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Social Complexity and Communication in Bottlenose Dolphins

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Primary supervisor Associate Professor Stephanie King

Co-supervisor Dr Frants Jensen

**A dissertation submitted to the University of Bristol in accordance with the
requirements for award of the degree of Doctor of Philosophy in the Faculty of Life
Sciences**

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*“An understanding of the natural world
is a source of not only great curiosity,
but great fulfilment.”*

Sir David Attenborough

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General abstract

Cooperation is widespread across the animal kingdom, serving a multitude of purposes from improving foraging efficiency to reproductive success. Often such cooperative behaviour is facilitated through the use of acoustic communication. In this thesis, I investigate the importance of communication for the coordination of cooperative behaviour and how sensory ecology can drive the evolution of cooperation. To address this, I focus on the bottlenose dolphin, a species well-known for its vocal flexibility and propensity for cooperative behaviour. First, I show that while dolphins performing a cooperative task when exposed to anthropogenic noise will increase their whistle amplitude and duration, their cooperative success still decreased with increasing noise (Chapter two). Thus, highlighting the importance of accounting for the impact of noise disturbance on wild animals that rely on communication to coordinate their behaviour. I then switch focus to the allied male bottlenose dolphins of Shark Bay, Western Australia. I first quantify the acoustic parameters of two vocalisations used extensively by male dolphins, whistles and pops, to estimate their communication range (Chapter three). I then investigate how habitat heterogeneity influences the active space of pops, which ultimately may influence alliance behaviour. I find that habitat heterogeneity is a major driver of cooperative group size and reproductive success in this population (Chapter four). Finally, I test the function of pop acoustic synchrony among allied male dolphins by using sound playbacks alongside drone-mounted video. I confirm the hypothesised function of pops as an agonistic signal to induce females to stay close, and while the results indicate acoustic synchrony could function as a coalitionary signal to promote social unity and cooperation among males, further research is needed (Chapter five). Combined, my findings highlight the importance of vocal communication for cooperative behaviour and how habitat heterogeneity and anthropogenic noise may impact cooperative strategies.

University of Bristol Author's Declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others is indicated as such. Any views expressed in the dissertation are those of the author.

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In the spring of 2020, I was preparing to travel to the Dolphin Research Center (DRC) in Florida, USA, to collect data for one of my thesis chapters. Unfortunately, due to the global pandemic this was not possible. However, soon after, our colleagues at DRC, Stephanie and I, decided to continue with our plans to conduct the experiment anyway, with the team at DRC collecting the data, while Stephanie and I provided support from Bristol. Equipment was shipped, manuals were written, new skills were acquired, data was offloaded and checked, and in the end successful data collection was completed. Abby Haddock, Emily Guarino, Kelly Jaakkola and Christina McMullen; it was an absolute pleasure working with all of you. Thank you for your positive attitude, your drive and for making this collaboration one that I am particularly proud of. I would also like to extend a huge thank you to all research interns and personnel who was involved with this project.

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Data chapter contributions

Below I (P.M.S) highlight the contributions of collaborators to this thesis. Associate Professor Stephanie King supervised all data chapters, and Dr Frants H. Jensen supervised data chapters two to four. I led and was involved with all aspects of the research presented in the chapters of this thesis unless otherwise stated; from designing the experimental setup, to collecting, processing, and analysing the data, to writing the manuscript. However, all chapters are ultimately the result of successful collaborations.

Chapter 2: Abby Haddock, Emily Guarino, Kelly Jaakkola, and Christina McMullen collected the experimental data. Frants H. Jensen provided code for analysis of whistle apparent output levels.

Chapter 3: Research assistants Emily Kelly, Mariella Zimmermann and Jeppe Kaczmarek assisted data collection in the field. Sound transmission data were extracted using code written jointly in collaboration with Frants H. Jensen.

Chapter 4: Long-term behavioural data from the dolphins in Shark Bay were collected by Stephanie King, Richard Connor, Simon Allen, and Michael Krützen. Frants H. Jensen prepared code for the sound propagation models. Ulysse Lebrech collected and provided high-resolution satellite-derived bathymetry data.

Chapter 5: Frants H. Jensen helped write code for creating playback stimuli, that P.M.S. adapted to the experimental study purpose. Stephanie King, Simon Allen, Richard Connor and P.M.S collected the data together. Stephanie King and P.M.S. both processed the video data.

Chapter 1 | General introduction

1.1 Cooperation

Cooperation is ubiquitous across the animal kingdom; from cooperative breeding in cichlid fishes (*Perciformes spp.*) (Taborsky, 1994) to alliance formation in chimpanzees (*Pan troglodytes*) (Watts, 1998). Cooperation can typically be explained by mechanisms such as kin selection, where individuals engage in self-sacrificial behaviour that benefits the genetic fitness of their relatives (Hamilton, 1964; Maynard Smith, 1964) or by reciprocity, that considers cooperation between non-relatives, or even different species, where individuals help one another with the expectation that this help will be reciprocated in the future (Trivers, 1971). Examples of kin selection can be found in cooperative breeders, where individuals help raise the offspring of dominant group members (Clutton-Brock, 2002). Reciprocity has also been observed in vampire bats (*Desmodus rotundus*), where adult individuals will share food with non-kin roost mates, who were unsuccessful in their nightly foraging attempt (Wilkinson, 1984).

Animals perform cooperative behaviours in a wide variety of contexts. For example, this includes cooperative hunting where individuals work together to catch prey that would otherwise be unattainable (e.g. lions, *Panthera leo* (Stander, 1992); hyenas, *Crocuta crocuta* (Smith et al., 2012); sailfish, *Istiophorus platypterus* (Herbert-Read et al., 2016)); sexual coercion in which males will form coalitions or alliances for exclusive access to females (e.g. Indo-Pacific bottlenose dolphins, *Tursiops aduncus* (Connor et al., 1992); lions (Packer and Pusey, 1982); chimpanzees (Watts, 1998)); territory defence (e.g. gorillas, *Gorilla beringei* (Morrison et al., 2020); dwarf mongooses, *Helogale parvula* (Christensen et al., 2016);

common marmosets, *Callithrix jacchus* (Lazaro-Perea, 2001)); inter-group conflicts, with implications for within-group cooperation (e.g. banded mongooses, *Mungos mungo*; Thompson et al., 2017); and even inter-species collaboration, such as the bottlenose dolphin-human (*Homo sapiens*) fisheries interactions in Brazil (Simões-Lopes, 1991; Simões-Lopes et al., 1998) and the honeyguide-human mutualism in Africa (*Indicator indicator*; Spottiswoode et al., 2016). In such cooperative endeavours, reciprocal communicative relationships often drive social coordination.

1.2 Communication

Traditionally, communication has been defined as the transmission of information from a sender to a receiver via the emission of a signal (Bradbury and Vehrencamp, 1998). More recently, this definition has been criticized of failing to provide a definition for the concept of information (Owren et al., 2010; Rendall and Owren, 2013). Instead, it has been suggested that signal evolution is driven by the benefits to the signallers, often with the purpose of influencing a receiver, and thus animal signalling is defined as the use of species-specific morphology or behaviour to influence the current or future behaviour of another individual (Owren et al., 2010).

Communication plays a central role in all animal societies, facilitating the exchange of information with respect to individual recognition, social affiliation, condition (i.e. quality) or motivational state, and it can facilitate behaviours such as group cohesion, cooperative foraging, mating and sexual coercion (Bradbury and Vehrencamp, 1998). Several different sensory modalities have evolved to enable communication (Laidre and Johnstone, 2013) encompassing chemical, electric, optical, tactile and acoustic modalities. How well a signal transmits depends on the modality used, the environment and the social context, with habitat type and social function driving which form a signal takes (Laidre and Johnstone, 2013). For

group-living animals acoustic signalling often, but not always, plays a major role in communication between conspecifics. This includes the roars of red deer (*Cervus elaphus*) as an honest advertisement of size, and thus quality, to attract females (Clutton-Brock and Albon, 1979); alarm calling in, for example, meerkats (*Suricata suricatta*) and jungle babblers (*Turdoides striatus*), during which sentinel individuals will emit alarm signals at the approach of a predator (Gaston, 1977; Manser et al., 2002); vocal discrimination of intra- and extra-group individuals in birds such as acorn woodpeckers (*Melanerpes formicivorus*) and green woodhoopoes (*Phoeniculus purpureus*) (Pardo et al., 2020; Radford, 2005); as an advertisement of cultural identity in sperm whales (*Physeter macrocephalus*) (Hersh et al., 2022; Rendell and Whitehead, 2003); and to address other individuals as a signal of referential labelling as seen in bottlenose dolphins (Bruck et al., 2022; King and Janik, 2013). Acoustic communication is thought to be important for coordinating cooperative behaviour, and while our knowledge of how signals and information is used to facilitate cooperative acts remains limited, a few recent studies have started to shed light on this; in chimpanzees, the “bark” vocalisation is a reliable signal of motivation for group hunting, and the use of barks increase hunter recruitment and hunting efficiency (Mine et al., 2022). Furthermore, in dolphin communication whistles have been shown to facilitate and increase cooperative success (King et al., 2021).

In favourable conditions, conspecifics may be able to communicate acoustically over very long ranges, whereas other sensory modalities may be limited to shorter ranges. The maximum range over which a receiver will be able to detect and decode an acoustic signal from a sender is described as the active space (Marten and Marler, 1977). The active space depends on the signal source level, the hearing sensitivity of the receiver, the properties of the environment with implications for sound degradation, and finally, the masking ambient noise level (i.e. the passive sonar equation (Urlick, 1983)). With respect to the latter, in the last couple

of decades terrestrial and aquatic soundscapes have transformed from being dominated by biological sources to being characterised increasingly more by the presence of anthropogenic noise due to large-scale industrialisation, which now dominates the soundscape in many areas (Duarte et al., 2021; Pijanowski et al., 2011).

1.3 The impact of anthropogenic noise on communication

Anthropogenic noise has over the last couple of decades become a substantially greater part of the soundscape. It is created as both a by-product and through the intentional use of sound, which in the aquatic environment includes low-frequency noise from vessels (e.g. recreational, freight and fishing vessels), offshore constructions and pile driving, military exercises, submarine sonar and seismic surveys (Duarte et al., 2021; Slabbekoorn et al., 2010). On land, anthropogenic noise sources include that of transportation (e.g. cars, planes, and trains), cities with aggregations of humans, and industrial activity (Barber et al., 2010). This pervasive pollutant comes with potential implications for animals, impacting animal communication, reproduction, development and physiology (Hotchkiss and Parks, 2013; Kight and Swaddle, 2011; Slabbekoorn et al., 2010; Southall et al., 2008), through causing stress, hearing damage or by distracting and masking signalling (Bradbury and Vehrencamp, 1998). In response to anthropogenic as well as biological noise disturbance, animals have developed a suite of mitigation strategies to compensate for the variations in noise to maintain their active space. Some animals may leave a noisy area only to return when the noise has ended (e.g. Blainville's beaked whale (*Mesoplodon densirostris*) in response to sonar; Tyack et al., 2011), while others may make temporal adjustments to continuous noise disturbance, increasing signal emission when the noise has ceased (e.g. European robins (*Erithacus rubecula*) increase nocturnal singing in urban environments; Fuller et al., 2007). Alternatively, animals may adjust their vocal behaviour to overcome the effects of noise by increasing signal amplitude (i.e. the

Lombard response; Brumm and Todt, 2002; Kragh et al., 2019; Lombard, 1911); by increasing signal duration (Brumm and Todt, 2002; Foote et al., 2004; Miller et al., 2000); by shifting the signal frequency to a frequency band outside of the noise (Ansmann et al., 2007; Lesage et al., 1999; Parks et al., 2007); by calling more redundantly (Di Iorio and Clark, 2010; Kaiser and Hammers, 2009); and/or by changing orientation relative to the noise to achieve spatial release from masking (Erbe et al., 2016). The use of compensatory mechanisms by the sender in response to noise disturbance has been well-studied in a variety of species and recently, new research has emerged investigating anti-predator behaviour and social defence responses of animal receivers exposed to noise (Morimura and Mori, 2019; Scarpaci et al., 2000; Visser et al., 2016), shedding light on the impact of noise on the entire communication network. Yet, little is still known about how noise pollution may impact social animals actively working together in coordinating a cooperative act. To address this data gap, I investigated the effect of increasing levels of noise on coordination between two bottlenose dolphins engaged in a cooperative task (Chapter two).

1.4 The impact of habitat structure on communication

Another component that can potentially influence the active space of an acoustic signal is the physical configuration of the habitat. A prerequisite for social associations or interactions is that individuals are within a distance that allows for successful communication, which is often within relatively close spatial proximity of each other (Farine et al., 2015). Such close spatial proximity can be facilitated or inhibited by the presence of physical components in the habitat, permitting or preventing animals from moving across a given area. The physical features of the habitat will therefore play a key role in shaping the rate of encounters between individuals, because of its impact on animal movement (He et al., 2019), but also due to its impact on acoustic detection range (Bradbury and Vehrencamp, 1998). The physical configuration of the

habitat will impact an animal's acoustic active space as barriers, corridors and other structural features will create reflective or absorbing boundaries that will impact how a sound is transmitted (Urick, 1983). As a result, the active space of the same signal travelling through two different habitats will vary as a function of habitat structure. Variation in active space with habitat has been demonstrated in a number of species, with implications for their vocal behaviour; for instance, variation in vegetation cover partially explain differences in prairie dog dialects (*Cynomys gunnisoni*) (Perla and Slobodchikoff, 2002), and the active space of brown-headed cowbirds (*Moluthrus ater*) varies depending on whether birds sing in urban versus natural habitats (Gall et al., 2012). It has also been shown that some animals will take direct advantage of variation in the active space. For example, some species favour signal transmission in habitats facilitating long-range transmission, as could be the case for animals advertising their presence to potential mates such as frogs (e.g. gray treefrogs, *Hyla versicolor*; Schwartz et al., 2016); and wrens (e.g. rufous-and-white wrens, *Thryothorus rufalbus*; Barker et al., 2009). In contrast, others may benefit from communicating in habitats that allow acoustic crypsis; indeed, it has been suggested that southern right whale (*Eubalena australis*) mother-calf pairs will retreat to shallow water nursery grounds with a small active space, to avoid eavesdropping from potential predators (Zeh et al., 2022). Likewise, Heaviside's dolphins (*Cephalorhyncus heavisidii*) may selectively relax acoustic crypsis to promote communication with conspecifics, but maintain their use of acoustic cryptic signals during foraging and navigation to avoid predation by killer whales (*Orcinus orca*) (Martin et al., 2018). As such, the impact of habitat structure on sound transmission is well-studied, but our knowledge of how changes in sensory ecology can impact social complexity remains limited. In this thesis, I address our lack of knowledge in this area of research by investigating the acoustic parameters of a vocalisation important for bottlenose dolphin reproductive behaviour (Chapter three) and combine this with satellite-derived bathymetry data and background ambient noise levels to

model how habitat structure, and thus communication range affects social behaviour (Chapter four).

1.5 Social interactions promoting cooperative behaviour

Maintaining social relationships between group-members is especially important for species where cooperative behaviour plays a major role. Many animals use physical contact behaviours such as grooming, petting, and preening to express affiliation between individuals and to maintain and strengthen social bonds (Connor et al., 2006; Kutsukake and Clutton-Brock, 2006; Morales Picard et al., 2020; Seyfarth and Cheney, 1984). Grooming has been shown to reduce tension in Talapoin monkeys (*Miopithecus talapoin*) through the release of endorphins (Keverne et al., 1989), and to decrease heart rates in female rhesus macaques (*Macaca mulatta*) (Aureli et al., 1999). Furthermore, there is evidence showing subordinate female meerkats will appease dominant females through grooming to avoid group eviction (Kutsukake and Clutton-Brock, 2006), and vampire bats will initiate low-cost grooming before sharing food with conspecifics (Carter et al., 2020). Preening is essential for successfully rearing offspring in pair-bonded wrens, where divorce rates are higher for those pairs that do not perform preening (Kenny et al., 2017). Preening behaviour is also shown to predict pair-bond stability, egg production and offspring survival rate, with preening individuals being more successful (Kenny et al., 2017; Spoon et al., 2007). Similarly, social contact through grooming and petting in primates and dolphins, respectively, allow male alliance members to mediate their social relationships with important implications for their future reproductive success (Berghänel et al., 2011; Connor and Krützen, 2015; Connor et al., 2006; Gerber et al., 2022; Seyfarth and Cheney, 1984; Watts, 2000). Recently, it has also been shown that allied male bottlenose dolphins (from here on referred to as dolphins) have a higher rate of vocal exchanges with allies with whom they share a weaker social bond, whereas they display a higher rate of

affiliative contact with allies that they share stronger social bonds with (Chereskin et al., 2022). As per Dunbar's social bonding hypothesis (Dunbar, 1996), this suggests that vocal exchanges can function as a replacement for physical affiliative contact allowing individuals to 'bond-at-a-distance' (Chereskin et al., 2022).

Another way to reinforce social bonds is through synchronous behaviours. Cooperative synchrony has been researched extensively in humans, where synchrony has been shown to be important for promoting cooperation and strengthening social bonds (Launay et al., 2016; von Zimmermann and Richardson, 2016). A well-known example of human synchrony is that of the haka "Ka Mate", a traditional Maori war dance, that is now performed by New Zealand's national rugby team, prior to each match (Savage et al., 2020). Through synchronised movements and vocals, the haka functions to signal coalitionary strength to intimidate the opposing team, while also diminishing their perceived formidability to the performing team (Fessler and Holbrook, 2014). Additionally, synchrony in humans has been shown to reduce tension, and to promote and enhance future cooperative actions (Valdesolo et al., 2010; von Zimmermann and Richardson, 2016). Cooperative synchrony is, however, not limited to humans. It has also been demonstrated between male bottlenose dolphins that form alliances to sexually coerce oestrus females (Connor et al., 2006). Previous studies suggest motor synchrony between allied male dolphins promotes cooperation, social unity and reduces tension between males that are ultimately competing over mating opportunities with the same female (Connor et al., 2006). In humans, the release of the neuropeptide oxytocin has been shown to be linked to synchronous behaviour, and to enhance trust and promote cooperation (De Dreu et al., 2010; De Dreu et al., 2011). While the role of oxytocin release during synchronous behaviour in dolphins is still unknown, a link between oxytocin and prosocial behaviour in other species has been shown (Crockford et al., 2014); such as during grooming

in chimpanzees (Crockford et al., 2013), and the peripheral administration of oxytocin to wild meerkats induced individuals to increase their rate of participation in cooperative behaviours, such as increasing the rate of alloparental care (Madden and Clutton-Brock, 2011). This suggests that, like in humans, oxytocin release promoted by synchronous behaviour may play a role in facilitating trust and reducing tension between male dolphin allies, however this is yet to be determined.

In addition to engaging in physical synchrony, allied male dolphins also engage in acoustic coordination, where males actively match the production and tempo of each other's vocalisations (Moore et al., 2020). In this thesis, I investigate the function of acoustic synchrony in male dolphins by testing three leading hypotheses based on our knowledge of motor synchrony. I propose acoustic synchrony functions to intimidate rivals or female consorts, to impress female consorts and/or to promote social bonding among allies (Chapter 5).

1.6 Study species: The Bottlenose Dolphin

The bottlenose dolphin is iconic, known by scientists and layman alike, and one of the most well-studied species of cetaceans to date. This is in large part due to their world-wide distribution in coastal and offshore habitats and their adaptability to be kept in human care, which over the years has led to an extensive understanding of their biology. There are currently two recognised species of bottlenose dolphins, the common bottlenose dolphin (*Tursiops truncatus*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), with indications that inshore and offshore 'ecotypes' may eventually be accepted as separate species (Costa et al., 2022; Hoelzel et al., 1998; Louis et al., 2021). Bottlenose dolphins exhibit fission-fusion grouping patterns, characterised by smaller groups that vary in size and composition as individuals leave and join, on a daily or even hourly basis (Connor et al., 2000; Würsig and

Würsig, 1977). Such frequent changes in social organisation require well-developed cognitive skills to allow individuals to navigate and maintain social relationships (Connor, 2007).

To mediate social interactions, bottlenose dolphins have developed a suite of different behaviours, including the use of signature whistles (Caldwell and Caldwell, 1965). These signals are learnt, and function as individually specific vocal labels (Bruck et al., 2022; King and Janik, 2013; Sayigh et al., 1990), through the encoding of identity information in the frequency modulation pattern of the whistle (Janik et al., 2006). In addition to advertising individual identity, they have been shown to be important for facilitating group cohesion (Janik and Slater, 1998; King et al., 2021), and dolphins are capable of long-term social recognition, remembering the signature whistles of conspecifics they have not seen for up to 20 years (Bruck, 2013). Although signature whistles are an important component of dolphins' vocal repertoire (Buckstaff, 2004; Cook et al., 2004; Watwood et al., 2005), bottlenose dolphins produce a variety of other acoustic communication signals, including burst pulsed sounds, squeals, creaks, and non-signature whistles. Yet, while signature whistles have been extensively studied, our knowledge on the function and behavioural context in which these other sounds are used is less well-known. However, it is extremely likely that these signals are involved in mediating the cooperative behaviours performed by bottlenose dolphins. For example, acoustic signals have been shown to be involved in cooperative foraging, such as that of role-specialised “driver-barrier feeding”, where a dolphin “driver” will herd mullet (*Mugil spp.*) towards the “barrier” dolphins (Gazda, 2016; Gazda et al., 2005; Hamilton et al., 2022). Other cooperative behaviours have been studied in the population of Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia. These include multilevel male alliance formation, and motor synchrony, important for expressing the social bonds between allied males (Connor and Krützen, 2015; Connor et al., 2006; Connor et al., 2022; Moore et al., 2020). I will present and introduce these in more detail in the following section.

