could be:
    a.   <u>stable</u> – a single individual leads
    b.   <u>semi-distributed</u> – a subset of individuals who share leadership over time
    c.   <u>distributed</u> – all members being able to lead in any given decision, whether equally or unequally

PARTIALLY SHARED (several leaders): An intermediate decision, between shared and unshared, where a subset of individuals make the decision (Conradt & Roper, 2005).

MIXED: where any combination of shared, unshared, and partially shared decision-making is used to achieve an outcome.
    e.g., where the decision of WHEN to move might be made separately from the decision of WHERE movement, resulting in a two-part process needed for movement to take place.

2.4 Results and Discussion

Six of the 29 extant mammal orders are represented by collective decision making studies. Cetacean decision making was better represented than decision making in bats, elephants, and carnivorans, but research effort in mammalian decision making was predominantly focused on primates and terrestrial ungulates (see Figure 2.2). Many well-researched groups of mammals (e.g. equids, bats) were represented by only a few non-experimental studies focusing on how they make their collective decisions.
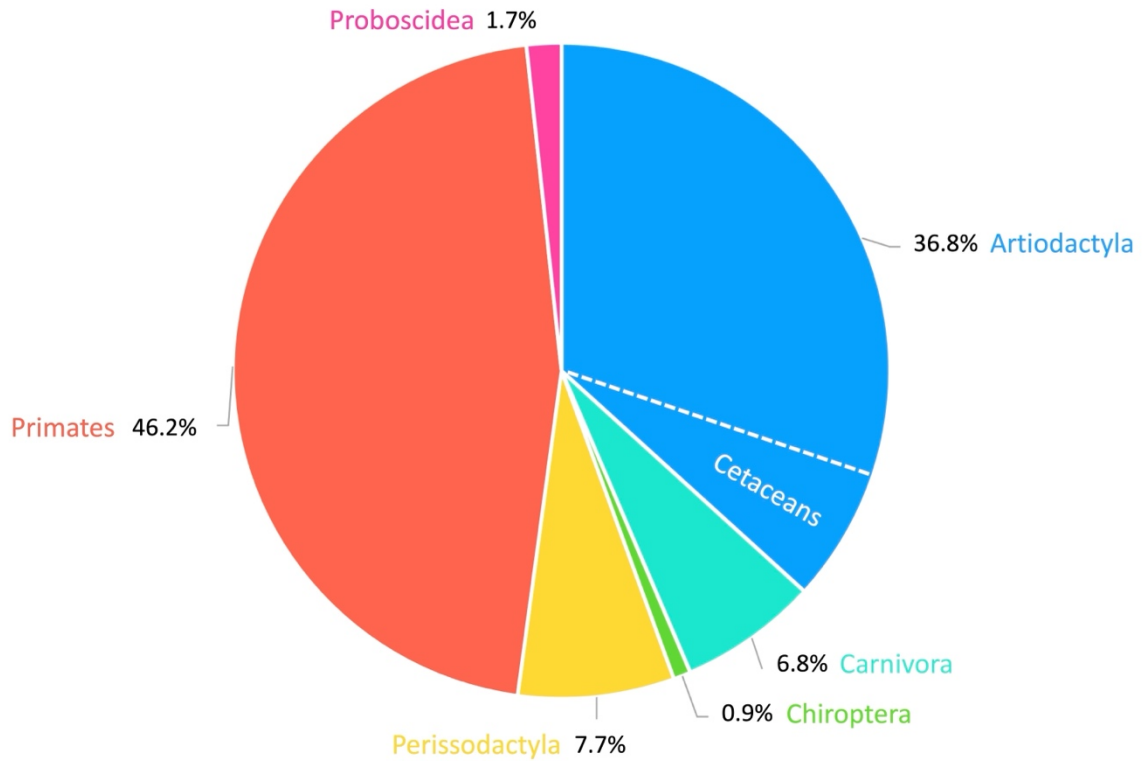
Figure 2.2 Representation of mammalian taxonomic orders from this decision making review (*n*=117), with the percentage of studies for each order. Cetaceans, part of the order Artiodactyla, make up only 8% of studies overall

Within mammalian collective decision making studies there was a wide range of species from diverse habitats and geographical locations. There were several examples of a species, e.g. chacma baboons, being studied on multiple occasions (see Table 2.2) – sometimes with different decision making tactics for different contexts or populations (Sellers et al. 2007, Stueckle & Zinner 2008), which is perhaps unsurprising given our knowledge of the complexity of many animal societies. However, these discrepant findings emphasise our limited understanding of decision making for species that have only been studied in one specific context or for a single population.

Table 2.2 Orders and species of mammals according to observed decision types (aquatic mammal species in bold, represented in the literature only by cetaceans). References are listed in the same order as the species to which they pertain.

Decision Type	Order	Species	References
Shared	Artiodactyla	Moose *Alces alces*, sheep *Ovis aries*, **sperm whale *Physeter macrocephalus***	Geist 1963; Pérez-Barbería & Walker 2018; Whitehead 2016
	Carnivora	Meerkat *Suricata suricata*	Bousquet et al. 2011
	Chiroptera	Leisler's bat *Nyctalus leisleri*	Naďo & Kaňuch 2015
	Primates	Chacma baboon *Papio ursinus*	Sellers et al. 2007
Partially Shared (several leaders)	Primates	Chacma baboon, vervet monkey *Chrorocebus pygerythrus*	Bonnell et al. 2017; Lee & Teichroeb 2016
	Carnivora	Wolf *Canis lupis*	Mech 2000
Unshared (single leader)	Artiodactyla	Barbary sheep *Ammotragus lervia*, caribou *Rangifer tarandus,* cattle *Bos taurus*, **common bottlenose dolphin *Tursiops truncatus*,** elk *Cervus canadensis*, European bison *Bison bonasus*, Giraffe *Giraffa camelopardalis*, goat *Capra aegagrus*, horse *Equus ferus*, **Indo-Pacific bottlenose dolphin *Tursiops aduncus*, Irrawaddy dolphin *Orcaella brevirostris*, killer whale *Orcinus orca*,** muskox *Ovibos moschatus*, Pyrenean chamois *Rupicapra pyrenaica*, roe deer *Capreolus capreolus*, sheep, wild boar *Sus scrofa*, zebu *Bos indicus*	Gray & Simpson 1982; Jakimchuk & Carruthers 1983, Naumov & Baskin 1969; Beilharz & Mylrea 1963, Dickson et al. 1967, Sato 1982, Šárová et al. 2007, Sueur et al. 2018; Lusseau 2007, Lusseau & Conradt 2009; Altmann 1956; Ramos et al. 2018; Berry & Bercovitch 2014; Escos et al. 1993; Wolter et al. 2014; Lewis et al. 2011, 2013b, a; Liew & Labadin 2017; Foster 2012, Brent et al. 2015; Ihl & Bowyer 2011; Gerard et al. 1993; Bresiński 1982, Mrlik 1991; Funk 1981, Carranza & de Reyna 1987; Rowell & Rowell 1993; Tsarev 1980, Zaitsev 1999; Reinhardt 1983
	Carnivora	Domestic dog *Canis familiaris*, wolf, spotted hyena *Crocuta crocuta*	Bonanni et al. 2010; Mech 2000, Peterson et al. 2002; Smith et al. 2010
	Perissodactyla	Horse, zebra *Equus zebra*	Jezierski & Gebler 1984, Krueger et al. 2014, Briard et al. 2015; Penzhorn 1984
	Primates	Bonobo *Pan paniscus*, chacma baboon, chimpanzee *Pan troglodytes*, Columbian white-faced capuchin monkey *Cebus capucinus,* diamemed sifaka *Propithecus diadema*, red lemur *Eulemur rufus*, hamadryas baboon *Papio hamadryas*, eastern lesser bamboo lemur *Hapalemur griseus*, gelada *Theropithecus gelada*, Geoffroy's spider monkey *Atelinae geoffroyi*, Guatemalan black howler	Tokuyama & Furuichi 2017; Stueckle & Zinner 2008, King et al. 2011; Chambers 2019; Leca et al. 2003; Erhart & Overdorff 1999, Rasolonjatovo & Irwin 2020; Romero & Castellanos 2010; Foreit 2016; Dunbar 1983; Palacios-Romo et al. 2019; van Belle et al. 2013; Jacobs et al. 2011; Nakagawa 1990; Ceccarelli et al. 2020; Smith et al. 2003; Makwana

		Alouatta pigra, Japanese macaque *Macaca fuscata*, mantled howler monkey *Alouatta palliata*, mustached tamarin *Saguinus mystax*, northern plains gray langur *Semnopithecus entellus*, Panamanian white-faced capuchin *Cebus imitator*, red-bellied lemur *Elemur rubriventer*, red-fronted lemur *Eulemur rufifrons*, Spix's saddle-backed tamarin *Leontocebus fuscicollis*, Tana River red colobus *Piliocolobus rufomitratus*, Tibetan macaque *Macaca thibetana*, Verreaux's sifaka *Propithecus verreauxi*, vervet monkey, white-faced capwhite-handed gibbon *Hylobates lar*	1979; Boinski & Campbell 1995; Tecot & Romine 2012; Pyritz et al. 2011, Sperber et al. 2019; Smith et al. 2003; Bonnell et al. 2013; Wang et al. 2016; Trillmich et al. 2004; Struhsaker 1967, Lee & Teichroeb 2016; Barelli et al. 2008
	Proboscidea	African bush elephant *Loxodonta Africana*, Asian elephant *Elephas maximus*	Lee & Moss 2012; Mizuno et al. 2017
Mixed	Artiodactyla	Caribou, cattle, European bison, giraffe, plains bison *Bison bison*, Przewalski's gazelle *Procapra przewalskii*, sheep	Lesmerises et al. 2018; Ramseyer et al. 2009b, Ramseyer et al. 2009c, Šárová et al. 2010; Merkle et al. 2015, Ramos et al. 2015; Innis 1958; You et al. 2013; Addison & Simmel 1980, Ramseyer et al. 2009a
	Carnivora	African wild dog *Lycaon pictus*, domestic dog, meerkat	Walker et al. 2017; Bonanni et al. 2011; Gall et al. 2017
	Perissodactyla	Horse, plains zebra *Equus quagga*	Bourjade et al. 2009, Bourjade et al. 2015; Fischhoff et al. 2007, Ozogány & Vicsek 2014
	Primates	Barbary macaque *Macaca sylvanus*, black and gold howler monkey *Alouatta caraya*, black-and-white ruffer lemur *Varecia variegata*, chacma baboon, Columbian white-faced capuchin monkey, golden snub-nosed monkey *Rhinopithecus roxellana*, olive baboon *Papio 17rocut*, Panamanian white-faced capuchin monkey, red-fronted lemur, rhesus macaque *Macaca mulatta*, Tibetan macaque, Tonkean macaque *Macaca tonkeana*, yellow baboon *Papio cynocephalus*	Seltmann et al. 2013, 2016; Fernández et al. 2013; Overdorff et al. 2005; King & Cowlishaw 2009, Zappala & Logan 2010, Sueur 2011, Marshall et al. 2012, Schweitzer et al. 2017; Petit et al. 2009; Wang et al. 2020; Strandburg-Peshkin et al. 2015, Farine et al. 2016; Boinski 1993; Sperber et al. 2017; Wang et al. 2015; Sueur & Petit 2008, Sueur & Petit 2010, Sueur et al. 2010b, Sueur et al. 2011, Sueur et al. 2013; Sueur et al. 2013; Sueur & Petit 2008, Sueur et al. 2009, Sueur & Petit 2010, Sueur et al. 2010b, a, Sueur et al. 2013; Norton 1986

The largest representative category of mammalian decision making is unshared (single leader) decisions, including examples from five of the six orders included in this review (Penzhorn 1984, Peterson et al. 2002, Barelli et al. 2008, Ihl & Bowyer 2011, Mizuno et al. 2017). Many of these studies looked specifically for physical leadership and individuals who initiated group movement. The second most prevalent category was mixed decision making, where a combination of unshared, partially shared, and/or shared decisions were made to reach a goal such as group movement initiation (Seltmann et al. 2016, Gall et al. 2017). There were few examples of species using an entirely shared decision making process (Bousquet et al. 2011, Whitehead 2016), and even fewer examples of partially shared decisions (as defined in Box 1) (Mech 2000, Lee & Teichroeb 2016). Both shared and partially shared decision types were common components within the mixed decision category.

Studies of several well-known cetacean populations made up the entirety of the literature available on collective decision making in aquatic mammals. This research covers five species: democratic consensus movement decisions in sperm whales (Whitehead 2016), spatial leadership observed in common bottlenose dolphins *Tursiops truncatus* and Indo-Pacific bottlenose dolphins *Tursiops aduncus* (Lusseau 2007, Lusseau & Conradt 2009, Lewis et al. 2011, 2013a, b) and killer whales (Foster 2012, Brent et al. 2015), and leadership potential in Irrawaddy dolphins *Orcaella brevirostris* (Liew & Labadin 2017). Evidence for leadership during synchronous surfacings was not found in Indo-Pacific bottlenose dolphins (McCue et al. 2020). There have been suggestions made for leadership in other species, including long-finned pilot whales *Globicephala melas* and sperm whales, particularly during stranding events (de Kock 1956, Mazzariol et al. 2018), but these observations are largely anecdotal, without detailed explanation or supporting evidence.

2.4.1 Hypotheses of Mammalian Collective Decision Making

The hypotheses tested in mammalian decision making studies were diverse, ranging from predicted drivers of leadership to different decision making types and mechanisms underlying the decision making process (see Table 2.3). Over 25% of studies (*n*=30) did not state clear hypotheses in the introduction or methods sections. Reasons for

the lack of stated hypotheses ranged from studies being purely observational without specific decision making goals, to technical papers where specific hypotheses were not tested.

Table 2.3 Hypotheses used in mammalian decision making studies

Hypothesis Category	Hypothesis Subcategory	Number of Studies
Leadership Drivers	Dominance	26
	Energetics*	21
	Ecological knowledge*	16
	Social connectedness*	19
	Kinship*	3
	Personality	3
	Other traits	2
Decision making Type	Consensus*	6
	Leadership – stable*	5
	Leadership – distributed	2
	Quorum	2
	Mimetic	3
Decision making Mechanism	Signal coordination	8
	As a process	4
	Consensus mechanisms	3
	Spatially driven*	3
	Temporally driven	1

* hypotheses presented in cetacean decision making studies

The most common hypotheses proposed centred around testing the drivers of leadership (57% of hypotheses, *n*=90), with dominance (*n*=26), energetics (*n*=21), social connectedness (*n*=19), and ecological knowledge (*n*=16) being the most frequently proposed explanations. These drivers were frequently tested in a similar manner, first by determining the independent variable(s); e.g. dominance rank, reproductive status, age, etc.) for each individual, followed by using a statistical model (e.g. Generalized Linear Mixed Model, Analysis of Variance, etc.) to test which factors successfully predicted observed leadership (Tecot & Romine 2012, Fernández et al. 2013, Ceccarelli et al.

2020). There was a wide variety of statistical methods used. The most common hypothesis was that dominant individuals were most likely to be leaders, particularly among primates where high-ranking individuals often play a key social role within their groups (Leca et al. 2003, Bonnell et al. 2017). Examples of dominance-driven leadership can be found in species such as sheep *Ovis aries*, chacma baboons, wolves *Canis lupus*, and cattle *Bos taurus* (Addison & Simmel 1980, Mech 2000, Peterson et al. 2002, Šárová et al. 2007, Romero & Castellanos 2010).

Not all mammalian species exhibit dominance hierarchies, and other studies were focused on alternative explanations for successful leadership. The hypothesis that females would be more likely to lead based on higher energetic needs when gestating or lactating was proposed as an explanation for species ranging from plains zebra *Equus burchellii* and spotted hyenas *Crocuta crocuta* to primates such as vervet monkeys *Chlorocebus pygerythrus* and red-fronted lemurs *Eulemur rufifrons* (Fischhoff et al. 2007, Smith et al. 2010, Lee & Teichroeb 2016, Sperber et al. 2019). In species where social connectedness was an important component of societies, it has been suggested that more connected individuals are frequent leaders (Strandburg-Peshkin et al. 2015). Socially central individuals in common bottlenose dolphins, Tibetan macaques *Macaca thibetana* and highland cattle have been observed with more followers and better leadership success (Lusseau 2007, Wang et al. 2016, Sueur et al. 2018).

The ecological knowledge of an individual was sometimes proposed to be the driver behind leadership. In killer whales, post-menopausal females were observed leading, likely because their age and experience meant that they held the best knowledge of where to find salmon (*Oncorhynchus sp.*) when food was scarce (Brent et al. 2015). Similarly, female Verreaux's sifakas *Propithecus verreaxi* were hypothesised to lead more often because they do not disperse from their natal habitats like males do, and therefore would have knowledge of where to find food (Trillmich et al. 2004). Kinship and personality (e.g. bold vs. shy) were also hypothesised to be drivers of successful leadership (Lee & Moss 2012, Briard et al. 2015), though far less often.

The second most common type of hypotheses were those that attempted to determine the mechanisms behind the decision making process (12% of hypotheses, *n*=19). Almost half of these were focused on whether signal coordination was important

in decision making (*n*=8). Testing for this hypothesis mainly occurred in primates (Boinski 1993, Boinski & Campbell 1995), though there were studies on both spotted hyenas and meerkats that also found vocal signals responsible for group conflict avoidance and group movement coordination respectively (Smith et al. 2010, Gall et al. 2017). Hypotheses in this category also focused on whether decision making was spatially driven (*n*=3; e.g. whether individuals in specific positions within a group consistently led directional changes) or temporally driven (*n*=1; e.g. whether leadership for direction changes depended upon the first individual to move, regardless of position within the group); what mechanisms underlay consensus decisions (*n*=3); and even suggested that decision making in some species was a process involving multiple decisions (*n*=4; Norton 1986, Petit et al. 2009, Ramseyer et al. 2009a, Seltmann et al. 2013).

The third category of hypotheses tested was composed of those testing for decision making type (11% of hypotheses, *n*=18), specifically if there were consensus decisions being made (broadly, *n*=6), what the type of leadership was being used (stable vs. distributed, *n*=7), whether a quorum determined the decision (*n*=2), or whether mimetics played a role in how groups moved (*n*=3). A study on Tibetan macaques discovered that a quorum system was used if the initiator had a simple majority of followers, but selective mimetics also played an important role if less than the majority initially followed (Wang et al. 2015).

2.4.2 Recommendations

There is great potential for future research to expand our understanding of leadership and shared decisions in non-human mammals. We have five recommendations for designing a study on collective decision making or analyzing opportunistic data collected for other studies.

Make clear delineations between temporal and non-temporal aspects of decision making

Like many areas of behavioural research, the literature available on mammalian collective decision making suffers from weak and overlapping definitions. What is leadership? Does the initiator also count as a leader even if they do not lead the

subsequent movement or only function in triggering a voting process? Are those pivotal first followers who are needed to meet a quorum also leaders? In their framework, Conradt and Roper (2005) defined unshared decisions as a single dominant individual acting as leader, which does not consider situations where leadership is not linked to dominance. In aquatic mammals such as cetaceans, dominance hierarchies are not apparent, perhaps because a three-dimensional and fluid habitat limits opportunities for the monopolization of resources (Strickland et al. 2017, Rendell et al. 2019). In cetaceans, social connectedness and ecological knowledge have been more commonly suggested as drivers of leadership (Lusseau 2007, Brent et al. 2015).

Conradt and Roper's (2005) broad definition of partially shared leadership as "a subset of individuals making a given decision" has a wide range of interpretations. Having several leaders for a specific decision, in contrast to several leaders rotating leadership at various times are quite different scenarios, although in both cases, the leadership is temporally stable with the same individual(s) leading across the study period. It appears that much of the confusion in terminology could be avoided if time was considered and incorporated into definitions. Further conflating this terminology is that distributed leadership (temporally unstable), where all individuals in the group are observed leading, is sometimes also interpreted as 'partially shared'. An example of this would be if some individuals (e.g. females) lead more often than others, even though everyone takes a turn at leading (Lee & Teichroeb 2016). Where then do these complexities fit into our understanding of decision making? We propose that a single decision made by one individual at a specific point in time to be termed as 'unshared', with a second temporally defined sub-category associated to capture these nuances (e.g. stable, semi-distributed, distributed unequally, or distributed equally; see Figure 2.3). Clarifying the temporal dimension of terminology, as well as the mechanisms of decision making and potential functions, will not only help facilitate the comparison of studies, but also give the reader a clear understanding of the goals and scope of the research.

Standardise methods to allow comparisons

There is a need for more standardized studies to facilitate comparisons of populations and species. There has been an attempt to standardise research methods in several cases, often as the result of researchers being involved in multiple similar studies or projects across populations or species (e.g. Sueur & Petit 2008, 2010, Sueur 2011). Much of the lack of standardization may result from studies that use opportunistic data, where understanding decision making is a secondary research goal. Targeted data collection may be necessary for undertaking comparative studies and furthering the field of decision making research.

Consider both shared and unshared decision making

Within mammalian decision making research, there is also a need to develop studies which consider both shared and unshared decisions. Many of the studies we reviewed were focused solely on testing a hypothesis for one or the other. For example, if one is testing specifically for physical leadership, the absence of an individual leading in front would not preclude leadership as it could be acoustic in nature or conducted from a central position in the group. The risk of not testing for both shared and unshared decision making is that the research will be limited in what it can say about these decisions and potential process complexities. Researchers have observed different decision making types within the same species, indicating that decision making may be influenced by the context in which it is made. If there is evidence for a physical leader when group movement begins, it can be difficult to determine whether this decision is truly unshared or whether the observed 'leader' is simply initiating movement in a direction that has already been agreed upon by the majority of the group through a shared decision making process.

That decision making can be a mix of shared and unshared processes is often overlooked. Events, such as group movement, that are initiated by an individual, who then triggers a consensus decision on direction by the group, have been found in several species including Panamanian white-faced capuchins *Cebus imitator*, and meerkats (Boinski 1993, Gall et al. 2017). Thus, shared and unshared decisions are not mutually

exclusive. For example, barbary macaques *Macaca sylvanus* have a two-fold process where the first part of the decision to move is shared by group members who display pre-departure behaviour to signal a readiness for movement, followed by an unshared decision when an initiator starts travel (Seltmann et al. 2013). Figure 2.3 outlines a framework for exploring decision making as a process.
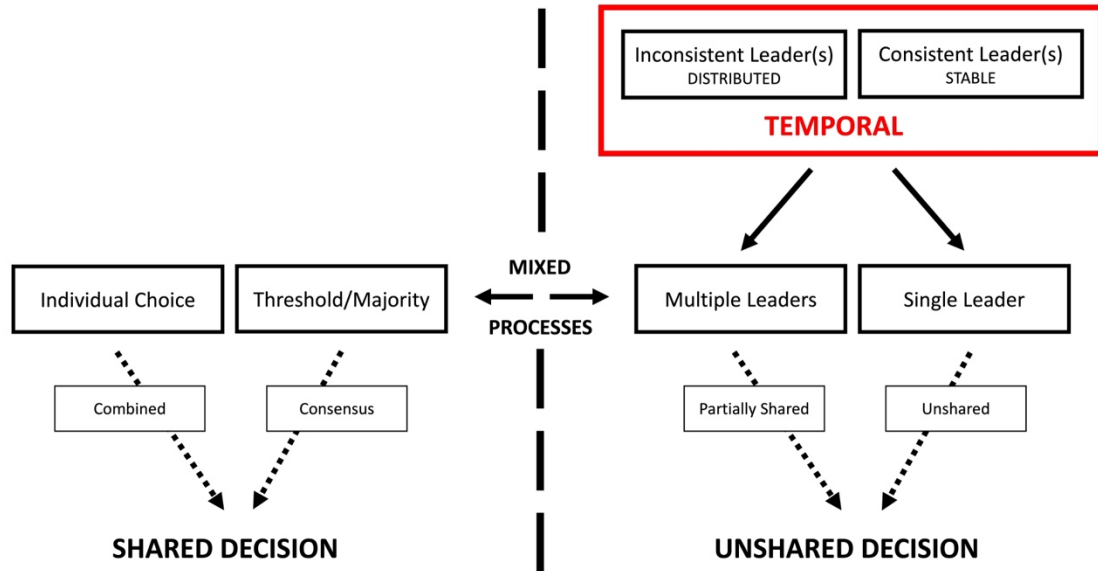
Figure 2.3 Decision making framework for a given collective decision or series of decisions, including consideration of temporal components

A decision making process may be simple or complex – and may require several hypotheses and analyses to clarify. Important questions to consider include: is the decision shared or unshared? If unshared, is there one leader or several? If leadership, is this leadership temporally consistent? Does the process start with leadership and result in a shared decision, or vice versa? If the decision is shared, does it result in group consensus or fission into subgroups?

Consider decision making in context

Studies that incorporate decision making for a population or species across different contexts are crucial for a broader understanding of how collective decisions are made. This was done in an observational study of mountain zebras *Equus zebra*, where

dominant mares led most herd movements, but stallions were observed consistently taking over leadership when the group went to drink (Penzhorn 1984). Many studies were focused on specific events or choices (Berry & Bercovitch 2014, Gall et al. 2017), resulting in important findings, yet a poor understanding of collective decision making beyond these behavioural contexts. If there are older female leaders in an endangered population who lead groups to food during scarcities (ecological knowledge), then prohibiting the removal of these older females and protecting known traditional foraging habitat would be important. However, other decisions within this population (e.g. where they breed, who defends against predators, etc.) may not use the same decision making strategies. Conservation measures based on a single context or study might be limited in their ability to protect the population and detrimental if the assumption is made that the population consistently makes decisions in the same manner.

How can shifts in behaviour, including those not associated with the initiation of group movement, tell us more about how decisions are made? Collecting consistent temporal (timing) and spatial (position) data, in addition to information on individual gestures, orientation, and even acoustic signals associated with group decisions will be important for facilitating the study of collective decision making across contexts.

Avoid anthropomorphising decision making in non-human mammals

Studies on decision making often use language that is anthropomorphic, implying assumptions about the underlying drivers of the decisions being made. Examples of these are words like 'democratic', used when referring to shared decisions, and 'despotic' when discussing leadership or an otherwise unshared decision. Do animals really count, as is implied when using the term 'quorum', or are they more sensitive to a different sort of threshold? Are the leaders of groups truly 'despots'? We should be careful when using wording that implies the intentions of the decision-makers in cases where this is still often unknown. Using terms such as shared and unshared in place of democratic and despotic, as well as threshold instead of quorum, are less assumptive and more objective.

2.4.3 Why are Continued Efforts to Study Collective Decision Making in Aquatic Mammals Important?

Perhaps the greatest challenge for aquatic mammals when it comes to collective decision making is the environment in which they live and how they use it. Many cetaceans have been observed diving to great depths to forage, the deepest of these being recorded for Cuvier's beaked whales *Ziphius cavirostris* reaching to 2992m (Schorr et al. 2014). Even species that are generally thought of as inhabiting surface waters have been occasionally shown to dive deeper, such as killer whales, where a 1087m deep dive was recorded for an individual in the Southern Ocean (Towers et al. 2019). Not only are these species diving to great depths where low visibility in addition to high pressure limit communication options and constrain movement patterns, but many of these departures and returns to the surface are also tightly coordinated with other conspecifics (Aguilar de Soto et al. 2020). Additionally, ocean environments are often patchy and unpredictable in resources (Martin et al. 2002), meaning that collective travel decisions are a critical part of life.

All but one of the studies on cetacean decision making found evidence of leadership in collective decisions, with examples in both long-term stable groups and societies with fission-fusion dynamics (Lewis et al. 2011, Brent et al. 2015). This comes as a bit of a surprise, as monopolizing resources in the ocean is difficult, given its patchy and unpredictable nature, and the added dimensionality of the habitat. Because of this, both territoriality and dominance are less commonly observed in cetaceans (Strickland et al. 2017, Rendell et al. 2019). We would expect unshared decision making to be less common than in terrestrial mammals, as leadership is frequently observed in species with strong dominance hierarchies (Peterson et al. 2002, Sueur et al. 2013). There are several possible reasons for the unexpected frequency of leadership in cetaceans. Firstly, in female-centred societies, such as those found in killer whales, the group may value the ecological knowledge of certain individuals and follow their lead at times when this information is needed (Brent et al. 2015). Secondly, several of these studies looked at small inshore dolphin populations (Lusseau & Conradt 2009, Lewis et al. 2011), where competition and potential temporal monopolization of restricted resources within a small area may be more common. Thirdly, shared decisions might be more difficult to detect in

cetaceans, particularly when studies are designed to look for physical leadership amongst animals that spend much of their time underwater.

It is important to consider how space use in three-dimensional aquatic environments with extreme pressure gradients and generally low or non-existent visibility impacts how collective decisions are made. An obvious problem would be the difficulty of maintaining communication between conspecifics over large distances and depths (Tyack & Clark 2000). Groups of sperm whales can spread out over several kilometres to hunt independently, yet they must make collective decisions on how to move directionally (Whitehead 2016) and then find each other when they return to the surface. Life in aquatic environments is compounded by an additional challenge. Light travels poorly and chemical signals do not function well, meaning that communication is often limited to acoustic signals (Tyack & Clark 2000). The use of sound is likely to be a much more integral element of collective decision making in cetaceans than for most terrestrial species (perhaps with the exceptions of bats and humans). While we know that cetaceans have developed advanced acoustic abilities to communicate (as well as forage and navigate in toothed whales), the importance and function of these signals in collective decision making remains largely unknown (Tyack & Clark 2000). It can be argued that the collection of acoustic data is just as important or even more critical than the collection of movement data for studying how cetaceans make collective decisions, given that this is their primary means of communication.

Studies of decision making also have the potential to contribute valuable insight into cetacean sociality. For example, finding a relationship between social connectedness in Indo-Pacific bottlenose dolphins, and discovering who leads within different social contexts (Lusseau 2007), allows us to address questions about the evolution and function of their social structure. Decision making studies can also help us understand the psychology of individuals. Research in horses and elephants found that personality can predict who leads (Lee & Moss 2012, Briard et al. 2015). While no studies in cetaceans have been focused on how personality and leadership are connected, a recent study in wild common bottlenose dolphins that looked at traits (e.g. shyness, boldness) in individuals showed that this would be an attainable next step (Díaz López 2020).

A phenomenon unique to cetaceans that Involves decision making is mass stranding. Various potential causes for strandings have been proposed (including military sonar exposure, navigational errors, and illness), and in many cases it can be hard to determine the exact cause (Moore et al. 2018; see Appendix C for further discussion on the causes of mass strandings). Sometimes, individuals have been observed close to the shore in the hours or days before a stranding takes place (Best & Reeb 2010). The singularity of mass strandings has resulted in much discussion and reporting from groups dedicated to rescue and response, but there are few peer-reviewed articles on potential causes. Literature pertaining to pre-stranding behaviour is even more scarce (Best & Reeb 2010). This is in part because strandings are typically identified as an issue only after they occur. Current technology and social media sharing means that access to footage of strandings that are 'in progress', showing behaviour as whales linger in nearshore waters and swim towards the beach, is more readily available. Understanding more about day-to-day and pre-stranding cetacean collective decision making would likely allow us to prevent or mitigate some (particularly anthropogenically-triggered) stranding events.