1.7 Study system: Male alliances in Shark Bay

The Indo-Pacific bottlenose dolphins of Shark Bay, Western Australia represent one of the best studied dolphin populations in the world. Following the social structure of other bottlenose dolphin populations, the dolphins in Shark Bay exhibit a fission-fusion grouping pattern with overlapping individual home ranges within an open social network (Randić et al., 2012). Long-term data have been collected for more than four decades (since 1982; www.sharkbaydolphins.org), providing detailed insight into their complex social lives including cooperative behaviour; communication; genetic relationships; ecology; and unique foraging specialisations (Connor and Krützen, 2015; Gerber et al., 2022; King et al., 2018; King et al., 2021; Wild et al., 2019a; Wild et al., 2019b). Among the most striking discoveries is perhaps that of the male alliance system. Male bottlenose dolphins, typically unrelated (Gerber et al., 2020), form the largest multilevel cooperative alliance network outside of humans. Alliances have been defined as enduring relationships with repeated instances of cooperation (de Wall and Harcourt, 1992), and in Shark Bay this system is driven by cooperation and competition over access to an indivisible resource: females (Connor and Krützen, 2015; Connor et al., 2022). In this system male dolphins form three alliance levels. At the first level, male pairs or trios (first-order alliance) will cooperate to aggressively pursue and herd oestrus females in events called consortships (Connor et al., 1992). Consortships can last from hours to weeks, with longer consortship durations increasing the chances for mating and securing offspring, but requiring more energy devoted to guarding and defending the female from rival alliances (Connor et al., 2022). Most adult males are members of a second-order alliance, the core social unit, which typically consist of 4-14 males that cooperate in competition against rival alliances over access to females (Connor and Krützen, 2015). Who a male forms an alliance with in his adult life is predicted by his associations during his early life, driven by similar ages, as opposed to kinship (Gerber et al., 2020). Males form first-order

alliances with males from within their second-order alliance (Connor et al., 2022). However, whereas second-order alliances remain stable across decades (Connor et al., 2022; King et al., 2021), the composition of first-order alliances is more variable, as some males prefer to consort females with the same allies, whereas others will engage in consortships with several different males from within their second-order alliance (Connor and Krützen, 2015; Connor et al., 2001; King et al., 2021). While it is yet to be determined how males share matings during a consortship, males with stronger and more homogeneous bonds with allies within their second-order will obtain more paternities (Gerber et al., 2022). Finally, male dolphins in Shark Bay sometimes cooperate in third-order alliances, when two or more second-order alliances cooperate in contests over females (Connor et al., 2011; Connor et al., 2022; King et al., 2021). Second- and third-order alliances may serve the same function, i.e. cooperation in competition for access to females, but are not interchangeable (Connor et al., 2022): Males are rarely observed with third-order allies without their second-order allies present, males almost exclusively form first-order alliances with males within their second-order, males rarely change to another second-order alliance once formed, males are more likely to engage in vocal exchanges with second-order allies compared to third-order allies, and categorise members of their second-order alliance as team members based on signature whistles and previous relationship history (Chereskin et al., 2022; Connor and Krützen, 2015; Connor et al., 2001; King et al., 2021). The importance of third-order alliance relationships are evident in that males with stronger social bonds to their third-order allies have more success consorting females, and thus higher reproductive success (Connor et al., 2022).

In addition to the complexity of the multilevel alliance system, alliance behaviour also varies as a function of habitat structure, with first-order alliance pairs more often observed in the southern part of the habitat, composed of shallow flats, subdivided by deeper channels, whereas

trios are more frequently observed in the northern, open water habitat (Connor et al., 2017). Similarly, consortship rates have been shown to be lower in the south compared to the north (Connor et al., 2017). This poses the question of whether male alliance behaviour is driven by the impact of habitat structure on acoustic communication range, however thus far empirical evidence has been lacking.

The social relationships and cooperative behaviours of male alliances are facilitated by acoustic signals. Using playback experiments, signature whistles have been shown to be used by males to classify second-order allies as members of their “team”, independently of social bond strength across all three alliance levels: males respond more strongly to members of their second-order alliance, compared to their third-order allies (King et al., 2021). Signature whistles are also used to maintain relationships between males with weaker social bonds within the second-order alliance, to compensate for the lower rate of physical affiliative behaviours (Chereskin et al., 2022). In addition to whistles, male dolphins produce ‘pops’, which are narrow-band, low-frequency pulsed signals usually produced in repetitive trains. They are almost exclusively produced during consortships and only by males, and function as a coercive female-directed signal of aggression, inducing the female to stay close to the popping male (Connor and Smolker, 1996; Moore et al., 2020; Vollmer et al., 2015). Pops are strongly associated with physical threats, but may also facilitate guard switching between first-order allies consorting a female (King et al., 2019). Finally, pops have been shown to be produced in synchrony by allied males while consorting a female, where males actively match each other’s tempo and pop production (Moore et al., 2020).

However, cooperative synchrony, which has not been documented in any other non-human species to date, is not limited to pops in this population. Male dolphins have been shown to perform synchronous displays, surfacings, and aerial leaps with coordinated precision (Connor

et al., 2006). These synchronous behaviours have been suggested to reduce tension and promote cooperation between allied males, who despite their strong bonds, are ultimately interested in the same resource; the consorted female (Connor et al., 2006).

The long-term research and the extensive knowledge on cooperation and communication already known from this population, provided a unique opportunity for further studies investigating the importance of acoustic signalling for cooperative behaviour.

1.8 Thesis outline

In this thesis, I present the results of four years of work during which I spent 10 months in Shark Bay, collecting empirical data for this PhD while also assisting in data collection for the Shark Bay Dolphin Research Projects' long-term database. I also remotely managed and provided support for data collection for this PhD at the Dolphin Research Center in Florida, as the global pandemic prevented me from travelling to Florida to collect the data myself. Using a wide range of experimental tools for acoustic data collection, including hydrophone arrays, autonomous acoustic recorders, sound and movement on-animal recording tags and underwater speakers, I explore the importance of acoustic communication for the coordination of cooperative behaviour and how signal characteristics can drive social evolution in the bottlenose dolphin. Furthermore, I investigate how the use of acoustic signalling may promote cooperation.

Each chapter is written as a stand-alone piece, allowing a reader to understand the context outside of this thesis. Chapter two is already published, and Chapter four is prepared for publication. Both chapters are formatted according to the formatting requirements of the relevant journals of which they have been published in or targeted to. Chapters three and five are both planned for publication, but not currently formatted for any specific journals. During this PhD I have been fortunate enough to be involved in other projects, one of which has led to

a publication that I am a co-author on (i.e., Chereskin et al., 2022). This publication as well as Chapter two can be found at the end of this thesis in their published format.

In Chapter two, I test the impact of anthropogenic noise on cooperation and acoustic communication between a pair of bottlenose dolphins performing a cooperative task. While the use of compensatory mechanisms in response to noise are well-documented in both terrestrial and marine animals (e.g. Brumm and Todt, 2002; Foote et al., 2004; Kaiser and Hammers, 2009; Kragh et al., 2019; Lesage et al., 1999; Parks et al., 2007), less is known about how efficient these mitigation strategies are in overcoming the effects of noise. This study highlights the importance of accounting for the impact of noise on wild animals performing cooperative tasks. In Chapter three, I quantify acoustic parameters of dolphin whistles and pops, ambient noise levels and sound transmission properties within the eastern gulf of Shark Bay. Combining these empirical measures, I estimate the communication range of whistles and pops, respectively, to help further our understanding of the use of these signals.

The evolution of social complexity has often been assumed to be driven purely by social processes, and an animal's social environment has been considered the product of individual movement decisions (Bonnell et al., 2017; Farine, 2015; Farine et al., 2016; He et al., 2019). However, while social cues are important drivers of animal social interactions, little is known of how habitat heterogeneity will impact the area over which animals can interact with implications for animal behaviour. In Chapter four, I use the empirical measures from Chapter three, and combine them with high-resolution, satellite-derived bathymetry data and measures of animal density to model how the active space of pops varies across the study site. Combining this with long-term male alliance behavioural data, I investigate how habitat heterogeneity, and thus sensory ecology, may have shaped cooperative mating behaviour of male dolphins. In Chapter five, I investigate the functional use of pop acoustic synchrony. Motor synchrony has previously been shown to play an important role in cooperative behaviour between male

dolphins and it is suggested to promote alliance unity. I test the function of pop synchrony by conducting playback experiments, playing back synchronous and asynchronous pop trains to focal subjects, while using drone-mounted video to record behavioural responses.

In summary, the aim of this thesis is to explore the importance of acoustic communication for dolphin cooperative behaviour. I demonstrate the importance of habitat heterogeneity for cooperative mating behaviour, how acoustic communication promotes cooperative behaviour, and how dolphins working together are impacted by noise disturbance.

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Chapter 2 | Anthropogenic noise impairs cooperation in bottlenose dolphins

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2.1 Summary

Understanding the impact of human disturbance on wildlife populations is of societal importance (Duarte et al., 2021), with anthropogenic noise known to impact a range of taxa, including mammals (Tyack, 2008), birds (Francis et al., 2009), fish (Bruitjes and Radford, 2013), and invertebrates (Morley et al., 2014). While animals are known to use acoustic and other behavioural mechanisms to compensate for increasing noise at the individual level, our understanding of how noise impacts social animals working together remains limited. Here, we investigated the effect of noise on coordination between two bottlenose dolphins performing a cooperative task. We previously demonstrated that the dolphin dyad can use whistles to coordinate their behaviour, working together with extreme precision (King et al., 2021). By equipping each dolphin with a sound-and-movement recording tag (DTAG-3 (Johnson and Tyack, 2003)) and exposing them to increasing levels of anthropogenic noise, we show that both dolphins nearly doubled their whistle durations and increased whistle amplitude in response to increasing noise. While these acoustic compensatory mechanisms are the same as those frequently used by wild cetaceans (Ansmann et al., 2007; Di Iorio and Clark, 2010; Foote et al., 2004; Kragh et al., 2019; Lesage et al., 1999; Parks et al., 2007), they were insufficient to overcome the effect of noise on behavioural coordination. Indeed, cooperative task success decreased in the presence of noise, dropping from 85% during ambient noise control trials to 62.5% during the highest noise exposure. This is the first study to demonstrate in any non-human species that noise impairs communication between conspecifics performing a cooperative task. Cooperation facilitates vital functions across many taxa and our findings highlight the need to account for the impact of disturbance on functionally important group tasks in wild animal populations.

2.2 Keywords: cooperation; active coordination; communication; anthropogenic noise; Lombard response; cognition; bottlenose dolphin; acoustic compensation.

2.3 Results and Discussion

Anthropogenic noise poses a significant problem for a wide range of animals (Kight and Swaddle, 2011; Shannon et al., 2016) in both marine and terrestrial environments (Barber et al., 2010; Morley et al., 2014; Tyack, 2008) and has been demonstrated to impact animal communication, physiology, reproduction and development (Hotchkin and Parks, 2013; Kight and Swaddle, 2011; Slabbekoorn et al., 2010; Southall et al., 2008). In response, individuals across taxa have been shown to take advantage of vocal and other behavioural mitigation strategies to compensate for variations in noise (Erbe et al., 2016). Individuals can attempt to compensate for increased noise disturbance by modifying the amplitude (Brumm and Todt, 2002; Kragh et al., 2019; Lombard, 1911), frequency (Ansmann et al., 2007; Lesage et al., 1999; Parks et al., 2007), duration (Foote et al., 2004) and/or redundancy of their calls (Di Iorio and Clark, 2010; Kaiser and Hammers, 2009), by changing their orientation relative to the noise source to achieve spatial release from masking (Erbe et al., 2016) or by moving to a new area entirely (Tyack et al., 2011). Previous studies have focused on the use of mitigation strategies at the individual level and on the social defence responses of groups exposed to disturbance from noise (Morimura and Mori, 2019; Scarpaci et al., 2000; Visser et al., 2016). However, little is known about how successful these compensatory mechanisms are at overcoming the impacts of noise disturbance when individuals are actively working together.

Noise disturbance impacts are of particular concern for cetaceans, which rely on sound for communication and coordination of complex behaviours, navigation, and for locating and capturing prey (King and Janik, 2015; King et al., 2019; King et al., 2021; Simpson et al., 2005;

Tyack, 2008; Vasconcelos et al., 2012). It is well established that anthropogenic noise can impair the ability of cetaceans to communicate with conspecifics or to find food e.g. through acoustic masking where their ability to detect and perceive vital signals is reduced (Erbe et al., 2016; Marten and Marler, 1977; Wisniewska et al., 2018; Wright et al., 2007). Noise exposure can also lead to both acute and chronic effects, such as shifts in signal frequency (Parks et al., 2007), increased levels of glucocorticoids (Pirotta et al., 2018; Rolland et al., 2012), and decreased reproductive success or elevated risk of death (Pirotta et al., 2018). Scientists and policymakers are therefore increasingly concerned about the impacts of anthropogenic noise on cetacean behaviour (King et al., 2015), as behavioural changes often precede ultimate indicators of population health (French et al., 2011; Harris et al., 2018; New et al., 2014).

Bottlenose dolphins (*Tursiops* spp.) are highly social and well-known for their behavioural and acoustic coordination (Connor et al., 2006; Moore et al., 2020), cooperative alliance behaviour (Connor and Krützen, 2015; Connor et al., 1992; King et al., 2019), and cooperative foraging (Gazda et al., 2005; Hamilton et al., 2022; Simões-Lopes et al., 1998). We have previously shown that dolphin dyads living in human care can work together to solve a cooperative task, understand the role their partner must play in the task, and use whistles to successfully coordinate their behaviour with extreme precision (Jaakkola et al., 2018; King et al., 2021). This task requires both members of a dyad to swim to different stations in a lagoon and each press their own underwater button simultaneously (within a 1 s time window) with the other dolphin, whether sent together or with a randomised delay between partners (Jaakkola et al., 2018; King et al., 2021). Here, we use the same cooperative task to investigate the effect of noise on coordination and cooperative behaviour between two male bottlenose dolphins (*Tursiops truncatus*) equipped with sound-and-movement recording DTAGs (Johnson and Tyack, 2003) while exposed to increasing levels of anthropogenic noise (Figure 2.1). We

examine how the dyads' ability to successfully solve this cooperative task is impacted by the presence of anthropogenic noise and how dolphins may attempt to compensate through the use of acoustic and other behavioural mitigation strategies.

The dolphin dyad was asked to perform the task under either ambient noise conditions (control) or when exposed to one of four noise treatments, consisting of either broadband filtered noise (1-20 kHz) or the noise of the pressure washer that the Animal Care and Habitat Staff used to clean the lagoons (Figure 2.1; see STAR methods). Noise levels quantified as 1-20 kHz broadband levels (NL) as recorded next to the push buttons corresponded to: (1) ambient noise control (mean \pm S.D.: 115 ± 6 dB re 1 μ Pa, rms); (2) low noise treatment (mean \pm S.D. = 119 ± 4 dB re 1 μ Pa, rms); (3) medium noise treatment (mean \pm S.D. = 126 ± 2 dB re 1 μ Pa, rms); (4) high noise treatment (mean \pm S.D. = 135 ± 1 dB re 1 μ Pa, rms) and; (5) very high noise treatment (pressure washer; mean \pm S.D. = 150 ± 4 dB re 1 μ Pa, rms). See Figure 2.2A for details on third-octave level (TOL) noise bands. A total of 200 trials, 40 trials for each of the four treatments and the control, were conducted with the dolphin dyad. We found that the dyad's success rate in the cooperative task decreased significantly when exposed to increasing levels of noise (GLMM: $\beta \pm \text{SE} = -0.03 \pm 0.01$, $z = -2.31$, $p = 0.021$; Figure 2.2B), with their overall success rate dropping from 85% during ambient noise control trials to 62.5% during the highest noise exposure treatment (Table 2.1).

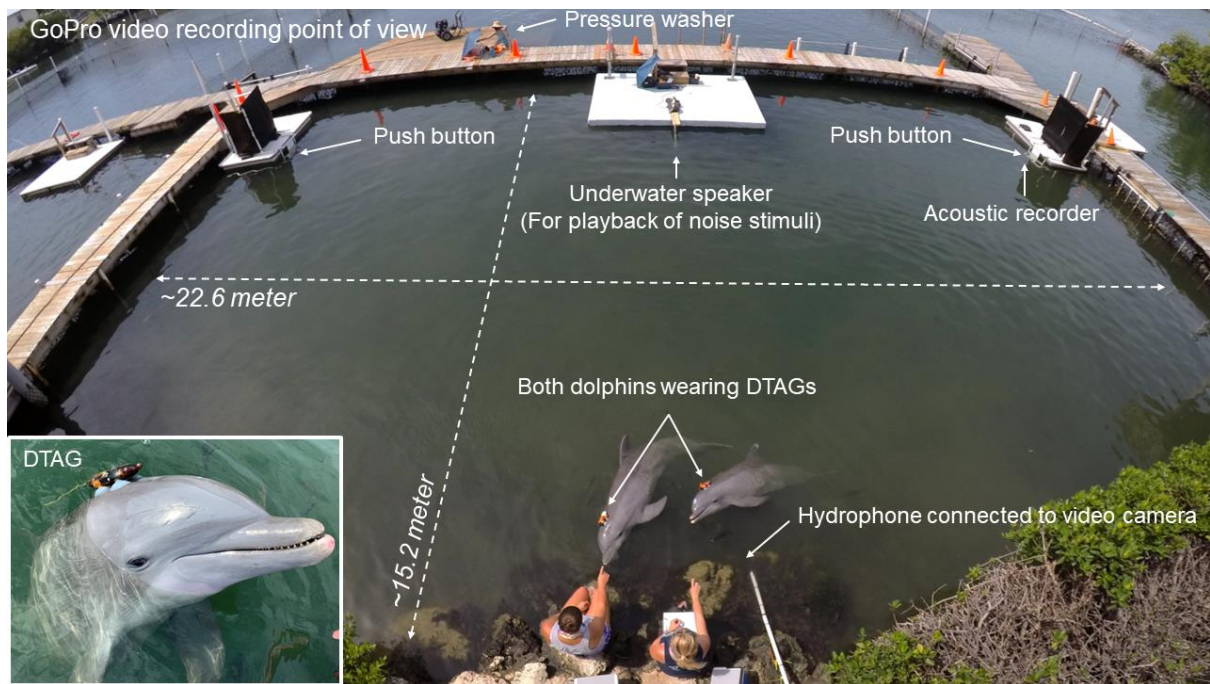


Figure 2.1. Experimental setup. Aerial view of the experimental lagoon and a close up of one member of the dyad (Reese) wearing a DTAG (Johnson and Tyack, 2003).

Table 2.1. Summary of experimental results

Number of experimental trials, success rate for each treatment, total number of whistles and number of signature whistles in parentheses, mean apparent output level (AOL, dB re 1 μ Pa, rms within a 95% energy window), mean duration (s) of all whistles and mean noise level (NL) as measured on the tags prior to whistle emission for the two dyad members, Delta and Reese, respectively. **See also Figure 2.2.**

Treatment	# Trials per treatment	Success rate (%)	Number of whistles		Mean whistle AOL (dB re 1 μ Pa, rms) \pm S.D.		Mean whistle duration (s) \pm S.D.		Mean noise level (dB re 1 μ Pa, rms) \pm S.D.	
			Reese	Delta	Reese	Delta	Reese	Delta	Reese	Delta
Ambient noise	40	85	41 (34)	11 (1)	151 \pm 6	142 \pm 8	0.62 \pm 0.5	0.50 \pm 0.3	123 \pm 15	122 \pm 9
Low noise	40	77.5	36 (34)	33 (5)	149 \pm 7	143 \pm 4	0.69 \pm 0.5	0.57 \pm 0.2	124 \pm 11	124 \pm 10
Medium noise	40	65	28 (24)	24 (5)	153 \pm 5	144 \pm 5	0.77 \pm 0.5	0.68 \pm 0.5	129 \pm 11	131 \pm 6
High noise	40	67.5	30 (22)	17 (2)	152 \pm 6	142 \pm 4	0.91 \pm 0.8	0.69 \pm 0.3	135 \pm 7	133 \pm 4
Very high noise	40	62.5	15 (15)	16 (5)	152 \pm 3	146 \pm 4	1.15 \pm 0.8	0.83 \pm 0.4	143 \pm 6	142 \pm 5

2.3.1 Acoustic compensatory mechanisms

Across all trials, the dolphin dyad produced a total of 251 whistles ($N_{\text{Reese}} = 150$, $N_{\text{Delta}} = 101$), identified as either signature whistles (individual identity signals (Caldwell et al., 1990; Janik et al., 2006)) or non-signature whistle types (Table 2.1). Reese's signature whistle spans 4-18 kHz while Delta's spans 6-20 kHz. For both individuals, there was a significant positive relationship between noise level (NL) measured prior to whistle emission and whistle apparent output level (AOL) (Reese, linear mixed-effects model (LMM): $\beta \pm \text{SE} = 0.08 \pm 0.03$, $t = 2.35$, $p = 0.02$; Delta, LMM: $\beta \pm \text{SE} = 0.14 \pm 0.05$, $t = 2.94$, $p = 0.005$; Figures 2.2C & 2.2D); both dolphins significantly increased the amplitude of their whistles as noise levels increased. This corresponds to an amplitude compensation, referred to as a Lombard response, of 0.08 dB per 1 dB increase in NL for Reese, and a 0.14 dB per 1 dB increase in NL for Delta; similar to that observed in wild bottlenose dolphins (Kragh et al., 2019). Noise levels were measured over a 100 ms window ending 50 ms prior to each whistle (see STAR methods), and the significant positive relationship between AOL and noise level suggests that dolphins adjust whistle AOL based on the amplitude of the noise experienced just before they produce the whistle, supporting the notion that it is important to account for *in-situ* received noise levels for each animal as experienced just prior to whistle emission.

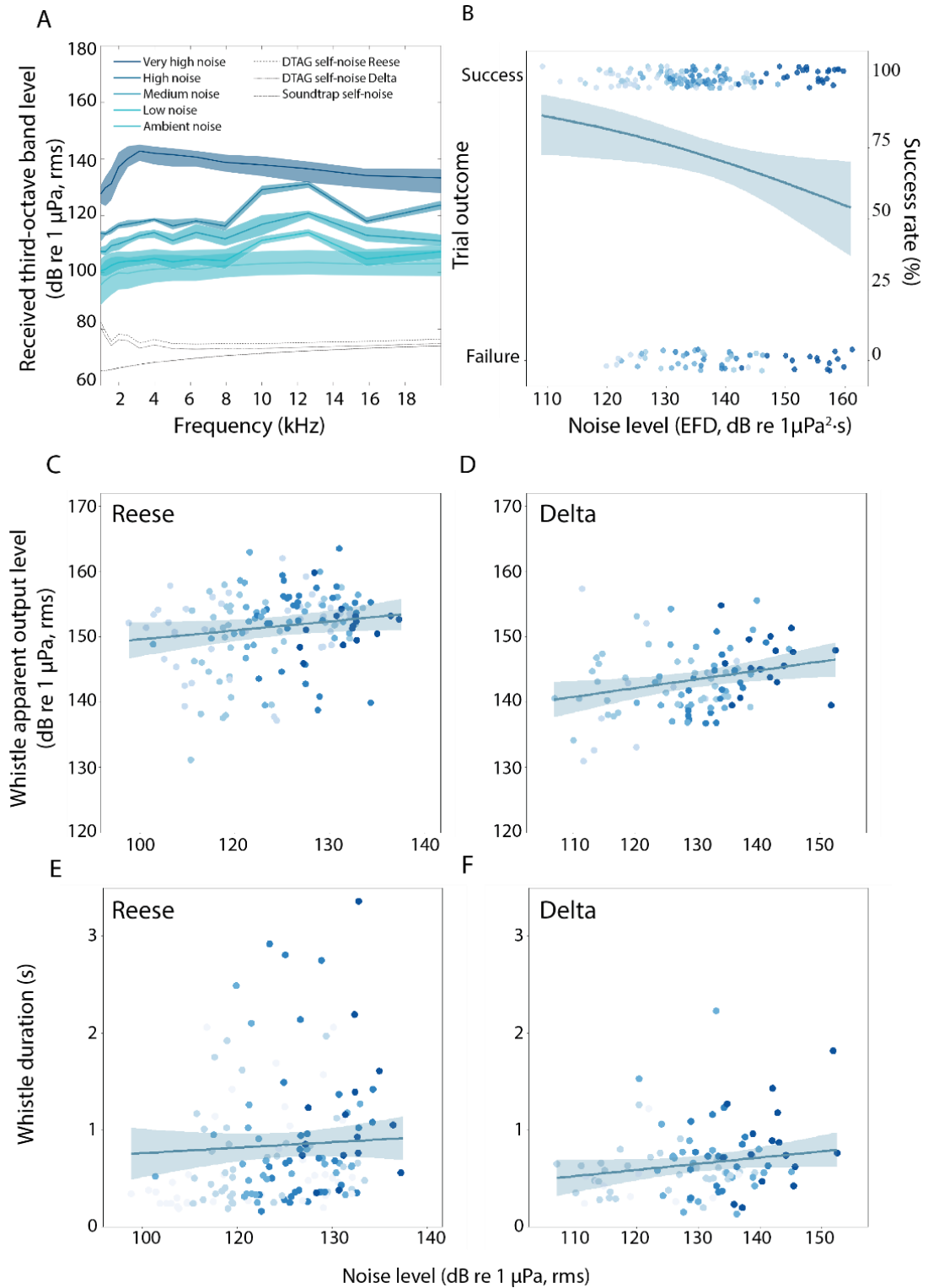


Figure 2.2. Noise exposure levels, success rate and acoustic compensatory measures. (A) The measured noise received levels (RL) recorded on a Soundtrap recorder at the location of the push buttons during experimental sessions quantified as third-octave level (TOL) bands in dB re 1 μ Pa, rms across third-octave level band frequencies 1 - 20 kHz (1 s integration bins). Noise treatment measurements are presented in graded colours of blue, with the lightest blue corresponding to the ambient noise control and the darkest blue the very high noise treatment. The ambient noise control corresponds to ambient noise at the push buttons during sessions,

where the speaker was deployed, but no stimuli played. The shaded areas represent the 25th and 75th TOL percentiles. Self-noise of the Soundtrap and DTAGs (also reported in TOLs) are plotted as dashed black lines. (B) Trial outcome (success or failure; left-hand y-axis) and success rate (%; right-hand y-axis) as a function of mean trial noise level as measured on the DTAGs (Energy flux density (EFD; dB re 1 $\mu\text{Pa}^2\cdot\text{s}$)). (C-F) Whistle apparent output level (AOL; dB re 1 μPa , rms, based on a 95% energy criterion) and whistle duration (seconds) as a function of noise level (NL) as measured on the tags just prior to whistle emission for the two dyad members (Reese C & E and Delta D & F). For (B-F) filled circles represent individual whistles and the colour represents the noise treatment category (lightest blue = ambient noise, darkest blue = very high noise). Model estimates are shown as the solid lines and the shaded area represent the 95% confidence intervals. **See also Table 2.7.S1 – 2.7.S3.**

We also provide experimental evidence that bottlenose dolphins will increase their call duration in response to noise. We found a positive relationship between whistle duration and NL for both dolphins, but this was only significant for Delta (Reese, LMM: $\beta \pm \text{SE} = 0.007 \pm 0.004$, $t = 1.81$, $p = 0.07$; Delta, LMM: $\beta \pm \text{SE} = 0.011 \pm 0.005$, $t = 2.09$, $p = 0.04$; Figures 2.2E & 2.2F); Delta produced significantly longer whistles as NL increased. While Reese's whistle durations were more variable and did not increase significantly, we should note his longest whistle was produced in the very high noise treatment (duration = 3.36 s), and on average, his whistles were longer during higher noise exposures (Table 2.1). For example, Reese's whistles were on average 1.85 times longer in the highest noise exposure trials compared to whistles emitted during the ambient noise trials, and Delta's whistles were on average 1.66 times longer in the very high noise trials compared to ambient noise trials (Table 2.1). Our model estimates showed that Reese increased the duration of his whistles by 2.8 ms per 1 dB increase in NL, whereas Delta increased his whistle duration by 7.2 ms per 1 dB increase in noise. It has previously been shown that male humpback whales (*Megaptera novaeangliae*) increase song duration when exposed to playbacks of low-frequency active sonar (Miller et al., 2000), and that killer whales (*Orcinus orca*) increase call duration in the presence of noise from vessels (Foote et al., 2004). In our experiment, both members of the dyad nearly doubled the duration

of their whistles in the highest noise treatment compared to ambient noise by both repeating whistle elements and stretching out the whole whistle contour. While the pattern of acoustic compensation is similar for the two dyad members, Reese also decreased the rate of whistle production with increasing noise (Table 2.1). This trend is less systematic for Delta, suggesting that increasing noise may impact individuals differently. Finally, both dolphins spent less time echolocating within each trial as the noise level increased (Reese, LMM: $\beta \pm SE = -0.008 \pm 0.001$, $t = -6.15$, $p < 0.0001$; Delta, LMM: $\beta \pm SE = -0.005 \pm 0.001$, $t = -3.96$, $p = 0.0002$).

2.3.2 Other behavioural compensatory mechanisms

We examined potential changes in physical behaviour as a response to increasing noise and found that each dolphin in the dyad was more likely to orient towards their partner with increasing noise (Generalised linear mixed-effects model (GLMM): $\beta \pm SE = 0.03 \pm 0.01$, $z = 2.08$, $p = 0.03$). Recent work has shown that bottlenose dolphin hearing sensitivity is directional, not only for echolocation clicks, but also for communication signals with energy below 30 kHz (Accomando et al., 2020). Each of our subjects increased their orientation towards their partner with increasing noise, but their echolocation decreased, suggesting that the dolphins were orientating towards each other not to use echolocation to track their partner, but to increase their chances of detecting their partner's signals. Their directional hearing may allow them to separate their partner's signals from that of the noise due to the spatial location of the two sources, also known as spatial release from masking (Accomando et al., 2020; Erbe et al., 2016). Listening to signal harmonics beyond the frequency band of the noise may also provide release from masking. Furthermore, we also found that each dolphin in the dyad was significantly more likely to visit the opposite half of the lagoon from where they pressed their buttons, ultimately coming closer to their partner, as the noise level increased (GLMM: $\beta \pm SE = 0.07 \pm 0.02$, $z = 4.00$, $p < 0.0001$). This behavioural strategy could also enable spatial release

for both signaller and receiver through a change in orientation and location relative to the noise and their partner, and facilitate the use of visual cues in a setting where noise may not only mask intentionally produced signals, but also passive acoustic cues, thus preventing eavesdropping on partner location (Götz et al., 2006; Gregg et al., 2007). Finally, we found no evidence that the dyad spent more time in sustained close physical proximity, i.e., swimming together in response to increasing noise (GLMM: $\beta \pm SE = 0.04 \pm 0.03$, $z = 1.71$, $p = 0.08$). Full results of all models can be found in the supplementary material (Table 2.7.S1 – 2.7.S3).

To summarise, we found that the dolphin dyad's success rate in the cooperative task decreased with increasing levels of anthropogenic noise, irrespective of their attempts to compensate by producing louder and longer duration whistles and by changing their physical behaviour to allow for better monitoring of their partner. This study is, to our knowledge, the first in any non-human species to show how increasing levels of anthropogenic noise negatively impacts coordination between conspecifics performing a cooperative task. Our findings reveal that noise can interfere with communication between individuals actively working together, and that behavioural compensatory adjustments are not necessarily sufficient to overcome the effect of noise.

Previous studies on the impact of noise have largely focused on the behavioural responses of the signaller, especially in terms of short- and long-term changes to signalling behaviour, however, in recent years studies on the response of receivers have emerged (Halfwerk et al., 2012; Kern and Radford, 2016; McMullen et al., 2014; Morris-Drake et al., 2017; Reed et al., 2021; Zhou et al., 2019), shedding new light on the impact of noise on the entire communication network. Using playbacks of conspecific signals overlapped by noise, these studies investigate the impact of noise on social interactions, including anti-predator behaviour

and territory defence. However, little is known about how noise impairs communication between conspecifics performing a cooperative task. Our study therefore provides new and compelling evidence that noise can have significant consequences on cooperative behaviour. This type of study would be very hard to replicate in the wild where we typically do not have a controlled understanding of cooperation or what the animals are attempting to achieve. However, given that cooperative behaviour is prevalent in many animal societies, and that anthropogenic noise is known to impact a range of taxa (Bruitjes and Radford, 2013; Francis et al., 2009; Morley et al., 2014; Tyack, 2008), our findings highlight that there is a need to account for the impact of noise disturbance on collective tasks in wild animal populations.

Finally, our study also sheds new light on the occurrence of actively coordinated collaboration among non-human animals (Duguid and Melis, 2020). While early studies on the Lombard response considered it to be an involuntary response in humans, later work showed that humans integrate information about noise and about the importance of getting the message across as they decide how much to modulate the level, and duration of their vocalizations (Lane and Tranel, 1971). In this study, the dolphins increased the level of their whistles in noise, nearly doubled whistle duration and oriented more towards their partner, indicating that both dolphins were actively attempting to compensate for noise to continue communicating with each other. These results support the interpretation that compensation for noise is more complex than a reflex in animals as well as in humans, and that our subjects flexibly modified their vocal signals and behaviour to facilitate cooperative success in response to noise (King et al., 2021).

2.4 Acknowledgements

We thank Peter Teglberg Madsen for valuable advice regarding the experimental setup and Kristian Beedholm for his help with creating the noise stimuli. We wish to thank Jesse Fox and Mandy Rodriguez for apparatus creation and troubleshooting, Marie Blanton and Sara Chi for assistance with training and data collection, research interns, and DRC's Animal Care and Habitat Team for assistance with the pressure washer. Finally, a special thanks to Delta and Reese and all the staff at DRC for their help and cooperation during this project. S.L.K. and P.M.S were supported by The Branco Weiss Fellowship – Society in Science awarded to S.L.K. This work was supported by a postgraduate research grant awarded to P.M.S. through the School of Biological Sciences at the University of Bristol. P.L.T. was supported by the US Office of Naval Research grants N00014-18-1-2062 and N00014-20-1-2709. The Dolphin Research Center staff were supported by a research grant from Jim and Marjorie Sanger.

2.5 Declaration of interests

The authors declare no competing interests.

2.6 STAR METHODS

2.6.1 EXPERIMENTAL MODEL AND SUBJECT DETAILS

Data were collected from September to November 2020 at the Dolphin Research Center (DRC) in Grassy Key, Florida. The subjects were two male bottlenose dolphins (*Tursiops truncatus*), Delta and Reese who at the time of data collection were 10 and 7 years, respectively. Both dolphins were born at DRC and lived together in natural seawater lagoons throughout the study period. All dolphins at DRC participate in three to five positive reinforcement training sessions each day (husbandry, research, play sessions, public interactions with trainers and guests, and research). The dolphin dyad was fed according to their normal daily routine during the study, which typically included capelin, herring, smelt, and squid three to five times per day, approximately 25-45% of which they received during each experimental session (up to three sessions per day). The University of Bristol granted animal ethics approvals and an internal committee at the Dolphin Research Center ethically approved this research. All aspects of animal care and habitat complied with the Standards and Guidelines of the Alliance of Marine Mammal parks and Aquariums. Research was non-invasive and strictly adhered to the laws of the United States of America.

2.6.2 METHOD DETAILS

2.6.2.1 Task apparatus and procedure

This task has previously been used in Jaakkola et al. (2018) and King et al. (2021), and a full description of the cooperative task setup and experimental procedure is provided in Jaakkola et al. (2018). Experiments were conducted in a natural seawater lagoon (dimensions 22.6 x 15.2 m) (Figure 2.1) and while there were other dolphins in nearby lagoons, the focal individuals were not able to physically interact with non-focal animals during the experiment.

The experimental setup consisted of two underwater push buttons equipped with pressure sensors and positioned 53 cm below the water's surface on either end of the lagoon (~18 meters apart).

During the experimental task the dolphins were required to swim across the lagoon and each press one of the underwater buttons simultaneously (within 1 s of each other), regardless of whether they were sent together or with a randomised delay of 5 or 10 s (where one individual was released first and the second individual was released after the delay). The push buttons were connected via a computer (Raspberry Pi model 3 B+) to an underwater speaker (University Sound UW-30). If the dyad pressed the buttons within the 1 s time interval, a 'success' sound would be played from the speaker, whereas if the buttons were pressed with > 1 s delay, a 'failure' sound would be played. In successful trials the dolphins would swim back across the lagoon for positive reinforcement of fish and social interaction, whereas no reinforcement was given in unsuccessful trials. Only the first press per button during each trial was registered, and thus the dolphins were not able to succeed by pressing the buttons repeatedly. The computer automatically recorded the following parameters for each trial: the time between button presses (accurate to 0.01 s), which button was pressed first, and the trial outcome (success or failure). A GoPro Hero5 (sampling at 59.94 frames/s; audio sample rate: 48 kHz) was positioned with a bird's-eye view of the lagoon to record the trials and a Canon Vixia HF R50 camera (sampling at 29.97 frames/s; audio sample rate: 48 kHz) in line with a HTI-96 min hydrophone was positioned behind the trainers (Figure 2.1). A Lubell underwater speaker (LL916C; Lubell Labs Inc., Columbus, OH, USA; frequency response: 0.2 – 23 kHz (0.5 – 21 kHz \pm 10 dB)) was deployed between the two push buttons at a depth of 1 meter (Figure 2.1). During each experimental session (duration: 6 m 24 s – 12 m 43 s) the dolphin dyad would perform 10 trials of the cooperative task while exposed to one of four noise

treatments or no added noise (referred to as ‘ambient noise’ trials) chosen at random. Three of the noise treatments were played back through the underwater speaker, but due to limitations of the speaker output we used the natural noise emitted from a pressure washer for the loudest noise treatment.

2.6.2.2 Noise stimuli

The dolphin dyad was asked to perform the task under either ambient noise conditions (control; mean 1-20 kHz broadband level \pm S.D.: 115 ± 6 dB re 1 μ Pa, rms) or when exposed to one of four noise treatments. Three broadband noise stimuli were created in MATLAB, using custom-written scripts, and filtered to correct for the uneven frequency response of the underwater speaker in the 1-20 kHz range as measured at 1 m distance, allowing a more uniform amplitude emission across frequencies. Each stimulus had a one-minute fade in and fade out period to avoid a startle response associated with the initiation of the noise. The fourth, and loudest, noise treatment was the familiar noise of the pressure washer that the Animal Care and Habitat Staff used to clean the lagoons (Figure 2.1). Prior to the experimental trials, the playback source levels of all noise stimuli were calibrated using a calibrated acoustic logger (Soundtrap; ST300-LF) and presented at four different 1-20 kHz broadband received levels (RL) as recorded at the location of the push buttons; (1) low noise (mean \pm S.D. = 119 ± 4 dB re 1 μ Pa, rms), (2) medium noise (mean \pm S.D. = 126 ± 2 dB re 1 μ Pa, rms), (3) high noise (mean \pm S.D. = 135 ± 1 dB re 1 μ Pa, rms) and (4) very high noise (pressure washer; mean \pm S.D. = 150 ± 4 dB re 1 μ Pa, rms). While performing the task the dolphins would experience a range of noise levels for each noise treatment as they moved from their release location to the push buttons. These noise levels overlap to some extent across treatments depending on where the dolphins were in the lagoon (Figure 2.2A).

Stimuli were presented through the Lubell Labs underwater speaker in line with a Lubell Labs modified power amplifier (TOA CA160) connected to a TASCAM DR-44WL digital recorder. The speaker was placed in the experimental lagoon directly between the two push buttons (Figure 2.1), to avoid the dolphins experiencing any potential spatial release from masking when located at the push buttons given their directional hearing (Accomando et al., 2020). For experimental trials with the very high noise exposure, the pressure washer was placed in the lagoon adjacent to the experimental lagoon (Figure 2.1). The dolphins were exposed and habituated to all noise stimuli prior to the experimental trials, but never engaged in the cooperative task while exposed to noise before the study was initiated (Table 2.7.S4). After a successful trial both individuals would typically leap out of the water in excitement, however, during the high and very high noise treatment it seemed the animals were sometimes not able to hear the success/failure sounds. In those instances, the dolphins would look to their trainers for visual confirmation and the trainers would provide them with the cue of success or the neutral response of failure.

2.6.2.3 Acoustic data collection

During all trials, a Soundtrap (ST300-LF; oceaninstruments.co.nz; sample rate: 288 kHz, clip level: 176 dB re 1 μ Pa, flat frequency response: 0.02 – 60 kHz \pm 3 dB) was deployed next to one of the two push buttons to continuously record noise level as received at the buttons. Both dolphins were equipped with high-resolution sound-and-movement recording tags (DTAG-3; (Johnson and Tyack, 2003; Johnson et al., 2009)) attached with four silicone suction cups recording 16-bit stereo sound (sample rate: 288 kHz, cliplevel: 178 and 180 dB re 1 μ Pa, flat frequency response: 0.5 – 150 kHz \pm 2 dB), allowing continuous recording of focal vocalisations as well as on-animal received noise levels (Figure 2.1). The tags also contain a pressure sensor, magnetometer, and tri-axial accelerometers sampling between 250 – 625 Hz.

Prior to each experimental session both dolphins were tasked to turn upside down, submerging the tags below water, after which a synchronisation signal (1 s downsweep; 20 – 1 kHz) was transmitted through the speaker to allow for time synchronisation of all acoustic recorders (DTAG-3s; HTI-96 min hydrophone; Soundtrap). The HTI-96 min hydrophone in line with the Canon video camera further allowed synchronisation of the acoustic recorders with video.

2.6.2.4 Noise recordings

The received noise levels during each trial were recorded on the Soundtrap next to the push buttons and were quantified as third-octave band levels (Figure 2.2A) and reported as mean 1-20 kHz broadband noise levels with a 1 s integration window (dB re 1 μ Pa, rms). For investigating the impact of noise on whistle acoustic parameters, noise level (NL, dB re 1 μ Pa, rms) was measured in a window prior to whistle emission. For examining the impact of noise on success rate, time spent echolocating and the occurrence of behaviours of interest within each trial, the average noise level as recorded on the tags was quantified as the energy flux density (dB re 1 μ Pa²·s).

2.6.2.5 Quantification of dolphin vocalisations

All DTAG acoustic data were extracted and audited using custom-written scripts in MATLAB R2013b (The Mathworks inc.). Each DTAG recording was processed by visual inspection of successive 5 s segments simultaneously displaying amplitude envelope, spectrogram (Hamming window, FFT: 512, 50% overlap) and dive profile with the option of listening to the synchronised audio (Johnson et al., 2009). During the auditing process the following parameters were marked: synchronisation sweeps, start and duration of whistles and echolocation click trains, start and duration of surface intervals (where the animal surfaced and the tag was above the water), and the start and end of all individual trials (as determined by

synchronising the acoustic data with the video data). Whistles were defined as tonal sounds with a duration exceeding 100 ms. Tonal sounds of less than 100 ms ('chirps' (Caldwell and Caldwell, 1968)) were excluded for the purpose of this study. Whistles produced by each of the tagged individuals were categorised as either signature or non-signature whistles through visual inspection of spectrograms (Hamming window, FFT: 1024, 50% overlap) for each individual whistle by two experienced observers. Whistles produced by the tagged individuals were further distinguished from those of non-focal individuals in nearby lagoons by 1) comparing whistle intensity between the two tags on the focal pair and 2) by a stereo angle-of-arrival (AOA) within ± 15 dB of the median AOA of each tagged individual's signature whistles (Johnson et al., 2009).

2.6.2.6 Quantifying in-situ noise exposure level

The noise exposure levels (NL, dB re 1 μ Pa, rms) as measured on the tags were filtered with a 1-25 kHz 6th pole bandpass filter and quantified as the root-mean-square (rms) sound pressure level (SPL_{rms}) in a 100 ms window ending 50 ms prior to each whistle. If loud whistles or clicks from the focal animal or nearby dolphins preceded the whistle, the 100 ms noise window was manually shifted to a period without clicks or whistles, 30 ms – 2 s (for one whistle we needed to use a noise window 2.96 s before the start of the whistle) before or after the whistle (N = 46). To examine the acoustic properties of dolphin whistles, the apparent output level (AOL, dB re 1 μ Pa, rms) of all whistles, as received on the tags while the animal was submerged, was quantified. First, the fundamental frequency contour of each marked whistle was manually tracked. Then, the fundamental, first and second harmonic were extracted using a custom-written time-frequency filter with a 1/8th octave bandwidth around each contour (Madsen et al., 2012). The filter captures the energy specific to each whistle, while removing noise outside each whistle contour. The energy in the fundamental, 1st and 2nd harmonic were extracted and

summed (Figure 2.7.S1). We then quantified whistle AOLs as the SPL_{rms} within a 95% energy window of each marked whistle (Jensen et al., 2012).

The noise level per trial as measured on the tags was filtered using a 1-25 kHz 6th pole bandpass filter and quantified as the energy flux density (EFD, dB re 1 $\mu Pa^2 \cdot s$) equal to the sum of the pressure squared across the duration of the noise. Prior to quantifying EFD for each trial, all periods of dolphin self-generated noise were removed (i.e., whistles, echolocation, surfacings, respirations), leaving only periods of noise present for assessment of the average noise level experienced on the tag within each trial. The measure of energy flux density was chosen to account for the difference in time periods available for noise level estimation within each trial. The final EFD noise level measure was averaged across the values for each dolphin. In two trials there were no periods available for quantifying noise on Reese's tag, as Delta pressed the button very shortly after Reese was released (0.5 and 3 s), both in 10 s delay trials. The noise level for these trials were therefore taken solely from Delta's tag.

2.6.2.7 Video coding

The dolphins' behaviours during the experimental trials were coded using the event-logging software BORIS (Friard and Gamba, 2016). Video recordings of trials were coded from the start of each trial (when dolphins were given a release hand signal) to the end of each trial as indicated by the success or failure sound (Example videos are available from the Dryad Digital Repository: doi:10.5061/dryad.g1jwstqv3) (Sørensen et al., 2023). Occasionally the success or failure sound was not audible, and the end of the trial was determined by the time of the first button press. For each experimental trial the following behaviours were coded (i) *waiting* defined as either of the dolphins not actively swimming for a minimum of 2 s, (ii) *time oriented towards the other dolphin* defined as the time each dolphin oriented their rostrum towards the

direction of their partner (anywhere along the full length of the other dolphin), (iii) *time spent in the other half of the lagoon* opposite to where each individual dolphin would push their button (the line separating the “two halves” goes from speaker location to the trainers location; see Figure 2.7.S2), (iv) *meet up* defined as the time the two dolphins crossed paths or were within one body length of each other and (v) *swimming together* defined as the time both dolphins have the same body orientation and are swimming within one body length of each other. All videos were coded by one observer. Additionally, two different observers independently coded 25% of all trials, corresponding to 10 randomly chosen trials per treatment and 50 trials in total. To assess agreement between raters, inter-reliability analyses were conducted for both experiments using the intraclass correlation coefficient (*ICC* function) for two-way models, using the ‘*irr*’ package in R studio (v. 1.4.11106). We found good agreement between our three observers for all behaviours combined ($ICC = 0.863$, $p < 0.0001$, $CI = 0.835 - 0.888$), however, when assessing behaviours separately the behaviours *meet up* and *wait* only scored moderate and poor agreement, respectively, and were, therefore, excluded from further analysis. We found good agreement for all remaining behaviours (*time oriented towards the other dolphin*, *time spent in the other half of the lagoon*, *swimming together*; $ICC = 0.894$, $p < 0.0001$, $CI = 0.864 - 0.919$).