2.5 Conclusions

Studies of mammalian collective decision making have advanced significantly in recent years. We have made five recommendations to move the study of decision making forward: 1) make clear delineations between temporal and non-temporal aspects of decision making, 2) standardize methods to allow comparisons, 3) consider both shared and unshared decision making, 4) consider decision making in context, and 5) avoid anthropomorphizing decision making by non-human mammals. While cetaceans are not the only group of aquatic mammals that make collective decisions, they represent the entirety of available literature on decision making for these animals. A better understanding of collective decision making across species will help us understand how these mammals have adapted to an environment with unique challenges not faced by their terrestrial counterparts. Additionally, research has the potential to provide new insights into both the function of social structures and the psychology of individuals (e.g. the role

of personality). With new technology, data needed to answer many of these research questions are becoming readily available (Figure 2.4). Learning from the successes and challenges in collective decision making studies conducted across other mammalian species is important in advancing the field of aquatic mammal behaviour and maximising future research opportunities.
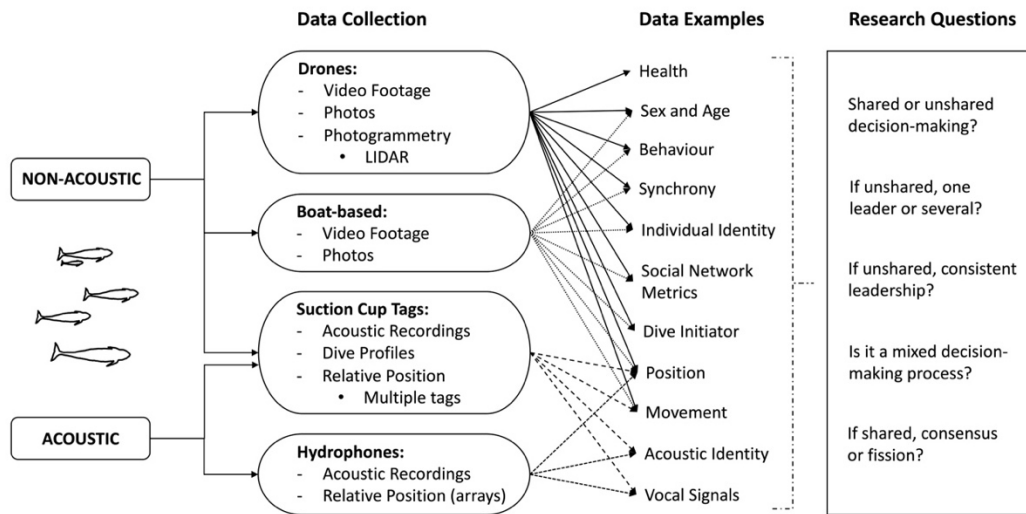
Figure 2.4 Suggested data collection methods and data types for studying decision making (including acoustic aspects) in aquatic mammals

CHAPTER 3 – FLANKING FEMALE GUIDES: COLLECTIVE DECISION MAKING IN LONG-FINNED PILOT WHALES[2]

> "A genuine leader is not a searcher for consensus,
> but a molder of consensus"
> ~ Martin Luther King Jr.

3.1 Abstract

Little is understood about how social cetaceans make collective decisions. Consensus processes are often beneficial for fitness at both a group and individual level, but most previous studies of decision making in whales and dolphins show evidence of a leader, frequently an individual with greater ecological knowledge or social connectedness. We used drone footage of long-finned pilot whales *Globicephala melas* off Cape Breton Island, Nova Scotia, Canada, to examine the characteristics of initial divers (age class/sex, relative position, accompanying calf) and the timing of when individuals dive (i.e. dive lag) within collective group dives (n=73). Resting groups of pilot whales had threefold higher mean dive lag and inter-individual dive intervals than groups in other behavioural states. Females initiated dives more often than expected by chance and initial divers were most frequently located peripherally on the left or right flank of the group. Dive lags following the initial diver had a heavily right-skewed distribution, suggesting that long-finned pilot whales within groups often respond to a stimulus (e.g. physical leadership, a vocal signal, approaching vessel). These findings are consistent with the hypothesis that unequally distributed leadership guides the temporal patterning of the collective deep dives of pilot whales.

3.2 Introduction

Group-living animals regularly make collective decisions, such as what direction to travel, how to avoid predators, and when to rest. These decisions are categorized as either unshared – where some form of leadership from one or several individuals occurs – or shared – a consensus decision with a threshold of individuals (e.g. a majority) (Conradt & Roper, 2005). Sometimes decisions are complex and involve a combination of both shared and unshared processes (Seltmann et al., 2013). If not all individuals agree on an outcome (e.g. where to move), it can lead to the splitting of a group (Courant & Fortin, 2012). Shared decisions benefit individual and group fitness, as they tend to result in less extreme decisions than those made by a single individual or small portion of the group (Conradt & Roper, 2005). However, leadership can outweigh the advantages generally attributed to shared decision making, including contexts where one individual holds important ecological knowledge, is dominant, or requires more access to resources (Brent et al., 2015; McComb et al., 2011).

Collective decision making has been studied across a wide range of terrestrial mammal species, with a range of processes and patterns being identified. For example, it was observed that most individuals are able to lead within groups of spotted hyenas *Crocuta crocuta*, but that certain traits (e.g. reproductive status, higher rank) predicted how often a particular hyena would lead (Smith et al., 2010). On the other hand, meerkats *Suricata suricatta* show evidence of shared decision making processes where a threshold number of individuals must make moving calls before the decision to move is made (Bousquet et al., 2010). Collective decision making styles often align with what is known about social structure in a species. For example, more egalitarian Tonkean macaques *Macaca tonkeana* involve almost all group members in collective decisions, while less egalitarian Rhesus macaques *M. mulatta* relied heavily on the input of just a few dominant individuals (Sueur & Petit, 2008).

There is considerably less known about collective decisions in aquatic mammal species, where the difficulties of observing groups for long periods at sea makes them more challenging to study than their terrestrial counterparts (Zwamborn et al., In Press). Many species of cetaceans live in groups and behave collectively, but little is known

about how group decisions are made. Shared decision making has been observed within groups of female sperm whales *Physeter macrocephalus*, who use slow "messy" group direction changes indicative of consensus decisions (Whitehead, 2016). In contrast, leadership by bottlenose dolphins *Tursiops spp.* can vary according to behavioural context (e.g. male bottlenose dolphins in Doubtful Sound, New Zealand, initiate travelling bouts while females terminate them; Lusseau & Conradt, 2009). Leadership has also been documented in post-menopausal southern resident killer whales (*Orcinus orca*), who hold important ecological knowledge and physically lead their matrilines in times of prey scarcity (Brent et al., 2015). Understanding how cetaceans make collective decisions helps elucidate how they overcome the unique challenges of living in aquatic environments, in comparison to terrestrial habitats where decision making is most often studied (Zwamborn et al. In Press). This is especially important for deep-diving odontocetes, where the loss of group cohesion on collective deep dives can result in an increased risk of predation (Aguilar de Soto et al., 2020; Alcázar-Treviño et al., 2021). Disruption of social bonds and loss of group coordination has been suggested as a reason for mass strandings (Oremus et al., 2013). Knowing who makes decisions within cetacean societies and how these processes work enhances our understanding of the role of individuals within known social structures (Brent et al., 2015).

Long-finned pilot whales *Globicephala melas* (henceforth referred to also as "pilot whales") live in stable social units thought to center around matrilines, with females and their offspring remaining together over long periods of time similar to resident killer whales (Amos et al., 1993; Bigg et al., 1990). The collective deep dives pilot whales make can function in foraging or simply be routine during travelling (perhaps offering the group an opportunity to assess prey abundance and location as they move). Pilot whales are known to be particularly susceptible to mass strandings, the causes and processes of which are still poorly understood (Moore et al., 2018). The common name "pilot whale" stems from perceived leadership within this species, with historical anecdotal reports often referring to the role of a sick leader as a causal reason for the stranding of entire groups (de Kock, 1956). However, there have been no studies investigating decision making processes in either pilot whale species.

We explore the characteristics of dive initiators and individual dive timing within group dives to assess how long-finned pilot whales make collective dive decisions. To determine whether some pilot whales are more likely to initiate dives than others, we looked at whether there were differences in age class and sex, relative position within the group, or the presence of an accompanying calf between initiating and non-initiating individuals. If the opportunity to initiate dives is equally distributed, we would expect no significant differences in initiators regardless of age class, sex, spatial positioning in the group, or presence of an accompanying calf. If long-finned pilot whales display leadership (unshared decision making), we would expect the distribution of the dive lags of individuals within collective dives to be right skewed, as all individuals would have a lag in responding to the leader.

3.3 Methods

3.3.1 Data Collection and Extraction

Aerial videos of groups of long-finned pilot whales were collected in the Gulf of St. Lawrence near the port of Cheticamp, Cape Breton Island, Nova Scotia (46.64, -61.01) from 2018-2021 during the months of July, August, and September using an unmanned aerial vehicle (drone). The study area covered was approximately 1300 km^2 including up to 18 km offshore and 74 km along the coast. Research surveys were conducted from 6.9 m long rigid hull inflatable boats and a 12.2 m long fishing vessel with a crew of four trained observers. During surveys, the waters were scanned continuously for groups of pilot whales. Focal groups were chosen when they could be clearly delineated from other pilot whales spatially (Table 1). Group behavioural states and composition (e.g. group size) data were collected (Table 2). Age classes were assigned using visual classification based on size and markings described as per Auger-Méthé & Whitehead (2007), using a combination of aerial images and boat-based identification photos (see Figure 1). A distinction was made between calves (<3 years) and other age classes with calves excluded from subsequent analyses, as calves generally exhibit a much greater dependence on accompanying adults than is observed in older age

classes (Fellner et al. 2006). Dive imitators were also further classified as mature male, female/subadult (which are difficult to tell apart at sea and thus included together for the purpose of this study), or juvenile. Most whales within the female/subadult category would be female – it has been found that sex ratios for North Atlantic long-finned pilot whales at birth are skewed (only 35% males) and that after the age of 10 years this ratio of males to females continuing to steadily decline (Desportes et al., 1994).

Figure 3.1 Visualization of long-finned pilot whale age class and sex information available from drone footage with (A) a mature male showing larger size, distinctive rectangular melon shape which overhangs and obscures the rostrum, as well as wider pectoral fins, (B) a grey calf showing lighter colouration and smaller size, (C) a mature female or subadult with much more rounded melon and rostrum visible, and (D) a juvenile showing the smaller size relative to females/subadults but darker colouration when compared calves.

During these encounters, a DJI Inspire 1 V2 drone fitted with an X5 camera and an Olympus Zuko 25mm lens was launched by hand to collect video footage. The drone maintained a minimum altitude of 25m when near pilot whales and was flown in wind conditions of 15 knots or less as per permit regulations. Flights had a maximum duration of 15 minutes. During these flights, an Apple iPad 9.7 was used by the drone pilot to monitor the focal group in real-time. If all whales within a group could be captured within the frame, a note was made on the behavioural datasheets to confirm this. Follows of a focal group ended when we moved on to a different group after successfully

collecting drone footage and necessary behavioural and compositional data, if groups merged with pilot whales from other groups and were no longer trackable, or if we ran out of daylight or boat time. Given the large local pilot whale population size (several thousand individuals) and turnover (Augusto et al., 2017), re-identifying the same individuals on different days over the course of the study was rare.

Table 3.1 Important pilot whale decision making terms and definitions

Term	Definition
Group	Delineated using chain rule as per the definition of party size in Clutton-Brock et al., (1982), where our definition of group contained all pilot whales within 200m of each other
Collective Deep Dive	When all pilot whales within a group leave the surface water and dive beneath the visible portion of the water column for a period of 45 seconds or more between last individual to dive and the first individual to surface again
Dive Lag	Time difference between the first individual– i.e. initiator – to dive (t=0) and another individual's last surfacing during a collective deep dive, as measured using the start of each individual's final breath
Inter-individual Dive Interval	Time interval between an individual's final dive relative to the pilot whale that dove just before it, as measured from the start of both individuals' final breaths

Table 3.2 Definitions of behavioural states at time of collective dive used in this study (as per Zwamborn & Whitehead, 2017).

Behavioural State	Definition
Travelling	Steady directional movement, travelling faster than vessel's idle speed (approximately 5.5 km/hr)
Socializing	Body contact between individuals, little to no directional movement, much activity at the surface
Foraging	Lifting tails when diving, no directional movement, often characterized by birds feeding in association with group, little to no surface social activity with individuals resurfacing on their own or in small groups
Resting	Either logging – resting at the surface – most of the time or travelling at a rate slower than vessel's idle speed, individuals come to the surface as a group

Only drone videos where the whole group was captured making their deep dives (a 'collective' deep dive) – as opposed to shallow dives, when pilot whales remained visible from the drone within the water column – were used for the analyses in this study. We did not analyze collective deep dives if each animal could not be individually tracked, which occurred when weather conditions (waves, lighting, water turbidity, etc.) were poor. A median of 2 collective dives (range 1-6) were included in the analyses across 33 days where usable data were collected. Wondershare Filmora software (2022) was used to review footage and extract frame numbers for the final dive time of each individual in a group, which were transformed into seconds. The terminal breath of each whale was chosen as a proxy for final dive time as it was clearly visible on the video and predictably coincided with individuals leaving the surface to initiate or join in on a collective deep dive. Only dives from groups comprised of four or more adult individuals were analyzed as dive lag distribution shape and other characteristics are difficult to determine for smaller groups.

3.3.2 Statistical Analyses

Characteristics of Initial Divers

To assess if certain traits were characteristic of deep divers, we considered the proportion of initiators based on sex/age class, whether the initial diver was accompanied by a calf, and the relative position of the initial diver in relation to the rest of the group. We used a *G*-test comparing age class and sex of dive initiating individuals with a randomly selected non-dive-initiating pilot whale from each analyzed dive (representing sex/age class within the larger dataset). To determine whether dive initiators were more likely to be accompanied by a calf than non-initiators, we used a *G*-test to compare the number of calf-accompanied and non-accompanied dive-initiating individuals to proportions found within the whole dataset (both dive-initiating and non-initiating individuals). To test the null hypothesis that dive initiators would be uniformly distributed throughout the group in terms of relative position, we first calculated the relative spatial order of pilot whales in a group both for file orientation – front to back relative to the direction of movement – and rank orientation – left to right relative to the direction of movement. For both orientations, we calculated the relative order of the dive initiator ($Relative\ Order = \frac{x+1}{n+0.5}$, where *x* is the number of individuals in front (file) or to the left (rank) of the initiator, and *n* is equal to the total number of individuals in the group). We then used *G*-tests for each of the four peripheral positions (furthest front, furthest back, outside left and outside right), with the null hypothesis that the number of dive-initiating pilot whales in these relative orders would not be significantly different from the expected proportions if dive-initiating individuals were uniformly distributed along file and rank continuums for each group.

Exploring drivers of dive timing

We fit four generalized linear mixed effects models (GLMEs) to explore drivers of variation in the timing of individual dives within groups of pilot whales. The units of these models were collective deep dives, and the response variables were inter-individual dive intervals (mean), inter-individual dive intervals (coefficient of variation), dive lag (mean), and dive lag (coefficient of variation). For each model, we included the

following predictor variables: (1) Group Size (integers), (2) Group behavioural state (categorical, see Table 2 for definitions), and (3) Year (continuous). We included year as a continuous variable as we were interested in possible trends across years given declining pilot whale observations within our field area (McComb-Turbitt et al. 2021). Models with mean dive interval or mean dive lag as a response were fit using Gamma error distribution and log link function, whereas models with coefficients of variation as responses were fit with Gaussian error distributions. All analyses were carried out in R (R Core Team 2022), using the *glmmTMB* package to fit GLMs (Brooks et al. 2017).

3.3.3 Simulations

We created simple simulations to visualize the possible distribution of dive times for different decision making scenarios (see Appendix D for more details on these simulations) including response to a stimulus (e.g. leadership), independent decisions of individuals to dive at a given time, and response to a threshold or majority (Figure 3.2). For all scenarios, we assumed that whales joining a collective deep dive remain submerged for the duration of each simulation after their dive (i.e. individuals are not resurfacing). These simulations were also created using R (R Core Team 2022).
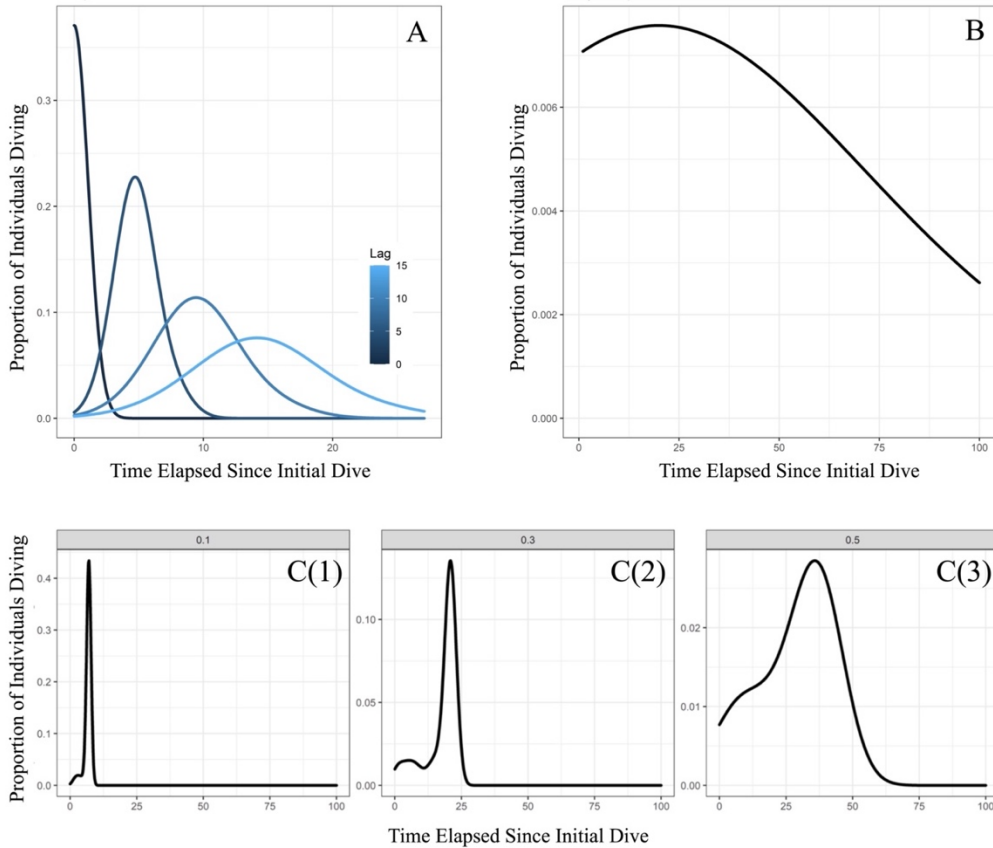
Figure 3.2 Simulation results of expected distributions of dive lag in collective deep dives of long-finned pilot whales for three different categories of decision making, including (A) response to a stimulus (e.g. leadership), (B) independent decision to dive made by each individual (e.g. non-collective decisions within a collective dive), and (C) quorum or threshold decision making for C1 – a 10% threshold, a C2 – a 30% threshold, and C3 – a 50% or majority threshold.

3.3.4 Ethical Note

The research for this project was conducted under the approval of the Dalhousie University Committee on Lab Animals (permits UCLA-18-020 and UCLA-20-050), which is part of the Canadian Council on Animal Care and oversees ethics approvals for research for our organization. Research for this project was also conducted under licences (SG-RHQ-18-032, GULF-MMDA-01-19, S.38 2020, and S.38 2021) from the Department of Fisheries and Oceans (government), which must grant data collection and ethics approval prior to any marine mammal research in Canada. We always maintained an appropriate minimum flight altitude above pilot whales (25m; see Christainsen et al.

2016) and did not observe visible disturbance or other behavioural changes during data collection.

3.4 Results

3.4.1 Collective Dive Timing Across Groups

The timing of individual dive lags were heavily right-skewed (Figure 3). Based on our simulations, this pattern was most consistent with leadership (see visualizations from simulations in Figure 2), while it does not fit what would be expected if pilot whales were making independent individual decisions to dive or using threshold or majority (shared) decision making. There were no distinctive patterns in ordered inter-individual dive intervals for independent dives across group size, behavioural state, or year (see Supplementary S1), with distributions generally showing a lot of variation between dives.
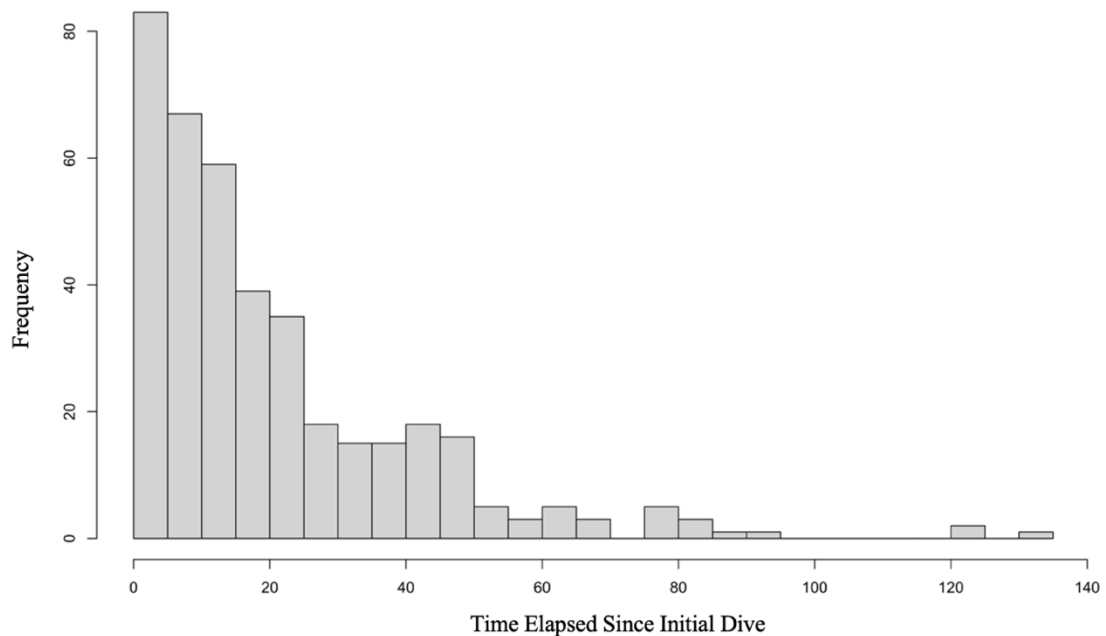
Figure 3.3 Distribution of dive lags (in seconds) of subsequent pilot whales (n=394) in relation to the start time of the collective dive from the last breath of the initiating individual

3.4.2 Which Individuals Initiate Collective Dives?

We made 187 flights across 38 days, which amounted to 30 hours of video footage of long-finned pilot whale groups. A total of 73 dives that met the study criteria were analyzed. Mature females/subadults were significantly and substantially more likely to initiate collective dives, while mature males and juveniles were less likely to initiate dives than expected by chance ($G = 13.7$, 2 d.f., $p<0.005$; Figure 4A). Pilot whales accompanied by a calf were not more likely to initiate dives than unaccompanied pilot whales ($G = 0.29$, 1 d.f., $p=0.59$; Figure 4B).
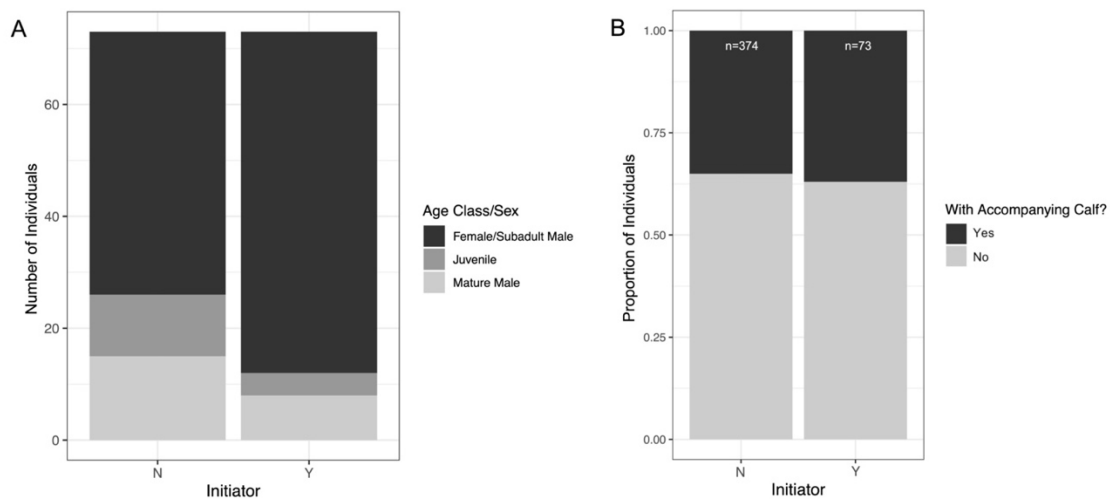
Figure 3.4 Comparison of (A) age class and sex proportions and (B) calf accompaniment of long-finned pilot whales, with Y indicating dive initiating and N non-initiating individuals

Dive-initiating individuals were more likely than expected by chance to be positioned on the periphery of the group: in the front ($G = 15.5$, 1 d.f., $p<0.005$), left ($G = 20.0$, 1 d.f., $p<0.005$), or right ($G = 9.8$, 1 d.f., $p<0.005$), but not in the back ($G = 0.21$, 1 d.f., $p=0.65$) (Figure 5).
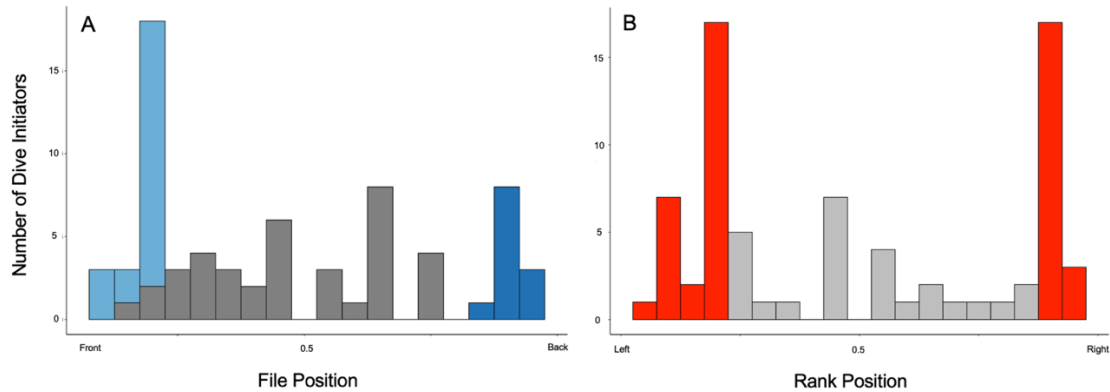
Figure 3.5 Relative position of collective dive initiating long-finned pilot whale from (A) front to back and (B) left to right in relation to the group's direction of movement – individuals in light and blue represented individuals who were in front and behind the rest of the group respectively, while those in red were in the furthest left or right positions (on the outside flank) relative to the rest of the group

3.4.3 The Relationship of Group Size, Group Behavioural State and Year to Dive Lags and Inter-individual Dive Intervals

Both mean dive lags and mean inter-individual dive intervals were larger (approximately threefold) while resting than during other behavioural states, varied slightly across years, and were lower at larger group sizes (Figure 3.6). Mean dive lag was higher when pilot whales were resting in comparison to travelling (the reference category; $\beta = 0.54$, s.e. $= 0.24$, $p = 0.024$) and increased over the years of the study ($\beta = 0.21$, s.e. $= 0.09$, $p = 0.014$), while the coefficient of variation for dive lag was not predicted by group size, group behaviour or year. Mean inter-individual dive intervals decreased with group size ($\beta = -0.12$, s.e. $= 0.03$, $p < 0.000$), increased when pilot whales were resting in comparison to travelling ($\beta = 0.50$, s.e. $= 0.22$, $p = 0.025$), and increased over the years of the study ($\beta = 0.19$, s.e. $= 0.08$, $p = 0.019$). Group size was also associated with the coefficient of variation for inter-individual dive intervals ($\beta = 0.04$, s.e. $= 0.02$, $p = 0.025$). Detailed results of the generalized linear models are summarized in Appendix E.
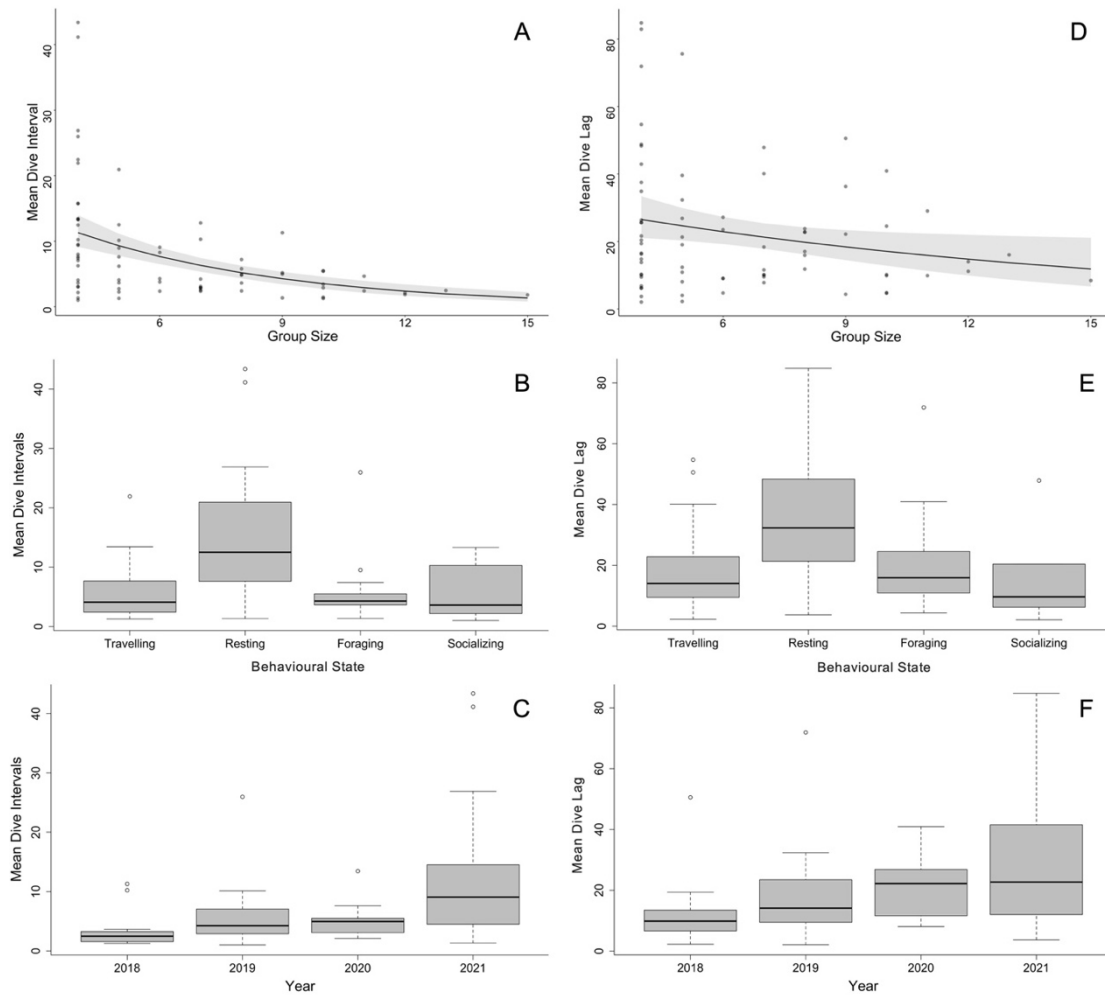
Figure 3.6 Visualization of dive time data for collective deep dives in groups of long-finned pilot whales, including how mean inter-individual dive interval varies across A) group size, B) group behavioural state, and C) year, as well as how mean dive lag varies across D) group size, E) group behavioural state, and F) year. Panels A) and D) also show model predictions with raw data shown as points (see Appendix F)

3.5 Discussion

Leadership (unshared decision making) is characteristic of mammalian societies with strong evidence of dominance hierarchies, such as those observed in many primate populations (Conradt & Roper, 2005; King & Sueur, 2011). It could be expected that consensus (shared) decision making would be common among cetaceans, who live in aquatic environments where there is little evidence for dominance and territoriality. This

apparent lack of territoriality likely arises from the patchy and ephemeral nature of ocean resources in a very three-dimensional space, which makes these resources challenging to guard or protect (Rendell et al., 2019).