2.6.3 Quantification and statistical analysis

All statistical analyses were conducted in R studio 1.4.1106 (R core Team, 2020 (R Core Team, 2020)). To determine whether an increase in NL impacted the ability of the dolphin dyad to successfully coordinate in the cooperative task, we built a binomial generalised linear mixed-effects model (GLMM; *lme4* package in R) with trial outcome as the response variable (0 = failure, 1 = success), average trial noise level (EFD, dB re $1\mu Pa^2 \cdot s$) as the predictor variable,

and session number (1-20) and day (data was collected over 8 days, hence 1-8) modelled as random effects.

To explore the impact of increasing noise on whistle apparent output level (AOL) we built linear mixed-effects models (LMM; *lme4* package in R), with whistle AOL (dB re 1 μ Pa, rms; 95 % energy window) as the response variable and noise level (NL, dB re 1 μ Pa, rms) as measured on the tag just prior to whistle emission as a continuous fixed effect for each of the two dolphins separately. We also built linear mixed-effects models to investigate the influence of NL on whistle duration for both individuals. Whistle duration was log transformed (to meet model assumptions) and set as the response variable with NL included as a continuous fixed effect. For both the AOL and duration models we included session number and trial (to account for the fact that some whistles were produced in the same trial) as random effects. Lastly, we investigated the use of echolocation by each member of the dyad during experimental trials by running a linear mixed-effects model with proportion of time spent echolocating as the response variable, average trial noise level (EFD, dB re 1 μ Pa²·s) as the continuous fixed effect, and session number (1-20) and day (1-8) as random effects.

We investigated potential changes in behaviour by examining the following behaviours in each trial: (i) *whether either dyad member looked towards their partner*, (ii) *whether the dyad visited the other half of the lagoon* and (iii) *whether the dyad members swam together* as a function of average trial noise level (EFD). We built binomial generalised linear mixed-effects models for each behaviour measure to investigate how noise level influences the occurrence of a given behaviour. The response variable was presence or absence of the behaviour in question, the fixed effect was trial noise level and session number (1-20) and day (1-8) were included as random effects.

For all models, we employed a traditional hypothesis testing approach where we used ANOVA (*stats* package in R) to test whether the full model (containing our fixed effect of interest) explained significantly more variance than the null model (without our fixed effect). Results of the full-null model comparisons can be found in the supplementary tables (Table 2.7.S1 – 2.7.S3). Model fit was assessed using residual diagnostic plots in the R *stats* package and the function *SimulateResiduals* from the R package *DHARMA* (Hartig, 2022). *SimulateResiduals* allows visual inspection of the overall deviations in residuals from the expected distribution and the model residuals as a function of the predicted values. It checks for normality, overdispersion and homogeneity of variance. The *effects* (Fox and Weisberg, 2019) and *ggplot2* (Wickham, 2016) packages in R were used to plot model estimates over the raw data. Data and R scripts associated with the analyses are available from the Dryad Digital Repository: doi:10.5061/dryad.g1jwstqv3 (Sørensen et al., 2023).

2.7 Electronic Supplementary Material

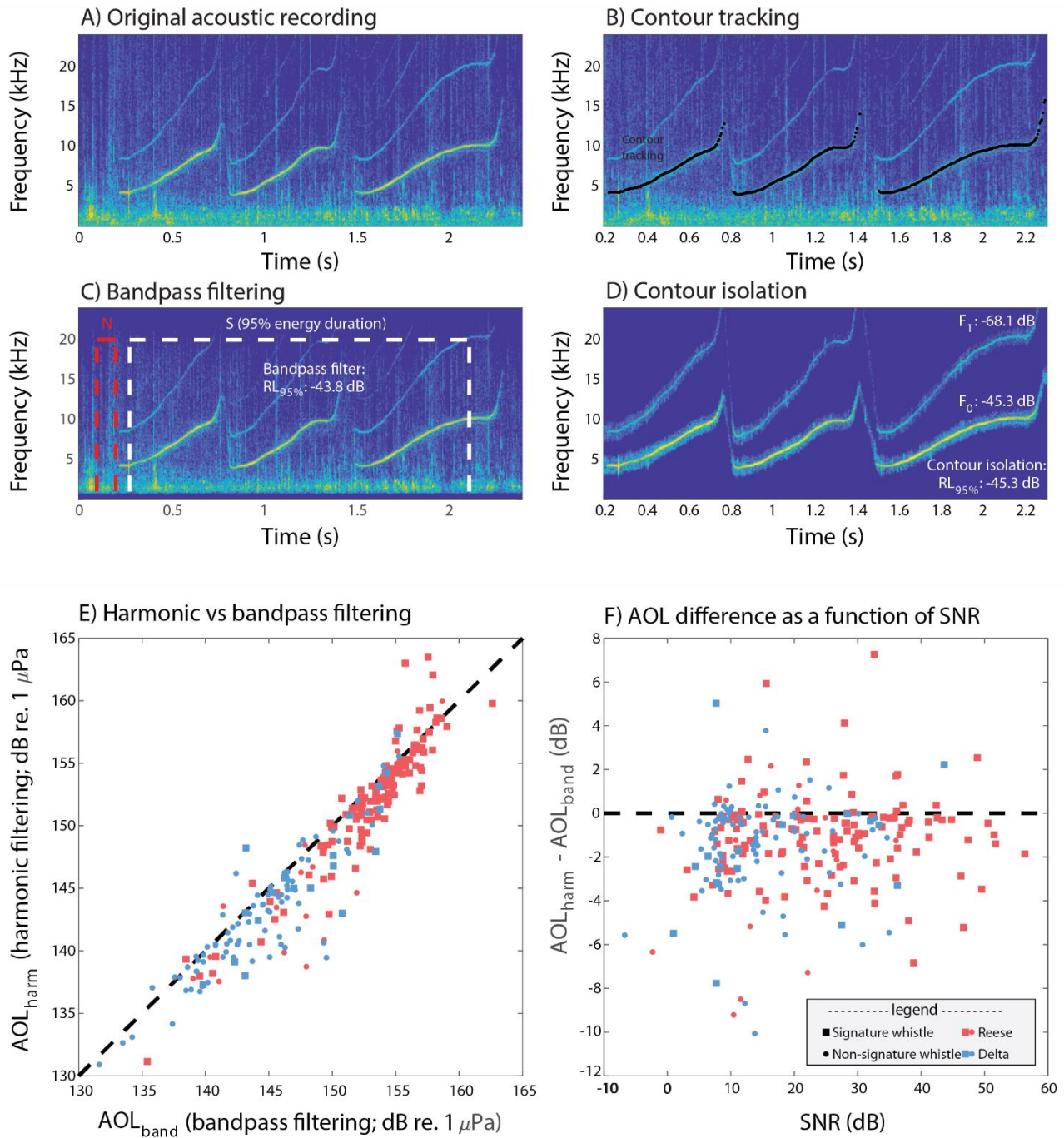


Figure 2.7.S1. Whistle contour isolation and comparison of a broadband and narrowband method for estimation of apparent output level. A time-varying narrow-band frequency filter was used to isolate the frequency contour and quantify the energy content of whistles of variable, and at times poor, signal-to-noise ratios. Here, we compare a standard broadband quantification of whistle apparent output level (AOL) to a narrow-band quantification of whistle AOL based on time-frequency contour isolation. For each whistle (A) a semi-

supervised algorithm was used to extract the fundamental frequency contour (B) at 5 ms temporal resolution. For broadband AOL quantification, the signal was then filtered with a 6-pole Butterworth bandpass filter with -3 dB cutoff points from 1 kHz to 25 kHz (C). For narrowband AOL quantification, the fundamental contour was used to isolate the fundamental and harmonic (using integer multiples of contour frequency) frequencies based on methods from Madsen et al. (2012), after which the narrow-band signal was reconstructed by summing waveforms of the fundamental and first two harmonics (D). For both approaches, the AOL was quantified by calculating the root-mean-square intensity within the 95% energy duration. (E) shows the difference in estimated AOL for the two methods which are generally highly correlated. (F) shows the difference in estimated AOL between the two methods as a function of SNR. Note that AOL tend to be lower using the contour isolation method, which is particularly true for some whistles that have a broadband burst-pulse component. Further, during the contour isolation method we exclude gaps between loops within a whistle of < 250 ms (Esch et al., 2009), which are not typically excluded during the bandpass filtering method and could therefore explain the lower AOLs for the contour isolation method. However, since the 95% energy duration is calculated separately for the bandpass filtered and narrow-band filtered waveform, estimated AOL can sometimes be higher for narrow-band filtering, and this is particularly true when occasional broadband signals such as clicks occur at the start or end of the whistle. **Related to STAR methods.**

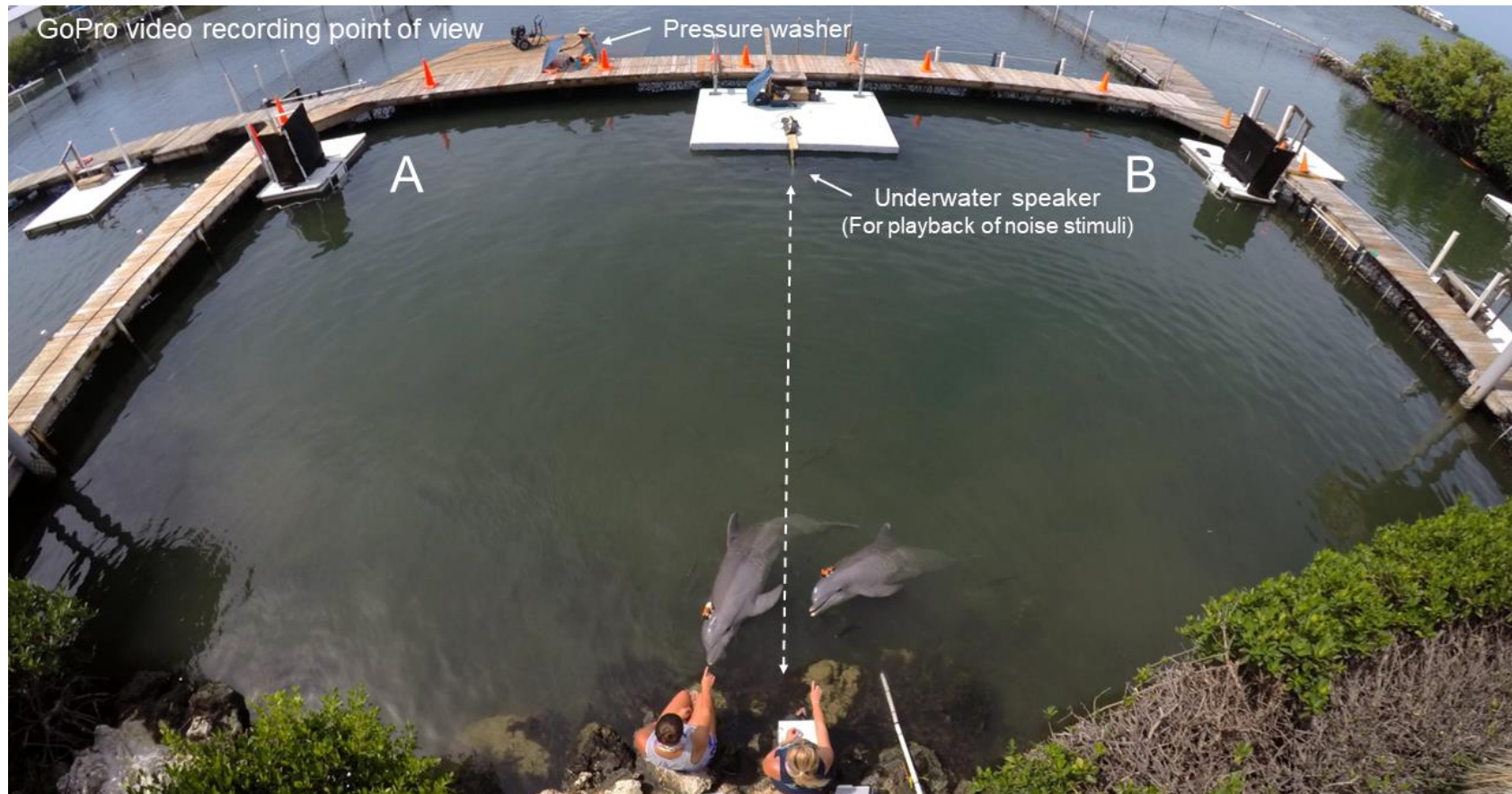


Figure 2.7.S2. Defining the behaviour “time spent in the other half of the lagoon”. Aerial view of the experimental lagoon showing how we define the “two halves” of the lagoon. The line separating the “two halves” goes from the location of the speaker to the location of the trainers. If one dolphin ends up pressing the button in part A, we show that it is more likely to visit part B of the lagoon prior to returning to part A in the high and very high noise treatment trials. **Related to STAR methods.**

Table 2.7.S1. Task success rate as a function of increasing noise. Model results for the generalised linear mixed-effects model with a binomial family investigating how noise level (NL quantified as energy flux density; dB re 1 μ Pa²·s) predicts the proportion of successful trials in the cooperative task. Trial outcome (success = 1, or failure = 0) was the response variable, noise level was the continuous fixed effect and session number (1-20) and day (1-8) were included as random effects. Significance codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05 < . < 0.1. **Related to Figure 2.2B and STAR methods.**

<i>Model</i>	<i>Parameter</i>	<i>Estimate (β)</i>	<i>CI (2.5 %)</i>	<i>CI (97.5 %)</i>	<i>Std. error</i>	<i>z/t-value</i>	<i>P value</i>
glmer(outcome ~ NL, EFD + (1 session) + (1 day))	Intercept	5.40868	1.61038	9.34040	1.96345	2.755	0.00587**
	NL	-0.03261	-0.06081	-0.00513	0.01414	-2.307	0.02105*

Table 2.7.S2. Investigating acoustic compensatory mechanisms. Model results of the linear mixed-effects models examining how noise impacted whistle apparent output level (AOL) and duration, and proportion of time spent echolocation; (i) Model results of the linear mixed-effects models examining how increasing noise levels predict whistle AOL (dB re 1 μ Pa) for the two individuals participating in the experiment (Reese and Delta). Whistle AOL (SPL_{rms} within a 95% energy window) is included in the model as the response variable and noise level (NL, dB re 1 μ Pa, rms) measured in a 0.1 s window prior to whistle emission as the continuous fixed effect. (ii) Model results of the linear mixed-effects models examining how increasing noise levels predict whistle duration (seconds) for the two participants. Whistle duration was included in the model as the response variable and noise level (NL, dB re 1 μ Pa, rms) as a continuous fixed effect. Whistle duration was log transformed to ensure the assumptions of the linear model were not violated. ^a The values here represent the slope of the log-transformed data. In the manuscript we report the slopes of the model based on non-transformed data as a proxy for how whistle duration increased as a function of NL (Reese: 2.8 ms per 1 dB increase; Delta: 7.2 ms per 1 dB increase). For both (i) and (ii), session number and trial number (accounting for the fact that some whistles were produced in the same trial) were included as random effects. (iii) Model results of the linear mixed-effects models investigating how noise level per trial as measured on the tags (NL quantified as energy flux density (EFD); dB re 1 μ Pa²·s) predicts the proportion of time each of the two dolphins (Reese and Delta) spent echolocating relative to trial duration. Proportion of time spent echolocating during each trial was included in the model as the response variable, noise level was included as the continuous fixed effect and session number (1-20) and day (1-8) were included as random effects. Significance codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05 < · < 0.1. **Related to Figure 2.2C-2.2F and STAR methods.**

<i>Model</i>	<i>ID</i>	<i>Parameter</i>	<i>Estimate (β)</i>	<i>CI (2.5 %)</i>	<i>CI (97.5 %)</i>	<i>Std. error</i>	<i>z/t-value</i>	<i>P value</i>
(i) lmer(AOL ~ NL + (1 session) + (1 trial))	Reese	Intercept	141.29409	132.16405	150.26331	4.55901	30.992	< 0.0001***
		NL	0.08178	0.01323	0.15165	0.03482	2.349	0.0203*
	Delta	Intercept	124.64311	112.35793	136.94940	6.31299	19.744	< 0.0001***
		NL	0.14219	0.047910	0.23629	0.04833	2.942	0.0048**
(ii) lmer(log(duration) ~ NL + (1 session) + (1 trial))	Reese	Intercept	-1.29000	-2.27692	-0.31547	0.500219	-2.579	0.0110*
		NL	0.00690 ^a	-0.00054	0.01444	0.003819	1.808	0.0729
	Delta	Intercept	-2.00689	-3.40755	-0.58836	0.69627	-2.882	0.00537**
		NL	0.01111 ^a	0.00026	0.0218	0.00532	2.090	0.04054*
(iii) lmer(proportion of time spent echolocating ~ NL, EFD + (1 session) + (1 day))	Reese	Intercept	1.50731	1.12093	1.91053	0.18371	8.205	< 0.0001***
		NL, EFD	-0.00819	-0.01111	-0.00539	0.00133	-6.152	< 0.0001***
	Delta	Intercept	1.20961	0.85381	1.56651	0.16493	7.334	< 0.0001***
		NL, EFD	-0.00476	-0.00736	-0.00216	0.00120	-3.959	0.000293***

Table 2.7.S3. Investigating behavioural compensation mechanisms. Model results of the generalised linear mixed-effects models with binomial families investigating the occurrence of the behaviours (i) ‘looking towards partner’, (ii) ‘visiting the other half of the lagoon’ and (iii) ‘swimming together’ as a function of within trial noise level (NL, quantified as energy flux density (EFD); dB re 1 μ Pa²·s). The presence or absence of the given behaviour was included as the response variable and NL as the continuous fixed effect. Session number (1-20) and day (1-8) were included as random effects. Significance codes: 0 < *** < 0.001 < ** < 0.01 < * < 0.05 < . < 0.1. **Related to Figure 2.7.S2 and STAR methods.**

<i>Behaviour</i>	<i>Model</i>	<i>Parameter</i>	<i>Estimate</i> (β)	<i>CI (2.5 %)</i>	<i>CI (97.5 %)</i>	<i>Std. error</i>	<i>z-value</i>	<i>P value</i>
(i) ‘looking towards partner’	glmer(behaviour[i] ~ NL, EFD + (1 session) + (1 day))	Intercept	-3.24577	-8.23851	0.59329	1.99046	-1.631	0.103
		NL, EFD	0.03045	0.00230	0.06709	0.01468	2.075	0.038 *
(ii) ‘visiting the other half of the lagoon’	glmer(behaviour[ii] ~ NL, EFD + (1 session) + (1 day))	Intercept	-9.80891	-14.77454	-4.84329	2.53353	-3.872	0.000108 ***
		NL, EFD	0.07418	0.03785	0.11051	0.01854	4.002	< 0.0001 ***
(iii) ‘swimming together’	glmer(behaviour[iii] ~ NL, EFD + (1 session) + (1 day))	Intercept	-8.68508	-15.77844	-1.31173	3.61730	-2.401	0.0164 *
		NL, EFD	0.04416	-0.00952	0.09341	0.02580	1.712	0.0870

Table 2.7.S4. Noise habituation and animal motivation. Related to STAR methods.

	Description
Noise habituation	<p>Prior to the start of the study, the two focal individuals, Delta and Reese, and the dolphins in the surrounding lagoons, were all habituated to the noise stimuli (low to high noise treatments) until they displayed normal behaviour as observed by their trainers and caretakers who know them extensively. The use of the pressure washer (very high noise treatment) to clean the lagoon was a normal part of their week before the experiments began, and the dolphins were fully habituated to this noise source. The dolphins live in natural sea water lagoons and will therefore experience unpredictable noises regularly, which they are used to being exposed to, such as boats of all sizes, jet skis, helicopters, planes/jets going to Marathon airport or Key West, visiting wild dolphins or manatees, various other marine life, work on neighbouring docks etc. There was never any visual or acoustic indication of an avoidance of the speaker or the pressure washer, and both focal dolphins would swim straight past the speaker during the noise trials. Between trials the dyad would also perform other behaviours (dives etc.), which took them around the lagoon without hesitation. We also observed no large difference in trial duration between the different treatments (mean trial durations \pm S.D: ambient noise = 14.0 ± 2.2 s; low noise = 14.8 ± 2.4 s; medium noise = 14.4 ± 2.3; high noise = 14.2 ± 2.2 s; very high noise = 16.7 ± 2.7 s). For the highest noise treatment, the trial duration was about 2s longer. For this treatment the pressure washer was placed outside of the lagoon. The results show that the dyad was significantly more likely to visit the opposite half of the lagoon (where they would experience a similar range of noise levels) as to where they would end up pressing the button (Table 2.7.S3), to check on their partner, perhaps explaining why they spent a few seconds longer in completing the trial.</p>
Animal motivation	<p>The dolphin dyad who participated in this experiment was one of three dyads trained to perform this cooperative task as per Jaakkola et al. (2018) and King et al. (2021). This dyad was chosen specifically for this study because of their high motivation and eagerness to participate in the task. Indeed, during the noise exposure trials, the dyad always attempted to complete the task by closely approaching their push button. Occasionally they would go to the button and not press (e.g., if their partner had already pressed and they heard the failure sound before reaching the button), but they would always go to the button i.e., they would always participate in the task. When the dyad was not successful the mean time between button presses was 1.8 s, revealing that they were still attempting to coordinate their button presses (failing the task by an average of 800 ms). Further evidence that both animals were highly motivated to participate in the task can be seen in their reactions to when they were successful; they would typically leap out of the water, which they do when they are excited. There was never any visual or acoustic indication of an avoidance of the speaker or the pressure washer, which we would have expected had the noise been painful to the animals. In fact, the dolphins would sometimes swim straight past the speaker during the noise trials, and they would also do other behaviours between trials (dives etc.) which took them around the lagoon without hesitation. Houser et al. (2013) showed that bottlenose dolphins rapidly habituate to received noise levels of ≤ 160 dB re 1 μPa, whereas a lack of habituation occurs at received noise levels of ≥ 175 dB re 1 μPa. Even the highest noise treatment in this study had received levels well below 160 dB re 1 μPa. Finally, the increase in whistle AOL and duration with increasing noise is strong evidence that the dolphins were attempting to compensate for the noise so that they could continue to communicate to succeed in the task. If the dolphins were demotivated or if the noise was “felt as painful” we would predict that they would cease to communicate.</p>

2.8 References

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Chapter 3 | Quantification of the acoustic parameters of pops and whistles produced by male bottlenose dolphins in Shark Bay, Western Australia

3.1 Summary

Sound is used by a variety of species across the animal kingdom, as it often allows communication over ranges that surpasses that of other sensory modalities. However, the range over which effective communication is available varies depending on the acoustic parameters of the signal, the properties of the environment and the hearing capabilities of the receiver. In Shark Bay, Western Australia, male Indo-Pacific bottlenose dolphins form multilevel alliances that compete against rival males over access to oestrus females. Alliance behaviour is mediated by whistles that function in aiding group cohesion and individual recognition, and pops that function as an agonistic, come-hither signal inducing sexually coerced females to stay close to the popping male. While the use and function of these sounds have been studied extensively, the properties and communication ranges of these signals have never been quantified. Here, empirical measures of whistle and pop apparent source levels, sound transmission loss and ambient noise levels were collected from across the Shark Bay study area. Dolphins produced whistles and pops with mean source levels of 141.4 ± 5.6 and 135.1 ± 4.9 dB re 1 μ Pa (rms) and centroid frequencies of 9.1 ± 4.3 and 1.8 ± 1.5 kHz, respectively. Transmission loss was near-spherical for whistles ($k = -20.7$) and was greater for whistles compared to pops ($k = -16.4$). Mean ambient noise levels varied widely across the study site, leading to large variations in detection range. Across sites, communication ranges were estimated as 246 to 1912 m for pops, and 154 to 1482 m for whistles. Pops therefore appear to transmit over slightly larger distances compared to whistles, which may have implications for eavesdropping by rival males.

3.2 Introduction

Communication is of vital importance in supporting social interactions in the animal kingdom, playing a role in group cohesion, social affiliation, individual recognition, and in more complex behaviours such as cooperative foraging or sexual coercion (Bradbury and Vehrencamp, 1998). To communicate with conspecifics, specialised sensory systems have evolved to facilitate the transmission of information (Laidre and Johnstone, 2013). For animals living in dispersed societies, where maintaining contact with conspecifics at a distance is especially important, acoustic signalling is often, but not always (Jackson and Ratnieks, 2006), used. This is true for animals living in both terrestrial and aquatic environments, but many animals living in aquatic environments rely heavily on sound as most other sensory modalities only allow communication over a few tens of meters (Vogel, 1981; Warrant and Locket, 2004). In contrast, the acoustic properties of sound allow long-range communication (Urlick, 1983). The acoustic communication range (i.e. the effective range over which a signal can be detected by conspecifics (Marten and Marler, 1977)) largely depends on the amplitude and frequency of the sound, with lower frequencies propagating further. As such, the very low frequency sounds of an elephant rumbling or a baleen whale singing are likely to travel over very long distances (Garstang et al., 1995; McComb et al., 2003; Payne and Webb, 1971), whereas the ultrasonic alarm calls of ground squirrels or communication calls of harbour porpoises will only be audible for conspecifics close by (Clausen et al., 2010; Sørensen et al., 2018; Wilson and Hare, 2006). However, the properties of the environment will also impact the effective communication range; variation in habitat structure (e.g. bathymetry and canopy cover) may act as reflective boundaries to amplify some sound frequencies, while attenuating others, and in the marine environment, temperature, salinity, bottom vegetation etc. can also impact sound transmission (Quintana-Rizzo et al., 2006; Urlick, 1983). Finally, the auditory capabilities of the receiving animal and especially the prevailing ambient noise levels also play a considerable role in signal detection (Bradbury and Vehrencamp, 1998; Urlick, 1983).

Communication has been defined as the transmission of information from a sender to a receiver, with benefits to both (Bradbury and Vehrencamp, 1998). As a result, social sounds often benefit from long-range transmission. However, when individuals communicate, there is the possibility that other animals may eavesdrop on the signal and exploit the information for their own benefit (Bradbury and Vehrencamp, 1998; Peake, 2006). This leads to a trade-off between maximising your own communication range, while reducing the risk of eavesdropping from potential rivals or predators (Morisaka and Connor, 2007; Wilson and Hare, 2006). For example, Heaviside's dolphins have evolved two types of clicks; narrow-band, high frequency clicks that allow them to forage and navigate outside the hearing range of a predator, the killer whale, and clicks of lower frequency that facilitate communication with conspecifics while they selectively relax their acoustic crypsis (Martin et al., 2018). Similarly, ground squirrels will switch to using ultrasonic alarm calls when closer to stimuli representative of a predator (Wilson and Hare, 2006).

In Shark Bay, Western Australia, a population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) have been studied for more than four decades (Connor and Krützen, 2015). Unrelated male dolphins in this population are well-known for their formation of multilevel alliances that comprise three levels or 'orders'; where the core social unit is the second-order alliance, consisting of 4-14 males (Connor and Krützen, 2015). Within the second-order alliance, males will work together in pairs or trios (first-order alliance) to pursue and herd single oestrus females in 'consortships'. Two or more second-order alliances will also associate preferentially and cooperate (third-order alliances) in the defence and theft of females from rival alliances (Connor et al., 2022).

To mediate the complex range of behaviours shown by this population is an impressive variety of acoustic communication signals; burst pulsed sounds, creaks, squeals, pops, and

whistles. Of these, the use of whistles and pops are the most well-studied (Connor and Smolker, 1996; King et al., 2018; King et al., 2019; King et al., 2021; Moore et al., 2020; Vollmer et al., 2015). Whistles are tonal, frequency modulated sounds normally categorised as non-signature and signature whistles. Signature whistles are individually distinctive identity signals that function as vocal labels (Bruck et al., 2022; Caldwell and Caldwell, 1965; King and Janik, 2013; Sayigh et al., 1990). Signature whistles are generally stable across an individual's life time (Sayigh et al., 2022) and facilitate individual recognition (Janik et al., 2006; Sayigh et al., 1990) and group cohesion (Janik and Slater, 1998; King et al., 2021). In Shark Bay, males from the same second-order alliance also have notably different signature whistles (King et al., 2018). Signature whistles have been shown to allow second-order allies with weaker social bonds and lower rates of affiliative physical contact to maintain vital cooperative relationships through whistle exchanges (Chereskin et al., 2022). Males will also respond strongly to the sound playbacks of signature whistles from second-order allies, as opposed to third-order allies, demonstrating that dolphins form a concept of team membership at the second-order level, independently of bond strength across all three alliance levels (King et al., 2021). While whistles are used by both sexes, pops are only produced by males and almost exclusively during consortships (Connor and Smolker, 1996; Vollmer et al., 2015). Pops are emitted in repetitive trains, consisting of 9-10 pops per train, and used by males as a 'come-hither', female-directed signal of aggression, which appears to induce the female to remain close to the popping male (Connor and Smolker, 1996; Moore et al., 2020; Vollmer et al., 2015). Pops largely function as a coercive signal with a strong association with physical threats (Connor and Smolker, 1996), but may also enable guard switching between first-order allies (King et al., 2019). A recent study also showed that allied males will engage in acoustic synchrony while consorting a female, by actively matching each other's pop tempo and pop production (Moore et al., 2020).

Yet, despite extensive knowledge on the use and function of these sounds for mediating complex social behaviours, the acoustic properties and communication ranges of pops and

whistles produced by the Shark Bay dolphins have never been investigated. Here, I quantify whistle and pop apparent source levels and frequency content and combine these estimates with empirical measures of background ambient noise levels and sound transmission loss to estimate communication range. Investigating the characteristics and effective communication range of both whistles and pops will help further our understanding of the use of these signals as well as how the social functions that these signals mediate may be impacted by increasing anthropogenic noise.

3.3 Methods

Sound transmission estimates, whistle and pop acoustic recordings and ambient noise level measurements were collected between September and early December 2019 in the eastern gulf of Shark Bay, Western Australia. Shark Bay is a shallow water, sub-tropical embayment characterised by significant variation in bathymetry (i.e. measures of depth below sea level) and habitat structure. Here, research on the Indo-Pacific bottlenose dolphins have been carried out on a near-annual basis, typically during the austral winter through spring for 40 years (www.sharkbaydolphins.org; Connor and Krützen, 2015). All experimental procedures were conducted from a 5.4-meter Quintrex Bowrider Vessel (Yamaha 100hp outboard engine) and only in optimal observational and recording conditions i.e. no rain, light wind, and a sea state ≤ 3 .

3.3.1 Sound transmission measurements

Sound transmission experiments followed a similar procedure to that of Jensen et al. (2009) and were conducted between 1 September and 29 October 2019 using six SoundTrap acoustic recorders (Ocean Instruments, Auckland, NZ). This setup permitted simultaneous recording of played back sounds at six receivers deployed in a straight line (cliplevels = 174 – 176 dB re 1 μ Pa; sampling rate: 96 kHz; 16-bit, flat (± 3 dB) frequency response from 0.02 – 60 kHz).

Each SoundTrap was deployed 1.5 meters below the water surface between a surface buoy and a ~8 kg anchor, permitting easy deployment and retrieval. The transmission experiments were performed at various locations across the study site, and at varying depths (range 4 – 14 meters), to ensure measurements were representative of the variation in habitat structure. Upon arrival at a location, each SoundTrap was deployed on a roughly straight line from the expected playback location, at a distance of approximately 20 m, 40 m, 80 m, 160 m, 320 m and 640 m (Appendix; Figure 3.7.1). Following deployment, the research vessel was anchored at approximately 20 meters from the location of the first SoundTrap along the same transmission line. Each SoundTrap was always deployed in the same position relative to the boat (i.e. SoundTrap with ID 1 was always deployed at the 20 m position). From the boat, an underwater speaker (Lubell Labs LL916C; frequency response: 0.2 – 23 kHz, ± 10 dB) was lowered to a depth of 1.5 m for playback of the sound stimuli. The underwater transducer was connected to a Lubell Labs modified amplifier (TOA CA160) powered by a 12V battery. Via the auxiliary port on the amplifier a handheld recorder (Tascam DR-44WL) was connected on which all sound stimuli were kept and played back. After the first eight playbacks, we switched to using a laptop for playback of sound stimuli due to technical difficulties with the TASCAM. Three types of stimuli were used for playbacks: (i) bottlenose dolphin signature whistles recorded from dolphins in human care (Dolphin Research Center, Florida), (ii), pseudo-random white noise (center frequencies of 2-24 kHz at 2 kHz increments) and (iii) fast and slow dolphin ‘pop’ trains. Each individual signal of each type was played back 15 times, except for the pop trains which were played back either two or three times as each sequence contained either 38 (slow pop sequence) or 71 individual pops (fast pop sequence). A downsweep (1 s duration, 25 to 1 kHz) was played back before and after each full playback sequence to allow for time synchronisation of all acoustic recorders. GPS waypoints were taken at deployment and retrieval of all SoundTraps and at the location of the underwater speaker before and after playback. Additionally, the distance between the speaker and the first three SoundTraps were

continuously measured during the playback session using a laser range finder (Bushnell laser range finder) and annotated via a microphone to a multitrack recorder (TASCAM DR-680 MKII) to ensure any changes in distance between the speaker and the array of SoundTraps were recorded.

3.3.2 Sound transmission analysis

Recordings from all six SoundTraps were visually inspected using Adobe Audition (Version 5.0). The start and end time of the synchronisation signal were marked in all six acoustic recordings, and additionally all played sounds were marked in the recording from the SoundTrap closest to the sound source (deployed at 20 m from the boat). This allowed extraction of the start and end times of all recorded stimuli across all loggers by calculating the time difference between the synchronisation signal and the stimuli in the closest SoundTrap. Any delays due to travel time (i.e. longer travel time to loggers further away from sound source) were accounted for by cross-correlating across synchronisation stimuli.

The received level of each recorded stimuli and a 0.5 s noise window preceding all recorded stimuli on all SoundTraps were then estimated using custom-written scripts in Matlab v. 2018b (Mathworks, Inc.). This was done by first bandpass filtering all stimuli using stimulus-specific 4th pole bandpass filters in a band around the minimum and maximum frequency content of the given stimuli and the noise preceding each stimulus, ending 0.1 s before the start of the stimulus. Secondly, the received level (RL) of all stimuli and the noise level (NL) were quantified as the root-mean-square (rms) sound pressure level (SPL_{rms} ; dB re 1 μ Pa, rms). The signal-to-noise ratio (SNR) was then calculated as the difference between the RL of the stimuli and the NL of the preceding noise window, and only stimuli with a $SNR > 6$ dB were included for further analysis. As each individual pop in the pop train stimuli was emitted with an inter-pop-interval less than 0.5 s, the same noise window of 0.5 s preceding the whole pop train was used to estimate SNR for each individual pop. Sound transmission within the habitat was not

straightforward; in some instances, the SNR of a recorder further away from the source (e.g. SoundTrap at location 4 relative to the sound source) would have a $\text{SNR} > 6$ dB, despite the fact that a recorder closer to the sound source (e.g. SoundTrap at location 3) had a $\text{SNR} < 6$ dB, which was consistent across repetitions of the same stimuli. In all cases, if the RL of a stimuli was recorded with a $\text{SNR} < 6$ dB, the RL of that same stimuli on any recorders further away from the source would be excluded from further analysis. For all repetitions of the same stimuli at each location, a linear regression model was fitted to correlate RL with log-transformed range using the *fitlm* function in Matlab. The slope of the line of best fit was extracted and considered the transmission loss coefficient (k). Finally, a mean estimate of k for each stimuli type was calculated.

3.3.3 Acoustic recordings

Acoustic recordings were collected from September – November 2019 during focal follows of adult male dolphins, primarily when they were consorting a female. Upon encountering a group of male dolphins, the group would be approached to within 30 meters and the team would conduct a minimum 5-minute survey to identify individuals, assess group composition (as defined by the 10 m chain rule; where each dolphin in the group is within 10 m of any another individual) and behavioural activity (Smolker et al., 1992). Individual dolphins were identified by trained observers based on the shape and pattern of their unique dorsal fins and their ID was confirmed with photo-identification data collected with a Canon 50D camera and a Canon 100-400 mm IS lens. After completion of the survey, we would initiate our focal follow of the group and deploy the hydrophones for acoustic recordings. Recordings were made using a horizontal, towed hydrophone array consisting of four HTI-96 MIN series hydrophones (clip level: 167 – 168 dB re 1 μPa , flat (± 1 dB) frequency response: 0.002 – 30 kHz) deployed in a rectangular formation around the research vessel, allowing estimation of the bearing to the vocalising animal(s) (King et al., 2018; Quick et al., 2008) (Figure 3.1). All hydrophones were suspended

to a depth of 1.5 meters and each in line with a TASCAM DR-680 MKII multi-track recorder (sample rate: 96 kHz), synchronised to a spoken track used to note bearing, individual identification, and distance to the focal individual(s).

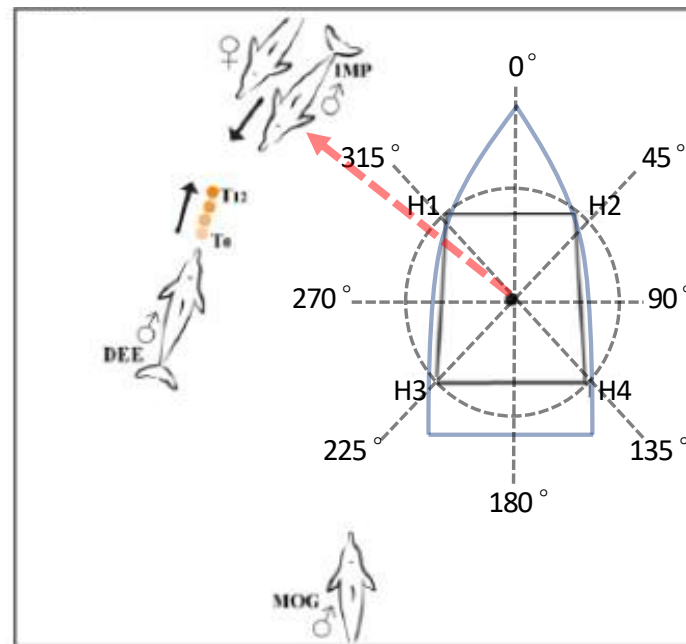


Figure 3.1. Experimental setup for acoustic recordings. Upon approaching a group of dolphins (three-letter codes represent animal identification), an array consisting of four hydrophones was deployed (H1-H4). During the focal follow a team member would stand in the middle of the boat (black dot) with a laser range finder to estimate distance to the individuals, as well as estimating the bearing to the focal individuals when whistle or pops were heard in real-time on the boat through the built-in speaker on our multi-track recorder (TASCAM DR-680 MKII). Voice notes were annotated on to a spoken track synchronised to the acoustic recordings. During acoustic analysis, the software TOADy (Quick et al., 2008) was used to confirm pop and whistle bearings allowing us to allocate bearing and distance estimates to the individual producing the vocalisation. Modified from King et al., 2019.

Distances were measured with a Bushnell Laser Range finder by a team member standing in the middle of the boat at the midpoint of the hydrophone array. The bearing was given according to a compass bearing with the bow considered 0° (Figure 3.1). The vessel engine was turned off during recordings to allow the hydrophones to settle to the desired depth and to avoid noise masking our acoustic recordings.

3.3.4 Hydrophone calibrations

A relative calibration of the acoustic sensitivity of all HTI-96 MIN hydrophones in line with the TASCAM (DR-680 MKII) were conducted prior to and after recordings using a calibrated acoustic recorder (SoundTrap ST300; Oceaninstruments.co.nz; cliplevel = 177 dB re 1 μ Pa) as a reference.

3.3.5 Whistle and pop analyses

All acoustic recordings were first analysed in Adobe Audition (Version 5.0) by visually inspecting the signal envelope and spectrograms (FFT = 1048, hamming window) simultaneously. Whistles and pop trains (sequences of pops with stereotyped inter-pop-intervals; Moore et al. 2020) were individually identified and marked. Similarly, the synchronised voice notes were aurally inspected and distance and bearing cues marked. Using custom-written Matlab code, start and duration information were extracted for each acoustic recording.

All source parameters were quantified in Matlab (v. 2018b) based on equations from Madsen and Wahlberg 2007. For each whistle, three measures of amplitude were quantified: The received level (RL) was estimated (i) as the root-mean-square (rms) sound pressure level (SPL_{rms} ; dB re 1 μ Pa, rms) within a 95% energy window, (ii) as the maximum value of a SPL_{rms} running average across a 200 ms window, corresponding to the dolphin auditory integration

time at whistle frequencies (Johnson, 1968) and (iii) as the energy flux density (EFD; dB re 1 $\mu\text{Pa}^2\cdot\text{s}$) calculated as the sum of the pressure squared over the 95% energy duration of each whistle. For each individual pop, the RL was calculated (i) as the peak-peak SPL (dB re 1 μPa), (ii) as the EFD and (iii) as the SPL_{rms} across the D-duration (D_{Dur}) of the pop, given by the -10 dB end points relative to the peak envelope of the waveform, estimated by using the absolute value of the analytical signal (Madsen and Wahlberg, 2007). The apparent source levels (ASL), defined as the back-calculated SPL at 1 meter in any direction from the source of unknown orientation relative to the acoustic axis, were calculated for both whistles and pops based on the passive sonar equation:

$$\text{ASL} = \text{RL} + \text{TL} [1],$$

where RL is the received level of the signal at the hydrophones and TL is the transmission loss. Separate TL estimates measured for whistles and pops were obtained based on the empirical measures of transmission loss: $\text{TL} = k \cdot \log(\text{range to focal animal})$ [2], where k is the transmission loss coefficient. Here, we used the k obtained from the playback of the 2 kHz and 10 kHz pseudo-random white noise stimuli, close to the centroid frequency of pops and whistles, respectively.

Frequency parameters for both whistles and pops were calculated as the centroid frequency (F_C), defined as the frequency midpoint dividing the signal into two halves of equal energy (Au, 1993), as the rms bandwidth ($F_{\text{rms BW}}$), given as the spectral standard deviation around F_C and finally, as the peak frequency (F_P) defined as the center frequency of the frequency band with the highest amplitude.

3.3.6. Localisation

The towed hydrophone formation allowed localisation of whistles and pops. Using the spoken track with annotated bearing and distance estimates, custom-written Matlab scripts were used to calculate localisation error by calculating 2D averaged MINNA (minimum number of receiver array) localisations (Schulz et al., 2006; Wahlberg et al., 2001). The array was calibrated using the methods of previous studies on pops and whistles with a localisation error for pops of 68% of within $\pm 5^\circ$, 94% within $\pm 10^\circ$, and 100% within $\pm 15^\circ$ of the true location and for whistles of 76% ± 15 degrees and 99% within ± 30 degrees of the true location (King et al., 2018; King et al., 2019; Moore et al., 2020).

3.3.7. Quantification of ambient noise

Six acoustic recorders (SoundTraps ST300; Ocean instruments, NZ; see further details in section 3.3.3) were deployed at six locations within the study area at depths of 8-14 meters between 30 October and 27 November in 2019 (Figure 3.2; Table 3.7.1). They were all spaced either greater than seven km's apart or on either side of some flats or banks to avoid overlap in recordings of background noise. All SoundTraps were moored 1 – 1.5 meters above the sea floor between a 50 kg concrete base and a 200 mm subsurface buoy (Figure 3.7.2) and recorded at a duty cycle of 30 minutes per hour and each 30-minute period was saved into a single file for 23-37 days providing a total of more than 1,700 hours of recordings (Table 3.7.1; Figure 3.7.2). All SoundTraps were retrieved by a local diver.

For each SoundTrap, the masking noise level was calculated as the spectral density of background noise added to the auditory critical ratios measured for bottlenose dolphins (Johnson, 1968). Spectral noise density corresponds to the amount of power per 1 Hz band (dB re 1 $\mu\text{Pa}^2/\text{Hz}$) and was calculated using a FFT length of 1024, a window length of 512 and a 50% window overlap. The critical ratio is the difference between the sound pressure level of a

pure tone just audible in the presence of continuous noise of constant spectral density and the sound pressure spectral density for that noise expressed in dB (Fletcher, 1940). For each acoustic recorder the ambient noise level was also quantified in third-octave band levels (TOL) using a 1 s integration window (dB re 1 μ Pa, rms).

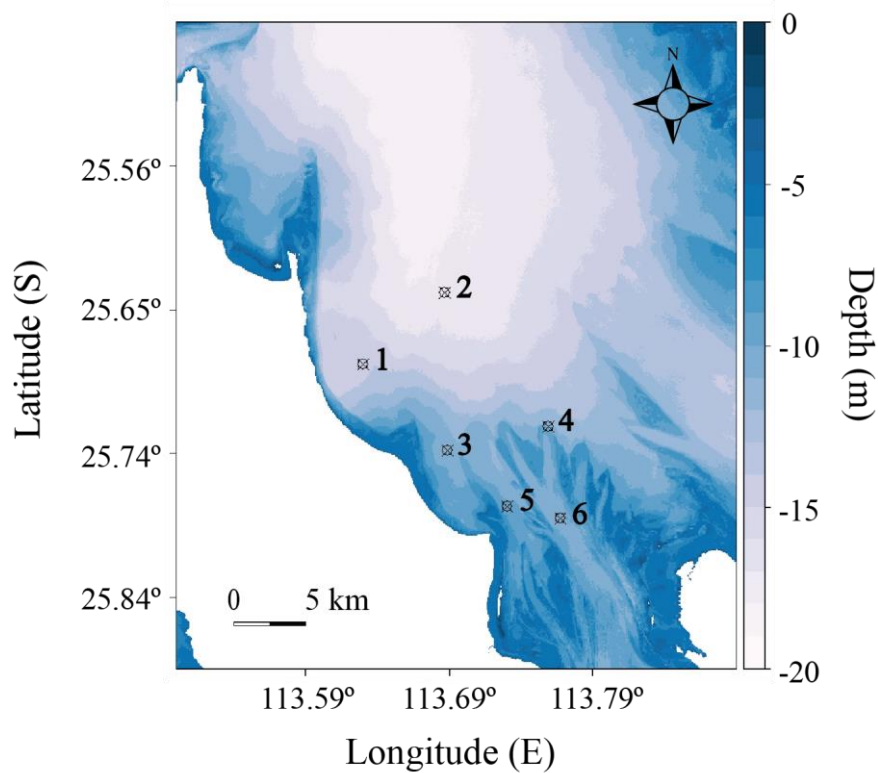


Figure 3.2. SoundTrap deployment locations for ambient noise recordings. The study area in the eastern gulf of Shark Bay, Western Australia, plotted with high-resolution (10 x 10 m) satellite-derived bathymetry data (Chapter four). The SoundTrap acoustic recorders deployed for recording ambient noise are superimposed on the map.