The common name 'pilot whale' suggests that long-finned pilot whales follow leading individuals, with historic accounts of strandings frequently recording the cause of beaching to be because a pod followed a sick leader to shore (de Kock, 1956). However, there are no scientific studies as to how pilot whales make collective decisions, and in the case of leadership, which individuals lead. While shared group decisions are generally thought of as producing more beneficial and less extreme solutions, the highly right-skewed and generally exponentially distributed nature of individual dive lags for the collective dives of long-finned pilot whales suggests that this species does not generally use shared decisions such as those requiring a threshold or majority for full group participation (see Appendix D). With some evidence for the unshared decision making processes in collective dives (e.g. leadership), one important question is: which individuals lead?

3.5.1 Characteristics of Initiating Whales

Mature females/subadults, mature males and juveniles were all found to initiate collective dives, suggesting that dive leadership in this species is distributed. Distributed leadership is often categorized as either equally distributed – where anyone can lead has an equal chance of being successful – or unequally distributed – where some individuals are more successful at initiating than others (Lee & Teichroeb, 2016). Mature female/subadult pilot whales initiated dives more often than expected, suggesting that diving leadership is unevenly distributed. Unequally distributed leadership is common in terrestrial mammals, particularly primates such as vervet monkeys (*Chrorocebus pygerythrus*) and white-faced capuchins (*Cebus imitator*) where one sex or age class has different motivations or experiences (Leca et al., 2003; Lee & Teichroeb, 2016).

Movement initiators and leaders (collectively termed "guides") are often female-biased in social mammals (Smith et al., 2022). Energetic needs, often higher in gestating and lactating females, are commonly found to drive sex-biased leadership during collective moments (Fischhoff et al., 2007; Smith et al., 2010). Gestation and lactation

are regular predictors of leadership across several primate species (Sperber et al., 2019), though they have never been documented to be a driver of cetacean leadership We found that individuals accompanied by calves (presumably lactating in most cases) did not initiate dives more than expected by chance, suggesting that energetic needs are not the primary motivator for dive leadership in long-finned pilot whales. Ecological knowledge may motivate initial diving pilot whales, as found in killer whales (Brent et al., 2015). Social connectedness and kinship can drive leadership in mammals, but these are less commonly observed than dominance, energetic needs, and ecological knowledge (Briard et al., 2015; Lee & Moss, 2012). Studies of bottlenose dolphins have provided some evidence that more socially connected individuals are more likely to lead but have found no suggestion that kinship is an important predictor of who makes these unshared decisions (Lewis et al., 2013; Lusseau & Conradt, 2009). We currently do not have enough information to test for the possible role of these additional predictors as they relate to dive initiators within Cape Breton long-finned pilot whales. Future studies that collect repeat dives from the same focal group over longer time frames (e.g. across days) will be important for determining whether specific individuals are consistently initiating dives.

Pilot whales that dove first were more likely to be on the periphery of the group, both from front to back (file) and from left to right (rank). This pattern was most obvious across rank, with initiating divers often being on the far outside of the group. Dive initiation from peripheral flanking positions is surprising, given that many mammals (e.g. primates, wolves, zebras) have been found to lead groups from front or central positions (Ceccarelli et al., 2020; Di Bitetti & Janson, 2001; Penzhorn, 1984; Peterson et al., 2002; Petit & Bon, 2010). One possible explanation for this is that flanking positions function in group cohesion in a similar way to flanking riders in cattle drives, where drivers on the outside left and right of the herd keep cows from wandering off or escaping. The role of individuals in flanking positions is important in the behaviours of some non-human terrestrial mammals. Studies of African Lion (*Panthera leo*) lionesses hunting showed that individuals in flanking (i.e. wing) positions were drivers of the hunt, while those in more central positions were largely waiting to catch the prey once the drivers flushed it towards them (Stander, 1992). Peripheral positions within animal groups are generally

more vulnerable to attack, so individuals that flank are often the most vigilant (Jennings, 1980). Cohesion is important in cetaceans, and it can be mediated acoustically (Moore et al., 2020; Zwamborn & Whitehead, 2017). The need for group coordination within long-fined pilot whales and the importance of vigilance (for predators, boats, etc.) by peripherally positioned individuals provides a possible explanation for why these flanking positions are important in a dive initiation (leadership) context.

3.5.2 Other Insights into Pilot Whale Collective Dives

When looking more closely at variation across group dives, we found that average inter-individual dive intervals decreased in large groups. Groups of pilot whales may benefit from increased coordination when less acquainted individuals travel, socialize, rest or forage in a collective manner. Perhaps counterintuitively, bottlenose dolphins show higher synchrony with dolphins they are not as familiar with, suggesting that this synchrony may function to reinforce bonds between individuals and aid in the organization of the group as a whole (McCue et al., 2020). It is important here to note that the coefficient of variation was found to increase with increased group size, which suggests that there might be more clustering within the final dives of these larger groups. Small groups of long-finned pilot whales in this study likely represent a single social unit (approx. 7 individuals; Augusto et al., 2017), where individuals have strong bonds with each other and perhaps less of a need for increased coordination during these routine dives. On the other hand, larger groups in this study are likely comprised of multiple social units and therefore contain animals that are less familiar with each other than they are with their more constant companions.

A puzzling finding was that both mean dive lag and mean inter-individual dive interval increased across the 4 years of study. Our models controlled for both group size and behavioural state, so these increases cannot be explained by variation in the types of groups that were encountered over the study period. Sighting rates of long-finned pilot whales have been generally declining in the area over the last 20 years, distributions are changing (McComb-Turbitt et al., 2021), and the species is arriving in inshore waters considerably later in the summer than earlier in this period. The cause(s) of these trends are unclear, but large-scale environmental shifts due to climate change that can affect

46

water temperatures and food availability are implicated. In particular, the Labrador Current that flowed into the Gulf of St. Lawrence from the North Atlantic through the Laurentian Channel is weakening and its cold waters are being replaced by warm water pulses (Galbraith, 2018). It is not obvious how these oceanographic changes, or secondary shifts in ecology, whale density or residency patterns might influence aspects of the timing of dives within groups. Decreased mean dive lags and inter-individual dive intervals would seem to suggest that decisions are being made more cohesively in recent years, which could be a sign of food stress.

Inter-individual dive intervals and dive lag times were approximately threefold longer when pilot whales were resting, while remaining quite similar across all other behavioural states. This is evidence that resting (including both slow travel and logging) is fundamentally different from other behavioural states and that our operational definitions capture much of this difference.

Longer focal follows of specific groups are needed to look at how dive initiators change across time and contexts (e.g. directional changes, approach from perceived threats, etc.). While the pilot whales in this study generally moved too quickly to collect simultaneous hydrophone recordings (especially as there were often other groups within acoustic range that would have been difficult to tease apart as the focal group moved further away from a fixed location standard hydrophone), future studies could investigate whether vocal behaviour predicts the initiation of deep dives by using suction cup tags equipped with hydrophones attached to whales within the focal group.

3.5.3 Conclusions

As suggested by their common name, pilot whales are likely using some form of leadership in their collective deep dives. Dive initiators were most often female and dove frequently from peripherally flanking positions within the group, but did not show any evidence of being motivated by energetic needs (e.g. lactating). This provides evidence for an unequally distributed leadership role in the initiation of group dives. Larger groups of pilot whales showed shorter mean inter-individual dive intervals than smaller groups, suggesting that increased coordination may be important when multiple social units are travelling, foraging, resting, or socializing together. Future studies should focus on how

leadership varies across contexts as well as whether there are consistent patterns within collective dive initiation for focal groups followed for hours or across days. The motivation behind the unequally distributed leadership during collective dives within pilot whale societies remains unclear.

CHAPTER 4 – ALL TOGETHER NOW: GROUP SYNCHRONY IN LONG-FINNED PILOT WHALES

4.1 Abstract

Many cetaceans synchronize behaviours as they breathe, swim, and dive together. Synchrony has been hypothesized to play an important role in social bonding and anti-predatory response, but the extent of its importance in the daily lives of whales and dolphins is not yet fully understood. I used aerial footage of groups of long-finned pilot whales *Globicephala melas* off Cape Breton Island, Nova Scotia, Canada to examine how synchrony varies across social contexts and whether synchronous behaviour is involved in collective decisions. Permutation tests showed that pilot whales within groups breathed more synchronously with each other than expected by chance ($p = 0.001$). Pilot whales decreased their synchrony just before the initiation of collective deep dives ($p > 0.001$), suggesting that groups anticipated an upcoming change in behaviour. There was also an increase in synchrony during the penultimate (second last) breathing period that appeared to be driven largely by calves, likely functioning as an anticipatory behaviour that serves to increase protection and decrease the energetic requirements of these young during following deep dives. Overall, grey calves (calves under 3 years old, not including newborns) were the most synchronous. Newborns displayed the lowest synchrony with other members of the group. A baseline understanding of synchronous behaviour in long-finned pilot whales and how it varies across age classes and different social contexts is important, as changes in synchrony have been found to be key indicators of disturbance in other cetacean species.

4.2 Introduction

Synchrony, defined as temporally coordinated behaviour amongst individuals (King & Cowlishaw, 2009), occurs in a wide range of species. Synchronous behaviour has been extensively studied in humans *Homo sapiens*, who partake in many activities – such as music, dance, team sports, and exercise – that involve elements of synchrony (Launay et al., 2016). Non-human animals display synchronous behaviour across a range of different contexts. During courting, male and female western grebes *Aechmophorus occidentalis* synchronize a series of behaviours (e.g. dipping heads and preening) before rising from the water and speeding across the surface of the lake, matched in both pace and proximity (Nuechterlein & Storer, 1982). In less conspicuous forms of synchrony, several species, including fallow deer *Dama dama*, red deer *Cervus elaphus*, cattle *Bos taurus*, and black-headed gulls *Chroicocephalus ridibundus* tightly coordinate their behaviour with conspecifics that are the closest in proximity to them (Evans et al., 2018; Hoyle et al., 2021; Rands et al., 2014; Stoye et al., 2012). While we often think of synchrony as manifesting through physically coordinated movements, synchrony in both vocalizations (e.g. the temporal adjustment of turn-taking vocalizations between calling pairs of Japanese macaques *Macaca fuscata* (Katsu et al., 2018) and behavioural processes (e.g. reproductive behaviours such as birthing synchrony in squirrel monkeys *Saimiri oerstedi* (Boinski, 1987) are also common.

Synchrony has several hypothesized functions, which are largely thought to be social and anti-predatory in nature. Synchronous behaviour may help reinforce bonds between individuals that have low familiarity with each other, particularly when they are in large groups (Launay et al., 2016; McCue et al., 2020). Coordinated behaviour(s) (such as dance) occurs in many human societies and may help facilitate large-scale cooperation as well as inter-individual bonding (Launay et al., 2016). However, social bonding is not as commonly hypothesized as a driver of synchrony in non-human animals. Bonding is facilitated predominately by grooming in non-human primates (Henzi & Barrett, 1999). Synchrony is frequently used in mating behaviours, including the aforementioned example of courting western grebes (Nuechterlein & Storer, 1982) as well as fiddler crabs *Austruca sp.*, where male crabs synchronously wave their enlarged claws to attract mates.

Female fiddler crabs preferred males that lead this waving, achieved by individuals which waved at a faster rate (Perez et al., 2021). Many animal species use reproductive synchrony as a predator-swamping strategy, where simultaneous births or hatchings decrease the overall risk of predation per offspring (e.g. green sea turtles *Chelonia mydas*; Santos et al., 2016). Even plants are thought to use synchronized reproduction as an anti-predatory measure to maximize the success of their offspring, such as is observed in the mast seeding of white spruce *Picea glauca* across North America (LaMontagne et al., 2020). Both the synchronized feeding of voles and air breathing of social fishes are also thought to be important anti-predator behaviours (Gerkema & Verhulst, 1990; Kramer & Graham, 1976).

Cetaceans display a wide range of synchronous behaviours, both in physical movements and vocalizations (Actis et al., 2018; Fellner et al., 2007; King & McGregor, 2016). As with other species of animals, synchrony in cetaceans has been hypothesized to serve several functions including predator avoidance and social bonding. Cuvier's *Ziphius cavirostris* and Blainville's beaked whales *Mesoplodon densirostris* make highly coordinated deep dives despite foraging independently at depth, suggesting that they may use synchrony to avoid having to use vocalizations at the surface to reconnect after dives and thus minimize the risk of predation from killer whales *Orcinus orca* which could use these vocalizations to locate them (Aguilar de Soto et al., 2020). Breathing synchrony has also been found to increase in response to disturbance (e.g. vessel, sonar, and tagging) in several cetacean species (Hastie et al., 2003; Visser et al., 2016). In Indo-Pacific bottlenose dolphins *Tursiops aduncus*, synchrony reinforces social bonds, particularly between individuals from different social companion groups (McCue et al., 2020). Despite cetaceans being considered highly synchronous animals, we have a limited understanding of the functions of synchrony across different species and behavioural contexts.

The use of drones to collect aerial footage of cetaceans can substantially increase the clarity of the behavioural recorded, giving better detail on spatial arrangements than conventional video methods (Hartman et al., 2020). These higher resolution data are important for answering questions that will help us begin to tease apart functions of synchrony, such as when it is being used socially versus when it is part of an anti-

predator strategy, as well as what the characteristic differences between synchronous behaviour employed for different functions might be.

The long-finned pilot whale *Globicephala melas* (hereafter also referred to as 'pilot whale'*)* is a gregarious social cetacean that lives in stable long-term groups (Augusto et al., 2017), providing a good species to further investigate group-level synchronous behaviour. Synchronous surfacings of pairs of long-finned pilot whales have been examined in two populations in the North Atlantic using boat-based videos (Senigaglia et al., 2012; Senigaglia & Whitehead, 2012). These studies hypothesized that synchronous behaviour in pilot whales functions as both an anti-predator response as well as an affiliative behaviour within social groups (Senigaglia et al., 2012; Senigaglia & Whitehead, 2012). However, these studies were not able to follow individuals over multiple surfacings, had limited spatial data, and did not differentiate between age classes. I used aerial footage of groups of long-finned pilot whales off Cape Breton Island, Nova Scotia, Canada to describe synchrony when whales surface to breathe. I predicted that this social group-living species will be highly synchronous similar to other species of cetaceans (Cioffi et al., 2021; Hastie et al., 2003; Senigaglia & Whitehead, 2012). I also hypothesized that synchrony might be used to help facilitate group decisions, representing a pre-decision behaviour (e.g. group anticipation of a deep dive), similar to those observed in barbary macaques (*Macaca sulvanus*; Seltmann et al., 2013) and African wild dogs (*Lycaon pictus*; Walker et al., 2017). Finally, I predicted that synchrony within groups would vary across behavioural states and group sizes.

4.3 Methods

4.3.1 Data Collection

Data were collected from a population of long-finned pilot whales that summers off the northwestern coast of Cape Breton Island, Nova Scotia, Canada. Rigid hull inflatable vessels (6.9m) and a fishing vessel (12.2m) were used to survey waters up to 11Nm offshore between the ports of Cheticamp (46.64, -61.01) and Bay St. Lawrence (47.00, -60.47). Data were collected during the months of July through September from

2018-2021. Encounters began when a group of pilot whales were sighted within 200m of the vessel. Groups were defined as all whales within 200m of each other and 200m of the vessel using the chain rule (Clutton-Brock et al. 1982). During encounters, group compositional (i.e. group size and number of calves) and behavioural data (see Table 4.1) were collected every 10 minutes until the encounter ended. Encounters ended if a) we successfully executed drone flights for our focal group, b) pilot whales were missing for two compositional and behavioural data collection periods (data collected every 10 minutes) or c) the vessel had to return to port.

Table 4.1 Definitions of long-finned pilot whale group behavioural states (Zwamborn & Whitehead, 2017)

Behavioural State	Definition
Travelling	Steady directional movement, travelling faster than vessel's idle speed (approximately 5.5 km/hr)
Socializing	Body contact between individuals, little to no directional movement, much activity at the surface
Foraging	Lifting tails when diving, no directional movement, often characterized by birds feeding in association with group, little to no surface social activity with individuals resurfacing on their own or in small groups
Resting	Either logging most of the time or travelling at a rate slower than vessel's idle speed, individuals come to the surface as a group

Aerial video data (4K; 24 frames per second) were collected with our 4-rotor vertical take-off and landing DJI Inspire 1 V2 drone (2.9kg; Transport Canada registration C-1917728238), which was equipped with an X5 camera and an Olympus Zuko 25mm lens. Footage was collected when weather conditions allowed for safe launch and retrieval of (wind <15 knots, swell < 1m, no fog or rain). The drone maintained at a minimum altitude of 25m while flying over pilot whales (in accordance with our research permit) and was piloted by a Transport Canada licensed drone pilot using manual remote flight control with a 6th generation Apple™ iPad tablet with real-

time camera output. Flights had a maximum duration of 15 minutes to conserve approximately 30% of the battery for safe return to the vessel. A team member observed the drone during the flight and also launched and caught the drone. The drone was only flown in visual line of sight. For all times when the whole group of pilot whales could be captured within the video frame, a note was made on the behavioural datasheet. The population's large size (several thousand individuals; Augusto et al., 2017), meant that the chance of resighting of the same individuals over multiple drone-captured encounters (where weather conditions lined up for sampling) was extremely small.

4.3.2 Data Extraction

Videos were annotated in BORIS (Friard & Gamba, 2016), where all encounters met a minimum standard of 30 seconds of continuous footage with all individuals present within the video frame and ended in a collective deep dive. A deep dive was defined as all pilot whales in a group diving below the surface (visible portion of the water column) for at least 45 seconds between the last individual diving and the first resurfacing (as in Zwamborn et al. 2023b). All individuals in a group had to be continuously trackable over the duration of time sampled or the data were discarded. Within BORIS, the time of the start of each breath taken was annotated for each individual during the duration of the video. Individual identity was attached to each annotation. All breaths (defined as the beginning of a breath where the first air bubbles/breath –white in colour - were clearly visible on the drone footage) were categorized as either BR (adult, subadult, and juvenile breaths) or BRC (calf breaths). Age class was also recorded (as in Zwamborn et al. 2023b; Auger-Méthé & Whitehead, 2007 and Augusto et al. 2017) including adults, juveniles (adult colouration, but smaller in size), grey calves (light grey colouration; several months to 3 years of age), and newborns (light grey colouration, deep fetal folds and/or bent dorsal).

4.3.3 Statistical Analyses

I explored long-finned pilot whale breathing intervals by calculating the median inter-breath interval for each individual, then using a Kruskal-Wallis test to test for statistical significance between age classes, visualized with a scatterplot.

Using MATLAB (MATLAB 2023a) to run permutations (1000 randomizations), I tested whether long-finned pilot whales within groups were more synchronous than expected by chance for four measures of group synchrony: MTCBreath (median time to closest (temporal) breath of another individual in the group), Prop <0.5s (the proportion of closest breaths that were <0.5s), Prop <1s (the proportion of closest breaths that were <1s), Prop <3s (the proportion of closest breaths that were <3s). In past studies of pilot whale synchrony, breaths within 1s of each other were considered highly synchronous while breaths within 3s of each other were considered moderately synchronous (Senigaglia et al., 2012). On a group level I looked at both of these, as well as a shorter 0.5s interval, to see whether they might be reasonable descriptors of synchrony across groups. Time to closest breath was defined as the time from one breath to next closest breath (either before or after) of another individual. To obtain random datasets, the data for each individual's breath times were shifted randomly (by random uniform variable lying between ±1/3 of the total length of the analyzed video) and the middle 1/3 time period was resampled for each encounter. Using a maximum time shift of 1/3 of the total video duration ensured that I would have ample data (in terms of breath times) remaining in the middle 1/3 to resample. Both real data and permuted data for MTCBreath were plotted as histograms. This analysis was performed twice: the first time only included adults and juveniles, while the second included calves in addition to the adults and juveniles. Calves were excluded from the first analysis as the calves of many species of cetaceans have been found to be highly synchronous with their mother or allocarer (Fellner et al. 2006), and therefore a dataset that included all age classes was predicted to show higher synchrony than the dataset that excluded calves. MTCBreath, as well as Prop <0.5s and Prop <1s were calculated (using the whole data set, not just the middle third used for testing) for the age class of each individual that was breathing (although the animal with the next closest breath could be of any age class).

To determine whether synchronous behaviour might be used to help facilitate collective decisions, I looked at whether synchrony varied in the time leading up to a collective deep dive. First, I calculated the breathing rate (inter-breath intervals) of individual pilot whales as well as medians across all individuals and within each age class. Leading up to the last breath of the individual who initiated the collective deep dive, I looked at three different time periods before the initiation of the dive, the Dive Imminent Period (DIP; 0-6.75s), the Penultimate Breath Period (PBP; 6.75-20.25s) and the Regular Surfacing Period (RSP; >20.25s) to investigate whether the previously calculated measures of breathing synchrony (MTCBreath, Prop <0.5s and Prop <1s) changed ahead of collective dives. Time intervals were chosen based on the median breathing interval for individual long-finned pilot whales (13.5s) calculated from the data. A deep dive was defined as all individuals leaving the visible surface water column with a minimum of 45 seconds between the last individual diving and the first individual resurfacing again. I then ran Gaussian generalized linear mixed models (GLMMs) with encounter as a random effect for both the adult/juveniles only and the all age class datasets using the glmmTMB package in R Statistics (Brooks et al., 2017; R Core Team 2023) to determine whether pre-dive period (the predictor) influenced the response variable (MTCBreath).

To explore whether group synchrony in pilot whales varies across behavioural and social contexts, I ran Gaussian generalized linear mixed models (GLMMs) with encounter as a random effect (glmmTMB package, Brooks et al., 2017; R Core Team 2023) to determine whether either group size or group behaviour (the predictors) influenced the response variables (MTCBreath, Prop <0.5s and Prop <1s).

4.4 Results

4.4.1 Respiration Rates

In total, I annotated 716 breathing events over 27 group encounters. The Kruskal-Wallis test showed that the median inter-breath interval for each individual was not significantly different across age classes ($\chi^2 = 2.62$; p = 0.454; Figure 4.1). The median

interval between breaths by an individual was 13.4s, which is approximately 4.5 breaths per minute, with juveniles exhibiting a slightly higher average respiration rate at 5.4 breaths per minute (see Appendix G).
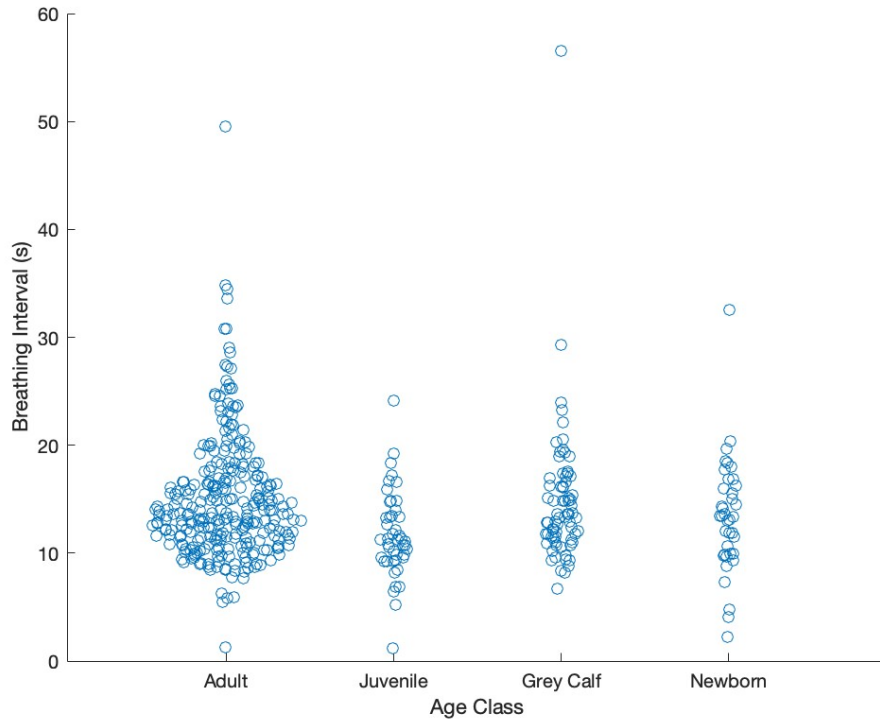
Figure 4.1. Median interval between consecutive breaths of individual long-finned pilot whales grouped by age class – adults (Median = 13.7), juveniles (Median = 11.2), grey calves (Median = 13.6), and newborns (Median = 13.4) – calculated from a sample of 716 breathing events.

4.4.2 Are Long-finned Pilot Whales Synchronous?

The distribution of time to closest breath for both the adult dataset and the all age class dataset were noticeably left-biased, indicating that individuals within the sampled groups of long-finned pilot whales were more synchronous than expected by chance (Figure 4.2). This left bias was more evident in the distribution of closest breath for the dataset that included calves with all other age classes (Tables 4.2 and 4.3).
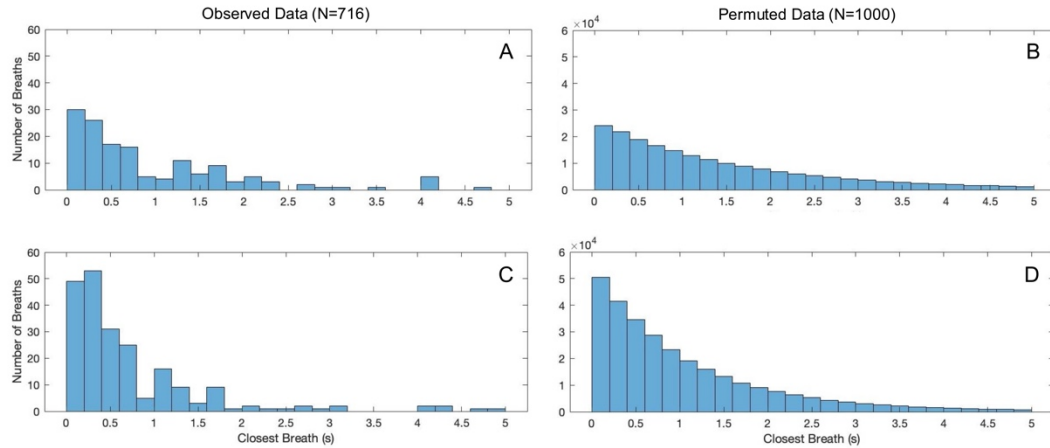
Figure 4.2. Time to closest breath(s) for groups of long-finned pilot whales for (A) adult and juvenile observed data, (B) adult and juvenile permuted data, as well as for (C) all age classes observed data, and (D) all age classes permuted data.

Table 4.2. Results for median time to closest breath (MTCBreath), proportions of closest breaths (Prop) <0.5s, <1s and <3s for adults and juveniles within groups of long-finned pilot whales (N =157 breaths)

Measure	Observed Data	Permuted Data	Proportion Permuted > Observed
MTCBreath	0.709	1.104	0.999
Prop <0.5s	0.389	0.270	0.000
Prop <1s	0.599	0.467	0.001
Prop <3s	0.879	0.847	0.116

Table 4.3. Results for median time to closest breath (MTCBreath), proportions of closest breaths (Prop) <0.5s, <1s and <3s for all age classes within groups of long-finned pilot whales (N = 212 breaths)

Measure	Observed Data	Permuted Data	Proportion Permuted > Observed
MTCBreath	0.417	0.747	1.000
Prop <0.5s	0.538	0.373	0.000
Prop <1s	0.738	0.603	0.000
Prop <3s	0.941	0.926	0.149

Across the complete dataset, newborn calves had the longest MTCBreath and the highest Prop CB <3s, while grey calves had the lowest MTCBreath and highest Prop <0.5s and Prop <1s (Table 4.4). Adults had a MTCBreath of 0.5s and the lowest Prop <1s. However, the Prop <0.5s, <1s and <3s were fairly consistent across age classes.

Table 4.4. Results for median time to closest breath (MTCBreath), proportions of closest breaths (Prop) across the full dataset (N = 716 breaths)

Age Class	No. of Breaths	MTCBreath (s)	Prop <0.5s	Prop <1s	Prop <3s
Adult	456	0.50	0.49	0.70	0.93
Juvenile	64	0.52	0.47	0.72	0.92
Grey Calf	135	0.42	0.55	0.76	0.93
Newborn	61	0.58	0.44	0.74	0.97

4.4.3 Synchrony and Collective Decisions

When looking at data from only adult and juvenile long-finned pilot whales for MTCBreath, there was an observable decrease in synchrony immediately before a collective dive (Dive Imminent Period (DIP); Table 4.5). When tested with GLMMs the difference in MRCBreath between pre-dive periods for adults and juveniles was statistically significant, with the DIP period MTCBreath being higher than both the regular surfacing period (RSP; β = -1.03, p > 0.001) and penultimate breathing period (PBP; β = -0.99, p > 0.001) periods. See Appendix H for model details.