3.3.8 Whistle and pop communication ranges

Measures of sound transmission loss, apparent source levels of pops and whistles, and ambient noise levels were all combined to estimate the communication range of whistle and pops. This was done using the modified passive sonar equation where the maximum communication range is considered the range at which the received level falls below the detection threshold, here assumed to be equal to the masking noise level (see equation [1], section 3.3.5). Masking noise levels were based on the ambient noise levels measured at the six acoustic recorders (Figure 3.2). For a pure tone in noise, the masking noise level depends on the spectral density and the auditory bandwidth of the listener. The critical ratio (CR) is defined as the level at which a pure tone is just audible in the presence of white noise at a constant spectral density (Erbe et al., 2016). We therefore followed previous studies (e.g. Jensen et al., 2012a) in estimating the masking noise level as the sum of the spectral noise density and the CR at the centroid frequency of pops and whistles. The rms measured within a 95% energy window was used as the received level (RL) for whistles, which is a commonly used measure for tonal sounds, whereas the rms measured within the -10 dB endpoints relative to the pop peak was used for pops. This measure is often used for pulsed sounds. To calculate transmission loss (TL), a mean value of k as estimated based on the transmissions of pseudo-random white noise near the centroid frequencies of pops (2 kHz) and whistles (10 kHz) were used.

3.4 Results

During nine encounters and follows of a total of 37 subjects (males, $N = 27$; females, $N = 10$), a total of ~9 hours of acoustic recordings were collected. Within this time, 237 whistles and 143 pop trains were recorded. Of these, 64 whistles and 559 individual pops were recorded within 5 s of a laser range estimate of distance to one individual or a group. A total of 30 whistles and 222 individual pops had a signal-to-noise ratio greater than 6 and 10 dB, respectively. All whistles were localised and two or three pops within the same pop train were localised using TOADy (Quick et al., 2008) to confirm the validity of the laser range estimate, and a total of 24 whistles and 168 pops were included for further analyses (Table 3.1). All pops and whistles were recorded at a distance of 8 - 73 m (mean, whistles = 28 ± 14 m; mean, pops = 43 ± 9 m) and most from a tight group of animals (consorting males with a female). Dolphin whistles were produced at a mean apparent source level (mean ASL \pm standard deviation) of 141.4 ± 5.6 dB re 1 μ Pa (95% energy window; Figure 3.3A), an ASL based on a 200 ms running average of 144.6 ± 5.9 dB re 1 μ Pa, and an ASL based on a measure of energy flux density (EFD) of 141.2 ± 6.3 dB re 1 μ Pa²·s. Pops were produced at an ASL of 135.1 ± 4.9 dB re 1 μ Pa (rms between -10 dB endpoints; Figure 3.3C), a peak-peak ASL of 163.5 ± 6.5 dB re 1 μ Pa, and an ASL based on EFD of 100.8 ± 6 dB re 1 μ Pa²·s. The mean centroid frequency (F_C) of whistles was 9.1 ± 4.3 kHz (Figure 3.3B), the mean rms bandwidth ($F_{rms,BW}$) was 3.9 ± 1.7 kHz, and the mean peak frequency (F_P) was 8.4 ± 5.1 kHz. For pops the mean F_C was 1.8 ± 1.5 kHz (Figure 3.3D), the mean $F_{rms,BW}$ was 1.8 ± 1.3 kHz and the mean F_P was 1.2 ± 1.4 kHz. Full summary of the results can be seen in Table 3.1.

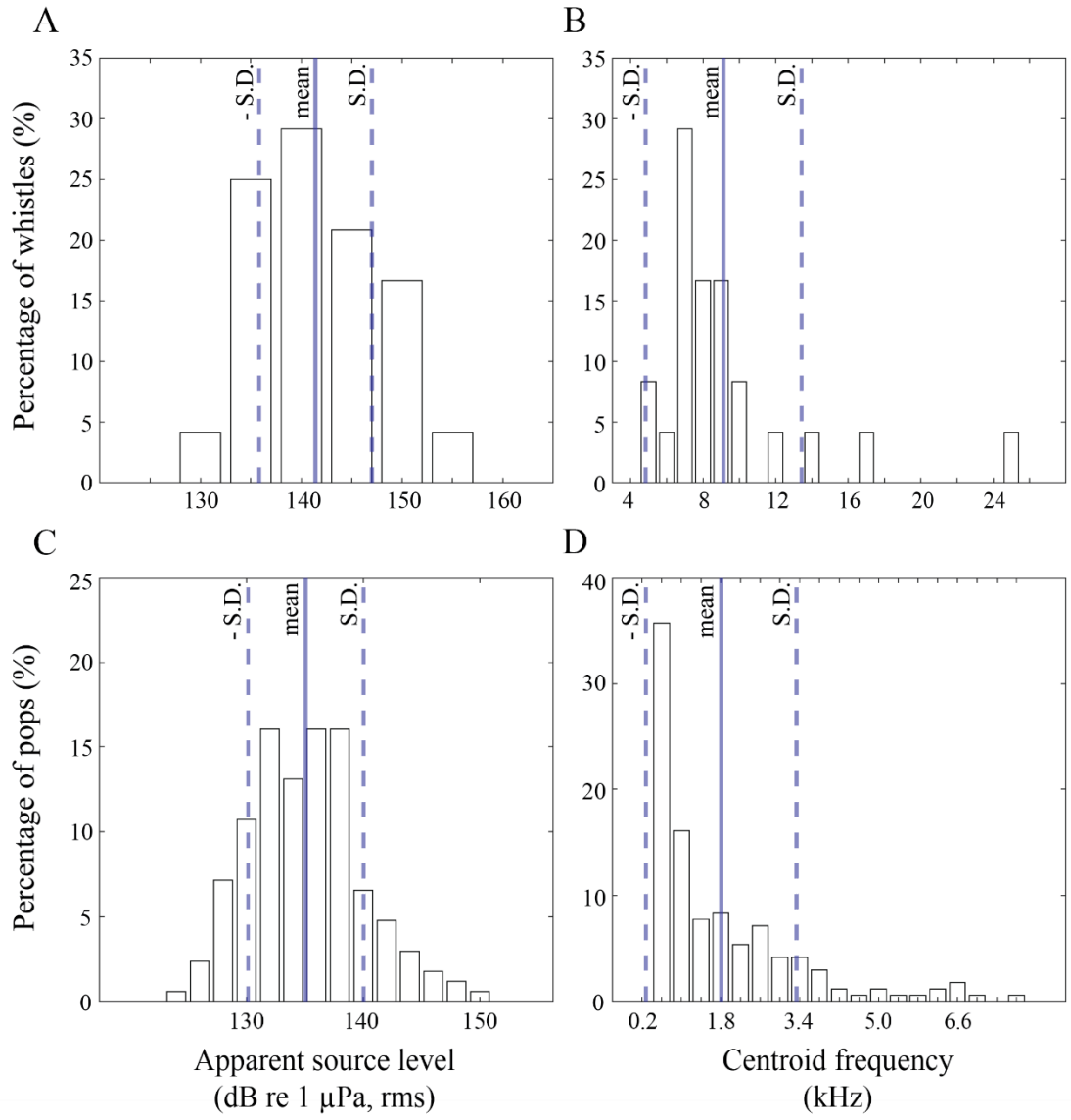


Figure 3.3. Pop and whistle source parameters. Histograms showing the distribution of whistle and pop apparent source levels (ASL; A & C) and centroid frequencies (F_C , kHz) (B & D). Shown are the ASL of whistles based on the rms across a 95% energy window and the ASL of pops over a duration defined by the -10 dB endpoints relative to the pop peak. Mean ASL and F_C are illustrated by the solid line, whereas standard errors are illustrated by dashed lines. Bin widths for whistle ASL and F_C are 5 dB and 1 kHz, respectively, whereas bin widths for pops are 2 dB and 0.4 kHz. $N_{\text{whistles}} = 24$, $N_{\text{Pops}} = 168$.

Table 3.1. Mean pop and whistle source parameters of Indo-Pacific bottlenose dolphins recorded in the eastern gulf of Shark Bay, Western Australia.

<i>Parameters</i>	<i>Whistles</i>	<i>Parameters</i>	<i>Pops</i>
	<i>Mean \pm S.D.</i>		<i>Mean \pm S.D.</i>
ASL _{95% rms} (dB re 1 μ Pa)	141.4 \pm 5.6	ASL _{-10dB, rms} (dB re 1 μ Pa)	135.1 \pm 4.9
ASL _{200ms rms} (dB re 1 μ Pa)	144.6 \pm 5.9	ASL _{pp} (dB re 1 μ Pa)	163.5 \pm 6.5
ASL _{95% EFD} (dB re 1 μ Pa ² ·s)	141.2 \pm 6.3	ASL _{95% EFD} (dB re 1 μ Pa ² ·s)	100.8 \pm 6.0
F _{centroid} (kHz)	9.1 \pm 4.3	F _{centroid} (kHz)	1.8 \pm 1.5
F _{rms BW} (kHz)	3.9 \pm 1.7	F _{rms BW} (kHz)	1.8 \pm 1.3
F _{peak} (kHz)	8.4 \pm 5.1	F _{peak} (kHz)	1.2 \pm 1.4
Range to vocalising animal (m)	28 \pm 14	Range (m)	43 \pm 9
N	24	N	168

A total of 18 empirical measures of sound transmission within the eastern gulf of Shark Bay were measured, at five locations in the northern habitat with a more homogenous depth contour, and 12 in the southern habitat, characterised by shallow flats, banks and channels (Figure 3.2). From repeated playbacks (N = 15) of the same stimuli at each location (19 different types of whistles, pops and pseudo-random noise) a mean estimate of transmission loss was calculated for each stimuli type (Figure 3.4). The estimated k for pseudo-random white noise at 2 kHz ($k = -16.4$) and 10 kHz ($k = -20.7$) were used as representative of the transmission loss of pops and whistles propagating through the environment in the subsequent estimation of communication ranges.

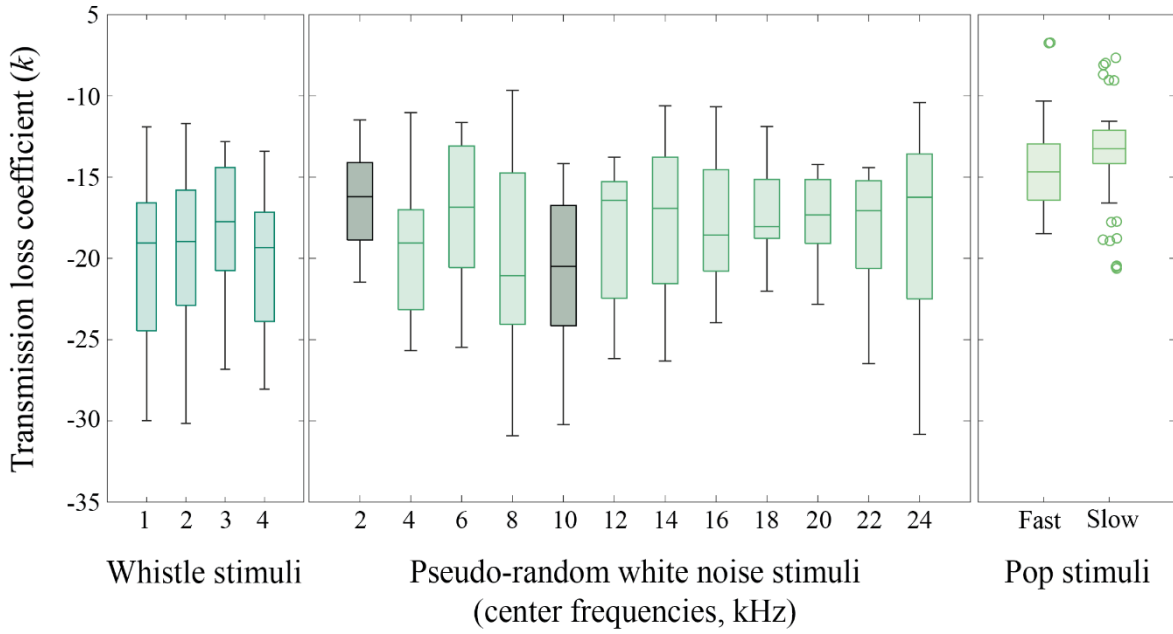


Figure 3.4. Sound transmission measurements. Boxplot showing the distribution of estimated transmission loss coefficients (k) for 18 different stimuli playback types (four whistle types; 12 pseudo-random noise stimuli; and pop trains, categorised as either fast or slow). The lower and upper bounds of each box represent the lower and upper quartile, and the whiskers the minimum and maximum point within $1.5 \cdot$ interquartile range. Hollow circles represent outliers. The two darker coloured boxes represent the pseudo-random noise stimuli with a center frequency of 2 and 10 kHz, from which the mean k was used to estimate apparent source levels and communication ranges of whistles and pops.

The masking noise levels were calculated as the sum of the spectral noise density of ambient noise and the critical ratios measured for bottlenose dolphins. At the centroid frequency (F_c) of whistles and pops, masking noise levels varied between 81 – 96 dB re 1 μ Pa and 75 – 96 dB re 1 μ Pa between the six acoustic loggers (Figure 3.5; Table 3.2). Third octave levels ranged between 82.6 – 97.5 dB re 1 μ Pa (rms) at 2 kHz (close to the center frequency of pops), and between 80.7 – 102.4 dB re 1 μ Pa (rms) at 10 kHz (close to the center frequency of whistles) (Figure 3.5).

By combining all empirical measures (i.e., ASL, masking noise level and transmission loss) the communication ranges of pops and whistles were estimated. A mean measure of ASL and k were used for each signal type and given the variation in ambient noise level, a measure of communication range was calculated including the masking noise level (i.e., spectral density plus CR) recorded at each logger. Communication ranges varied from 246 – 1912 m for pops and from 154 – 1482 m for whistles, with communication ranges decreasing along a north-south gradient, with larger ranges in the north for both signal types (Table 3.3).

Table 3.2. Masking noise levels. Median ambient noise level, dB re 1 μ Pa (Spectral density (dB re 1 μ Pa²/Hz) + critical ratio (dB re 1 Hz) (Johnson, 1968) at the centroid frequency of pops (~ 2 kHz) and whistles (~9 kHz)), and 5th and 95th percentiles as recorded on six acoustic recorders (SoundTraps) deployed within the eastern gulf of Shark Bay, Western Australia. The six loggers were all deployed for one month in November 2019 recording at a duty cycle of 30 minutes per hour. SoundTrap 1 and 2 were deployed in the northern, more uniform habitat, whereas 5 and 6 were deployed in the southern, subdivided habitat. SoundTrap 3 and 4 were deployed between the two northern recorders and the two southern recorders.

<i>Location</i>	<i>Masking noise level</i> $\pm S.D. (2\text{ kHz})$	<i>P₅:P₉₅</i> (2 kHz)	<i>Masking noise level</i> $\pm S.D. (9\text{ kHz})$	<i>P₅:P₉₅</i> (9 kHz)
1 (Inshore WB)	81.0 \pm 4.9	[71.4:87.1]	76.1 \pm 2.6	[72.0:80.0]
2 (Offshore WB)	85.9 \pm 2.6	[82.8:90.0]	84.1 \pm 2.4	[81.1:88.7]
3 (Red Cliff Bay)	84.3 \pm 2.0	[81.9:87.4]	80.7 \pm 1.8	[79.0:83.1]
4 (N of 2 nd channel)	85.7 \pm 3.1	[82.7:92.4]	81.8 \pm 7.0	[78.9:98.3]
5 (1 st channel)	95.8 \pm 2.6	[92.9:101.5]	97.0 \pm 1.9	[94.1:100.3]
6 (2 nd channel)	92.3 \pm 1.8	[89.8:95.2]	88.1 \pm 2.0	[85.3:91.7]

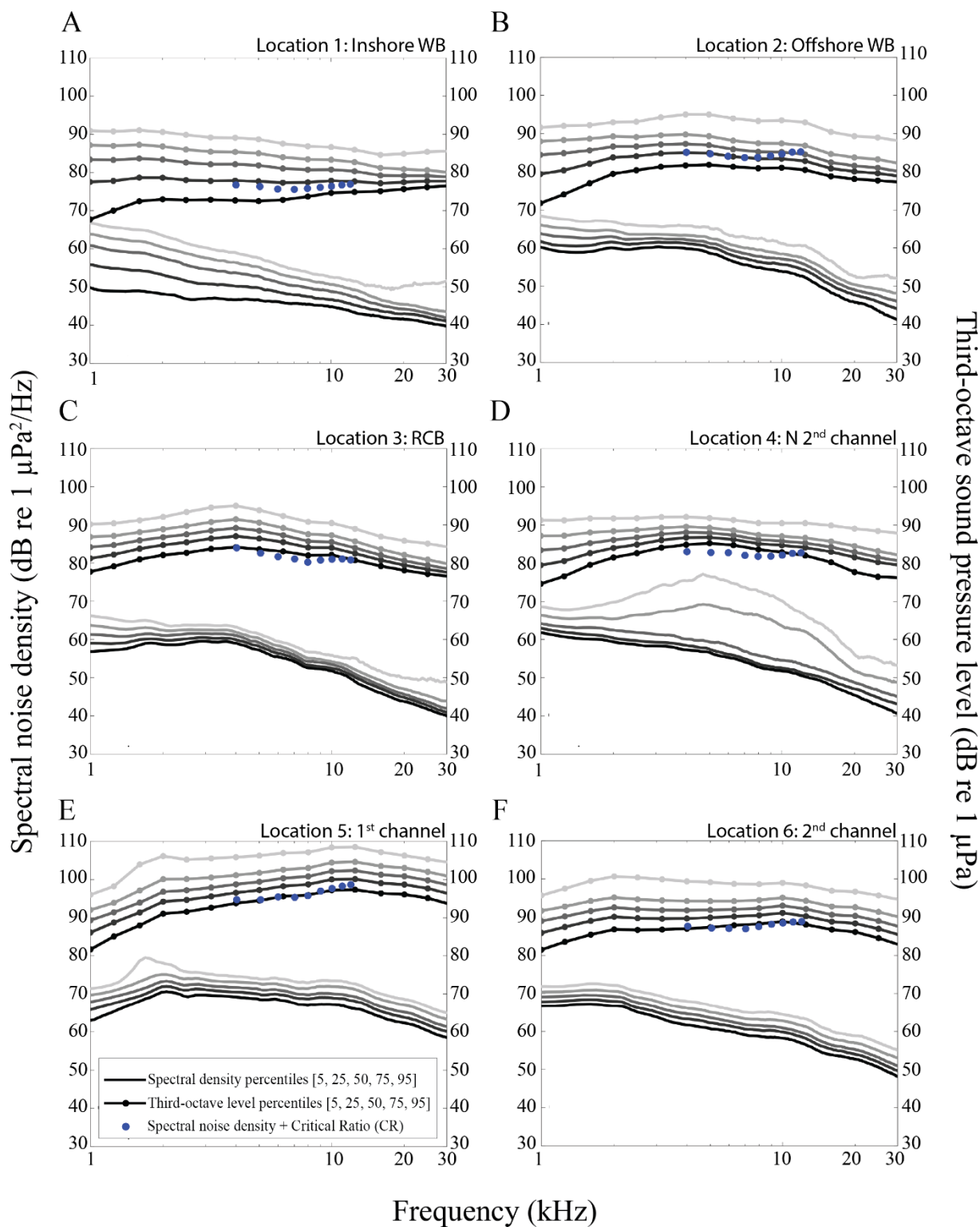


Figure 3.5. Ambient noise levels recorded on six acoustic recorders. Ambient noise levels as recorded on six SoundTraps between 30 November and 27 October 2019 deployed in our study area in the eastern gulf of Shark Bay, Western Australia, quantified as spectral noise density (dB re 1 $\mu\text{Pa}^2/\text{Hz}$) and third-octave band levels (TOL; dB re 1 μPa , rms) between 1 and 20 kHz. For both spectral noise density and TOLs the 5th, 25th, 50th, 75th and 95th percentiles are shown (5th percentile as dark grey; 95th percentiles as light grey). The masking noise level

in 1 kHz increments between 4 and 12 kHz is given as the sum of the spectral density and bottlenose dolphin critical ratios (CR) (From Johnson 1968) and presented as *. The top two panels (A and B) represent deployment areas of uniform bathymetry (Inshore and offshore Whale Bight), while the bottom two panels (E and F) represent locations in the southern, more subdivided habitat (First and Second channel). The background noise presented in the two middle panels represent deployment locations in areas in between A-B and E-F.

Table 3.3. Pop and whistle communication ranges. Estimated communication ranges (m) based on empirical measures of sound transmission loss at the centroid frequency of pops and whistles (transmission coefficient, $k = -16.4$ for pops and $k = -20.7$ for whistles), apparent source levels, and masking noise levels recorded on six acoustic SoundTraps deployed within the eastern gulf of Shark Bay, Western Australia.

<i>Estimated communication ranges (m)</i>		
<i>Location</i>	<i>Pops</i> <i>($k = -16.4$ at 2 kHz)</i>	<i>Whistles</i> <i>($k = -20.7$ at 10 kHz)</i>
1 (Inshore WB)	1912	1482
2 (Offshore WB)	975	622
3 (Red Cliff Bay)	1216	898
4 (N of 2 nd channel)	1002	789
5 (1 st channel)	246	154
6 (2 nd channel)	401	406

3.5 Discussion

The bottlenose dolphins of Shark Bay, Western Australia have been extensively studied for more than 40 years. While the use and context in which pops and whistles are produced are well-studied, the acoustic parameters of these social sounds and the range over which they permit communication have never been quantified. Here, I quantified whistle and pop apparent source levels, their transmission properties, and ambient noise levels across the study site to investigate their effective communication range. Whistles were produced at apparent source levels (141.4 ± 5.6 dB re 1 μ Pa) and at an average centroid frequency (9.1 ± 4.3 kHz) similar to that of bottlenose dolphins that reside in another shallow water habitat in Western Australia (Jensen et al., 2012). Pops were emitted at slightly lower apparent source levels compared to that of whistles (135.1 ± 4.9 dB re 1 μ Pa) and at a much lower centroid frequency (1.8 ± 1.5 kHz). Empirical measures of sound transmission showed a close to spherical spreading loss for whistles, whereas the transmission loss of pops was smaller. The ambient noise level varied extensively across the whole study area, with 10-20 dB differences in noise level across the six recording locations at the frequencies at which pops and whistles are emitted. The variation in ambient noise levels and transmission loss between the two social sounds were clearly reflected in the estimations of communication range; pops had a slightly larger communication range compared to whistles, however, the differences in noise levels resulted in highly variable communication ranges for both social sounds across the study area.