Table 4.5. Results for median and the proportions of closest breaths for adults and juveniles leading up to the initiation of a collective deep dive in groups of long-finned pilot whales

Pre-dive Period	Breaths	MTCBreath (s)	Prop <0.5s	Prop <1s	Prop <3s
Dive Imminent (DIP)	77	1.17	0.26	0.42	0.81
Penultimate Breath (PBP)	123	0.83	0.35	0.56	0.91
Regular Surfacing (RSP)	320	0.77	0.34	0.60	0.88

When looking at data across all age classes of pilot whales, the MTCBreath was also longest immediately before the initiation of the collective deep dive (Table 4.6; Figure 4.3). However, during the PBP there was a more exaggerated increase in synchrony than seen in the dataset with only adults and juveniles, with the all ages dataset showing a decrease in MTCBreath and an increase in the Prop <0.5s. This difference in MTCBreath between pre-dive periods across all age classes was statistically significant, with the DIP period MTCBreath being higher than both the RSP (β = -0.82, $p > 0.001$) and PBP (β = -0.83, $p > 0.001$) periods. MTCBreath for the PBP period was lower than for the RSP period.

Table 4.6. Median time to closest breath (MTCBreath), proportions of closest breaths (Prop) for all ages leading up to the initiation of a collective deep dive in groups of long-finned pilot whales

Pre-dive Period	Breaths	MTCBreath (s)	Prop <0.5s	Prop <1s	Prop <3s
Dive Imminent (DIP)	99	0.75	0.38	0.56	0.87
Penultimate Breath (PBP)	173	0.38	0.58	0.73	0.95
Regular Surfacing (RSP)	444	0.50	0.49	0.74	0.93
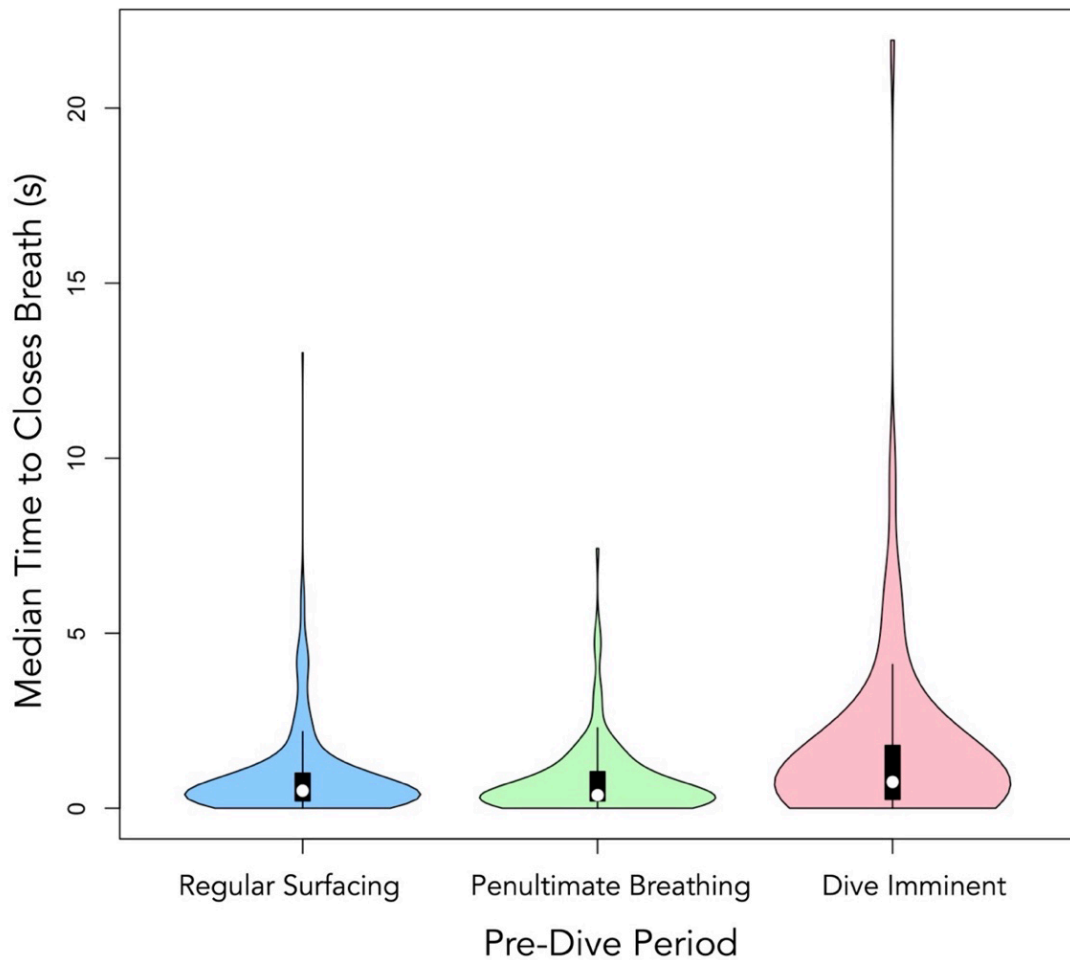
Figure 4.3. Violin plot of MTCBreath across three pre-dive period for long-finned pilot whales (all age classes; $n = 716$)

4.4.4 Does Synchrony Vary Across Social Contexts?

MTCBreath decreased with group size ($\beta = -0.02$, $p = 0.007$) while Prop <0.5s increased with increasing group size ($\beta = 0.01$, $p = 0.005$), suggesting that large groups were more synchronous. However, there was no significant relationship observed between group behavioural state and any measure of breathing synchrony. Detailed results of the generalized linear mixed models and accompanying figures are summarized in Appendix H.

4.5 Discussion

My results showed that the breaths of long-finned pilot whales within groups were more synchronous than expected by chance. When I looked at pilot whale individual interbreath intervals, they weren't significantly different when compared across age classes. I found that breathing synchrony in pilot whale groups decreased right before collective deep dives, suggesting that individuals may be anticipating these behavioural changes. Larger groups of pilot whales showed an increase in breathing synchrony, but there was no relationship found between breathing synchrony and group behavioural state.

4.5.1 Long-finned Pilot Whale Respiration Rates

The mean respiration rate of 4.5 breaths per minute found in my study was close to the predicted baseline rate of 4.6 breaths per minute (before dives of 2-minute duration or longer) reported in a study of long-finned pilot whales off Norway (Isojunno et al., 2018). Unlike humans and some terrestrial mammals, breathing rate in long-finned pilot whales does not significantly decrease with age (Mortola, 1987). Juveniles had slightly higher median respiration rates than other age classes, though not significantly so. In killer whales and northern elephant seals (*Mirounga agustirostris*), juveniles have been observed to have higher respiration rates than other age classes (Miller et al. 2010; le Boeuf et al. 2000). A proposed explanation for these higher respiration rates in other marine mammal species is that juveniles might have a higher metabolism and therefore require more oxygen than adults. Despite quite clearly having different metabolic needs and exhibiting different behaviours (e.g. calves travelling in energy-saving echelon position), we do not yet have a good understanding as to why there is such similarity in respiration rate across all age classes of long-finned pilot whales.

Understanding the basal respiration rates across age classes, as well as overall, is important as these rates can be used to understand the impacts of anthropogenic disturbances. A number of other toothed whale species have been observed to increase

respiration rates when facing threats (e.g. whale-watching disturbance; Senigaglia et al., 2016).

4.5.2 Group Synchrony

Long-finned pilot whales have been the subject of two focal studies on breathing synchrony, which looked specifically at breathing/surfacing synchrony of individuals within one body width in the Cape Breton and Gibraltar populations (Senigaglia et al., 2012; Senigaglia & Whitehead, 2012). However, my study shows that synchrony can also work over larger spatial scales, such as within groups of pilot whales that are within vocal and sometimes visual range. I found that long-finned pilot whales within a group context were more synchronous than expected by chance, which aligns with the idea of high synchrony as being characteristic of many cetaceans species (Actis et al., 2018; Fellner et al., 2007; King & McGregor, 2016). The majority of individuals were found to breath within 3s of the next closest breath, so this does not represent as valuable of a measure of synchrony on a group level as it has in past studies of paired synchrony within pilot whales (Senigaglia et al., 2012). Rather, on a group level, breaths within 0.5s could be considered highly synchronous while breaths within 1s are moderately synchronous.

My study shows support for calves being more dependent on (and thus more likely to be synchronous with) their mothers and allocarers, as has been found for other cetacean species (e.g. bottlenose dolphins; Connor et al., 2006). For juveniles and adults, patterns for MTCBreath as well as Prop <0.5s and <1s were similar, aligning with the idea that juveniles have gained more independence than calves (Krzyszczyk et al., 2017) and are therefore more likely to display surfacing behaviours similar to adults within the group. Interestingly, newborn calves (within about a month of birth) had the highest median time to closest breath and the lowest proportion of closest breaths within 0.5s. A possible explanation for this is that newborn pilot whales might lack the coordination or skills needed to synchronize as tightly with members of their group. In studies of bottlenose dolphin mother-calf pairs, it was noted that mothers responded rapidly to deviations in calves' surfacing behaviours in order to remain highly synchronized with their offspring for several months after birth, likely for calf protection (Fellner et al.,

2013). For pilot whales, accompanying mothers and allocarers may not adapt their swimming patterns, perhaps because their newborns face fewer threats than young calves in other delphinid species (i.e. Cape Breton may be a location with fewer natural predators or that predatory attacks targeting calves are rare within groups of pilot whales).

4.5.3 Synchrony and Collective Dives

Many species that make collective decisions display pre-decision behaviour indicating that the group is aware of what is about to occur. Pre-decision behaviour (also known as pre-departure behaviour in studies of collective movement) often involves some form of signalling (Zwamborn et al., 2023b), such as the directional orientation of group members in barbary macaques (*Macaca sylvanus*) and the sneezing of African wild dogs (*Lycaon pictus*) before group movement initiation (Seltmann et al., 2013; Walker et al., 2017). While there is now evidence for unequally distributed leadership in the initiation of collective deep dives in long-finned pilot whales, where predominantly flanking female guides are the first to dive (Zwamborn et al., 2023a), we do not know whether the collective dive is anticipated by the group before it occurs. Given the importance of synchrony in the lives of cetaceans, a change in synchronous behaviour before the initiation of a collective dive could be used as a signalling mechanism or other form of pre-departure behaviour within groups of pilot whales.

My study shows that, when including all age classes, there is a slight increase in synchrony during the 6.75-20.25s period before the initiation of a collective deep dive, indicated by both an increase in the proportion of closest breaths within 0.5s and a decrease in the median interval to the next closest breath. After this, synchrony decreases significantly in the 6.75s before dive initiation. This implies that individuals within a group increase synchronization during the penultimate, or second last, breathing cycle followed by a more variable period of submersion before dive initiation.

When considering only the data from adults and juveniles, this increase in synchrony during the penultimate breath is no longer apparent, suggesting that the increase in synchrony during the penultimate breath is being driven predominantly by calves or their companions. Calves may benefit from increasing their synchrony with

other members of the group shortly before a deep dive begins, both through moving into echelon position which would make diving less energetically costly for young individuals (Weihs, 2004; Noren and Edwards, 2007) and by adding protection from the mother or allocarer (Fellner et al., 2013). While calves may increase synchrony of their own volition or be responding to less conspicuous cues from companions or other group members (e.g. vocalizations or body language), it is also possible that the companions of the calves themselves are responsible for driving this increase of synchrony before deep dives. Future studies could look at the spatial positions of calves relative to accompanying adults to assess how breathing synchrony within these pairs changes during the period leading up to collective deep dives.

Regardless of the mechanism driving these changes in synchrony, periods of increased synchronization followed by a significant decrease likely indicate that collective dives are premeditated to some degree within the group before they occur. Pre-departure behaviours before movement initiation have been observed in a number of terrestrial mammal species, but never before documented within cetaceans (Zwamborn et al., 2023b). Future studies looking for pre-dive vocalizations that may act as signals as well as other clues (e.g. changes in speed or group formation prior to dive initiation) may lend more insight into what signals initiate pre-departure behaviour in long-finned pilot whales.

4.5.4 Synchrony and Social Context

There was no statistically significant difference in synchrony between group behavioural states, contrary to what I hypothesized. However, with an increase in group size, median interval decreased and the proportion of closest breaths within <0.5s increased significantly. It could be expected that time to closest breath would decrease with larger group size (as there are more whales expected to breathe within the same time period), which reaffirms what has been observed in a previous study on paired synchrony in this population (Senigaglia et al., 2012) as well as in other cetacean species (Hastie et al., 2003).

4.5.5 Conclusions

Groups of long-finned pilot whales display increased synchrony during the penultimate breathing period before the beginning of a deep dive. This is followed by a decrease in synchrony within the 6.75s before dive initiation, which can be interpreted as pre-departure behaviour that may suggest the group is anticipating a collective dive. The increase in synchrony during the penultimate breathing period appears to be driven by an increase in calf synchrony, which could be due to increased protection and possibly energetic benefits for calves diving in the echelon position. Grey calves showed the highest synchronization within the group, while newborns had the lowest synchrony and highest median intervals to the next closest breath (perhaps due to a lack of coordination and skill at such a young age). Future studies in long-finned pilot whales should focus on whether and if there might be more evidence for pre-departure vocal signals or behaviours such as changes in speed, direction or group formation.

CHAPTER 5 – POD PATTERNS: LONG-FINNED PILOT WHALE GROUP FORMATIONS VARY ACROSS SOCIAL CONTEXTS

"Ina 'au ka nai'a ma Hilo, 'a, e malie ana ke kai.
Ke 'au ka nai'a ma Ka'u, 'a, e 'ino'ino ana ka moana"
~ Hawaiian Proverb

5.1 Abstract

Distinct spatial formations have been observed across of number of animal species, hypothesized to function in enhancing group cohesion, predator vigilance, foraging success, and travelling efficiency. Long-finned pilot whales (*Globicephala melas*) are highly social cetaceans with long-term stable associations (termed "social units"), which often form ephemeral groups composed of multiple social units. This study describes group formation characteristics in long-finned pilot whales off Cape Breton Island, Nova Scotia, using aerial footage collected using a DJI Inspire V2 drone. I hypothesized that pilot whale group formations would vary in shape, spread, and orientation, as well as vary across social contexts. Pilot whale groups are more clumped when resting and socializing, while travelling groups have a higher median rank width than in other behavioural states ($\eta_p^2 = 0.12$). Pilot whales align themselves within groups and display less circular formations as they approach a collective deep dive ($\eta_p^2 = 0.11$), indicating awareness of the impending dive and emphasizing the importance of group coordination for this species. Group size also influences pilot whale group formations ($\eta_p^2 = 0.34$), with larger groups being more circular and displaying more clumping than smaller groups. This heightened cohesion in larger groups may stem from the need for coordination among less familiar individuals or increased vigilance. Understanding these formation patterns is vital for baseline knowledge of group dynamics and can aid in managing mass stranding events, where abnormal group formations might signal distress. Future research should compare free-ranging in-habitat and out-of-habitat pre-stranding group formations to identify indicators of stranding risk, as well as assess the impact of anthropogenic disturbances on group behaviour

5.2 Introduction

Distinct spatial patterns are commonly observed within many species of gregarious animals. From the characteristic 'v' formation that many species of waterfowl use during their long migratory flights to the single-file movement of matrilines of African elephants *Loxodonta africana* as they travel across the savannah, these patterns often serve an important role in the organization and function of animal groups (Allen et al., 2020; Heppner, 1974). For example, the tight spatial groups observed during the foraging trips of Adélie penguins *Pygoscelis adeliae* are thought to allow for increased predator vigilance, as well as more efficiency in travelling and cooperative foraging (Imaki et al., 2024).

Our understanding of formation for groups of cetaceans is limited to a handful of relatively well-studied species. Examples of formations amongst whales and dolphins include the resting lines of northern resident killer whales *Orcinus orca* (Ford, 1989) and the clustered rank formations (where group spread is perpendicular to group movement) observed in foraging sperm whale *Physeter macrocephalus* groups (Whitehead, 1989). In sperm whales, this rank formation is hypothesized to increase the feeding success of individuals, by allowing for cooperative hunting or localization of prey across a larger area and minimizing interference between whales during foraging dives (Whitehead, 1989).

Long-finned pilot whales *Globicephala melas* are a gregarious social species of cetacean that forms long-term stable (likely matrilineal) associations (Amos et al., 1993; Augusto et al., 2017; de Stephanis et al., 2008). They travel in social units composed of approximately seven individuals, but often form larger temporary groups comprised of multiple units (Augusto et al., 2017). Recent research has revealed unequally distributed leadership within these groups, where flanking females initiate deep dives the majority of the time (Zwamborn et al., 2023). However, patterns of group formation and possible functions have not yet been studied for this species.

In this study, I described the group formations of long-finned pilot whales that summer off Cape Breton Island, Nova Scotia, Canada using unmanned aerial vehicles (drones). I hypothesized that pilot whales have group formation patterns that can be characterized by shape, spread or the orientation of individuals. I also hypothesized that

these group formations will vary according to behavioural state, group size, or in the lead-up to collective deep dives. Understanding group formations in free-swimming pilot whales is important for building baseline knowledge of group dynamics (e.g. formations and how they relate to behavioural state) within this species. Long-finned pilot whales are the species of cetacean that most frequently mass strands (Brownlow et al., 2015; de Kock, 1956; Oremus et al., 2013). Thus, the findings of this study can be compared to the behaviours and formations of out-of-habitat, pre-stranded, and refloated pilot whale groups to inform management of future stranding events.

5.3 Methods

5.3.1 Field Methods

Aerial videos of long-finned pilot whale groups were collected during the months of July-September from 2018-2021 off northwestern Cape Breton Island, Nova Scotia, Canada. Rigid inflatable boats (6.9m) and a fishing vessel (12.2m) from the ports of Bay St. Lawrence (46º59.5'N, 60º27.5'W) and Cheticamp (46º38.4'N, 61º0.6'W) were used as observation platforms. Each research survey was crewed by a captain and 2-4 trained observers. A group of long-finned pilot whales was defined using chain rule (Clutton-Brock et al., 1982) as all pilot whales within 200m of each other. I selected focal groups when they could be clearly spatially delimited from other individuals in the vicinity. Encounters started once pilot whales were within 200m of our vessel and ended when we finished data collection and left the focal group, if the focal group merged with another group or were otherwise no longer trackable, or we had to return to port. Additional data on group size and behavioural state (see Table 1 for definitions) were also collected during these encounters. The local population size is large (several thousand individuals) with a relatively high turnover (Augusto et al., 2017), so re-encountering identifiable individuals during subsequent research surveys when the conditions were appropriate for droning was rare.

Table 5.1 Definitions of behavioural states in long-finned pilot whales (from Zwamborn & Whitehead, 2017)

Behavioural State	Definition
Travelling	Steady directional movement, travelling faster than the vessel's idle speed (approximately 5.5 km/h)
Socializing	Body contact between individuals, little to no directional movement, much activity at the surface
Foraging	Lifting tails when diving, no directional movement, often characterized by birds feeding in association with group, little to no surface social activity with individuals resurfacing on their own or in small groups
Resting	Either logging (resting at the surface) most of the time or travelling at a slower rate than the vessel's idle speed; individuals come to the surface as a group

For video data collection, a 4-rotor vertical take-off DJI Inspire 1 V2 drone (2.9kg; Transport Canada registration C-1917728238) fitted with an X5 camera and Olympus Zuko 25mm lens was used to fly (maximum 15 minutes in duration to conserve 30% of the battery for return to our vessel; 4K video; 24 frames per second) over groups of pilot whales during encounters when weather conditions allowed (wind <15 knots, swell <1m, no fog or rain). A 6th generation Apple[TM] iPad was used by the drone pilot to monitor the focal group throughout the flight. The minimum altitude flown above groups of pilot whales was 25m and a visual observer monitored the drone's position at all times in addition to hand launching and catching for each flight. The pilot was Transport Canada licensed and always flew in visual line of sight.

5.3.2 Data Extraction

Drone videos in which the entire group of whales were captured within the frame of view were used for data extraction. I specifically used videos that included a surfacing sequence that culminated in a collective deeper dive (defined as a dive where all individuals within the group dove beneath the visible portion of the water column for a

period of 45s or more as in Zwamborn & Whitehead, 2023). I extracted video frames at 10 second intervals up until the initiation of the collective deep dive (Frame Grab, 2024).

Data on the position and orientation of all individuals visible within a frame were then extracted using Matlab (see Appendix I for a visual example). For each individual, a mark was placed on the most anterior part of the body visible (typically the rostrum) and another on a posterior location (typically the dorsal fin or fluke notch). Individuals were assigned a six-character alphanumeric code (e.g., A01TQ3). The first letter denotes age class, with individuals classified either as adults, juveniles, calves or newborns (as per Auger-Méthé & Whitehead, 2007). The next two characters are an individual numeric identification for that frame. The fourth character was a letter denoting what the spacing between the two points of measurements represented, which was classified as either a total measurement (T; rostrum to medial fluke notch), partial measurement (P; rostrum to the posterior inset of the dorsal fin) or random (R; where specific features of the whale were not clear and thus a specific portion of the whale was not measured). The final two characters indicate quality, with Q1 being a pilot whale where only orientation can be denoted, Q2 being when the outline of the pilot whale can be seen, but no further details, Q3 when I could determine the shape of the pilot whale well as well as specific anatomical parts. , and Q4 when the pilot whale is perfect or near perfect in both clarity and details. See Appendix I for an annotated photo example.

Using drone height, a scaling factor was calculated by repeatedly measuring an object of known length (our research vessel). Using the two points extracted for each pilot whale within a frame, in addition to the drone height and scaling factor, I calculated for each frame the mean heading of whales in the frame, standard deviation from the mean heading, rank width (metres across group perpendicular to movement direction), file length (metres from front to back of group in movement direction), mean distance to nearest neighbour (m), major axis heading angle, the proportion of variance on the major axis, and the clumping statistic for each frame (Table 1; Figure 5.1 for visualization of rank and file). The major axis is defined as the axis that accounts for the most variance (Sokal & Rohlf, 1981). The proportion of variance was calculated using the following formula: $\frac{Major\ Axis\ Length}{Major\ Axis\ Length * Minor\ Axis\ Length}$, where values near 1.0 represented more collinear groups and values close to 0.5 represented more circular groups of pilot whales.

The clumping statistic measured the spread of individuals (Durbin, 1965). When individuals within a group were distributed according to a Poisson process (i.e. uniformly and independently of one another along the major axis), we would expect a clumping statistic value of 0.0 (SD = 1.0), whereas clustering in pilot whales would give a clumping statistic greater than 0.0 and spaced-out pilot whales would result in a clumping statistic of less than 0.0. At the individual level, I extracted the age class, portion of whale measured, and quality of individual images using their assigned six-character alphanumeric code.
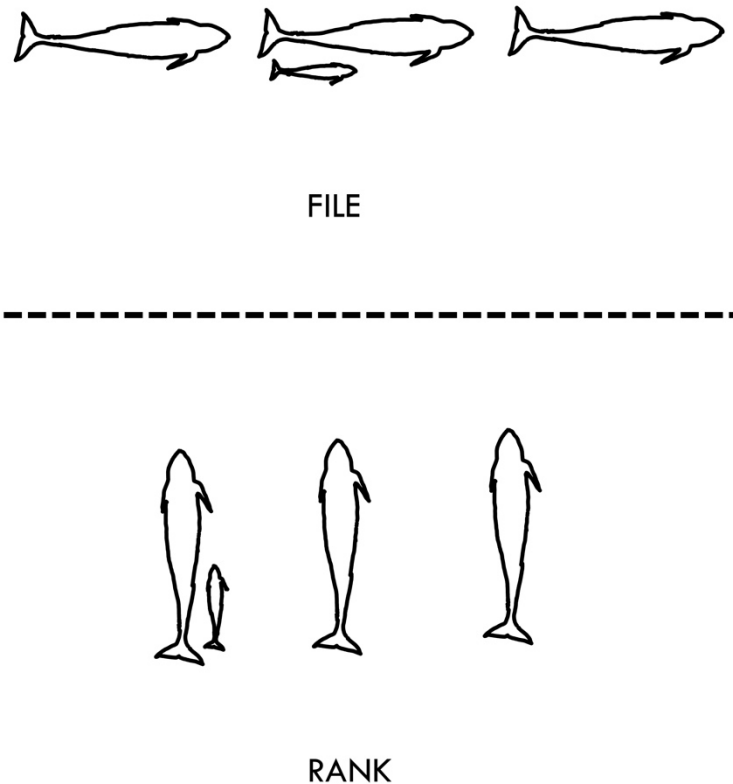
FILE

RANK

Figure 5.1 Visualization of rank (colinear perpendicular to direction of movement) and file (colinear in line with direction of movement) formations

5.3.3 Data Analysis

The distributions of our formation characteristics variables were visualized using violin plots. I used a principal component analysis (PCA) to explore whether there were

any relationships between eight dependent formation variables. Multivariate analysis of variance (MANOVA) then examined how these variables related to group behavioural state, group size (each different group size treated as a different class), and time to collective dive. A canonical variate analysis was also used to further investigate the relationship between group formation variables and behavioural state, group size and time to dive. All statistical analyses were performed in R (R Core Team, 2024).

5.4 Results

Most formation characteristics calculated for groups of long-finned pilot whales showed considerable variation (Table 2). The modal group size in the images analyzed included 8 individuals. Groups were typically arranged in a more collinear than circular formation (modal proportion of variance on the major axis 92%), with a median heading of approximately 15 degrees from the minor axis. This meant that the rank width (median 12.3m) was generally longer than the file length (median 8.0m). Members of groups were slightly more often clumped as opposed to spaced along the major axis (the clumping statistic was greater than zero for 55% of frames).

Table 5.2 Median and interquartile range for formation characteristics in long-finned pilot whales

Formation Characteristic	Median	Interquartile Range
SD Heading (^{o})	8.16	4.77 – 13.66
Rank Width (m)	12.36	8.63 – 15.59
File Length (m)	8.02	5.27 – 12.75
Mean Distance to Nearest Neighbour (m)	2.38	1.81 – 3.27
Major Axis Heading Angle (^{o})	15.21	-10.58 – 60.76
Proportion of Variance on the Major Axis	0.91	0.83 – 0.96
Clumping Statistic	0.18	-0.63 – 0.94

The first principal component of the Principal Components Analysis (PCA; Figure 5.2) was positively correlated with standardized file length and major axis heading angle, while negatively correlated with standardized rank width. Thus, positive values of the first principal component represented groups in file formation aligned to the direction of movement and negative values represent groups in rank formation and those aligned

perpendicular to the direction of movement. The second principal component was positively correlated with the standard deviation of the heading, mean nearest neighbour (m), and the proportion variance on the major heading, while it is negatively correlated with group size and the clumping statistic. Therefore, positive values of the second principal component represented groups that are more spaced, have a higher standard deviation of heading in comparison to the group mean heading, and are less circular (more collinear), while negative values aligned with larger groups and those that showed more clumping. There appeared to be some clumping based on group behavioural state in the PCA plot (along the second principal component), with foraging and resting showing different distributions, but this was not very distinctive.
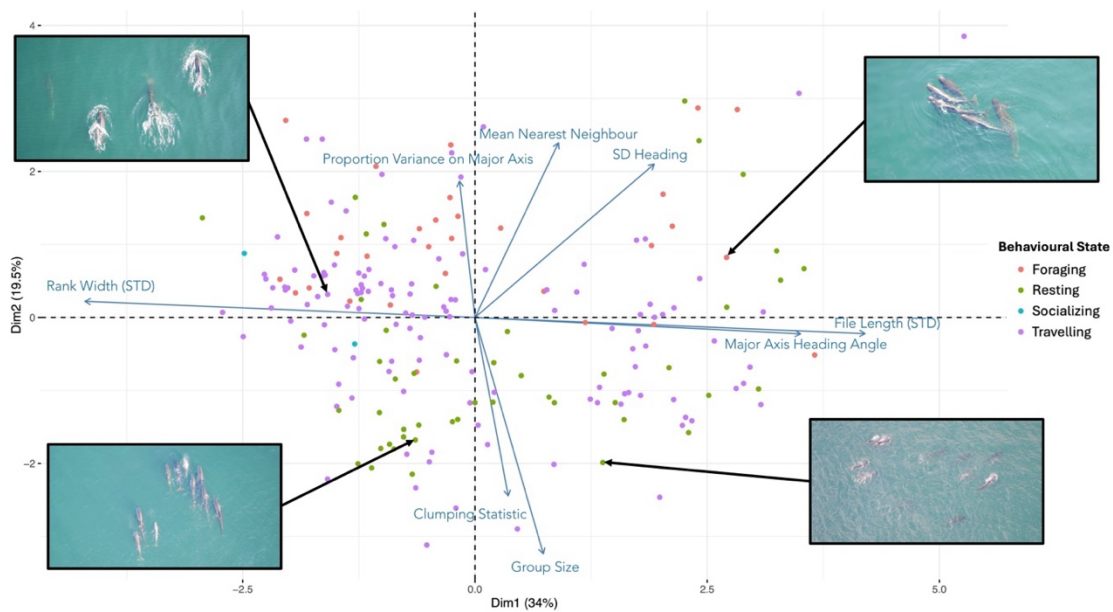
Figure 5.2 Principal component analysis (PCA) biplot of group formation variables for long-finned pilot whales, including samples coloured by group behavioural state and video frame grabs linked to data points ($n = 208$). The first two axes of the PCA explained 53.5 % of the variance, while the third axis explained 13%.