Whistles have been shown to be important for facilitating group cohesion, for advertising individual identity (i.e. signature whistles), maintaining social bonds, and promoting cooperative behaviours (Chereskin et al., 2022; Janik and Slater, 1998; King et al., 2019; King et al., 2021). In contrast, pops are produced by males herding females, inducing her to stay close to the popping male, and sometimes used in acoustic synchrony between two males (Connor and Smolker, 1996; Moore et al., 2020; Vollmer et al., 2015). The estimated communication ranges measured here for whistles are similar to those found in previous studies

in shallow water habitats (Jensen et al., 2012; Quintana-Rizzo et al., 2006), and pops were estimated to travel slightly further than whistles. This follows the prediction of lower frequency signals travelling further than high frequency signals. However, given pops are almost exclusively produced in consortships, and given that male alliances compete intensively over access to females, it seems surprising that pops transmit further than whistles. Indeed, it would appear more advantageous for an agonistic signal used in a reproductive context to be more inconspicuous rather than advertising the consortship, and thus the presence of a female, to potential eavesdropping rival alliances. In addition to potentially losing a female to theft by rivals, male competition can also lead to direct fitness consequences, such as physical injury (Connor et al., 1992; King et al., 2021).

While pops *may* have evolved to travel further than whistles, certain limitations of the communication ranges estimated in this study should be highlighted. First, we defined masking noise level as the sum of the spectral density and the critical ratio (CR) to allow for comparison between signal types. These values of CR were estimated based on pure tones between 4 and 12 kHz in 1 kHz increments (Johnson, 1968). As pops are produced at 2 kHz, the CR of pops was assumed to correspond to a CR at 4 kHz. Furthermore, pops are pulsed sounds, and because the assumed CR used is derived based on pure tones, we may be overestimating the communication range of pops. A masking noise level based on a CR estimated using pure tones may therefore not be the most appropriate measure and reveals a gap in our current knowledge of CR for low-frequency pulsed sounds. Second, in this study we measured sound transmission at 18 locations across the study area. Shark Bay is characterised by a northern habitat, with a relatively homogeneous bathymetry contour compared to the southern habitat, which is characterised by huge variation in habitat structure from shallow flats to deeper channels. Despite the effort to quantify sound transmission across the whole study area, the small-scale variations in habitat structure greatly influences sound transmission, which is reflected in the large variation in the estimated transmission loss coefficient (k). For the 2 and 10 kHz pseudo-

random white noise stimuli the measures of k varied by ~6 and ~8 dB respectively between the lower and upper quartiles. Such variation corresponds to differences in estimated communication ranges of ~400 m to 6 km for both signal types, depending on the ambient noise level, with the biggest potential variation found in the northern habitat. This leads to another limitation of using empirical measurements to understand transmission loss in complex, shallow water habitats; empirical measurements allow estimation of sound transmission in one direction at a given location, whereas estimation of sound transmission perpendicular to this direction may reveal completely different results. As such, while empirical measurements are important in understanding the use of social sounds, they only provide information about sound transmission at one point in space and time, and it can be challenging to collect enough samples to accurately represent 2-dimensional sound propagation in complex habitats.

The ambient noise recordings were collected in the peak of the dolphin mating season from September to December (Connor et al., 1996). Ambient noise levels were overall very high, and characterised by the presence of snapping shrimp, but they also varied as a function of habitat, with noise levels in the southern part of the study site considerably louder than those recorded further north. This leads to large variations in communication range for both signals, which are limited to few hundreds of meters in the southern, subdivided habitat, compared to communication ranges of more than 1 km further north in the habitat characterised by a more homogenous bathymetry. For estimating communication range, a single mean value of k for each signal type was used due to the large overall variation in transmission loss across the study site. Thus, the variation between estimated communication ranges for each location represent differences in the recorded mean ambient noise levels. While these variations are primarily natural fluctuations in noise level caused by snapping shrimp in particular, this highlights the impact masking noise may have on communication range and emphasises the possible implications of anthropogenic noise pollution.

Like ambient noise, alliance behaviour interestingly also varies along a north-south gradient. First-order level alliances are more likely to form pairs in the south, and trios in the north, and northern males engage in consortships at a higher rate than males in the south (Connor et al., 2017). The variation in communication range suggests that variation in alliance behaviour could, to some extent, be driven by habitat heterogeneity, and thus sensory ecology. A large communication range allows males to maintain acoustic contact with allies over greater ranges and may increase their chances of locating the whereabouts of oestrus females, potentially explaining the increased consortship rate of males in the north compared to the south. However, a larger communication range also increases the risk of eavesdropping by rival males. Males may encounter rival alliances more often in the north where the cost of reducing your own success at securing paternities by forming trios, may be outweighed by the benefits of a third ally in defending females against competing alliances. I explore the impact of habitat heterogeneity, and thus sensory ecology, on male alliance behaviour in Chapter four.

3.6 Conclusion

In this study, I quantify the communication ranges of bottlenose dolphin whistles and pops based on empirical measures of apparent source levels, ambient noise level measurements and sound transmission within the eastern gulf of Shark Bay. The empirical measures of sound transmission suggest that pops experience less attenuation compared to whistles, leading to slightly larger communication ranges for pops compared to whistles, which may have implications for detection by and encounters with rival alliances. The effective communication range varied greatly across the study area for both pops and whistles; in the southern subdivided habitat ambient noise levels are high, and pops and whistles are unlikely to be detected at more than a couple of hundred meters at most. In contrast, both pops and whistles may be heard at ranges of 1 km or more in the northern, more homogeneous habitat. While empirical studies allow for a very fine-scale understanding of sound transmission at specific locations,

collecting representative data for a complex habitat can be challenging. Furthermore, estimating masking noise levels are based on assumptions for low-frequency, pulsed sounds. Future work might benefit from an approach combining empirical estimates with a sound transmission modelling approach to estimate communication range, and from studies exploring how dolphins perceive low-frequency pulsed sounds in noise.

3.7 Appendix

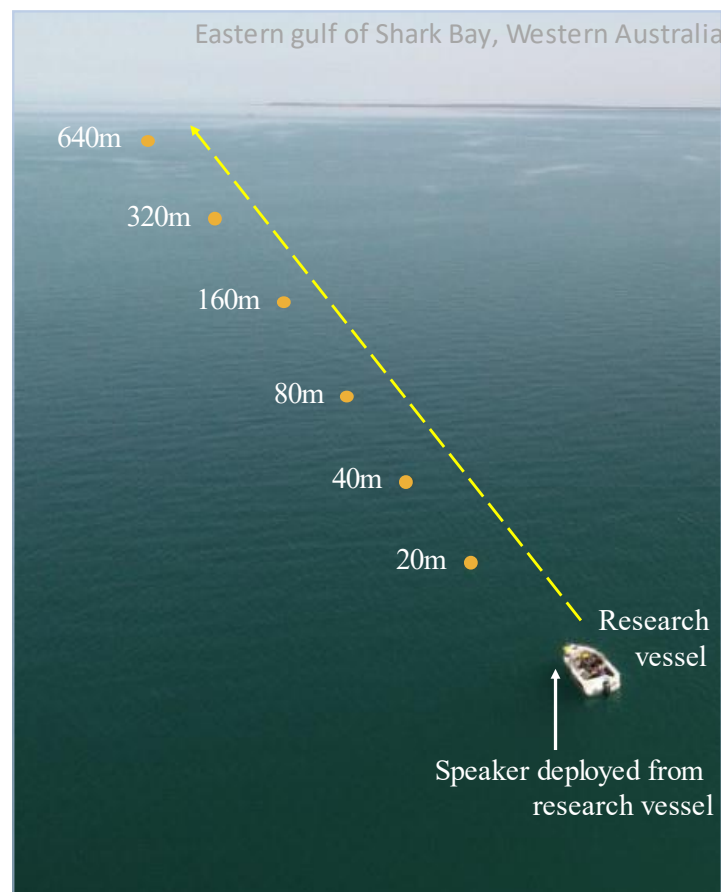


Figure 3.7.1. Sound transmission experimental setup. Sound transmission experiments were conducted by deploying six SoundTraps on a line at a predetermined distance of 20m, 40m, 80m, 160m, 320m and 640m from the research vessel. After deployment of all SoundTraps the research vessel was anchored in line with the array, 20m from the first SoundTrap. All SoundTraps were always deployed at the same location relative to the vessel. The playback speaker was lowered from the side of the vessel prior to playback 1.5 meters below the surface, the same depth at which SoundTraps were deployed.

Table 3.7.1. SoundTrap deployment details. Six acoustic recorders (ST300; Oceaninstruments.co.nz) were deployed at six different locations within the eastern gulf of Shark Bay. Shown in the table is logger ID, deployment location (latitude and longitude), deployment date and depth (m) and retrieval date and depth at retrieval.

Logger ID	Latitude	Longitude	Deployment date	Deployment depth (meters)	Retrieval date	Retrieval depth
5153	S25°41'18.5"	E113°37' 49.3"	30.10.2019	11.7	26.11.2019	11.7
5154	S25°38'31.2"	E113°41'09.7"	30.10.2019	13.3	26.11.2019	13.2
5155	S25°44'29.5"	E113°41'26.2"	02.11.2019	7.8	26.11.2019	8.1
5156	S25°46'32.9"	E113°43'56.9"	04.11.2019	9.2	27.11.2019	9.1
5158	S25°46'57.5"	E113°46'10.7"	04.11.2019	9.4	27.11.2019	9.7
5159	S25°43'30.1"	E113°45'36.6"	04.11.2019	9.2	27.11.2019	9.8

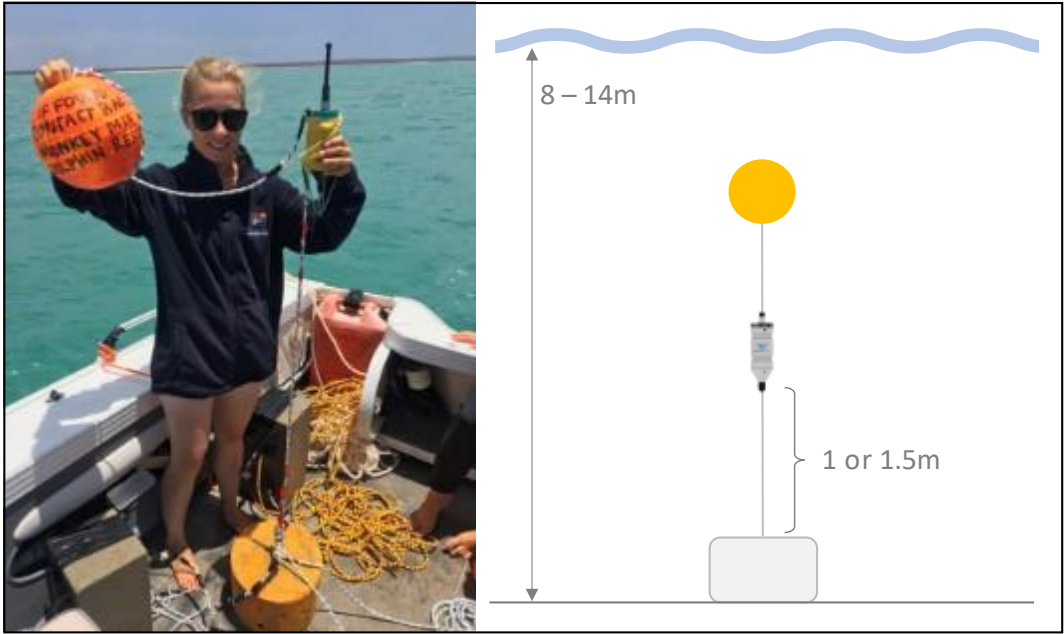


Figure 3.7.2. Deployment setup for ambient noise recordings. All acoustic recording SoundTraps were deployed 1 or 1.5 meters above the bottom between a 50 kg concrete mooring base and a 200 mm subsurface buoy.

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Chapter 4 | Communication range shapes cooperation dynamics in a dolphin alliance system

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Key Words: Active space; habitat heterogeneity; habitat structure; social complexity; Indo-Pacific bottlenose dolphins; social behaviour; alliance behaviour

Author contributions:

P.M.S co-designed the study with S.L.K, F.H.J and R.C.C. P.M.S collected the empirical data in 2019, and S.L.K., R.C.C., S.J.A. and M.K. collected the long-term data used in this study. U.L collected and provided the satellite-derived bathymetry data. P.M.S processed and analysed the data with support from S.L.K and F.H.J. F.H.J prepared the sound propagation and active space reconstruction models and P.M.S and F.H.J implemented habitat-scale modelling of active space. P.M.S conducted the statistical analyses with support from S.L.K. P.M.S. drafted the manuscript with support from S.L.K and F.H.J.

4.1 Abstract

Social complexity is often viewed as the product of exclusively social processes. However, sociality demands spatial proximity, and the physical configuration of the environment directly influences the range over which individuals can communicate and interact with each other. Yet, empirical evidence linking variations in communication range with the evolution of social behaviour remains lacking. In Shark Bay, Western Australia, unrelated male bottlenose dolphins form multilevel alliances in competition over females. Within this alliance system, pairs or trios of males (first-order alliances) cooperate to herd individual oestrus females in events termed consortships. Notably, first-order alliance size varies along a north-south gradient, and it has been speculated that this variation relates to underlying habitat heterogeneity. Here, we use empirical measures of male dolphin vocalisations, ambient noise levels and high-resolution bathymetry data to model how detection range and resulting active space of dolphin communication signals varies across habitat. We combined these measures of active space with long-term data on alliance behaviour and animal density to determine the social and ecological drivers of first-order alliance size. We show that active space is the sole predictor of the number of preferred alliance partners and contributes significantly to the rate at which males consort females. Our findings illustrate that variation in sensory ecology driven by heterogeneous habitat structure plays a major role in influencing cooperative group size and reproductive success in an alliance mating system. This study represents an important advance in the field by demonstrating the role of habitat heterogeneity in shaping cooperation and social evolution.

4.2 Significance statement

Habitat structure is known to influence the range over which animals can detect each other's communication signals, yet how this may impact the evolution of social behaviour remains unknown. Here, we show that the detection range of vocalisations used by individual allied male dolphins in a reproductive context varies with habitat heterogeneity, exclusively predicts the number of alliance partners with whom individuals cooperate and contributes significantly to male access to mating opportunities. These results reveal that habitat heterogeneity not only affects communication range, but also drives optimal cooperative group size and mating success within a single population of wild animals. This work highlights that habitat structure, and thus communication range, are major contributors in shaping social evolution.

4.3 Introduction

The evolution of social complexity has often been considered the product of social processes, with social complexity typically defined by both qualitative (i.e., dominance hierarchy, mating strategy (Tibbetts et al., 2020) and prosocial behaviours (Clutton-Brock, 2002; Connor, 2007)) and quantitative (i.e., group size, density or the number of differentiated relationships (Bergman and Beehner, 2015; Dunbar, 1995; Dunbar, 2009)) measures of sociality. Spatial proximity is a prerequisite for social interactions, therefore an animal's social environment is largely determined by individual movement decisions (Bonnell et al., 2017; Farine, 2015; Farine et al., 2016; He et al., 2019). However, while social cues are important drivers of animal movement, animal movement patterns will also be influenced by the physical components of the habitat in which an animal lives, facilitating or preventing movement, with implications for social interactions and organisation (He et al., 2019).

While habitat configuration is a well-established driver of animal movement, it remains unknown how variation in sensory ecology driven by heterogeneous habitat structure impacts the evolution of social behaviour. For a wide range of species, the detection of conspecifics is mediated by sound, due to its long-range transmission properties, making it an efficient carrier of social information (Urick, 1983). The physical configuration of the environment will, however, influence the maximum range over which individuals can detect the vocal signals of others, also known as the active space (Marten and Marler, 1977). Thus, variations in active space as a result of habitat heterogeneity are important to consider when predicting animal movement patterns and spatial proximity. Active space has been shown to vary with habitat structure in a number of species (Gall et al., 2012; Perla and Slobodchikoff, 2002), with some animals exploiting this variation by modifying sound production to facilitate advertisement, or acoustic crypsis from predators (Barker et al., 2009; Martin et al., 2018; Schwartz et al., 2016; Zeh et al., 2022). Whilst the impact of habitat structure on sound transmission is well studied,

empirical data linking variations in active space with measures of social complexity are lacking.

Here, we test how the active space of a dolphin communication signal influences social complexity within a population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia. In Shark Bay, bottlenose dolphins exhibit a fission-fusion grouping pattern within an open social network, with individuals residing in a continuous mosaic of overlapping home ranges (Randić et al., 2012). Male dolphins form three alliance levels, or orders, in competition against other alliances over access to females (Connor and Krützen, 2015). At the first level (first-order alliance), male pairs or trios will cooperate to herd single oestrus females in events termed consortships. A consortship can last from days to weeks (Connor and Krützen, 2015), with longer consortships providing males with an increased opportunity to copulate with females and secure paternities (Connor et al., 2022), but requiring more effort to guard and defend the female from rival alliances. Almost all adult males are members of a second-order alliance, which comprise 4 - 14 members that compete with other alliances over females and is considered the core unit of male social organisation (Connor and Krützen, 2015; Connor et al., 1992; Randić et al., 2012). Multiple second-order alliances will also cooperate in third-order alliances (Connor et al., 2011; Connor et al., 2022). While the composition of second- and third-order alliances are relatively stable across decades (Connor et al., 2022; King et al., 2021), the stability of first-order alliances may be highly variable. Some males have consistent first-order allies, while others will consort females with numerous males from within their second-order alliance in a given mating season (Connor and Krützen, 2015; Connor et al., 2001; Connor et al., 2022; King et al., 2021). While it is yet to be determined how matings are shared between males within the first-order alliance, it has recently been shown that males with stronger and more homogenous social bonds within their second-order alliance are more successful at securing paternities (Gerber et al., 2022).

Interestingly, first-order alliance size varies as a function of the physical habitat structure, with trios more frequently observed in the northern, open water habitat, whereas pairs are formed in the southern habitat, composed of shallow flats, subdivided by deeper channels (Connor et al., 2017). Furthermore, male consortship rates have also been shown to be lower in the southern habitat compared to the north (Connor et al., 2017). The physical differences in habitat structure between the north and south may impact how sound is transmitted and thus an individual's active space. Previously, we have shown that male alliance behaviour is mediated through the use of tonal, frequency modulated whistles and narrowband, pulsed 'pop' vocalisations produced in repetitive trains (King et al., 2018; King et al., 2021; Moore et al., 2020). While whistles play an important role in keeping track of individuals and are produced by both males and females (King et al., 2018; King et al., 2019; King et al., 2021), the pop vocalisation plays a major role in mating behaviour. Pops are only produced by males and almost exclusively when males are consorting a female (Connor and Smolker, 1996). The pop acts as an agonistic 'come-hither' signal or warning, inducing the female to stay close to the popping male (Connor and Smolker, 1996; Moore et al., 2020; Vollmer et al., 2015), and increases in the context of guard switches (King et al., 2019).

Here, we combine extensive empirical measures of dolphin vocalisations (including apparent source levels and frequency content) and background ambient noise levels with satellite-derived, high-resolution bathymetry data to model communication range and active space and how it varies across the dolphin habitat. Given the importance of pops for reproductive behaviour and their advertisement of the presence of an oestrus female to potential rival alliances, we focus on the pop vocalisation to investigate this question. We model active space of pops across the eastern gulf of Shark Bay and combine these measures with comprehensive long-term association and consortship behaviour data collected between 2001 and 2006 on 102 well-known focal males (12 different second-order alliances), to investigate

whether active space, and thus habitat configuration, is driving the variation in first-order alliance size and consortship rate along the north-south gradient (Connor et al., 2017). We also investigate the influence of active space on maximum consortship duration, a measure of the potential of an individual to keep a female (Connor et al., 2022). We use survey data collected within the same period to account for dolphin density, for the number of rival males within the home range of each individual male, and for second-order alliance size and social bond strength with second-order allies, as possible predictors of variation in first-order alliance size and/or reproductive behaviour. The combination of this data provides an unparalleled and comprehensive opportunity to investigate how variation in sensory ecology driven by habitat heterogeneity within a single population of animals may shape the behaviour of a complex cooperative mating system.

4.4 Results

Our results showed that the active space of pops significantly predicted the number of preferred first-order alliance partners (GLMM; $\beta \pm \text{S.E.} = 2.16 \pm 0.67$, $z = 3.23$, $p = 0.001$; Figure 4.1A-C, Table 4.1): males that reside in a home range with greater active space of pops were significantly more likely to form trios rather than pairs when consorting females. Model averaging likewise showed that the mean active space of pops within a male's home range significantly predicted trio formation with no evidence that the other fixed effects affected trio formation (Table 4.9.S1).

Active space of pops was also positively correlated with consortship rate (GLMM; $\beta \pm \text{S.E.} = 0.25 \pm 0.083$, $z = 3.054$, $p = 0.002$; Figure 4.1D, Table 4.1); as active space of pops increases, the rate at which males consort females increases. Consortship rate also decreased with increasing animal density (individuals per km² within each male's home range) (GLMM; $\beta \pm \text{S.E.} = -0.011 \pm 0.005$, $z = -2.40$, $p = 0.01$; Table 4.1), but increased as a function of a male's

cumulative social bond strength with their second-order allies (GLMM; $\beta \pm \text{S.E.} = 0.58 \pm 0.19$, $z = 3.12$, $p = 0.001$; Table 4.1). Our model averaging approach showed the same relationship (Table 4.9.S1).

Finally, when examining how active space of pops influences consortship duration we found a significant positive relationship between a male's cumulative social bond strength with their second-order allies and consortship duration (LMM; $\beta \pm \text{S.E.} = 9.76 \pm 3.39$, $t = 2.88$, $p = 0.004$; Table 4.1); males that are well-connected within their second-order alliances tended to consort individual females for longer. We found no evidence that active space of pops predicted consortship duration (LMM; $\beta \pm \text{S.E.} = 1.73 \pm 1.27$, $t = 1.36$, $p = 0.19$; Figure 4.1E, Table 4.1). Our model averaging approach showed the same relationship (Table 4.9.S1).

When investigating whether forming trios, rather than pairs, has a reproductive benefit, we found that trio formation was positively correlated with consortship rate (GLMM; $\beta \pm \text{S.E.} = 1.69 \pm 0.24$, $\text{CI} = 1.22 - 2.20$, $z = 6.83$, $p < 0.0001$) and maximum consortship duration (LMM; $\beta \pm \text{S.E.} = 12.07 \pm 4.04$, $\text{CI} = 11.86 - 12.38$, $t = 2.98$, $p = 0.005$). While whistles were not the focus of our study, we did investigate whether the active space of whistles impacted trio formation, using the same statistical model presented here, but found no significant relationship between trio formation and any of our fixed effects. These results can be found in the supplementary material (Table 4.9.S2 – 4.9.S3).