More obvious clustering was seen in the canonical variate analysis (CVA) (Figure 5.3) in comparison to the PCA, where travelling groups were spread out, but resting groups had generally lower values along the CV2 axis and foraging groups had generally higher values along this same CV2 axis.
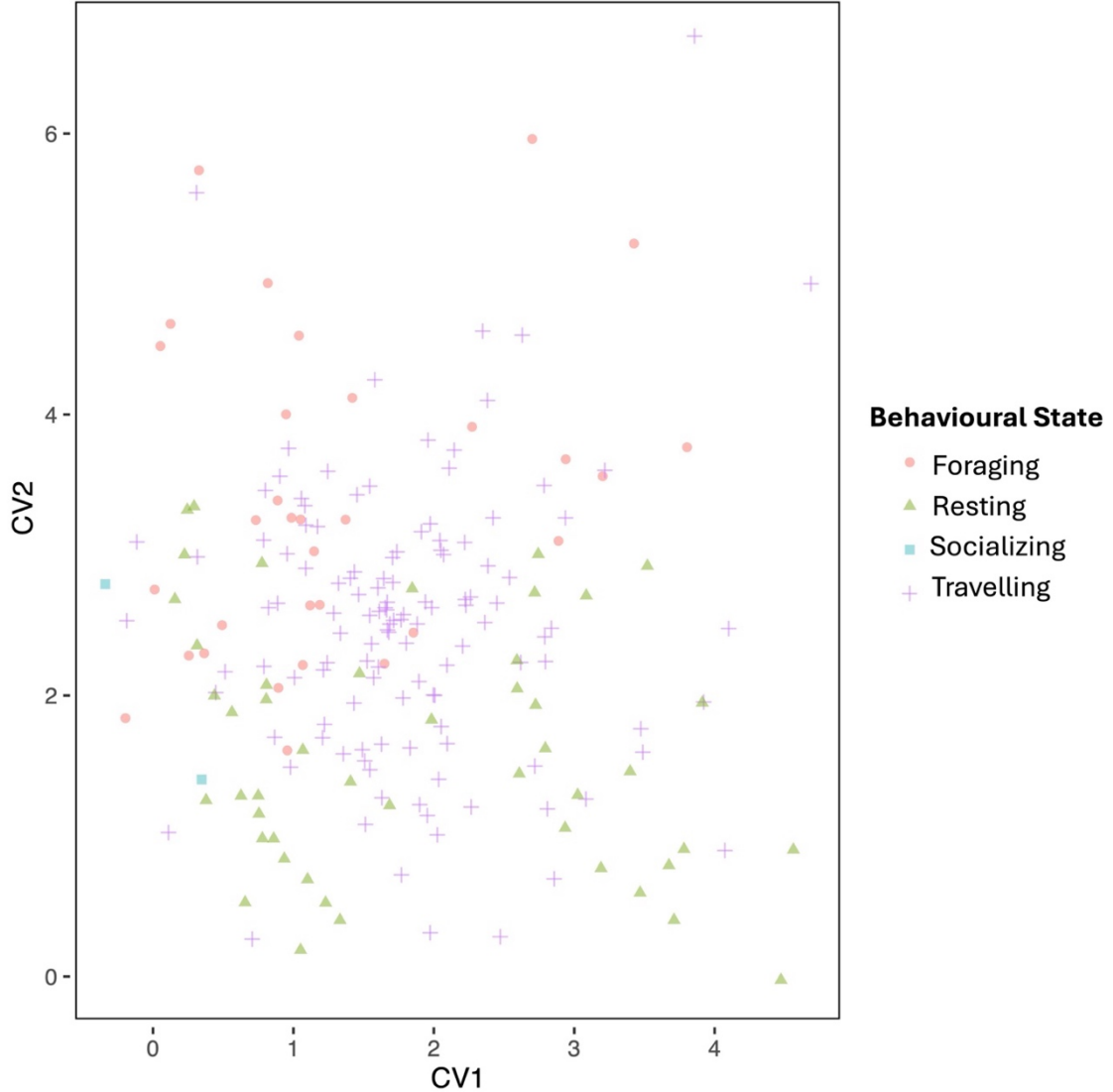
Figure 5.3 Canonical Variate Analysis (CVA) group formation variables for long-finned pilot whales, including samples coloured by group behavioural state

My multivariate analysis of variance (MANOVA) comparing these formation variables to group behavioural state was statistically significant (F = 3.78; p = 3.96e-08; $\eta_p^2 = 0.12$), with file length (m) being generally shorter and less variable in foraging and travelling then during resting (F = 2.99; p = 0.032) and clumping being lower in travelling and foraging groups, but higher in resting and socializing ones (F = 4.50; p = 0.004). Rank width was also statistically significant between behavioural states (F = 2.66; p = 0.049), with travelling pilot whales showing higher median rank widths than foraging

and resting groups. Distinctions between behavioural states in the standard deviation of the heading of the different whales in the frame were near significant ($F = 2.53$; $p = 0.058$) with foraging groups of pilot whales showing more variation and a higher median than other behavioural states. See Figure 5.4 for violin plots of these significant and near significant variables with behavioural state (and Appendix J for violin plots of non-significant formation characteristics).
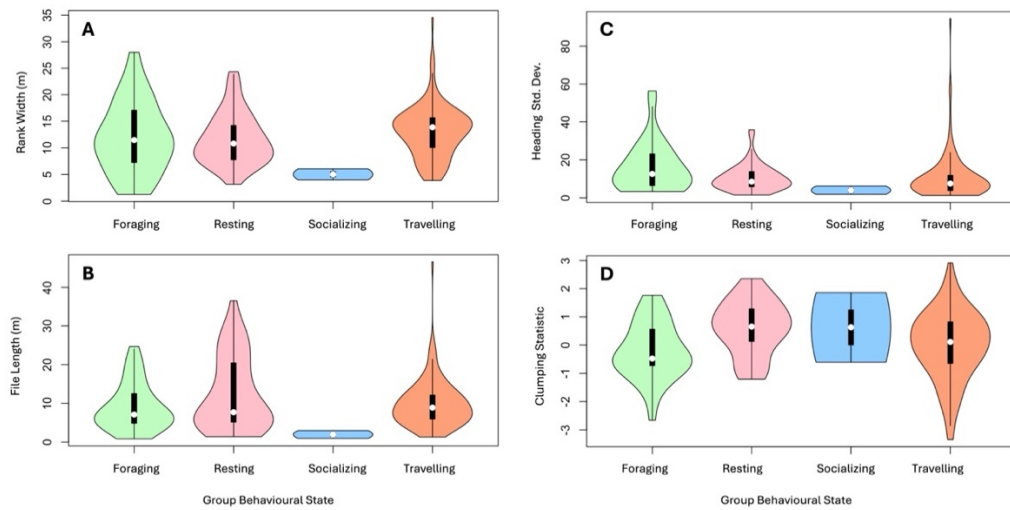
Figure 5.4 Violin plots of (A) rank width (B) file length (C) standard deviation of the heading and (D) clumping by group behavioural state for groups of long-finned pilot whales off Cape Breton, Nova Scotia.

A multivariate analysis of variance (MANOVA) comparing time to dive initiation with formation variables was also statistically significant ($F = 3.63$; $p = 0.001$; $\eta_p^2 = 0.11$; Figure 5.5), with the standard deviation of heading generally decreasing closer to the group dive ($F = 6.02$; $p = 0.015$), groups becoming less circular as they near the initiation of the dive ($F = 9.08$; $p = 0.003$). Clumping increases ($F = 2.80$; $p = 0.096$) and mean distance to nearest neighbour (m) decreases shortly before the collective dive ($F = 3.69$; $p = 0.056$), but neither are statistically significant at $p<0.05$. See Appendix J for additional supporting figures.
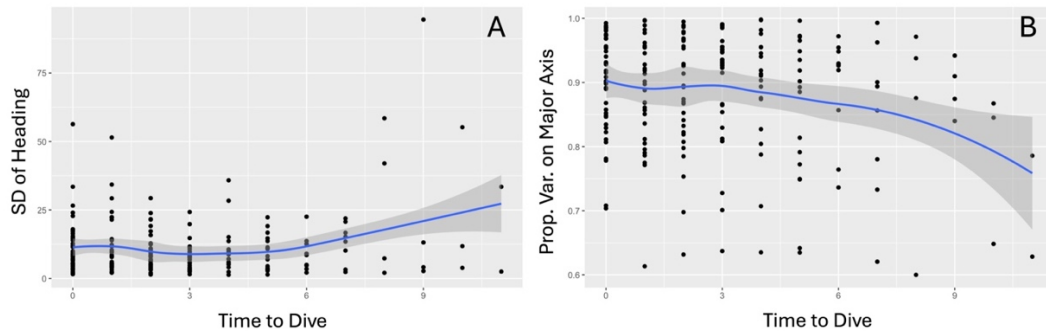
Figure 5.5 Group formation variables (A) standard deviation of heading and (B) the proportion variance on major axis that changed significantly in the time leading up to collective deep dives (time in seconds) in long-finned pilot whales off Cape Breton, Nova Scotia

A multivariate analysis of variance (MANOVA) comparing group size with formation variables was also statistically significant (F = 14.90; p = 1.37e-15; $\eta_p^2 = 0.34$), with file length (m) increasing as groups got larger (F = 5.65; p = 0.018), and mean distance to nearest neighbour (m) decreasing with larger groups (F = 16.39; p = 7.29e-05), as shown in Figure 5.6. Additionally, groups became more circular as they got larger (F = 11.13; p = 0.001) and moderate-sized groups were less clumped than both small and large ones (F = 9.06; p = 0.003). See Appendix J for additional supporting figures.
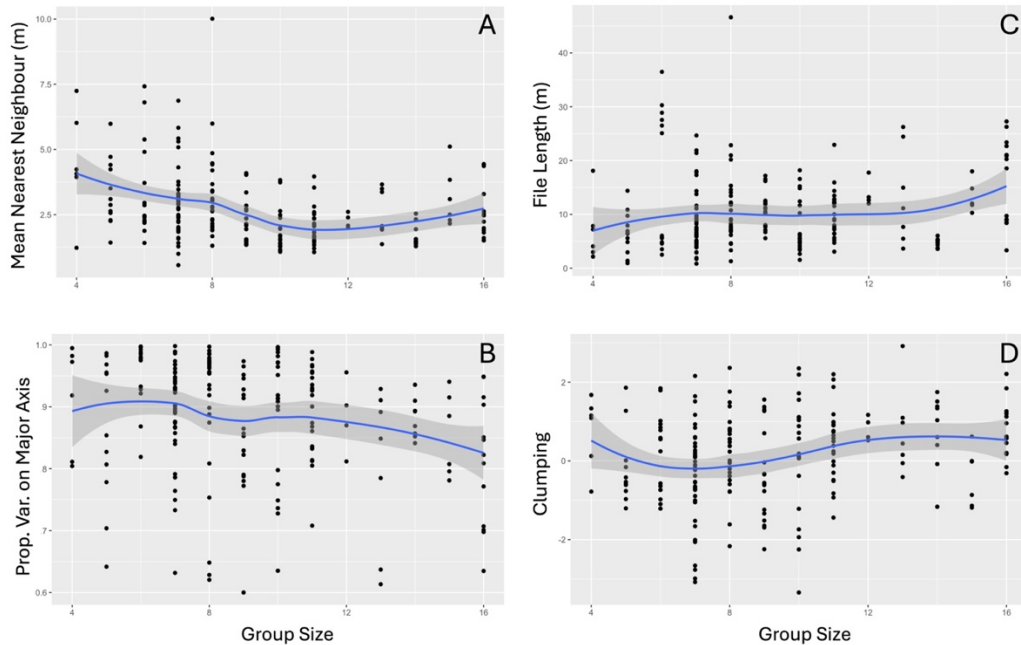
Figure 5.6 Group formation variables (A) mean distance to nearest neighbour (m), (B) proportion variance on major axis, (C) file length (m) and (D) clumping statistic that varied significantly with group size in long-finned pilot whales off Cape Breton, Nova Scotia

5.5 Discussion

My study found that group formation characteristics in long-finned pilot whales do vary across group behavioural states, time to collective dive and group size. However, there was also a fair amount of variation across the formation variables looked at. Overall individuals within groups tended to be oriented in a similar direction to the mean heading and groups were broader in width than length. Pilot whale groups were more often collinear in shape than circular, and more regularly clumped than spaced. These results provide an important baseline for understanding how groups of free-ranging pilot whales move together as a group.

5.5.1 Formations Across Behavioural States

Pilot whales were more clumped when resting and socializing than when foraging and travelling. A number of cetacean species have been documented to rest in close proximity to other group members, including spinner dolphins *Stenella longirostris*, dusky dolphins *Lagenorhynchus obscurus* and killer whales (Norris & Dohl, 1980; Würsig & Würsig, 1980; Ford,1989; Norris et al. 1994). Resting individuals are more vulnerable to predation and other disturbances (Lima, 1995). Therefore, close clumping and coordination can help increase group vigilance and decrease vulnerability (Beauchamp, 2015). Clumping during socializing can be explained by groups of individuals interacting with each other, often in tactile ways that necessitate close contact.

File length (m) was generally shorter and less variable in foraging and travelling than during resting, which contrasts with the observed resting lines of northern resident killer whales which are typically in rank formation (Ford, 1989). Unlike killer whales, distinctive resting lines have not been observed in long-fined pilot whales. This observed difference between these two species may result from an increased vulnerability to predation in pilot whales (whereas killer whales have no natural predators) or from other social differences.

While some formation variables did come out as significant across group behavioural states, many did not. This is likely explained by the amount of variation observed across different groups exhibiting this same behaviour, indicating that long-finned pilot whales perhaps do not have as clear and stereotyped formations as are observed in some other species of cetaceans (e.g. the resting lines of northern resident killer whales or the cooperative bubble net feeding of humpback whales *Megaptera novaeangliae* (Jurasz & Jurasz, 1979; Ford, 1991)).

5.5.2 Formations Leading Up to Collective Dives

When I looked at whether formation variables changed leading up to the initiation of a collective dive, I found that pilot whales generally aligned themselves with other group members and became more collinear in formation shortly before these dives

occurred. This alignment of heading suggests that members of the group are aware of the dive that is about to occur, which is referred to as pre-departure behaviour in studies of collective decision-making (Seltmann et al., 2013; Walker et al., 2016; Zwamborn et al., 2023). While dive initiators – often female and in flanking positions – have been observed in long-finned pilot whales, there was no previous evidence as to whether other individuals within the group anticipate collective dives before they occur (Zwamborn et al., 2023).

Decreasing circularity before collective dives could function in strengthening group coordination, as pilot whales would be spatially and temporally aligning themselves with other individuals. Studies on other odontocete species have observed that groups are often broader in the direction of movement and have suggested that this may increase the success rate of finding dispersed prey patches (Norrish and Dohl 1980, Whitehead 1989). Shifting into a more collinear formation would allow pilot whales to use these collective dives more efficiently if the dives involve scouting for prey. Group coordination is an important part of cetacean (and more specifically long-finned pilot whale) ecology, as it is important for maintaining social bonds as well as group cohesion (Senigaglia et al., 2012; Senigaglia & Whitehead, 2012; Zwamborn & Whitehead, 2017). Strong group coordination before collective dives (through spatial and temporal alignment) could be an essential component of ensuring that pilot whales dive and resurface in a cohesive group.

5.5.3 Formations Across Group Size

Comparing formation variables across group sizes, I found that file length (m) increased and the distance between individuals decreased as groups got larger, in addition to larger groups being more collinear in shape. Additionally, clumping was highest in small and large groups, but less so in medium-sized groups.

It makes sense that file length increases are related to the shape of a group becoming more circular, as many groups that displayed higher file lengths were also more circular in terms of formation (and single file formations were rarely observed,

whereas collinear rank formations were common). Reasons for this may also link back to the importance of coordination and cohesion. Larger groups of long-finned pilot whales are less likely to belong to the same long-term social unit (Augusto et al., 2017; Ottensmeyer & Whitehead, 2003), and therefore may benefit from maintaining higher cohesion than would be found in smaller groups. There is evidence for this in other cetaceans, including bottlenose dolphins *Tursiops truncatus*, where individuals were more synchronous with lesser-known acquaintances than with their constant companions (McCue et al., 2020). This also is a possible explanation for why both small and large groups were more clumped, with small groups representing very small social units and large groups representing multiple social units, while medium sized (and less clumped) groups are likely representative of larger social units, in which coordination is perhaps slightly less important. Increases in group size often correlate with a decreased need for individual vigilance resulting from an increased collective vigilance (Beauchamp, 2019). This is a possible driver of circular formations in larger pilot whale groups, especially given that collinear rank formations allow for better predatory vigilance in other species of animals (Beauchamp, 2019). However, the preference of collinear rank formations (as opposed to single file) in long-finned pilot whales may also be driven by benefits such as higher success finding dispersed prey patches, as has been proposed for sperm whales (Whitehead, 1989).

5.5.4 Importance of Formations in Pilot Whales

There has been little work done to quantify the group formations of most cetacean species. A baseline understanding of free-ranging group formations in long-finned pilot whales is of particular importance as they are the most common species involved in mass strandings globally (Moore et al., 2018). In some cases, groups have been observed before these beachings occur (Best & Reeb, 2010), but it is often unclear as to whether they are behaving normally or showing signs of distress. Many strandings appear to be the result of confusion and errors in navigation, though they also are known to have a number of other correlates (Moore et al., 2018). Having a good understanding of normal group formations in this species (and others) can help us to determine when abnormal

behaviour is occurring so that stranding responses can attempt to mitigate these events. For example, pre-stranded long-finned pilot whales have been observed floating at the surface in extremely tight formations for long periods of time, unlike any of the formations observed in free-ranging pilot whales during this study (see Appendix K for examples). If groups of pilot whales in danger of stranding are found to show unique group formation characteristics, this information can be used to help responders determine whether groups of pilot whales seen close to shore are in distress and how to best mitigate the risk of stranding if they are. These insights into free-ranging long-finned pilot whale group formations can also help to understand the behavioural effects of disturbance, such as that from whale-watching or seismic surveys, as has been observed in other species where it is not uncommon for disturbed individuals to cluster more tightly together (Senigaglia et al., 2016).

5.5.5 Conclusions

Long-finned pilot whales display group formations that varied with group behavioural state, time to collective group dives, and group size. While these formation characteristics seem quite variable overall, they do not cluster as distinctly as might be expected, showing some consistency across different social contexts. This study provides the first spatial evidence for pre-departure behaviour in a cetacean species, where groups of long-finned pilot whales anticipate deep dives and alter their formations in preparation for diving. Future studies could compare these observed formations of free-ranging long-finned pilot whales with groups that have been filmed pre-stranding to determine whether there are clear differences that can indicate risk of beaching and allow for possible mitigation. Further research could also look at how these formations change with specific behavioural disturbances, such as from whale-watching or seismic surveys.

CHAPTER 6 – DISCUSSION

"The sea does not reward those who are too anxious, too greedy, or too impatient…
Patience, patience, patience, is what the sea teaches. Patience and faith.
One should lie empty, open, choiceless as a beach – waiting for a gift from the sea."
~ Anne Morrow Lindbergh

6.1 Leadership, Synchrony, and Formations

Leadership, synchrony, and formations are all important components of group social behaviour and are often related. For example, collective decision making frequently involves coordinated group behaviours, which can manifest through synchronous behaviour (temporal), group formations (spatial), or a combination of both (Andrieu et al., 2016; Reinhardt, 1983; Walker et al., 2017). We know that leadership in cetaceans, particularly species with complex social interactions like common bottlenose dolphins *Tursiops truncatus* and killer whales *Orcinus orca*, includes key individuals who guide group movements (Brent et al., 2015; Lusseau & Conradt, 2009). These leaders have been found to be more socially connected or hold greater ecological knowledge than other individuals within their group. This is similar to what is found more broadly across terrestrial mammals, though dominance plays a much more important role in determining which individuals lead in taxa such as primates (Conradt & Roper, 2005; Zwamborn et al., 2023). Conversely, the messy movements of foraging sperm whales *Physeter macrocephalus* provide evidence for shared decision making in cetaceans (Whitehead, 2016).

While the prevalence of leadership in cetaceans can be, in part, explained by the behavioural ecology of the species in which these decision making processes have been observed, there are also possible reasons for this bias linked to study design. When researching decision making in non-human animals, scientists generally survey for a visible (often related to movement) or audible cue preceding group behavioural change (Zwamborn et al., 2023). There is a tendency towards looking for leadership without considering other types of decision making, as a change in behaviour initiated by one or several individuals is often more intuitive to study than investigating subtler clues that

could point towards other decision making processes. Therefore, the lack of evidence for more shared decision making amongst cetaceans may not reflect reality, but rather be an artifact of study design coupled with the challenge of observing animals that spend much of their time out of view.

While collective decision making is important for many aspects of group life, one unique context which requires group-level decisions in cetaceans is collective deep dives. Both synchrony and formations can be important during these dives, as they are hypothesized to reduce predation risks associated with deep-water foraging (Aguilar de Soto et al., 2020; Alcázar-Treviño et al., 2021). For instance, Cuvier's beaked whale *Ziphius cavirostris* and Blainville's beaked whale *Mesoplodon densirostris* whales dive and return to the surface together (even though they disperse at depth), synchronized temporally and close spatially which should minimize predation risk from killer whales (Aguilar de Soto et al., 2020).

Collective decision making, synchrony and group formations also can stand alone as important components of group behaviour. Groups do not have to be tightly temporally or spatially coordinated during collective decisions, such as was observed with groups of (independently) foraging sperm whales that seem to make messy consensus decisions (Whitehead, 2016). Additionally, synchrony and formations are often observed outside of the context of important group decisions, thus not relating exclusively to the decision making aspect of group behaviour (Connor et al., 2006; Hastie et al., 2003; Hoyle et al., 2021). This is because the benefits of coordination (temporally and spatially) as both antipredator and affiliative behaviour extend beyond discrete decision making events.

6.2 Research Findings

In this section, I provide a summary of each of my research chapters and highlight their contributions to the main objective of my thesis, which was to enhance understanding of group life in long-finned pilot whales.

In the second chapter, I systematically reviewed studies of collective decision making in terrestrial mammals and compared what I found to current information on

collective decision making in aquatic mammals. Most studies in non-human mammals focused on primates and artiodactyls. There were only a few studies (N= 9) looking at collective decision making within cetaceans, with no representation of other aquatic mammalian taxa. Studies observed leadership within killer whales, common bottlenose dolphins, Indo-Pacific bottlenose dolphins *Tursiops aduncus* and Irrawady dolphins *Orcaella brevirostris* (Zwamborn et al., 2023). Shared (e.g. consensus) decision making processes were only described in sperm whales (Whitehead, 2016). I provided five suggestions for improving studies in the field of collective decision making: clearly delineating between temporal and non-temporal aspects, standardizing methods to allow for better comparisons, considering the possibility of both shared and unshared decision making (instead of focusing solely on whether leadership is observed), considering the context of decision making, and avoiding the anthropomorphizing of decision making in non-human animals. We now have the tools (e.g. drones, suction cup tags with camera and acoustic capabilities) to learn more about these processes in a group of taxa that were historically challenging to observe at the level of detail needed for these studies. Research in captivity has looked at individual decision making and prosocial choice in cetaceans but has not investigated group-level decisions (Nakahara et al., 2017; Shyan et al., 2002).

In chapter three I analyzed drone footage of long-finned pilot whales *Globicephala melas* to learn more about what decision making processes were used in their collective deep dives. The results, published in Zwamborn et al. (2023), show that there is evidence for leadership during dive initiation and that these initiators are generally females in flanking positions. A higher proportion of female leadership may be driven by a disparity in ecological knowledge between the sexes, as has been found in other matrilineal cetaceans (Brent et al., 2015). However, more studies will be necessary to clarify the drivers of this unequally distributed leadership. Leadership from flanking positions is hypothesized to aid in coordination and cohesion, akin to what has been observed in lions as well as cattle drives in human societies (Stander, 1992; Zwamborn et al., 2023). Larger groups of pilot whales, which likely represent multiple social units, showed shorter average interindividual intervals (and an increased coefficient of variation suggesting more clustering in final dives) compared to smaller groups. These shorter

average interindividual intervals may function akin to what has been observed in Indo-Pacific bottlenose dolphins, where individuals exhibit higher synchrony within larger groups of less familiar dolphins as a way of reinforcing social bonds and aiding group coordination (McCue et al., 2020).

In the fourth chapter, I used breath times of individuals extracted from aerial drone footage within groups of long-finned pilot whales to explore synchronous behaviour. My research showed that pilot whales increased within-group synchrony during the penultimate (second-to-last) breathing period, followed by decreased synchrony just before initiating a collective deep dive, suggesting anticipation of these collective dives by group members. This increase in synchronous behaviour appears to be primarily driven by calves, likely to enhance their protection and minimize their energy expenditure during deep dives. Overall, grey calves were the most synchronous age class, while newborns showed the lowest synchrony with other group members. In terms of the relation of synchrony to group size, larger groups of pilot whales were found to be more synchronous than smaller groups as could be expected as more whales would be breathing within the same time period. This is supported by similar observations in other cetacean species, such as common bottlenose dolphins (Hastie et al., 2003). There was no clear correlation between group behavioural state and the synchrony measures studied.

In chapter five I used drone footage to explore how long-finned pilot whale group formations change in relation to decision making context (collective deep dives), group size and behavioural state. I found that pilot whales often align themselves with other individuals within their groups, becoming more collinear and less circular in formation shortly before deep dives occurred. This provides further evidence that members of the group are aware of the dive that is about to occur (i.e. pre-departure behaviour; Seltmann et al., 2013; Walker et al., 2016; Zwamborn et al., 2023). The decrease in circularity before these collective dives may serve to enhance group cohesion and coordination, as the whales spatially and temporally align themselves with one another. Clustering was most pronounced in large groups. Large groups likely consist of multiple social units, providing a context in which coordination is more important (Connor et al., 2006). In terms of the relationship between group formations and behavioural state, pilot whales were more clumped during resting and socializing behaviours similar to other cetacean

species (Würsig & Würsig, 1980; Ford,1989; Norris et al. 1994). However, the length of the group from front to back in the direction of movement (i.e. file length) was shorter and less variable during foraging and travelling when compared to resting, which contrasts with the rank formations observed in resting northern resident killer whales (Ford, 1989). Significant variation was observed across different groups displaying the same behavioural state, suggesting that long-finned pilot whales may not exhibit clear and stereotyped formations as sometimes seen in other cetacean species (e.g. the distinctive resting lines of northern resident killer whales; Ford, 1989).

Overall, the results of this thesis have provided important baseline information into the spatial and temporal aspects of group life in long-finned pilot whales, as well as information as to how collective decisions are made within these groups. There are flanking female guides that typically initiate deeper collective dives. This peripheral position likely functions in coordination and cohesion, similar to the role of horse riders during cattle drives in human societies. The eyes of long-finned pilot whales are located peripherally (similar to cows), and thus flanking locations for leaders would be the best positions to keep track of the group, as well as of any possible threats outside of the group. Before collective deep dives happen, pilot whales within the group adjust their synchrony and align themselves with other individuals in a colinear fashion (typically rank-wise), providing the first evidence for pre-departure behaviour in a cetacean species. Larger groups showed higher temporal synchrony, as well as increased spatial clustering, which was expected. Temporally (synchrony-wise) there was little variation across behavioural states but spatially (formations-wise) there was, with resting and socializing groups being more clustered, while foraging and travelling groups were more often in a rank-like formation with shorter and less variable file lengths. Despite these observations, long-finned pilot whales showed variation across both synchrony and formations. This variation might be explained by other aspects of group life that weren't investigated during this research, or may be characteristic of this species (similar to the great variation noted in their vocal repertoires; Zwamborn and Whitehead, 2017). In general, groups of long-finned pilot whales are highly synchronous and favour more collinear rank-like, evenly-spaced formations.

6.3 Research Contributions

One of the most exciting contributions of this thesis is a baseline understanding of group life in long-finned pilot whales as related to decision making, synchrony and formations. While synchrony in pilot whales has been studied before (Senigaglia et al., 2012; Senigaglia & Whitehead, 2012), it had not been looked at on a group level. Before this thesis, there were no scientific studies on collective decision making and group formations within pilot whales. There were only a handful of studies looking at collective decision making in situ for other cetacean species (and none in captive settings; Zwamborn et al., 2023). Group formations are often anecdotal or observational mentions (Würsig & Würsig, 1980; Ford,1989; Norris et al. 1994) where spatial arrangements weren't described quantitively (see notable exception for sperm whales; Whitehead, 1989).

Long-finned pilot mass strand more frequently than any other species of cetacean (Moore et al., 2018). Without a baseline understanding of how long-finned pilot whale groups make collective decisions and organize both spatially and temporally, we are unable to look at whether decision making processes and temporal (synchrony) and/or spatial (formations) characteristics present differently when it comes to pre-stranded or refloated groups of pilot whales. Does the way decisions are made change leading up to mass-stranding events? Or perhaps it is a lack of decisions or a collapse in leadership that leads to these beachings. The findings of this study hold great potential for informing stranding response and management worldwide. For example, pilot whales have been documented in extremely tightly clustered large groups shortly before mass strandings (see Appendix K for example image) in a way unlike any of my observations of healthy free-ranging pilot whales. Long-finned pilot whales commonly use inshore waters in some areas of the world (e.g. McComb-Turbitt et al., 2021), so an understanding of the difference between normal and abnormal (pre-stranding) behaviours in pilot whales is critical for management decisions on whether or not to intervene (e.g. actively shepherding groups considered at risk away from shallow habitats). Stranding response groups across the world have often used herding by vessels to successfully shepherd pilot

whales at risk of stranding away from the dangerous shallows (Mrusczok pers. comm., 2023; Stockin pers. comm., 2024).

While this thesis furthers our understanding of some specific aspects of group life in long-finned pilot whales, it also contributes significantly beyond this focused field to other cetacean studies and across animals more generally. My systematic review of collective decision making in terrestrial and aquatic mammals suggested a modified framework to move forward within studies of group decisions, as well as a number of other suggestions to strengthen this field of research. Additionally, many of the research and analytical techniques used in my studies are directly applicable to other study systems in cetaceans, as well as other aquatic and terrestrial mammal species.

6.4 Research Challenges and Future Directions

Studying far-ranging and often elusive cetaceans presents a number of significant challenges, especially for deep-diving and pelagic living species that spend much of their time in out of the sight of researchers who use traditional data collection methods (e.g. boat-based observations). While we now have better tools to study species such as the long-finned pilot whale (e.g. drones), there are still a number of challenges that limit what we can learn about decision making, synchrony and formations.

For analyzing aerial footage, we are dependent on favourable weather conditions for data collection and constrained by the visibility in the water column for data analysis (particularly for individual-level tracking). While advances in drone technology and flying techniques make it easier to fly in more extreme conditions and from inopportune platforms (Zwamborn et al., 2023), in-water visibility remains a challenge. The waters off Cape Breton Island have extremely low visibility and often present challenging weather conditions that limited my data collection, but there are many other parts of the world where this is less of a problem and a larger portion of collected data would be usable for analysis.

When it comes to collective decision making in cetaceans, as well as its relationship to synchrony and formations, observations of visual behaviour are limiting without accompanying acoustic data. This is because sound is the primary sense for

cetaceans, who live in light- and visibility-limiting waters (Tyack, 2000). Long-finned pilot whales often travel at speeds that are too quick for small boat-deployed hydrophones or fixed arrays, so my studies relied primarily on visual observations. So, questions remain. Are there acoustic cues that pilot whales use to signal a plan to the group before a dive? Do call rates or types link to synchronous or formation behaviour? Would we be able to gain a better understanding of the drivers of dive initiators if we could also listen to groups of pilot whales? One practical way of gathering this information would be to use suction cup acoustic tags on one or more individuals within a focal group of pilot whales. Another solution might be to use hydrophones set at a distance behind the vessel, if the vessel is under sail or powered by a quiet engine (e.g. a hybrid vessel with an electric option that can be used during encounters).

The population of long-finned pilot whales that summers off Cape Breton Island is quite large (of the order of thousands of individuals) and therefore reencountering the same group on multiple days during this study (when weather conditions were favourable) was rare. Without resightings of the same groups, we are unable to talk about how decision making, synchrony, and formations vary over time and contexts within a social unit or group. Focal follows of known groups are the next step in understanding more about the distribution of leadership, as well as looking in more detail at synchrony and formations within known groups. Do all pilot whale groups follow the same general patterns? Or is there consistency within groups but variation between them?

This brings up the challenge of identifying individuals from drone footage. Northern hemisphere long-finned pilot whales *G. melas melas* are relatively poorly marked (Auger-Méthé & Whitehead, 2007) and therefore images from drones are difficult to match to boat-based photos unless the drone is at lower altitude (which is not always practical for capturing the activities of the whole group on video and can be disruptive, resulting in behavioural changes). Even when matching individuals on drone footage to boat-based images is feasible, it is time-consuming (especially in larger groups where tracking is not straightforward). While there is much to be learned by looking at a group level for decision making, synchrony, and formations as I did in this thesis, understanding the nature and history of relationships at an individual level would add more to our understanding of group life in this species. Are older females leading,

implying ecological knowledge may play an important role? Or are more socially connected individuals taking on this role? Do specific individuals lead consistently or is leadership distributed over time within a group? None of these questions can be answered without the ability to identify individuals. Future studies could aid in these efforts by identifying the range of flying altitudes (drone) for which matching of individuals from aerial to boat-based photos is practical.

Analyzing drone footage at the level of detail needed for these studies is also extremely time-consuming and would benefit from technological advances that help streamline the data extraction process. Because of the often-turbid nature of the aquatic environments these cetaceans live in, current automated tracking methods such as EthoVision XT (Noldus Information Technology, 2024) often do not work as efficiently for cetaceans as they do for species that are consistently and clearly visible. While this will likely remain a challenge for the time being, automated tracking routines that are able to use individual characteristics like fine-scale scarring or relative size to help track individuals within cetacean groups would greatly help in studies that use aerial drone footage where individuals might switch places rapidly or briefly slip out of visibility.

These challenges underscore the need for innovative methodologies that can reliably capture and analyze cetacean behaviour under less-than-ideal conditions. In addition to the directions mentioned above, future research should look at a broader range of behavioural and social contexts (as we know that collective decision making happens in scenarios other than deep dives). Further studies could also explore the drivers of leadership (e.g. whether identifiable leaders are known to be more socially connected or more likely to have greater ecological knowledge).

6.5 Conclusion

My thesis has advanced our understanding of some of the intricate aspects of group life in long-finned pilot whales, particularly as they relate to decision making, synchrony, and formations. I have found evidence for leadership in the initiation of deep dives, undertaken primarily by flanking female guides. This research has also shed light on how within-group synchrony and clustering appear more prevalently in larger groups,

supporting their proposed affiliative function (Connor et al., 2006; Senigaglia et al., 2012). These findings underscore the complex relationship between collective decisions, synchrony and formations for cetaceans, as well as how they relate to other contexts such as group size and behavioural state. Beyond long-finned pilot whales (and cetaceans), this thesis also contributed an updated framework for collective decision making in animals more generally. Understanding more about the group life of social cetaceans is necessary for investigating drivers of decision making, synchrony and formations across different social and behavioural contexts. These studies are also critical for providing a baseline for the future comparison of how these behaviours vary across time and within the context of challenges faced by cetaceans (e.g. disturbance, mass strandings, climate change).

BIBLIOGRAPHY

Actis PS, Danilewicz D, Cremer MJ, Bortolotto GA (2018) Breathing synchrony in franciscana (*Pontoporia blainvillei*) and Guiana dolphins (*Sotalia guianensis*) in Southern Brazil. *Marine Mammal Science* 34: 777–789. https://doi.org/10.1111/mms.12480

Addison WE, Simmel EC (1980) The relationship between dominance and leadership in a flock of ewes. *Bulletin of the Psychonomic Society* 15: 303–305. https://doi.org/10.3758/BF03334540

Altmann M (1952) Social behavior of elk, *Cervus canadensis nelsoni*, in the Jackson Hole area of Wyoming. *Behaviour* 4: 116-143. http://www.jstor.org/stable/4532747

Aguilar de Soto N, Visser F, Tyack PL, Alcazar J, Ruxton G, Arranvi P et al.(2020) Fear of killer whales drives extreme synchrony in deep diving beaked whales. *Scientific Reports* 10: 13. https://doi.org/10.1038/s41598-019-55911-3

Aivaz AN, Ruckstuhl KE (2011) Costs of behavioral synchrony as a potential driver behind size-assorted grouping. *Behavioral Ecology* 22: 1353–1363. https://doi.org/10.1093/beheco/arr141

Alcázar-Treviño J, Johnson M, Arranz P, Warren VE, Pérez-González CJ, Marques T, Madsen PT, Aguilar De Soto N (2021) Deep-diving beaked whales dive together but forage apart. *Proceedings of the Royal Society B: Biological Sciences* 288: 20201905. https://doi.org/10.1098/rspb.2020.1905

Amos B, Bloch D, Desportes G, Majerus TMO, Bancroft DR, Barrett JA, Dover GA (1993) A review of the molecular evidence relating to social organisation on breeding system in the long-finned pilot whale. *Reports of the International Whaling Commission* Special Issue 14: 209–217.

Archie EA, Moss CJ, Alberts SC (2006) The ties that bind: Genetic relatedness predicts the fission and fusion of social groups in wild African elephants. *Proceedings of the Royal Society B: Biological Sciences* 273: 513–522. https://doi.org/10.1098/rspb.2005.3361

Auger-Méthé M, Whitehead H (2007) The use of natural markings in studies of long-finned pilot whales (*Globicephala melas*). *Marine Mammal Science* 23: 77–93. https://doi.org/10.1111/j.1748-7692.2006.00090.x

Augusto JF, Frasier TR, Whitehead H (2017a) Characterizing alloparental care in the pilot whale (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada. *Marine Mammal Science* 33: 440–456. https://doi.org/10.1111/mms.12377

Augusto JF, Frasier TR, Whitehead H (2017b) Social structure of long-finned pilot whales (*Globicephala melas*) off northern Cape Breton Island, Nova Scotia. *Behaviour* 154: 509–540. https://doi.org/10.1163/1568539X-00003432

Backwell PRY (2018) Synchronous waving in fiddler crabs: A review. *Current Zoology* 65: 83–88. https://doi.org/10.1093/cz/zoy053

Badgerow J, Hainsworth F (1981) Energy savings through formation flight? A re-examination of the vee formation. *Journal of Theoretical Biology* 93: 41–52. https://doi.org/10.1016/0022-5193(81)90055-2

Bales K, Dietz J, Baker A, Miller K, Tardif SD, Allocare W, Marmoset W, Tamarin W (2000) Effects of allocare-givers on fitness of infants and parents in callitrichid primates. *Folia Primatol* 71: 27-38. https://doi.org/10.1159/000021728

Barelli C, Boesch C, Heistermann M, Reichard UH (2008) Female white-handed gibbons (*Hylobates lar*) lead group movements and have priority of access to food resources. *Behaviour* 145: 965–981. https://www.jstor.org/stable/40295873

Beauchamp G (2015) *Animal Vigilance. Monitoring and Competitors.* Academic Press.

Beilharz RG, Mylrea PJ (1963) Social position and movement orders of dairy heifers. *Animal Behaviour* 11: 529–533. https://doi.org/10.1016/0003-3472(63)90275-6

Bekoff M, Daniels TJ, Gittleman JL (1984) Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics* 15: 191-232. https://www.jstor.org/stable/2096947

van Belle S, Estrada A, Garber PA (2013) Collective group movement and leadership in wild black howler monkeys (*Alouatta pigra*). *Behavioral Ecology and Sociobiology* 67: 31–41. https://doi.org/10.1007/s00265-012-1421-5

Bernard HJ, Reilly SB (1999) Pilot whales *Globicephala* Lesson, 1828. In S. H. Ridgway & R. Harrison (Eds.), *Handbook of marine mammals. Volume 6: The second book of dolphins and propoises* (pp. 245–279). Academic Press.

Berry PSM, Bercovitch FB (2014) Leadership of herd progressions in the Thornicroft's giraffe of Zambia. *African Journal of Ecology* 53: 175–182. https://doi.org/10.1111/aje.12173

Berthold P (2001) Bird migration: a novel theory for the evolution, the control, and the adaptability of bird migration. *Journal Für Ornithologie* 142: 148–159. https://doi.org/10.1007/BF01651453

Best PB, Reeb D (2010) A near mass stranding of cetaceans in St Helena Bay, South Africa. *African Journal of Marine Science* 32: 163–166. https://doi.org/10.2989/18142321003715234

Betty EL, Zwamborn EMJ, Weyn M, Luck E, Alves F (2023) Life history parameters, sociobiology, and reproductive strategies of pilot whales. In *Sex in Cetaceans* (pp. 327–351). Springer International Publishing. https://doi.org/10.1007/978-3-031-35651-3_15

Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales *(Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Report of the International Whaling Commission* 12: 383-405.

Boinski S (1993) Vocal coordination of troop movement among white-faced capuchin monkeys, *Cebus capucinus*. *American Journal of Pathology* 30: 85–100. https://doi.org/10.1002/ajp.1350300202

Boinski S, Campbell AF (1995) Use of trill vocalizations to coordinate troop movement among white-faced capuchins: a second field test. *Behaviour* 132: 875–901. https://doi.org/10.1163/156853995X00054

Bonanni R, Cafazzo S, Valsecchi P, Natoli E (2010) Effect of affiliative and agonistic relationships on leadership behaviour in free-ranging dogs. *Animal Behaviour* 79: 981–991. https://doi.org/10.1016/j.anbehav.2010.02.021

Bonanni R, Natoli E, Cafazzo S, Valsecchi P (2011) Free-ranging dogs assess the quantity of opponents in intergroup conflicts. *Animal Cognition* 14: 103–115. https://doi.org/10.1007/s10071-010-0348-3

Bonnell TR, Campennì M, Chapman CA, Gogarten JF, Reyna-Hurtado RA, Teichroeb JA, Wasserman MD, Sengupta R (2013) Emergent group level navigation: an agent-based evaluation of movement patterns in a folivorous primate. *PLoS ONE* 8: e78264. https://doi.org/10.1371/journal.pone.0078264

Bonnell TR, Clarke PM, Henzi SP, Barrett L (2017) Individual-level movement bias leads to the formation of higher-order social structure in a mobile group of baboons. *Royal Society Open Science* 4: 170148. https://doi.org/10.1098/rsos.170148

Bourjade M, Thierry B, Hausberger M, Petit O (2015) Is leadership a reliable concept in animals? An empirical study in the horse. *PLoS One* 10: e0126344. https://doi.org/10.1371/journal.pone.0126344

Bourjade M, Thierry B, Maumy M, Petit O (2009) Decision making in Przewalski horses (*Equus ferus przewalskii*) is driven by the ecological contexts of collective movements. *Ethology* 115: 321–330. https://doi.org/10.1111/j.1439-0310.2009.01614.x

Bousquet CAH, Sumpter DJT, Manser MB (2011) Moving calls: a vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society B: Biological Sciences* 278: 1482–1488. https://doi.org/10.1098/rspb.2010.1739

Brent LJN, Franks DW, Foster EA, Balcomb KC, Cant MA, Croft DP (2015) Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Current Biology* 25: 746–750. https://doi.org/10.1016/j.cub.2015.01.037

Bresiński W (1982) Grouping tendencies in roe deer under agrocenosis conditions. *Acta Theriologica* 29: 427–447.

Briard L, Dorn C, Petit O (2015) Personality and affinities play a key role in the organisation of collective movements in a group of domestic horses. *Ethology* 121: 888–902. https://doi.org/10.1111/eth.12402

Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M & Bolker BM (2017) glmmTMB balances speed and flexibility

among packages for zero-inflated generalized linear mixed modeling. *The R journal*, 9: 378-400. https://doi.org/10.3929/ethz-b-000240890

Buckland ST, Bloch D, Cattanach KL, Gunnlaugsson, T, Hoydal K, Lens S, Sigurjónsson J (1993) Distribution and abundance of long-finned pilot whales in the North Atlantic, estimated from NASS-87 and NASS-89 data. *Reports of the International Whaling Commission* Special Issue 14: 33–49.

Carranza J, de Reyna LA (1987) Spatial organization of female groups in red deer (*Cervus elaphus* L.). *Behavioural Processes* 14: 125–135. https://doi.org/10.1016/0376-6357(87)90039-8

Ceccarelli E, Rangel Negrín A, Coyohua-Fuentes A, Canales-Espinosa D, Dias PAD (2020) Sex differences in leadership during group movement in mantled howler monkeys (*Alouatta palliata*). *American Journal of Primatology* 82: 1–9. https://doi.org/10.1002/ajp.23099

Chambers LM (2019) Follow the leader: correlates of juvenile leadership in wild chimpanzees. PhD thesis, The George Washington University, Washington, D.C., USA.

Christal J, Whitehead H, Lettevall E (1998) Sperm whale social units: variation and change. *Canadian Journal of Zoology* 76: 1431-1440. https://doi.org/10.1139/z98-087

Christiansen F, Rojano-Doñate L, Madsen PT, Bejder L (2016) Noise levels of multi-rotor unmanned aerial vehicles with implications for potential underwater impacts on marine mammals. *Frontiers in Marine Science* 3: 277. https://doi.org/10.3389/fmars.2016.00277

Cioffi WR, Quick NJ, Foley HJ, Waples DM, Swaim ZT, Shearer JM, Webster DL, Friedlaender AS, Southall BL, Baird RW, Nowacek DP, Read AJ (2021) Adult male Cuvier's beaked whales (*Ziphius cavirostris*) engage in prolonged bouts of synchronous diving. *Marine Mammal Science* 37: 1085–1100. https://doi.org/10.1111/mms.12799

Clutton-Brock TH, Guinness FE, Albon SD (1982) *Red deer: Behavior and ecology of two sexes*. University of Chicago Press.

Collignon B, Cervantes Valdivieso LE, Detrain C (2014) Group recruitment in ants: who is willing to lead? *Behavioural Processes* 108: 98–104. https://doi.org/10.1016/j.beproc.2014.09.033

Connor R, Smolker R, Bejder L (2006) Synchrony, social behavior and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops adunucus*. *Animal Behavior* 72: 1371–1378. https://doi.org/10.1016/j.anbehav.2006.03.014

Conradt L, Roper TJ (2005) Consensus decision making in animals. *Trends in Ecology and Evolution* 20: 449–456. https://doi.org/10.1016/j.tree.2005.05.008

Courant S, Fortin D (2012) Time allocation of bison in meadow patches driven by potential energy gains and group size dynamics. *Oikos*, 121: 1163–1173. https://doi.org/10.1111/j.1600-0706.2011.19994.x

Covidence Systematic Review Software (accessed 2021) Veritas Health Innovation, Melbourne, Australia. http://www.covidence.org

Creel S, Creel, N. (2002). *The African wild dog: behavior, ecology, and conservation* (Vol. 25). Princeton University Press.

Díaz López B (2020) When personality matters: personality and social structure in wild bottlenose dolphins, *Tursiops truncatus*. *Animal Behaviour* 163: 73–84. https://doi.org/10.1016/j.anbehav.2020.03.001

Di Bitetti MS, Janson CH (2001) Social foraging and the finder's share in capuchin monkeys, *Cebus apella*. *Animal Behaviour* 62: 47–56. https://doi.org/10.1006/anbe.2000.1730

Dickson DP, Barr GR, Wieckert DA (1967) Social relationship of dairy cows in a feed lot. *Behaviour* 29: 195–203. https://www.jstor.org/stable/4533190

Dunbar RIM (1983) Structure of gelada baboon reproductive units: IV. Integration at group level. *Zeitschrift für Tierpsychologie* 63: 265–282. https://doi.org/10.1111/j.1439-0310.1983.tb00743.x

Dunbar, RIM (1992). Time: A hidden constraint on the behavioural ecology of baboons. *Behavioral Ecology and Sociobiology, 31, 35-49.* https://doi.org/10.1007/BF00167814

Erhart EM, Overdorff DJ (1999) Female coordination of group travel in wild *Propithecus* and *Eulemur*. *International Journal of Primatology* 20: 927–940. https://doi.org/10.1023/A:1020830703012

Escos J, Alados CL, Boza J (1993) Leadership in a domestic goat herd. *Applied Animal Behaviour Science* 38: 41–47. https://doi.org/10.1016/0168-1591(93)90040-V

Evans MHR, Lihou KL, Rands SA (2018) Black-headed gulls synchronise their activity with their nearest neighbours. *Scientific Reports* 8: 9978. https://doi.org/10.1038/s41598-018-28378-x

Fellner W, Bauer GB, Harley HE (2007) Cognitive implications of synchrony in dolphins: A review. *Aquatic Mammals* 32: 511–516. https://doi.org/10.1578/am.32.4.2006.511

Farine DR, Strandburg-Peshkin A, Berger-Wolf T, Ziebart B, Brugere I, Li J, Crofoot MC (2016) Both nearest neighbours and long-term affiliates predict individual locations during collective movement in wild baboons. *Scientific Reports* 6: 27704. https://doi.org/10.1038/srep27704

Fernández VA, Kowalewski M, Zunino GE (2013) Who is coordinating collective movements in black and gold howler monkeys? *Primates* 54: 191–199. https://doi.org/10.1007/s10329-013-0342-x

Fernández A, Sierra E, Diaz-Delgado J, Sacchini S, Sánchez-Paz C, Suárez-Santana, M et al. (2017) Deadly acute decompression sickness in Risso's dolphins. *Scientific Reports* 7: 13621. https://doi.org/10.1038/s41598-017-14038-z

Fischhoff IR, Sundaresan SR, Cordingley J, Larkin HM, Sellier MJ, Rubenstein DI (2007) Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. *Animal Behaviour* 73: 825–831. https://doi.org/10.1016/j.anbehav.2006.10.012

Foreit K (2016) Leading behaviour, positioning, and group spacing as indicators of dominance in *Hapalemur griseus*. PhD thesis, Northern Illinois University, DeKalb, USA.

Foster EA (2012) Exploring the mechanisms and functions underpinning the social networks of an endangered population of killer whales, *Orcinus orca*. PhD thesis, University of Exeter, Exeter, UK.

Friard O, Gamba M (2016) BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution* 7: 1325–1330. https://doi.org/10.1111/2041-210X.12584

Funk E (1981) The behavior of 2 red deer family groups - an enclosure observation. *Zeitschrift Fur Jagdwissenschaft* 27: 33–41.

Galbraith PS (2018) *Conditions océanographiques physiques dans le golfe du Saint-Laurent en 2017*. Pêches et Océans Canada, Région du Québec, Institut Maurice-Lamontagne.

Gall GEC, Strandburg-Peshkin A, Clutton-Brock T, Manser MB (2017) As dusk falls: collective decisions about the return to sleeping sites in meerkats. *Animal Behaviour* 132: 91–99. https://doi.org/10.1016/j.anbehav.2017.08.001

Geist V (1963) On the behaviour of the North American moose (*Alces alces andersoni* Peterson 1950) in British Columbia. *Behaviour* 20: 377–416. https://www.jstor.org/stable/4533040

Gerard JF, Richard-Hansen C, Maublanc ML, Bideau E (1993) Probable exaptations within the" distributed" herd. *Revue d'Ecologie, Terre et Vie* 48: 239-248.

Gerkema MP, Verhulst S (1990) Warning against an unseen predator: a functional aspect of synchronous feeding in the common vole, *Microtus arvalis*. *Animal Behaviour*, 40: 116–1178. https://doi.org/0.1016/S0003-3472(05)80183-6

Giraldeau LA, Caraco T (2000) *Social foraging theory* (Vol. 73). Princeton University Press.

Gray GG, Simpson CD (1982) Group dynamics of free-ranging Barbary sheep in Texas. *Journal of Wildlife Management* 46: 1096–1101. https://www.jstor.org/stable/3808250

Hartman K, van der Harst P, Vilela R (2020) Continuous group follows operated by a drone enable analysis of the relation between sociality and position in a group of male Risso's dolphins (*Grampus griseus*). *Frontiers in Marine Science* 7: 283. https://doi.org/10.3389/fmars.2020.00283

Hastie GD, Wilson B, Tufft LH, Thompson PM (2003) Bottlenose dolphins increase breathing synchrony in response to boat traffic. *Marine Mammal Science* 19: 74–84. https://doi.org/10.1111/j.1748-7692.2003.tb01093.x

Hay K (1982) Aerial line-transect estimates of abundance of humpback, fin, and long-finned pilot whales in the Newfoundland-Labrador area. *Reports of the International Whaling Commission* 32: 475–486.

Henzi SP, Barrett L (1999) The value of grooming to female primates. *Primates,* 40: 47–59. https://doi.org/10.1007/BF02557701

Heyman WD, Graham RT, Kjerfve B, Johannes RE (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. *Marine Ecology Progress Series* 215: 275–282. https://doi.org/10.3354/meps215275

Hindell MA, Harcourt R, Waas J, Thompson D (2002) Fine-scale three-dimensional spatial use by diving, lactating female Weddell seals *Leptonychotes weddellii*. *Marine Ecology Progress Series* 242: 275–284. https://doi.org/10.3354/meps242275

Hoyle ZE, Miller RA, Rands SA (2021) Behavioural synchrony between fallow deer *Dama dama* is related to spatial proximity. *BMC Ecology and Evolution* 21: 79. https://doi.org/10.1186/s12862-021-01814-9

Ihl C, Bowyer RT (2011) Leadership in mixed-sex groups of muskoxen during the snow-free season. *Journal of Mammalogy* 92: 819–827. https://doi.org/10.1644/10-MAMM-A-109.1

Innis AC (1958) The behaviour of the giraffe, *Giraffa camelopardalis*, in the eastern Transvaal. *Proceedings of the Zoological Society of London* 131: 245–278.

Isojunno S, Aoki K, Curé C, Kvadsheim PH, Miller PJO (2018) Breathing patterns indicate cost of exercise during diving and response to experimental sound exposures in long-finned pilot whales. *Frontiers in Physiology* 9:1462. https://doi.org/10.3389/fphys.2018.01462

Jacobs A, Watanabe K, Petit O (2011) Social structure affects initiations of group movements but not recruitment success in Japanese macaques (*Macaca fuscata*). *International Journal of Primatology* 32: 1311–1324. https://doi.org/10.1007/s10764-011-9554-3

Jakimchuk RD, Carruthers DR (1983) A preliminary study of the behaviour of barren-ground caribou during their spring migration across Contwoyto Lake, N.W.T., Canada. *Acta Zoologica Fennica* 175: 117–119.

Jákupsstovu SH (2002) The pelagic fish stocks, pilot whales and squid in Faroese waters – migration patterns, availability to fisheries and possible links to oceanographic events. *ICES CM* 7: 1-37.

Jankowski M (2007) Long-finned pilot whale movement and social structure: residency, population mixing and identification of social units. *PhD Thesis.* Dalhousie University, Halifax, Canada.

Janson CH, Van Schaik CP (1988) Recognizing the many faces of primate food competition: Methods. *Behaviour* 105: 165-186. https://www.jstor.org/stable/4534685

Jefferson TA, Stacey PJ, Baird RW (1991) A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal Review* 21:151-180. https://doi.org/10.1111/j.1365-2907.1991.tb00291.x

Jennings T (1980) Influence of position in the flock and flock size on vigilance in the starling, *Sturnus vulgaris*. *Animal Behaviour* 28: 634–635. https://psycnet.apa.org/doi/10.1016/S0003-3472(80)80071-6

Jeschke JM, Tollrian R (2007) Prey swarming: Which predators become confused and why? *Animal Behaviour* 74: 387–393. https://doi.org/10.1016/j.anbehav.2006.08.020

Jezierski T, Gebler E (1984) Observations on behavior of Polish feral horses. *Zeitschrift fuer Tierzuechtung und Zuechtungsbiologie* 101: 143–152.

Katsu N, Yamada K, Okanoya K, Nakamichi M (2018) Temporal adjustment of short calls according to a partner during vocal turn-taking in Japanese macaques. *Current Zoology* 65: 99–105. https://doi.org/10.1093/cz/zoy077

King AJ, Cowlishaw G (2009) All together now: behavioural synchrony in baboons. *Animal Behaviour* 78: 1381–1387. https://doi.org/10.1016/j.anbehav.2009.09.009

King AJ, Sueur C, Huchard E, Cowlishaw G (2011) A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour* 82: 1337–1345. https://doi.org/10.1016/j.anbehav.2011.09.017

King SL, McGregor PK (2016) Vocal matching: the what, the why and the how. *Biology Letters* 12: 20160666. https://doi.org/10.1098/rsbl.2016.0666

de Kock LL (1956) The pilot whale stranding on the Orkney Island of Westray, 1955. *Scottish Naturalist* 68: 63–70.

Konrad CM, Frasier TR, Whitehead H, Gero S (2019) Kin selection and allocare in sperm whales. *Behavioral Ecology* 30: 194–201. https://doi.org/10.1093/beheco/ary143

Kramer DL, Graham JB (1976) Synchronous air breathing, a social component of respiration in fishes. *Copeia* 30: 689–697. https://doi.org/10.2307/1443450

Krueger K, Flauger B, Farmer K, Hemelrijk C (2014) Movement initiation in groups of feral horses. *Behavioural Processes* 103: 91–101. https://doi.org/10.1016/j.beproc.2013.10.007

Krzyszczyk E, Patterson EM, Stanton MA, Mann J (2017) The transition to independence: sex differences in social and behavioural development of wild bottlenose dolphins. *Animal Behaviour* 129: 43–59. https://doi.org/10.1016/j.anbehav.2017.04.011

LaMontagne JM, Pearse IS, Greene DF, Koenig WD (2020) Mast seeding patterns are asynchronous at a continental scale. *Nature Plants* 6: 460–465. https://doi.org/10.1038/s41477-020-0647-x

Launay J, Tarr B, Dunbar RIM (2016) Synchrony as an adaptive mechanism for large-scale human social bonding. *Ethology* 122: 779–789. https://doi.org/10.1111/eth.12528

Leca JB, Gunst N, Thierry B, Petit O (2003) Distributed leadership in semifree-ranging white-faced capuchin monkeys. *Animal Behaviour* 66: 1045–1052. https://doi.org/10.1006/anbe.2003.2276

Lee PC, Moss CJ (2012) Wild female African elephants (*Loxodonta africana*) exhibit personality traits of leadership and social integration. *Journal of Comparative Psychology* 126: 224–232.

Lee HC, Teichroeb JA (2016) Partially shared consensus decision making and distributed leadership in vervet monkeys: older females lead the group to forage. *American Journal of Physical Anthropology* 161: 580–590. https://doi.org/10.1002/ajpa.23058

Lesmerises F, Johnson CJ, St-Laurent M (2018) Landscape knowledge is an important driver of the fission dynamics of an alpine ungulate. *Animal Behaviour* 140: 39–47. https://doi.org/10.1016/j.anbehav.2018.03.014

Lewis JS, Wartzok D, Heithaus MR (2011) Highly dynamic fission-fusion species can exhibit leadership when traveling. *Behavioral Ecology and Sociobiology* 65: 1061–1069. https://doi.org/10.1007/s00265-010-1113-y

Lewis JS, Wartzok D, Heithaus MR (2013a) Individuals as information sources: could followers benefit from leaders' knowledge? *Behaviour* 150: 635–657. https://doi.org/10.1163/1568539X-00003075

Lewis JS, Wartzok D, Heithaus M, Kruetzen M (2013b) Could relatedness help explain why individuals lead in bottlenose dolphin groups? *PLoS ONE* 8: e58162. https://doi.org/10.1371/journal.pone.0058162

Liew C, Labadin J (2017) Leadership in species: a bipartite-network-based approach. *First International Conference on Computer and Drone Applications (ICONDA)*, 66–70.

Lima SL (1995) Back to the basics of anti-predatory vigilance: the group-size effect. Animal Behaviour 49: 11-20. https://doi.org/10.1016/0003-3472(95)80149-9

Loehle C (1995). Social barriers to pathogen transmission in wild animal populations. *Ecology*, 76: 326-335. https://doi.org/10.2307/1941192

Lusseau D (2007) Evidence for social role in a dolphin social network. *Evolutionary Ecology* 21: 357–366. https://doi.org/10.1007/s10682-006-9105-0

Lusseau D, Conradt L (2009) The emergence of unshared consensus decisions in bottlenose dolphins. *Behavioral Ecology and Sociobiology* 63: 1067–1077. https://doi.org/10.1007/s00265-009-0740-7

Macnulty DR, Tallian A, Stahler DR, Smith DW (2014) Influence of group size on the success of wolves hunting bison. *PLoS ONE* 9: 112884. https://doi.org/10.5061/dryad.nf043

Majolo B, de Bortoli Vizioli A, Schino G (2008) Costs and benefits of group living in primates: group size effects on behaviour and demography. *Animal Behaviour* 76: 1235–1247. https://doi.org/10.1016/j.anbehav.2008.06.008

Makwana SC (1979) Infanticide and social change in two groups of the Hanuman langur, *Presbytis entellus*, at Jodhpur. *Primates* 20: 293–300. https://doi.org/10.1007/BF02373381

Marshall HH, Carter AJ, Coulson T, Rowcliffe JM, Cowlishaw G (2012) Exploring foraging decisions in a social primate using discrete-choice models. *American Naturalist* 180: 481–495. https://doi.org/10.1086/667587

Martin AP, Richards KJ, Bracco A, Provenzale A (2002) Patchy productivity in the open ocean. *Global Biogeochemical Cycles* 16: 9-1–9-9. https://doi.org/10.1029/2001GB001449

Mazzariol S, Centelleghe C, Cozzi B, Povinelli M, Marcer F, Ferri N et al. (2018) Multidisciplinary studies on a sick-leader syndrome-associated mass stranding of sperm whales (*Physeter macrocephalus*) along the Adriatic coast of Italy. *Scientific Reports* 8: 11577. https://doi.org/10.1038/s41598-018-29966-7

McComb K, Shannon G, Durant SM, Sayialel K, Slotow R, Poole J, Moss C (2011) Leadership in elephants: The adaptive value of age. *Proceedings of the Royal Society B: Biological Sciences* 278: 3270–3276. https://doi.org/10.1098/rspb.2011.0168

McComb-Turbitt S, Costa J, Whitehead H, Auger-Méthé M (2021) Small-scale spatial distributions of long-finned pilot whales change over time, but foraging hot spots are consistent: Significance for marine wildlife tourism management. *Marine Mammal Science* 37: 1196-1211. https://doi.org/10.1111/mms.12821

McCue L, Cioffi W, Heithaus M, Barrè L, Connor R (2020) Synchrony, leadership, and association in male Indo-pacific bottlenose dolphins (*Tursiops aduncus*). *Ethology* 126: 741–750. https://doi.org/10.1111/eth.13025

Mech D (2000) Leadership in wolf, *Canis lupus*, packs. *Canadian Field Naturalist* 114: 259–263.

Merkle JA, Sigaud M, Fortin D (2015) To follow or not? How animals in fusion-fission societies handle conflicting information during group decision making. *Ecology Letters* 18: 799–806. https://doi.org/10.1111/ele.12457

Mizuno K, Sharma N, Idani G, Sukumar R (2017) Collective behaviour of wild Asian elephants in risky situations: how do social groups cross roads? *Behaviour* 154: 1215–1237. https://doi.org/10.1163/1568539X-00003465

Moore KM, Simeone CA, Brownell Jr RL (2018) Strandings. *Encyclopedia of Marine Mammals*, 945–951. Academic Press.

Mortola JP (1987) Dynamics of breathing in newborn mammals. *Physiological Reviews* 67: 187-243. https://doi.org/10.1152/physrev.1987.67.1.187

Mrlik V (1991) Active protective behaviour of roe deer (*Capreolus capreolus*) in an open habitat during the winter season. *Folia Zoologica* 40: 13–24.

Naďo L, Kaňuch P (2015) Swarming behaviour associated with group cohesion in tree-dwelling bats. *Behavioural Processes* 120: 80–86. https://doi.org/10.1016/j.beproc.2015.09.005

Nakagawa N (1990) Decisions on time allocation to different food patches by Japanese monkeys (*Macaca fuscata*). *Primates* 31: 459–468. https://doi.org/10.1007/BF02382530

Naumov NP, Baskin LM (1969) Leadership in herds of reindeer as group adaptation. *Zhurnal Obshchei Biologii* 30: 147–156.

Nemiroff, L., & Whitehead, H. (2009). Structural characteristics of pulsed calls of long-finned pilot whales *Globicephala melas*. *Bioacoustics*, *19*, 67–92. https://doi.org/10.1080/09524622.2009.9753615

Norris KS, Schilt CR (1988) Cooperative societies in three-dimensional space: on the origins of aggregations, flocks, and schools, with special reference to dolphins and fish. *Ethology and Sociobiology* 9: 149–179. https://doi.org/10.1016/0162-3095(88)90019-2

Norton G (1986) Leadership: decision processes of group movement in yellow baboons. In *Primate Ecology and Conservation* (pp. 145–156). Cambridge University Press.

Nowacek DP, Friedlaender AS, Halpin PN, Hazen EL, Johnston DW, Read AJ, Espinasse B, Zhou M, Zhu Y (2011) Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. *PLoS ONE* 6: e19173. https://doi.org/10.1371/journal.pone.0019173

Nuechterlein G L, Storer RW (1982) The pair-formation displays of the western grebe. *The Condor* 84: 350-369. https://doi.org/10.2307/1367437

Oremus M, Gales R, Kettles H, Baker CS (2013) Genetic evidence of multiple matrilines and spatial disruption of kinship bonds in mass strandings of long-finned pilot whales, *Globicephala melas*. *Journal of Heredity* 104: 301–311. https://doi.org/10.1093/jhered/est007

Ottensmeyer CA, Whitehead H (2003) Behavioural evidence for social units in long-finned pilot whales. *Canadian Journal of Zoology* 81: 1327–1338. https://doi.org/10.1139/Z03-127

Overdorff DJ, Erhart EM, Mutschler T (2005) Does female dominance facilitate feeding priority in black-and-white ruffed lemurs (*Varecia variegata*) in southeastern Madagascar? *American Journal of Primatology* 66: 7–22. https://doi.org/10.1002/ajp.20125

Ozogány K, Vicsek T (2014) Modeling the emergence of modular leadership hierarchy during the collective motion of herds made of harems. *Journal of Statistical Physics* 158: 628-646. https://doi.org/10.1007/s10955-014-1131-7

Palacios-Romo TM, Castellanos F, Ramos-Fernandez G (2019) Uncovering the decision rules behind collective foraging in spider monkeys. *Animal Behaviour* 149: 121–133. https://doi.org/10.1016/j.anbehav.2019.01.011

Payne PM, Heinemann DW (1993) The distribution of pilot whales (*Globicephala sp.)* in shelf/shelf edge and slope waters of the northeastern United States, 1978-1988. *Reports of the International Whaling Commission* Special Issue 14: 51–68.

Penzhorn BL (1984) A long-term study of social organisation and behaviour of Cape Mountain zebras *Equus zebra zebra*. *Zeitschrift für Tierpsychologie* 64: 97–146. https://doi.org/10.1111/j.1439-0310.1984.tb00355.x

Perez DM, Klunk CL, Araujo SBL (2021) Imperfect synchrony in animal displays: Why does it occur and what is the true role of leadership? *Philosophical Transactions of the Royal Society B: Biological Sciences* 376: 20200339. https://doi.org/10.1098/rstb.2020.0339

Pérez-Barbería FJ, Walker DM (2018) Dynamics of social behaviour at parturition in a gregarious ungulate. *Behavioural Processes* 150: 75–84. https://doi.org/10.1016/j.beproc.2018.01.013

Peterson RO, Jacobs AK, Drummer TD, Mech LD, Smith DW (2002) Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*. *Canadian Journal of Zoology* 80: 1405–1412. https://doi.org/10.1139/z02-124

Petit O, Gautrais J, Leca JB, Theraulaz G, Deneubourg JL (2009) Collective decision making in white-faced capuchin monkeys. *Proceedings of the Royal Society B: Biological Sciences* 276: 3495–3503. https://doi.org/10.1098/rspb.2009.0983

Plötz J, Weidel H, Bersch M (1991) Winter aggregations of marine mammals and birds in the north-eastern Weddell Sea pack ice. *Polar Biology* 11: 305–309. https://doi.org/10.1007/BF00239022

Pitcher, T. (1993). Functions of shoaling behaviour in teleosts. In *The behaviour of teleost fishes* (pp. 294–337). Springer US.

Pyritz LW, Kappeler PM, Fichtel C (2011) Coordination of group movements in wild red-fronted lemurs (*Eulemur rufifrons*): processes and influence of ecological and reproductive seasonality. *International Journal of Primatology* 32: 1325–1347. https://doi.org/10.1007/s10764-011-9549-0

Ramos A, Manizan L, Rodriguez E, Kemp YJM, Sueur C (2018) How can leadership processes in European bison be used to improve the management of free-roaming herds. *European Journal of Wildlife Research* 64: 1–16. https://doi.org/10.1007/s10344-018-1175-0

Ramos A, Petit O, Longour P, Pasquaretta C, Sueur C (2015) Collective decision making during group movements in European bison, *Bison bonasus*. *Animal Behaviour* 109: 149–160. https://doi.org/10.1016/j.anbehav.2015.08.016

Ramseyer A, Boissy A, Dumont B, Thierry B (2009a) Decision making in group departures of sheep is a continuous process. *Animal Behaviour* 78: 71–78. https://doi.org/10.1016/j.anbehav.2009.03.017

Ramseyer A, Boissy A, Thierry B, Dumont B (2009b) Individual and social determinants of spontaneous group movements in cattle and sheep. *Animal* 3: 1319–1326. https://doi.org/10.1017/S1751731109004790

Ramseyer A, Thierry B, Boissy A, Dumont B (2009c) Decision making processes in group departures of cattle. *Ethology* 115: 948–957. https://doi.org/10.1111/j.1439-0310.2009.01686.x

Rands S, Muir H, Terry N (2014) Red deer synchronise their activity with close neighbours. *PeerJ* 2: e344. https://doi.org/10.7717/peerj/344

Rasolonjatovo SM, Irwin MT (2020) Exploring social dominance in wild diademed sifakas (*Propithecus diadema*): females are dominant, but it is subtle and the benefits are not clear. *Folia Primatologica* 91: 385–398. https://doi.org/10.1159/000503345

Reinhardt V (1983) Movement orders and leadership in a semi wild herd cattle herd. *Behaviour* 83: 251–264. https://doi.org/10.1163/156853983X00183

Rendell L, Cantor M, Gero S, Whitehead H, Mann J (2019). Causes and consequences of female centrality in cetacean societies. *Philosophical Transactions of the Royal Society B* 374: 20180066. https://doi.org/10.1098/rstb.2018.0066

Riedman ML (1982) The evolution of alloparental care and adoption in mammals and birds. *The Quarterly Review of Biology* 57: 405-435. https://www.jstor.org/stable/2826887

Romero T, Castellanos MA (2010) Dominance relationships among male hamadryas baboons (*Papio hamadryas*). *Journal of Ethology* 28: 113–121. https://doi.org/10.1007/s10164-009-0162-z

Rowell TE, Rowell CA (1993) The social organization of feral *Ovis aries* ram groups in the pre-rut period. *Ethology* 95: 213–232. https://doi.org/10.1111/j.1439-0310.1993.tb00472.x

Ryan JP, Benoit-Bird KJ, Oestreich WK, Leary P, Smith KB, Waluk CM, Cade DE, Fahlbusch JA, Southall BL, Joseph JE, Margolina T, Calambokidis J, DeVogelaere A, Goldbogen JA (2022) Oceanic giants dance to atmospheric rhythms: Ephemeral wind-driven resource tracking by blue whales. *Ecology Letters* 25: 2435–2447. https://doi.org/10.1111/ele.14116

Šárová R, Špinka M, Panamá JLA (2007) Synchronization and leadership in switches between resting and activity in a beef cattle herd - a case study. *Applied Animal Behaviour Science* 108: 327–331. https://doi.org/10.1016/j.applanim.2007.01.009

Šárová R, Špinka M, Panamá JLA, Šimeček P (2010) Graded leadership by dominant animals in a herd of female beef cattle on pasture. *Animal Behaviour* 79: 1037-1045. https://doi.org/10.1016/j.anbehav.2010.01.019

Santos RG, Pinheiro HT, Martins AS, Riul P, Bruno SC, Janzen FJ, Ioannou CC (2016) The anti-predator role of within-nest emergence synchrony in sea turtle hatchlings. *Proceedings of the Royal Society B: Biological Sciences*, 283: 20160697. https://doi.org/10.1098/rspb.2016.0697

Sato S (1982) Leadership during actual grazing in a small herd of cattle. *Applied Animal Ethology* 8: 53–65. https://doi.org/10.1016/0304-3762(82)90132-8

Schorr GS, Falcone EA, Moretti DJ, Andrews RD (2014) First long-term behavioral records from Cuvier's beaked whales (*Ziphius cavirostris*) reveal record-breaking dives. *PLoS One* 9: e92633. https://doi.org/10.1371/journal.pone.0092633

Schweitzer C, Gaillard T, Guerbois C, Fritz H, Petit O (2017) Participant profiling and pattern of crop-foraging in chacma baboons (*Papio hamadryas ursinus*) in Zimbabwe: why does investigating age–sex classes matter? *International Journal of Primatology* 38: 207–223. https://doi.org/10.1007/s10764-017-9958-9

Sellers WI, Hill RA, Logan BS (2007) An agent-based model of group decision making in baboons. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 362: 1699–1710. https://doi.org/10.1098/rstb.2007.2064

Seltmann A, Franz M, Majolo B, Qarro M, Ostner J, Schülke O (2016) Recruitment and monitoring behaviors by leaders predict following in wild Barbary macaques (*Macaca sylvanus*). *Primate Biology* 3: 23–31. https://doi.org/10.5194/pb-3-23-2016

Seltmann A, Majolo B, Schuelke O, Ostner J (2013) The organization of collective group movements in wild Barbary macaques (*Macaca sylvanus*): social structure drives processes of group coordination in macaques. *PLoS One* 8: e67285. https://doi.org/10.1371/journal.pone.0067285

Senigaglia V, Christiansen F, Bejder L, Gendron D, Lundquist D, Noren DP, Schaffar A, Smith JC, Williams R, Martinez E, Stockin K, Lusseau D (2016) Meta-analyses of whale-watching impact studies: Comparisons of cetacean responses to disturbance. *Marine Ecology Progress Series* 542: 251–263. https://doi.org/10.3354/meps11497

Senigaglia V, de Stephanis R, Verborgh P, & Lusseau D (2012) The role of synchronized swimming as affiliative and anti-predatory behavior in long-finned pilot whales. *Behavioural Processes* 91: 8–14. https://doi.org/10.1016/j.beproc.2012.04.011

Senigaglia V, Whitehead H (2012) Synchronous breathing by pilot whales. *Marine Mammal Science* 28: 213–219. https://doi.org/10.1111/j.1748-7692.2011.00465.x

Shen SF, Akçay E, Rubenstein DR (2014) Group size and social conflict in complex societies. *American Naturalist* 183: 301–310. https://doi.org/10.1086/674378

Smith AC, Buchanan-Smith HM, Surridge AK, Mundy NI (2003) Leaders of progressions in wild mixed-species troops of saddleback (*Saguinus fuscicollis*) and mustached tamarins (*S. mystax*), with emphasis on color vision and sex. *American Journal of Primatology* 61: 145–157. https://doi.org/10.1002/ajp.10117

Smith JE, Gavrilets S, Mulder MB, Hooper PL, El Mouden C, Nettle D et al. (2016) Leadership in mammalian societies: emergence, distribution, power, and payoff. *Trends in Ecology and Evolution* 31: 54–66. https://doi.org/10.1016/j.tree.2015.09.013

Smith JE, van Horn RC, Powning KS, Cole AR, Graham KE, Memenis SK, Holekamp KE (2010) Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behavioral Ecology* 21: 284–303. https://doi.org/10.1093/beheco/arp181

Smith JE, Ortiz CA, Buhbe MT, van Vugt M (2020) Obstacles and opportunities for female leadership in mammalian societies: a comparative perspective. *The Leadership Quarterly* 31: 1–15. https://doi.org/10.1016/j.leaqua.2018.09.005

Smith JE, Fichtel C, Holmes RK, Kappeler PM, van Vugt M, Jaeggi AV (2022) Sex bias in intergroup conflict and collective movements among social mammals: male warriors and female guides. *Philosophical Transactions of the Royal Society B*, 377: 20210142. https://doi.org/10.1098/rstb.2021.0142

Sorato E, Gullett PR, Griffith SC, Russell AF (2012) Effects of predation risk on foraging behaviour and group size: Adaptations in a social cooperative species. *Animal Behaviour* 84: 823–834. https://doi.org/10.1016/j.anbehav.2012.07.003

Sperber AL, Kappeler PM, Fichtel C (2019) Should I stay or should I go? Individual movement decisions during group departures in red-fronted lemurs. *Royal Society Open Science* 6: 180991. https://doi.org/10.1098/rsos.180991

Sperber AL, Werner LM, Kappeler PM, Fichtel C (2017) Grunt to go—vocal coordination of group movements in redfronted lemurs. *Ethology* 123: 894–905. https://doi.org/10.1111/eth.12663

Strandburg-Peshkin A, Farine DR, Couzin ID, Crofoot MC (2015) Shared decision making drives collective movement in wild baboons. *Science* 348: 1358–1361. https://doi.org/10.1126/science.aaa5099

Stander PE (1992) Cooperative hunting in lions: the role of the individual. *Behavioral Ecology Sociobiology* 29: 445–454. https://doi.org/10.1007/BF00170175

Stoye S, Porter MA, Stamp Dawkins M (2012) Synchronized lying in cattle in relation to time of day. *Livestock Science*, 149: 70–73. https://doi.org/10.1016/j.livsci.2012.06.028

Strickland K, Levengood A, Foroughirad V, Mann J, Krzyszczyk E, Frère CH (2017) A framework for the identification of long-term social avoidance in longitudinal datasets. *Royal Society Open Science* 4: 170641. https://doi.org/10.1098/rsos.170641

Struhsaker TT (1967) Social structure among vervet monkeys (*Cercopithecus aethiops*). *Behaviour* 29: 6–121. https://www.jstor.org/stable/4533186

Stueckle S, Zinner D (2008) To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. *Animal Behaviour* 75: 1995–2004. https://doi.org/10.1016/j.anbehav.2007.12.012

Sueur C (2011) Group decision making in chacma baboons: leadership, order and communication during movement. *BMC Ecology* 11: 1–14. https://doi.org/10.1186/1472-6785-11-26

Sueur C, Deneubourg JL, Petit O (2010a) Sequence of quorums during collective decision making in macaques. *Behavioral Ecology and Sociobiology* 64: 1875–1885. https://doi.org/10.1007/s00265-010-0999-8

Sueur C, Deneubourg JL, Petit O (2011) From the first intention movement to the last joiner: macaques combine mimetic rules to optimize their collective decisions.

Proceedings of the Royal Society B: Biological Sciences 278: 1697–1704. https://doi.org/10.1098/rspb.2010.2084

Sueur C, Kuntz C, Debergue E, Keller B, Robic F, Siegwalt-Baudin F, Richer C, Ramos A, Pelé M (2018) Leadership linked to group composition in highland cattle (*Bos taurus*): implications for livestock management. *Applied Animal Behaviour Science* 198: 9–18. https://doi.org/10.1016/j.applanim.2017.09.014

Sueur C, MacIntosh AJJ, Jacobs AT, Watanabe K, Petit O (2013) Predicting leadership using nutrient requirements and dominance rank of group members. *Behavioral Ecology and Sociobiology* 67: 457–470. https://doi.org/10.1007/s00265-012-1466-5

Sueur C, Petit O (2008) Shared or unshared consensus decision in macaques? *Behavioural Processes* 78: 84–92. https://doi.org/10.1016/j.beproc.2008.01.004

Sueur C, Petit O (2010) Signals use by leaders in *Macaca tonkeana* and *Macaca mulatta*: group-mate recruitment and behaviour monitoring. *Animal Cognition* 13: 239–248. https://doi.org/10.1007/s10071-009-0261-9

Sueur C, Petit O, Deneubourg JL (2009) Selective mimetism at departure in collective movements of *Macaca tonkeana*: an experimental and theoretical approach. *Animal Behaviour* 78: 1087–1095. https://doi.org/10.1016/j.anbehav.2009.07.029

Sueur C, Petit O, Deneubourg JL (2010b) Short-term group fission processes in macaques: a social networking approach. *Journal of Experimental Biology* 213: 1338–1346. https://doi.org/10.1242/jeb.039016

Tecot SR, Romine NK (2012) Leading ladies: leadership of group movements in a pair-living, co-dominant, monomorphic primate across reproductive stages and fruit availability seasons. *American Journal of Primatology* 74: 591–601. https://doi.org/10.1002/ajp.22011

Tokuyama N, Furuichi T (2017) Leadership of old females in collective departures in wild bonobos (*Pan paniscus*) at Wamba. *Behavioral Ecology and Sociobiology* 71: 55. https://doi.org/10.1007/s00265-017-2277-5

Towers JR, Tixier P, Ross KA, Bennett J, Arnould JPY, Pitman RL, Durban JW (2019) Movements and dive behaviour of a toothfish-depredating killer and sperm whale. *ICES Journal of Marine Science* 76: 298–311. https://doi.org/10.1093/icesjms/fsy118

Trillmich J, Fichtel C, Kappeler PM (2004) Coordination of group movements in wild Verreaux's sifakas (*Propithecus verreauxi*). *Behaviour* 141: 1103–1120. https://www.jstor.org/stable/4536187

Tsarev SA (1980) Behavior of the wild boar in the northern limits of its range. *Vestnik Leningradskogo Universiteta Biologiya*: 15–21.

Tyack P, Clark C (2000) Communication and acoustic behavior of dolphins and whales. In: Au W, Popper A, Fay R (eds) *Hearing by Whales and Dolphins*, 156–224. Springer-Verlag, New York, USA.

Visser F, Curé C, Kvadsheim PH, Lam FPA, Tyack PL, Miller PJO (2016) Disturbance-specific social responses in long-finned pilot whales, *Globicephala melas*. *Scientific Reports* 6: 28641. https://doi.org/10.1038/srep28641

Walker RH, King AJ, McNutt JW, Jordan NR (2017) Sneeze to leave: African wild dogs (*Lycaon pictus*) use variable quorum thresholds facilitated by sneezes in collective decisions. *Proceedings of the Royal Society B: Biological Sciences* 284: 20170347. https://doi.org/10.1098/rspb.2017.0347

Wang C, Pan R, Wang X, Qi X, Zhao H, Guo S et al. (2020) Decision making process during collective movement initiation in golden snub-nosed monkeys (*Rhinopithecus roxellana*). *Scientific Reports* 10: 480. https://doi.org/10.1038/s41598-019-57191-3

Wang X, Sun L, Li J, Xia D, Sun B, Zhang D (2015) Collective movement in the Tibetan macaques (*Macaca thibetana*): early joiners write the rule of the game. *PLoS ONE* 10: e0127459. https://doi.org/10.1371/journal.pone.0127459

Wang X, Sun L, Sheeran LK, Sun BH, Zhang QX, Zhang D, Xia DP, Li JH (2016) Social rank versus affiliation: which is more closely related to leadership of group movements in Tibetan macaques (*Macaca thibetana*)? *American Journal of Primatology* 78: 816–824. https://doi.org/10.1002/ajp.22546

Ward AJW, Herbert-Read JE, Sumpter DJT, Krause J (2011) Fast and accurate decisions through collective vigilance in fish shoals. *Proceedings of the National Academy of Sciences of the United States of America* 108: 2312–2315. https://doi.org/10.1073/pnas.1007102108

Weimerskirch H, Martin J, Clerquin Y, Alexandre P, Jiraskova S (2001) Energy saving in flight formation. *Nature*, 413: 697–698. https://doi.org/10.1038/35099670

Whitehead H (1989) Formations of foraging sperm whales, *Physeter macrocephalus*, off the Galapagos Islands. *Canadian Journal of Zoology* 67: 2131–2139. https://doi.org/10.1139/z89-303

Whitehead H (2016) Consensus movements by groups of sperm whales. *Marine Mammal Science* 32: 1402–1415. https://doi.org/10.1111/mms.12338

Wilson EO (2000) *Sociobiology: The New Synthesis*. Harvard University Press, Cambridge, USA.

Wolter R, Pantel N, Stefanski V, Moestl E, Krueger K (2014) The role of an alpha animal in changing environmental conditions. *Physiology & Behavior* 133: 236–243. https://doi.org/10.1016/j.physbeh.2014.05.025

Wrona FJ, Jamieson Dixon RW (1991) Group size and predation risk: A field analysis of encounter and dilution effects. *The American Naturalist* 137: 186-201. https://doi.org/10.1086/285153

You W, Shi J, Lu F, Dong S, Li X, Zhang Z (2013) Traits and process of group decision making in Przewalski's gazelle (*Procapra przewalskii*). *Acta Theriologica* 33: 293–299.

Zaitsev V (1999) Guides, leaders and scouts in wild boar. *Bulletin of the Moscow Society of Natural Scientists* 104: 10–16.

Zappala J, Logan B (2010) Effects of resource availability on consensus decision making in primates. *Computational and Mathematical Organization Theory* 16: 400–415. https://doi.org/10.1007/s10588-010-9080-4

Zhang Y, Lauder GV (2023) Energetics of collective movement in vertebrates. *Journal of Experimental Biology* 226: jeb245617. https://doi.org/10.1242/jeb.245617

Zwamborn EMJ, Whitehead H (2017a) Repeated call sequences and behavioural context in long-finned pilot whales off Cape Breton, Nova Scotia, Canada. *Bioacoustics* 26: 169-183. https://doi.org/10.1080/09524622.2016.1233457

Zwamborn EMJ, Whitehead H (2017b) The baroque potheads: Modification and embellishment in repeated call sequences of long-finned pilot whales. *Behaviour* 154: 963-979. https://doi.org/10.1163/1568539X-00003451

Zwamborn EMJ, Boon N, Whitehead H (2023) Collective decision making in aquatic mammals. *Mammal Review* 53: 238–253. https://doi.org/10.1111/mam.12321

Zwamborn EMJ, Walmsley SF, Whitehead H (2023) Flanking female guides: Collective decision making in long-finned pilot whales. *Animal Behaviour* 205: 149–159. https://doi.org/10.1016/j.anbehav.2023.09.007

APPENDIX A – Further Details on Past Mammalian Decision Making Reviews

Smith et al. (2016) reviewed leadership in mammalian societies (both small scale human and non-human) and found that non-human mammalian leadership was seldom studied outside the context of group movement and foraging. A second review by Smith and colleagues (2020) on female mammalian leadership, showed that female leaders typically emerge without coercion and that their followers often benefit from their ecological knowledge. Though this review was focused largely on how what we learn about non-human female leadership can be applied to challenges faced by women in human societies, its suggestions that forthcoming research focus on the evolutionary and ecological factors that lead to successful female leadership are important for our understanding of non-human mammalian leadership. King and Sueur (2011) provided a useful overview and critique of the literature on non-human primate collective decision making. Specifically, they note how context-specific the majority of studies have been and how difficult it can be to track the position of all individuals within a group (King & Sueur 2011). Suggestions for solutions to these challenges include studying decision making across different behavioural contexts (e.g. group vigilance, conflict resolution), using GPS trackers to make monitoring individual positions easier, and including social networks to provide valuable insight into how collective decisions are made (King & Sueur 2011). Fischer and Zinner (2011) focus more on the role of communication in group movement decisions and coordination in their review, showing that past research has determined the importance of vocal signals in many primates, but that few studies have tried to determine the underlying reasons of why these vocal signals are such an important part of collective movement decisions in comparison to alternative non-vocal signals

APPENDIX B – Cetacean Decision Making Literature Search Terms

WEB OF SCIENCE

(cetacea* OR dolphin* OR whal* OR porpois* OR mysticet* OR odontocet*) AND ("decision making" OR "decision making" OR leader* OR democratic OR despotic OR consensus) NOT (optimization* OR policy)

(266 results)

BIOLOGICAL ABSTRACTS

(cetacea* OR dolphin* OR whal* OR porpois* OR mysticet* OR odontocet*) AND ("decision making" OR "decision making" OR leader* OR democratic OR despotic OR consensus) NOT (optimization* OR policy)

(170 results)

PROQUEST (DISSERTATIONS AND THESES GLOBAL)

ab(cetacea* OR dolphin* OR whal* OR porpois* OR mysticet* OR odontocet*) AND ab("decision making" OR "decision making" OR leader* OR democratic OR despotic OR consensus) NOT ab(optimization* OR policy)

(605 results for scholarly articles, theses and conference proceedings)

SCOPUS

TITLE-ABS-KEY (cetacea* OR dolphin* OR whal* OR porpois* OR mysticet* OR odontocet*) AND TITLE-ABS-KEY ("decision making" OR "decision making" OR leader* OR democratic OR despotic OR consensus) AND NOT TITLE-ABS-KEY (optimization* OR policy)

(2172 results)

Mammal Decision making Literature Search Terms

WEB OF SCIENCE

(mammal* OR primate* OR roden* OR elephant* OR bat* OR bats OR ungulate*) AND ("decision making" OR "decision making" OR leader* OR democratic OR despotic OR consensus) AND (group* OR social) NOT (optimization* OR policy OR brain* OR disease* OR medical OR genome OR person OR people)

(3552 results)

BIOLOGICAL ABSTRACTS

(mammal* OR primate* OR roden* OR elephant* OR bat* OR bats OR ungulate*) AND ("decision making" OR "decision making" OR leader* OR democratic OR despotic OR consensus) AND (group* OR social) NOT (optimization* OR policy OR brain* OR disease* OR medical OR genome OR person OR people)

(3812 results)

PROQUEST (DISSERTATIONS AND THESES GLOBAL)

ab(mammal* OR primate* OR roden* OR elephant* OR bat* OR bats OR ungulate*) AND ab("decision making" OR "decision making" OR leader* OR democratic OR despotic OR consensus) AND ab(group* OR social) NOT ab(optimization* OR policy OR brain* OR disease* OR medical OR genome OR person OR people)

(365 theses and conference proceedings)

SCOPUS

TITLE-ABS-KEY (mammal* OR primate* OR roden* OR elephant* OR bat* OR bats OR ungulate*) AND TITLE-ABS-KEY ("decision making" OR "decision making" OR leader* OR democratic OR despotic OR consensus) AND TITLE-ABS-KEY (group* OR social) AND NOT TITLE-ABS-KEY (optimization* OR policy OR brain* OR disease* OR medical OR genome OR person OR people)

(2172 results)

APPENDIX C – Further Notes and References on the Cause of Mass Strandings in Cetaceans

Mass stranding events (MSEs) involving cetaceans are defined as two or more individuals (not including mother/calf pairs) that strand in the same geographic area at the same time (Geraci & Lounsbury 2005). Evidence of strandings can be found far back in the fossil record, indicating that these events have occurred throughout history (Pyenson et al. 2014). There are a number of natural causes that have been proposed to contribute to MSEs including disease, confusion in nearshore waters due to difficulty navigating certain underwater features (e.g. sandbars, gently sloping beaches), beaching to escape predation, injured or sick individuals, and unusual environmental conditions (Moore et al. 2018). MSEs can also be caused by anthropogenic factors, with some strandings linked to Navy sonar, seismic surveys, and underwater explosions (Southall et al. 2006; Southall et al. 2013; Brownlow et al. 2015). These events most often involve pelagic-living species with strong social bonds, such as pilot whales (*Globicephala melas* and *G. macrorhynchus),* melon-headed whales (*Peponocephala electra*) and false killer whales (*Pseudorca crassidens*), which are not always as familiar with navigating shallow coastal waters (Moore et al. 2018). Strong social bonds (or disruption of these bonds; Oremus et al. 2013) are an underlying factor in MSEs, often resulting large numbers of animals beaching together regardless of the reasons for the stranding.

Selected references on the causes of mass strandings in cetaceans:

Brownlow A, Baily J, Dagleish M, Deaville R, Foster G, Jensen SK, Krupp E, Law R, Penrose R, Perkins M, Read F (2015) Investigation into the long-finned pilot whale mass stranding event, Kyle of Durness, 22nd July 2011. SRUC Wildlife Unit, Inverness, UK.

D'Amico A, Gisiner RC, Ketten DR, Hammock JA, Johnson C, Tyack PL et al. (2009) Beaked whale strandings and naval exercises. *Aquatic Mammals* 35: 452-472.

Endo T, Hisamichi Y, Kimura O, Haraguchi K, Baker CS (2008). Contamination levels of mercury and cadmium in melon-headed whales (*Peponocephala electra*) from a mass stranding on the Japanese coast. *Science of the Total Environment* 401: 73-80.

Geraci JR, Lounsbury VJ (2005). *Marine Mammals Ashore: A Field Guide for Strandings*, *2nd Ed*. National Aquarium in Baltimore, MD.

Jepson PD, Deaville R, Acevedo-Whitehouse K, Barnett J, Brownlow A, Brownell Jr RL et al. (2013) What caused the UK's largest common dolphin (*Delphinus delphis*) mass stranding event? *PLoS One* 2013 8: e60953.

Lodi L, Siciliano S, Capistrano L (1990) Mass stranding of *Peponocephala electra* (Cetacea, Globicephalinae) on Piracanga Beach, Bahia, northeastern Brazil. *Scientific Reports of Cetacean Research* 1: 79-84.

Mazzariol S, Di Guardo G, Petrella A, Marsili L, Fossi CM, Leonzio C et al. (2011) Sometimes sperm whales (*Physeter macrocephalus*) cannot find their way back to the high seas: a multidisciplinary study on a mass stranding. *PLoS One* 6: e19417.

Mazzuca L, Atkinson S, Keating B, Nitta E (1999). Cetacean mass strandings in the Hawaiian Archipelago, 1957-1998. *Aquatic Mammals* 25: 105-114.

Moore KM, Simeone CA, Brownell Jr RL (2018) Strandings. *Encyclopedia of Marine Mammals*, 945–951.

Oremus M, Gales R, Kettles H, Baker CS (2013). Genetic evidence of multiple matrilines and spatial disruption of kinship bonds in mass strandings of long-finned pilot whales, *Globicephala melas*. *Journal of Heredity* 104: 301-311.

Parsons ECM (2017) Impacts of Navy sonar on whales and dolphins: Now beyond a smoking gun? *Frontiers in Marine Science* 4: 1–11.

Pyenson ND, Gutstein CS, Parham JF, Le Roux JP, Chavarría CC, Little H, Metallo A, Rossi V, Valenzuela-Toro AM, Velez-Juarbe J, Santelli CM (2014) Repeated mass strandings of Miocene marine mammals from Atacama Region of Chile point to sudden death at sea. *Proceedings of the Royal Society B: Biological Sciences* 281(1781): 20133316.

Sampson K, Merigo C, Lagueux K, Rice J, Cooper R, Weber III, ES et al. (2012) Clinical assessment and postrelease monitoring of 11 mass stranded dolphins on Cape Cod, Massachusetts. *Marine Mammal Science* 28: 404-425.

Sergeant DE (1982) Mass strandings of toothed whales (Odontoceti) as a population phenomenon. *Scientific Reports of the Whales Research Institute* 34: 1-47.

Southall BL, Braun R, Gulland FMD, Heard AD, Baird RW, Wilkin SM, Rowles TK (2006) Hawaiian melon-headed whale (*Peponocephala electra*) mass stranding event of July 3-4, 2004. *NOAA Technical Memorandum* NMFS-OPR-31.

Southall BL, Rowles T, Gulland F Baird RW and Jepson PD (2013) Final report of the Independent Scientific Review Panel investigating potential contributing factors to a 2008 mass stranding of melon-headed whales (*Peponocephala electra)* in Antsohihy, Madagascar. *Independent Scientific Review Panel* 75.

Walker RJ, Keith EO, Yankovsky AE, Odell DK (2005) Environmental correlates of cetacean mass stranding sites in Florida. *Marine Mammal Science* 21: 327-35.

Zellar R, Pulkkinen A, Moore K, Rousseaux CS, Reeb D (2021) Oceanic and atmospheric correlations to cetacean mass stranding events in Cape Cod, Massachusetts, USA. *Geophysical Research Letters* 48: e2021GL093697.

APPENDIX D – Decision Making Simulations

We considered the following processes of collective dive initiation in pilot whales:

A. *Response to a Stimulus* (e.g. a leading whale, vocal signal, vessel presence or predator): This would be expected in the case of leadership, as well as a few other circumstances, where the assumptions are:

    a. every individual perceives the stimulus in some way (from the first whale to dive or vocalize, etc.)

    b. there is normally distributed variation in individual response times – centred on a mean lag relative to the first diver

B. *Independent Decision making*: This would be expected if each individual was deciding when to join independently of others around them, where the assumptions are:

    a. the decision to join in on the dive is made independently of any stimulus or other underlying process after the first whale dives

    b. all whales are diving within a given time frame

    c. whales are diving at random at a time-invariant base rate (e.g. on average once every 25 timesteps) following the first dive

C. *Consensus (Threshold) Decision making:* This would be expected in the case of a quorum or threshold being needed to trigger a collective deep dive. The simulated distribution assumes that the probability of an individual diving is influenced by the proportion that have already dove (with thresholds of 10%, 30%, and 50% percent modeled). Here we assumed:

    a. a specific quorum/threshold is needed to trigger the rest of the group to dive (above a threshold, everyone dives)

The simulations showed that dive lag distributions when collective dives were initiated by an individual (either physically or vocally) or response to an external stimulus (e.g. approaching vessel or predator) would range from heavily positively skewed if there was a short-lag time to a more normal distribution if there were longer lags in individuals diving. Contrarily, shared decisions with a required quorum or threshold displayed an

initial dive, then a lag before most of the individuals then join in, creating this bimodal distribution that is quite distinctive from what is expected under leadership.

APPENDIX E – Generalized Linear Mixed Effects Model Results

Table E1 Results from generalized linear mixed effects model estimating the influences of year, group behaviour, and group size on mean dive lag in long-finned pilot whales.

Model 1: Mean Dive Lag				
Variable	**Estimate**	**s.e.**	**z**	**p**
Intercept	-424	174	-2.44	0.015
Year	0.21	0.09	2.45	0.014
GrB (Resting)	0.54	0.24	2.26	0.024
GrB (Foraging)	0.20	0.22	0.92	0.359
GrB (Socializing)	-0.38	0.33	-1.17	0.241
Group Size	0.01	0.04	0.27	0.784

Table E2 Results from generalized linear mixed effects model estimating the influences of year, group behaviour, and group size on the coefficient of variance for dive lag in long-finned pilot whales.

Model 2: Coefficient of Variance for Dive Lag				
Variable	**Estimate**	**s.e.**	**z**	**p**
Intercept	16.5	61.1	0.27	0.787
Year	-0.01	0.03	-0.26	0.793
GrB (Resting)	-0.16	0.09	-1.80	0.072
GrB (Foraging)	-0.12	0.08	-1.48	0.139
GrB (Socializing)	0.01	0.12	0.07	0.946
Group Size	0.02	0.01	1.44	0.151

Table E3 Results from generalized linear mixed effects model estimating the influences of year, group behaviour, and group size on mean inter-individual dive intervals in long-finned pilot whales.

Model 3: Mean Inter-individual Dive Interval				
Variable	**Estimate**	**s.e.**	**z**	**p**
Intercept	-381	164	-2.32	0.020
Year	0.19	0.08	2.34	0.019
GrB (Resting)	0.50	0.22	-2.25	0.025
GrB (Foraging)	0.04	0.21	0.18	0.854
GrB (Socializing)	-0.34	0.31	-1.11	0.267
Group Size	-0.12	0.03	-3.54	0.000*

Table E4 Results from generalized linear mixed effects model estimating the influences of year, group behaviour, and group size on the coefficient of variance inter-individual dive intervals in long-finned pilot whales.

Model 4: Coefficient of Variance for Inter-individual Dive Interval				
Variable	**Estimate**	**s.e.**	**z**	**p**
Intercept	-98.4	87.3	-1.13	0.260
Year	0.05	0.04	1.14	0.256
GrB (Resting)	0.18	0.12	1.50	0.133
GrB (Foraging)	0.17	0.11	1.45	0.148
GrB (Socializing)	0.05	0.17	0.31	0.754
Group Size	0.04	0.02	2.05	0.040*

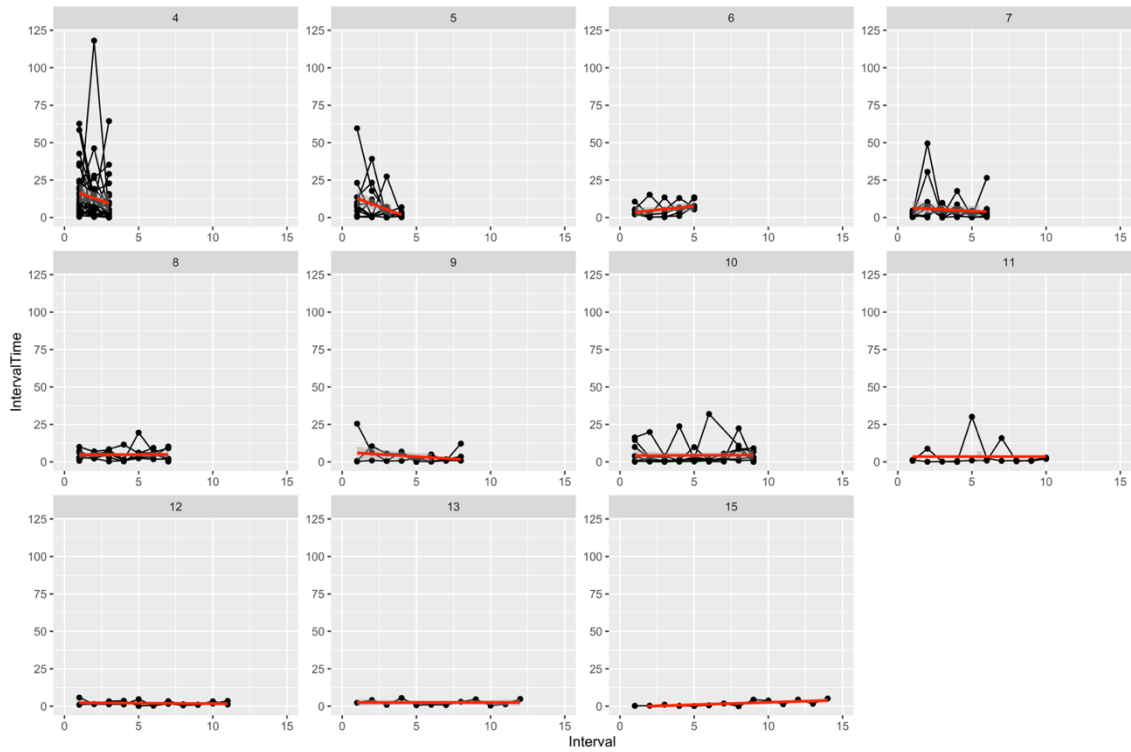## APPENDIX F – Inter-individual Dive Interval Variation Across Group Size, Behavioural State and Year

Figure F1 Ordered inter-whale interval times across group size for long-finned pilot whale collective deep dives
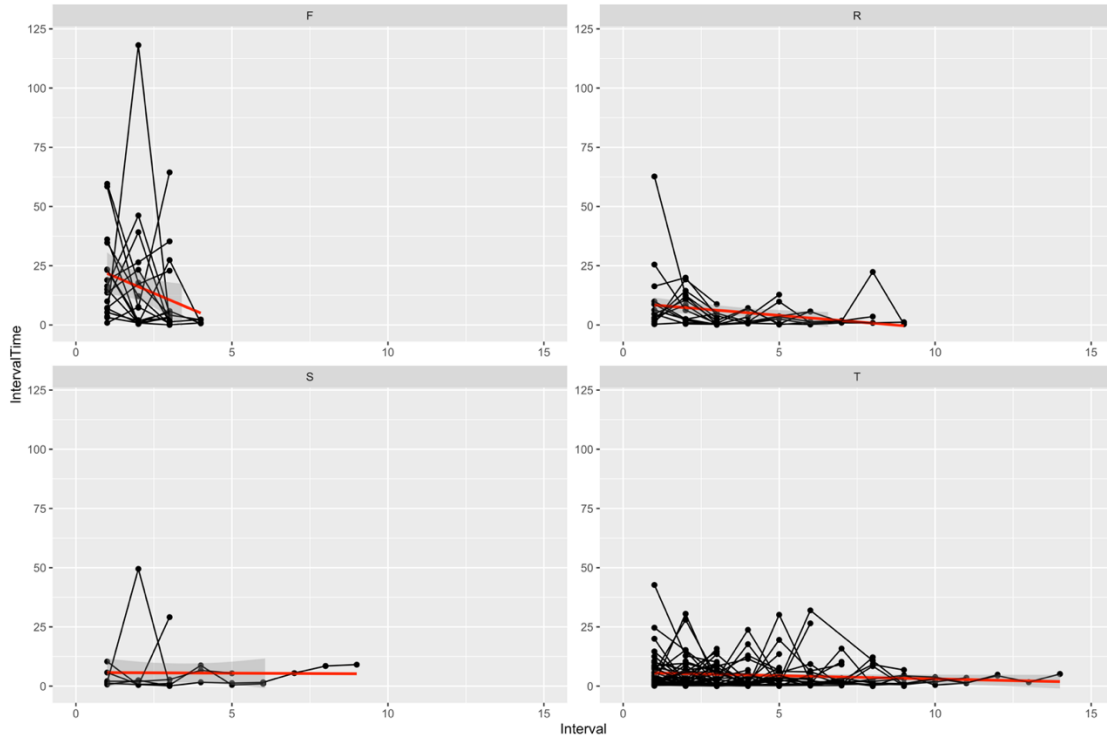
Figure F2 Ordered inter-whale interval times across group behavioural state for long-finned pilot whale collective deep dives
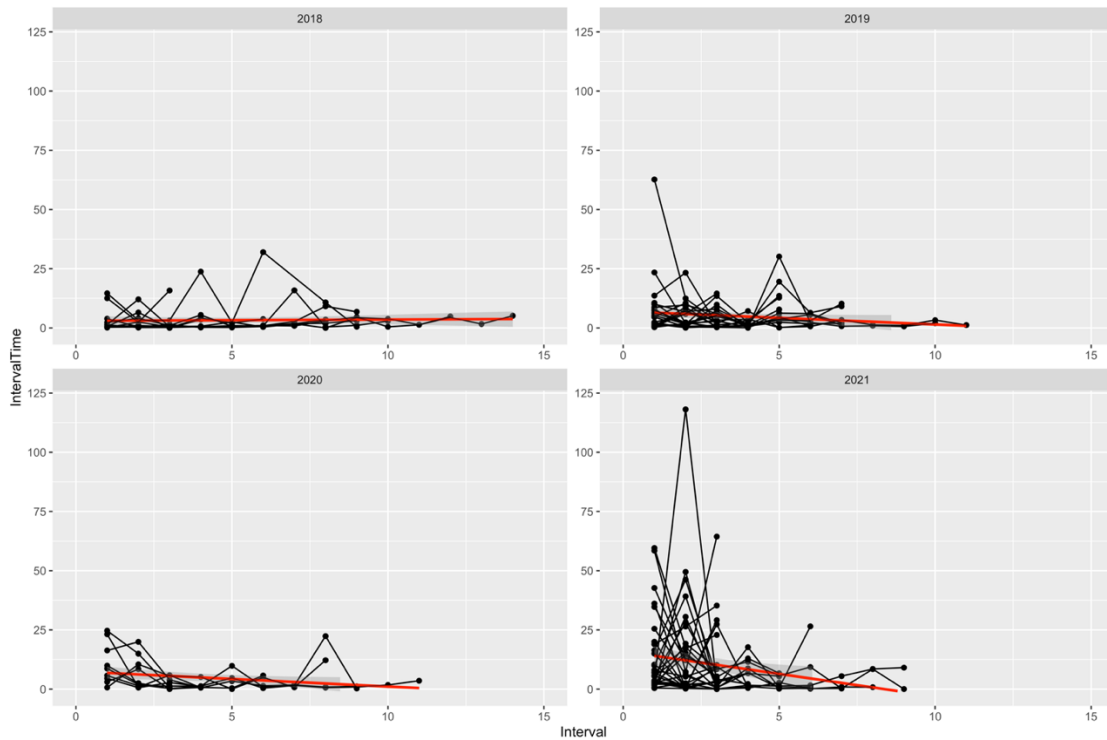

Figure F3 Ordered inter-whale interval times across years for long-finned pilot whale collective deep dives

APPENDIX G – Median Breath Intervals by Age Class

Table G1 Median interval between an individual's consecutive breaths by age class

Age Class	No. of Breaths	Median Interval	Standard Deviation
Adult	289	13.7	5.5
Juvenile	46	11.2	4.0
Grey Calf	73	13.6	6.4
Newborn	39	13.4	5.3

APPENDIX H – Synchrony Generalized Linear Mixed Models (Detailed Results)

How does synchrony change across pre-dive periods?

Median time to closest breath (MTCBreath) was significantly longer during the dive imminent period (DIP), in comparison with the penultimate breathing period (PBP; $\beta = -1.03$, s.e. $= 0.23$, $p < 0.001$) and the regular surfacing period (RSP; $\beta = -0.99$, s.e. $= 0.21$, $p < 0.001$) for the dataset including just adults and juveniles (Table H1).

Table H1 Results from generalized linear mixed model (Gaussian) estimating the influences of pre-dive period on median time to closest breath in adult and juvenile long-finned pilot whales.

Model 2: Median time to closest breath (s)				
Variable	**Estimate**	**s.e.**	**z**	**p**
Intercept	1.98	0.21	9.55	0.000
Penultimate Breathing Period (PBP)	-1.03	0.23	-4.38	**< 0.001**
Regular Surfacing Period (RSP)	-0.99	0.21	-4.80	**< 0.001**

Significant outcomes are show in bold

Median time to closest breath (MTCBreath) was also observed to be significantly longer during the dive imminent period (DIP), in comparison with the penultimate breathing period (PBP; $\beta = -0.82$, s.e. $= 0.19$, $p < 0.001$) and the regular surfacing period (RSP; $\beta = -0.83$, s.e. $= 0.17$, $p < 0.001$) for the all age class dataset (Table H2).

Table H2 Results from generalized linear mixed model (Gaussian) estimating the influences of pre-dive period on median time to closest breath across all age classes long-finned pilot whales.

Model 1: Median interval to closest breath (s)				
Variable	**Estimate**	**s.e.**	**z**	**p**
Intercept	1.79	0.18	9.89	0.000
Penultimate Breathing Period (PBP)	-0.82	0.19	-4.39	**< 0.001**
Regular Surfacing Period (RSP)	-0.83	0.17	-4.99	**< 0.001**

Significant outcomes are show in bold

How does synchrony vary across social contexts?

As might be expected, median time to closest breath decreased (β = -0.02*, s.e. = 0.01*, p = 0.007; Table H3, Figure H1) and the proportion of individuals breathing within 0.5s of the closest breath increased (β = 0.01*, s.e. = 0.00*, p = 0.005) with increasing in group size (Table H4, Figure H2). There was no significant relationship observed between group behavioural state and median time to closest breath or the proportion of individuals breathing within 0.5s of the closest breath. There was also no significant relationship observed between group behavioural state or group size and the proportion of individuals breathing within 1s of the closest breath (Table H5).

Table H3 Results from generalized linear mixed model (Gaussian) estimating the influences of group size and group behavioural state on median interval to closest breath in long-finned pilot whales (all age classes).

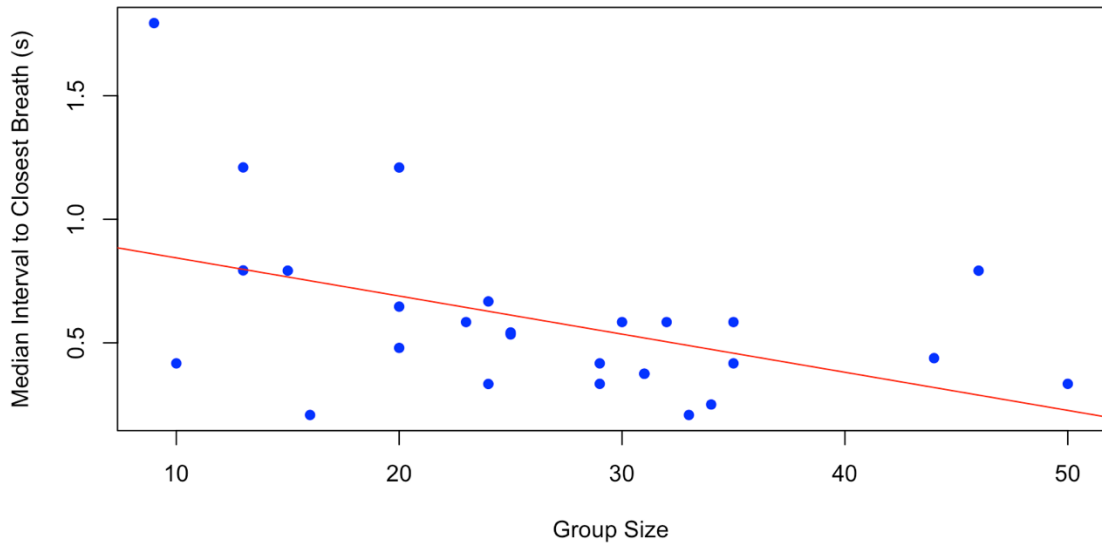| Model 1: Median interval to closest breath (s)				
Variable	**Estimate**	**s.e.**	**z**	**p**
Intercept	1.00	0.18	5.43	0.000
Group Size	-0.05	0.02	-2.23	**0.026**
GrB (Resting)	-0.01	0.18	-0.10	0.923
GrB (Travelling)	0.04	0.16	0.24	0.813

Significant outcomes are show in bold

Figure H1 Median time to closest breath as a measure of breathing synchrony in relation to group size for long-finned pilot whales

Table H4 Results from generalized linear mixed model (Gaussian) estimating the influences of group size and group behavioural state on proportion of closest breaths within <0.5s in long-finned pilot whales (all age classes).

Model 2: Proportion of closest breaths within <0.5s				
Variable	**Estimate**	**s.e.**	**z**	**p**
Intercept	0.22	0.14	1.60	0.109
Group Size	-0.04	0.02	-2.08	**0.037**
GrB (Resting)	0.26	0.14	1.87	0.062
GrB (Travelling)	0.18	0.12	1.50	0.133

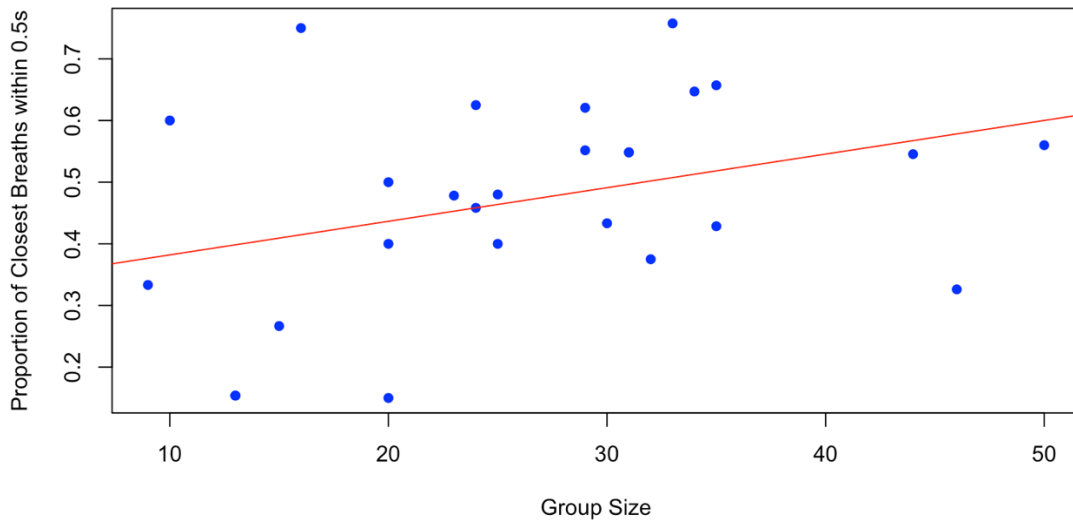Significant outcomes are show in bold

Figure H2 Proportion of closest breaths within 0.5s as a measure of breathing synchrony in relation to group size for long-finned pilot whales

Table H5 Results from generalized linear mixed model (Gaussian) estimating the influences of group size and group behavioural state on proportion of closest breaths within <1s in long-finned pilot whales (all age classes).

Model 2: Proportion of closest breaths within <1s				
Variable	**Estimate**	**s.e.**	***z***	***p***
Intercept	0.36	0.29	1.28	0.202
Group Size	0.03	0.04	0.95	0.344
GrB (Resting)	0.01	0.28	0.03	0.975
GrB (Travelling)	-0.10	0.25	-0.42	0.676

APPENDIX I – MATLAB Data Extraction of Long-finned Pilot Whale Formation Characteristics (Example)

Figure I1 Example of data extracted for each visible individual, which codes information on age class (adult, juvenile, calf, newborn, and unknown), distance between points (total length – rostrum to medial notch of fluke, partial length – rostrum to posterior inset of dorsal fin, or unknown), and quality of individual being annotated (Q1-Q4).
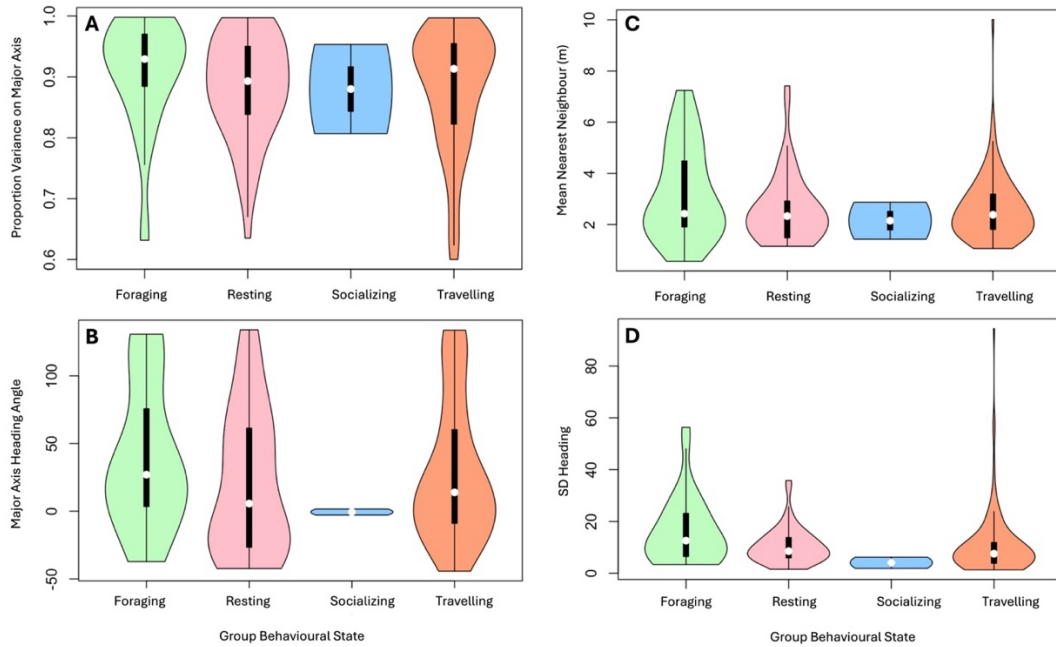
Figure J1 Violin plots of (A) proportion of variance on major axis (B) major axis heading angle (C) mean distance to nearest neighbour (m) and (D) standard deviation of heading by behavioural state for groups of long-finned pilot whales off Cape Breton, Nova Scotia.
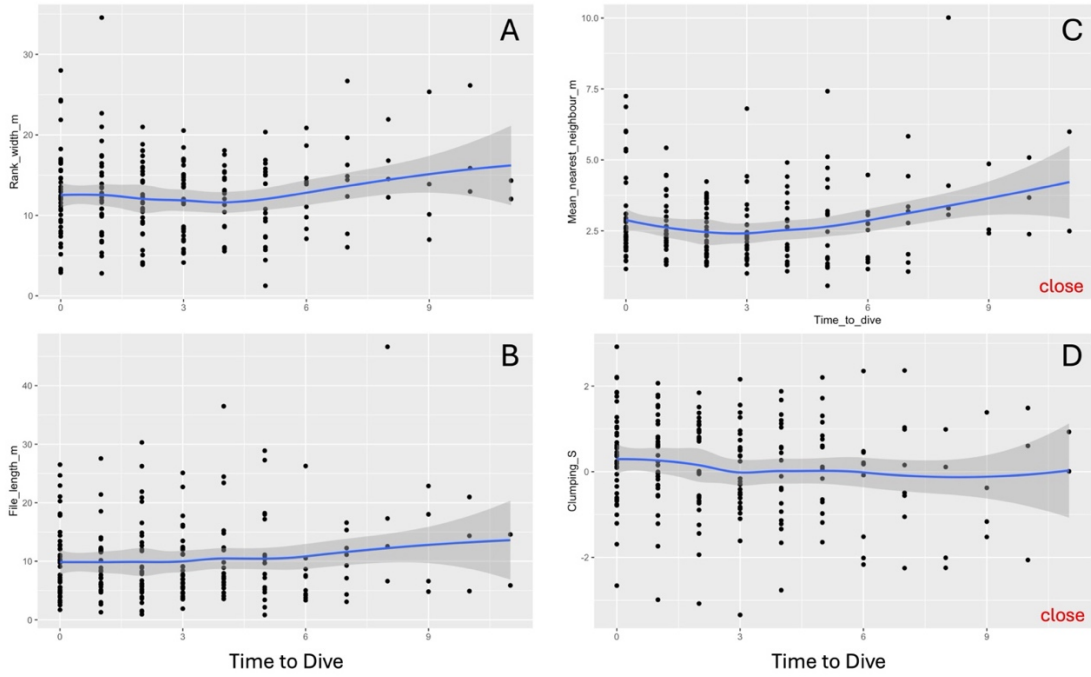
Figure J2 Group formation variables (A) rank width (m) and (B) file length (m) (C) mean distance to nearest neighbour (m) and (D) clumping statistic major axis in the time leading up to collective deep dives in long-finned pilot whales off Cape Breton, Nova Scotia (marginally significant variables labelled as "close").
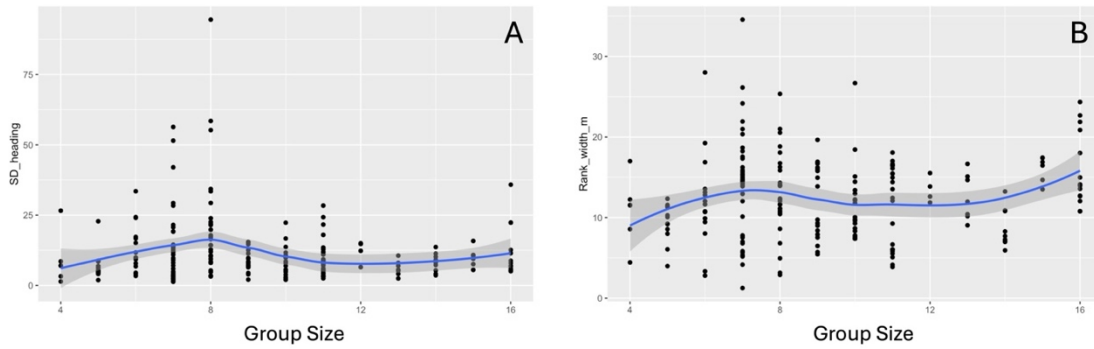

Figure J3 Group formation variables (A) standard deviation of heading and (B) rank width across group sizes in long-finned pilot whales off Cape Breton, Nova Scotia

APPENDIX K – Photo Examples of Pre-stranding Behaviour in Long-finned Pilot Whales

Figure K1 Aerial photo of a large group of long-finned pilot whales (*G. melas edwardii*) that subsequently stranded and died on Cheynes Beach, Australia (Eden Harris, DBCA).

Figure K2 Aerial photo of a group of long-finned pilot whales (*G. melas melas*) that had been herded out to sea after a near-stranding in Rif, Iceland in 2023 (Róbert A. Stefánsson).