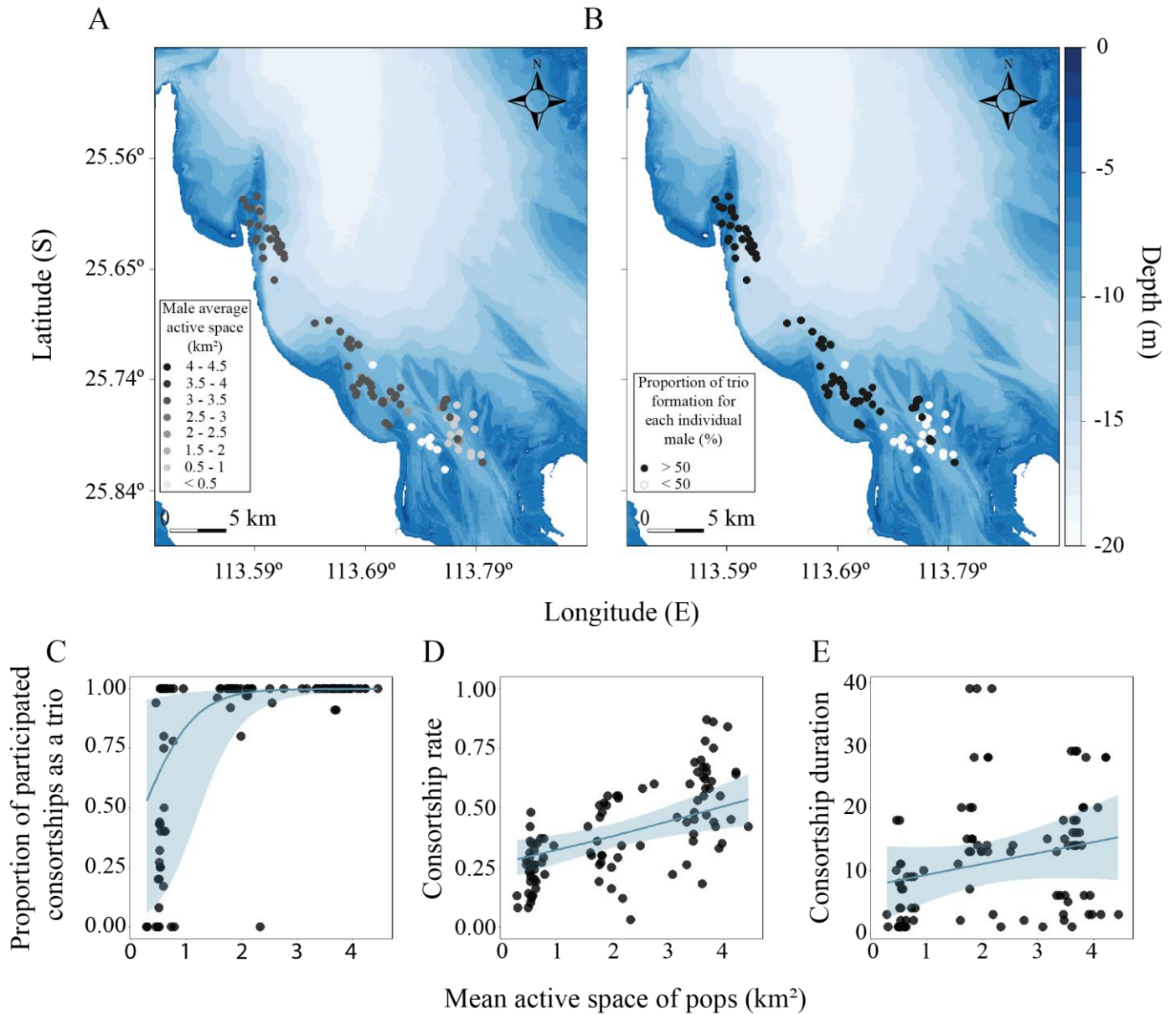


Figure 4.1. Male active space and cooperation dynamics. (A) and (B) show the high-resolution bathymetry contour of the study site (10 x 10 m) obtained from satellite derived bathymetry data. (A) shows the centroid of each male's core home range (50% kernel density estimation (KDE)) colour-coded according to the average active space (km²) within each male's core home range (N = 102), with increasingly darker colours (from light grey to black) representing a greater active space. (B) shows the centroid of each male's core home range (50%) KDE colour-coded with respect to the proportion of consortships that each male has participated in as a trio, with black representing more than 50% (N = 78) and white less than 50% (more often as a pair, N = 24). (C) The proportion of participated consortships as a trio, (D) consortship rate (number of days spent consorting/number of days observed) and (E) maximum consortship duration in days for each male as a function of the mean active space of pops (km²). In panels C-E, the raw data is shown as black, filled circles, the model estimates as the solid line and the 95% confidence interval is presented as the shaded area.

Table 4.1. Summary of model results using a traditional hypothesis testing approach to test whether the full model including our fixed effect of interest (active space) significantly predicted the variance in our response variables. (a) trio formation, (b) consortship rate and (c) maximum consortship duration. Results from a model averaging approach showed the same relationship and are presented in Table 4.9.S1.

Response:				
Proportion of trios	Estimate	Std. error	z-value	Pr (> z)
<i>Intercept</i>	-2.564	4.316	-0.594	0.553
Active space	2.164	0.671	3.226	0.001 **
Animal density	-0.034	0.033	-1.038	0.299
Rival males	0.040	0.027	1.477	0.140
Second-order alliance size	0.166	0.392	0.422	0.673
Foraging group size	-0.506	0.354	-1.429	0.153
Response:				
Consortship rate	Estimate	Std. error	z-value	Pr (> z)
<i>Intercept</i>	-1.901	0.691	-2.749	0.006 **
Active space	0.255	0.083	3.054	0.002 **
Animal density	-0.011	0.005	-2.396	0.017 *
Rival males	0.003	0.006	0.509	0.611
Second-order alliance size	0.060	0.046	1.308	0.191
Cumulative bond strength	0.578	0.186	3.115	0.002 **
Response:				
Consortship duration	Estimate	Std. error	t-value	Pr (> z)
<i>Intercept</i>	3.805	13.045	0.292	0.771
Active space	1.734	1.273	1.362	0.189
Animal density	-0.088	0.076	-1.168	0.246
Rival males	-0.137	0.121	-1.130	0.261
Second-order alliance size	0.781	0.726	1.075	0.307
Cumulative bond strength	9.756	3.387	2.880	0.005 **

4.5 Discussion

Here, we integrated satellite-derived, high-resolution bathymetry data with habitat-specific ambient noise measurements and empirical data on dolphin vocalisations to model the consequences of habitat heterogeneity in a cooperative bottlenose dolphin society. We combined this sound propagation model with long-term data collected on dolphin behaviour to effectively show that variation in habitat configuration experienced by a single population of wild animals shapes the two-dimensional communication range (the active space) of individuals, and ultimately influences cooperation dynamics in a complex alliance mating system.

We show that the active space of the pop vocalisation, a frequently used, male-specific acoustic signal used to mediate reproductive behaviour, varies depending on habitat structure. In the northern part of Shark Bay, characterised by a more uniform bathymetry contour, dolphins had larger effective active space compared to the southern, subdivided habitat, where the active space was smaller. These differences in active space of pops significantly predicted first-order alliance group size, with males residing in areas with larger active space more likely to form trios when herding females. The active space of pops was the only significant predictor of trio formation, driving the number of preferred alliance partners, while animal density, second-order alliance size, number of rivals, and optimum foraging group size within this population had no significant influence on trio formation. Thus, it is the rate at which males encounter each other in competition over females as a function of detection distance that directly influences first-order alliance size.

We also found that the active space of pops predicted a male's consortship rate; the greater the mean active space within a male's home range, the higher the rate at which a male participates in consorting females. The influence of active space on consortship rate may be explained by

females not being able to hide as easily in habitat where active space is greater as they will be acoustically detected by males over much larger distances. Our finding that the active space of whistles did not influence trio formation (see supplementary material) argues against this explanation: while whistles are produced by both sexes, it is the active space of a male-specific vocalisation, and not whistle active space, that predicts consortship rate. Instead, males may be detecting consortships by rivals over greater distances and, as a result, female captures or thefts are more common in these areas resulting in higher consortship rates overall. Alternatively, there may be some direct fitness benefits to forming trios if, for example, it is harder for females to escape trios compared to pairs. Our additional analysis supports this idea, as males that are more likely to form trios consorted females at significantly higher rates and for significantly longer. However, active space of pops was not the only factor influencing consortship rate; our results showed that as the number of individuals within a male's home range increases, the rate at which he consorts females decreases, suggesting that density plays a role in driving male consortship rate, but not in the direction we would predict. Consortship rate and maximum consortship duration were also significantly influenced by a male's cumulative bond strength with his second-order allies. Both these results are in line with previous research (Connor et al., 2022), which demonstrated that socially integrated males within second-order alliances spend more time consorting females and can consort them for longer.

The habitat heterogeneity in Shark Bay is striking; the subdivided south with channels and shallow flats as a contrast to the open water habitat in the north with a more uniform bathymetry contour makes it reasonable to assume that ecology contributes to shaping variation in alliance behaviour. Such ecological factors include prey abundance, predator abundance, dolphin density and detection range as investigated here. While the availability of prey cannot explain the variation in consortship rate between the two habitats, Connor et al. (2017) hypothesised

that the shift in food distribution could explain the shift from pair to trio formation within first-order alliances, through a greater abundance of schooling fish in the northern habitat which would reduce the cost of grouping. To address the foraging hypothesis, we estimated average foraging group size outside of the main mating season and included this in our trio-formation model (Table 4.1). We found no effect of foraging group size on trio formation.

Tiger sharks are the main predators of bottlenose dolphins in Shark Bay, and it has been hypothesised in other populations that predator abundance influences dolphin group size (Wells et al., 1987). Within Shark Bay it has been shown that tiger sharks are close to absent during the cold austral months but found in high density during the summer months (Heithaus and Dill, 2002). There is no evidence of seasonal changes in group size of first-order alliances as might be expected if they were influenced by the presence of large predators. Another potential factor influencing the variation in male alliance behaviour is animal density, with higher densities increasing encounter rates with competitors. Here, we quantified density by using surveys from our long-term database to estimate male home range size and within each male's home range; the number of individuals and rival males per km². Regardless of what metric we included in our models, none predicted trio formation, thus density cannot explain the shift in first-order alliance group size along the north-south habitat gradient.

In this study, we were interested in investigating how habitat structure and, as a result, acoustic detection range, may prohibit or allow individuals to detect, identify, and eavesdrop on rival males and receptive females. The active space of pops was the only predictor explaining the proportion of time a male spent consorting in a trio. Given pops are almost exclusively produced in consortships (there has been very few observations of pops produced outside a

consortship context), it is highly likely that males producing pops are herding an oestrus female, indicative to rivals of a potential mating opportunity. In the northern habitat, the greater active space of pops results in greater distances over which rival males can detect and eavesdrop on alliances consorting females, compared to the southern habitat. Hence, males in habitats that favour the transmission of pops are likely detected by rivals over much greater distances, favouring larger first-order alliance sizes as means of defending females against attempted thefts by rivals. Thus, the acoustic detection range of pops has a strong influence on the number of preferred alliance partners, and consequently drives mating success. Together, our results highlight the importance of habitat heterogeneity in shaping the opportunities for social interactions and ultimately driving variation in complex cooperative behaviour within a single population of wild animals.

4.6 Materials and Methods

Data for this study were collected in the Eastern gulf of Shark Bay, Western Australia, where research on the Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) has been conducted on a near-annual, seasonal basis since 1982 (www.sharkbaydolphins.org). The habitat within the study area is highly heterogeneous, characterised by a uniform depth contour in the northern part of the gulf, whereas the southern area varies extensively in depth, and is subdivided by channels, flats and banks (Figure 4.2A).

4.6.1 Long-term data on alliance behaviour

Data on male alliance behaviour were collected from 2001 to 2006, where there was extensive focus on collecting consortship data on 102 focal males who were all members of 12 second-order alliances. However, data collected during these years are representative of male behaviour; males are loyal to their core home range across years and individual male's cooperation dynamics persist throughout their lives, with males forming trios in the north, and pairs in the south. Male association and consortship data were collected during boat-based surveys from June to December between 2001 and 2006, which includes the peak mating season from September to November. Survey data were used to calculate the strength of social relationships between pairs of males. A survey was defined as a minimum 5-min snapshot of dolphin group composition (as defined by the 10 m chain rule, where each dolphin in the group is within 10 m of any other dolphin (Smolker et al., 1992)) and behavioural activity. We removed all foraging surveys (defined based on interindividual spacing, relative orientation, dive type, and direct observations of prey or feeding), as animals tend to loosely aggregate in large groups at the same foraging patch but are not necessarily associating preferentially (Connor et al., 2022).

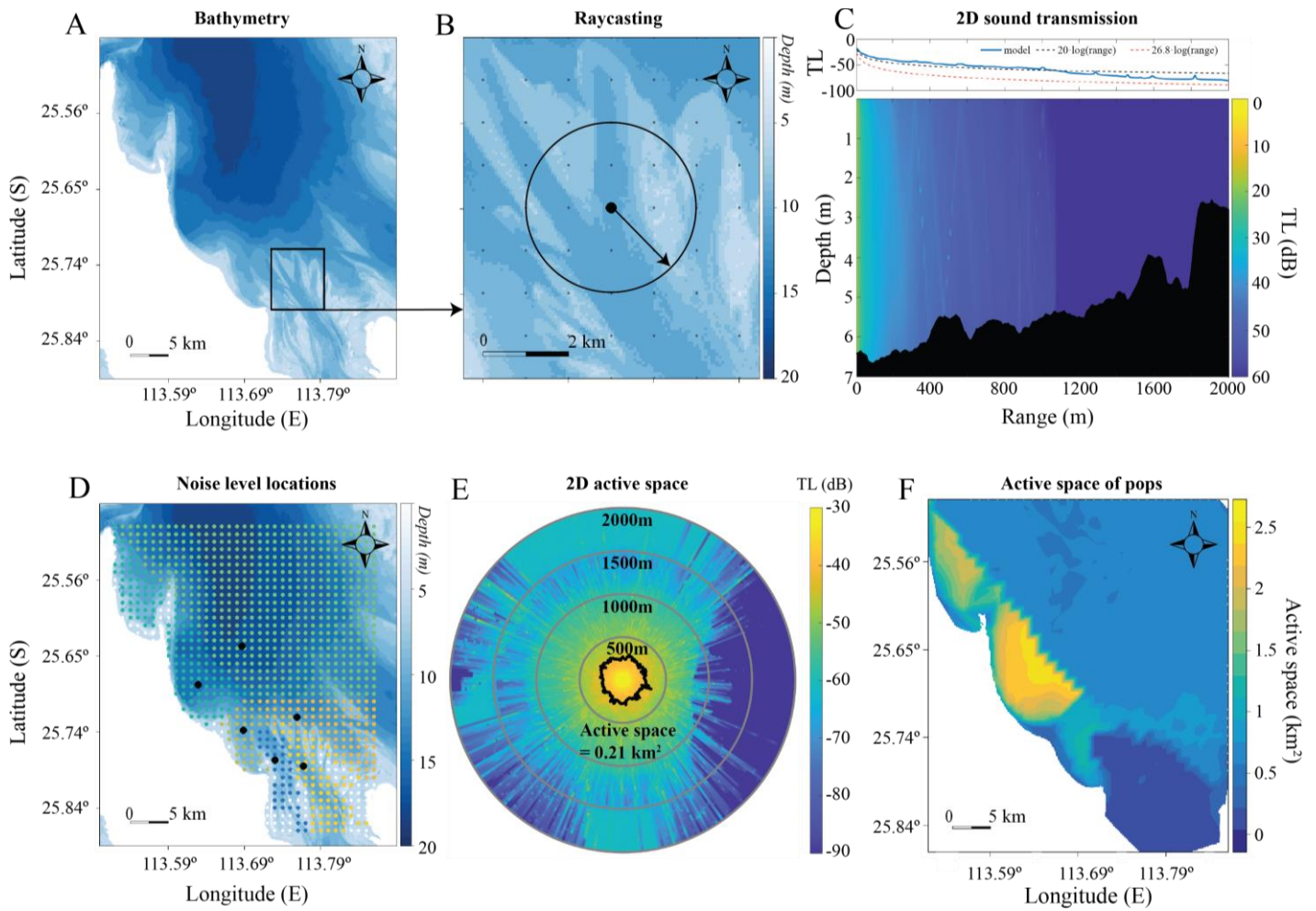


Figure 4.2. Modelling two-dimensional active space within the eastern gulf of Shark Bay, Western Australia. (A) shows the bathymetry based on a 10 x 10 m spatial resolution obtained from satellite derived bathymetry data. (B) shows a close-up of the southern habitat, characterised by channels subdivided by shallow flats. Sampling points (black dot) for sound transmission modelling were spatially organised in grids of 1 x 1 km. From each sampling point the transmission loss (TL) and acoustic detection range was estimated in 1-degree increments, providing 360 detection range estimations per sampling point, in a range of 2 km from the sampling point. (C) 2D sound transmission model in a single direction (the 135° increment) from the sampling point. The main plot shows the modelled TL as a function of range and depth of receiver, with the transition from yellow to blue representing an increasingly larger TL, and the black area representing the seabed. The top panel shows the TL as a function of range (m) from the source (blue solid line) compared to either a spherical ($20 \cdot \log(\text{range})$) spreading model (black dashed line) or an average TL coefficient (red dashed line) estimated based on the total TL at a range of 2 km (in this example 26.8). (D) Each sampling point (small dots, 1 x 1 km grid) was assigned a SoundTrap (large dots) recorded noise level (NL) based on

which SoundTrap would have recorded ambient noise most representative of the ambient NL in the area of the given sampling point. This is shown here using the same colour for the sampling points (small dots) and the SoundTrap (large dots) to which the sampling points were assigned. White dots represent shallow areas with sampling points at a depth of < 1 meter. Sound transmission modelling was not performed for these sampling points. (E) For each sampling point we modelled transmission loss and combined this with site-specific masking noise level and signal-specific source level to estimate communication range along each of 360 radials. Finally, we integrated across all radials to estimate the total two-dimensional active space (km^2) at each sampling point (black line). (F) Doing this for all sampling points provided a 1×1 km resolution of active space across the study site, visualised here using triangular irregular surface interpolation between sampling points (R package *interp* and *raster*).

Association data from surveys were used to calculate each male's cumulative bond strength within their second-order alliance (their core unit) i.e. the sum of each male's social bonds to his second-order allies (see also (Connor et al., 2022; Gerber et al., 2022)). Only associations observed within the first minutes of a survey were included, and any resights of the same group within two hours of each other were excluded. Furthermore, all surveys in which the primary behavioural activity was foraging were excluded, as animals may aggregate around the same foraging patch without directly associating. Social bond strength was then quantified using the Simple Ratio Index (SRI) using the R package *asnipe* (Farine, 2013), which is an estimate of the proportion of time two animals spend together (0 for two animals never observed together; 1 for animals always observed together). The male dolphins are all well-known and identifiable based on the unique patterns of their dorsal fins, meeting the assumptions of the SRI which assumes that all individuals are correctly identified and that no observations of interactions are overlooked (Farine, 2013). Next, the *sna* package (Butts, 2008) was used to calculate each male's cumulative bond strength, which was then normalised by dividing each male's cumulative bond strength by the highest cumulative social bond strength within a male's second order alliance, thus scaling cumulative social bond strength between 0 and 1 for each alliance.

For each male, we calculated their consortship rate as the number of days observed in a consortship divided by the total number of days observed (Connor et al., 2001; Connor et al., 2017; Connor et al., 2022) and their maximum consortship duration in days, which is the length in days of the longest consortship with the same female in which a male participated. Except in cases where we see the female captured, escape, or taken by rivals, consortship durations are conservative, given that we are unable to monitor males every day (Connor et al., 2022). For each male we calculated the proportion of participated consortships as a trio (0 for males that

have only been observed consorting in pairs; 1 for males that have only been seen consorting in trios).

4.6.2 Acoustic recordings of dolphin vocalisations

To quantify the apparent source level of pops, acoustic data were collected between September and November 2019. Pops were recorded during focal follows of male alliances, primarily in the context of consorting a female. Focal follows were conducted from a small (5.4m) research vessel using a horizontal, towed hydrophone array consisting of four HTI-96 MIN series hydrophones (sensitivity: -164 dB re 1 V/ μ Pa, flat (± 1 dB) frequency response: 0.002 – 30 kHz) permitting acoustic localisation of the vocalising animal(s) (King et al., 2018; Quick et al., 2008). All hydrophones were calibrated prior to and after the field season by the method of relative calibration using a calibrated acoustic recorder (SoundTrap ST300; Oceaninstruments.co.nz; cliplevel: 177 dB re 1 μ Pa/V). Hydrophones were suspended to a depth of 1 or 1.5 meters depending on the location depth. All hydrophones were in line with a TASCAM DR-680 MKII multi-track recorder sampling at 96 kHz. Concurrently, a spoken track was used to note the bearing, distance (measured with a Bushnell Laser range finder) and ID of the focal individuals. Individual dolphins were identified by trained observers based on the shape and pattern of their unique dorsal fins and their ID was confirmed with photo-identification data collected with a Canon 50D camera and Canon 100-400 mm IS lens. The vessel engine was turned off during recordings.

All acoustic recordings were first analysed in Adobe Audition (Version 5.0) by visually inspecting the signal envelope and spectrograms simultaneously (FFT = 1024, hamming window). Pops were individually identified and marked. Similarly, the synchronised voice notes were aurally inspected and distance and bearing cues labelled. Using custom-written MATLAB code, start and duration information of pops were extracted from each acoustic

recording. All source parameters were quantified based on Madsen and Wahlberg (Madsen and Wahlberg, 2007) in MATLAB (version 2018b). For each pop the received level (RL) was quantified as the root-mean-square (rms) sound pressure level (SPL_{rms} ; dB re 1 μ Pa) within a 95% energy window (Madsen and Wahlberg, 2007). Only pops with a received signal-to-noise (SNR) ratio of more than 10 dB were used for further analysis. The apparent source levels (ASL) of pops, defined as the back-calculated SPL 1 meter in any direction from the source of unknown orientation relative to the acoustic axis, were calculated based on the passive sonar equation: $ASL = RL + TL$, where TL is the transmission loss, calculated based on the assumption of spherical spreading and ignoring absorption due to the short range to the focal animals (22m – 71m) and relatively low frequency signals: $TL = 20 \cdot \log(R)$ (where R is range to focal animal). Finally, the mean ASL for pops was calculated (mean ASL = 140.9 ± 4.9 dB re 1 μ Pa, rms).

The MATLAB based program TOADy (Quick et al., 2008) was used to calculate the localised bearing of pops. Localised bearings were compared to the bearing and distance measurements of individuals recorded in the field to confirm the distance from the array of the animal producing the pop. Localisation accuracy of the array was calculated using custom-written MATLAB routines to calculate 2D averaged MINNA (minimum number of receiver array) localisations using the methods described in (Schulz et al., 2006; Wahlberg et al., 2001). As per King et al. (King et al., 2019; Moore et al., 2020) the localisation accuracy for pop directions ($n = 50$) were calculated as 68% within $\pm 5^\circ$, 94% within $\pm 10^\circ$, and 100% within $\pm 15^\circ$ of the true location. The centroid frequency (F_C) of pops was calculated (pop mean centroid frequency, $F_C = 1.8 \pm 1.4$ kHz), and defined as the frequency midpoint dividing the signal into two halves of equal energy (Au, 1993).

4.6.3 Quantification of ambient noise

To quantify ambient noise, six acoustic recorders (SoundTraps ST300; OceanInstruments.nz) were deployed at six locations (Figure 4.2D) at water depths of 8-14 meters between 30 October and 27 November in 2019. SoundTraps were either spaced > 7 km apart or on either side of the flats and banks to avoid overlap in the recorded soundscape. Two SoundTraps were placed in the more uniform, open water habitat, two in the complex, subdivided habitat and two in intermediate locations (Figure 4.2D). They were moored 1 or 1.5 meters above the seafloor between a 50 kg concrete base and a 200 mm subsurface buoy. The SoundTraps recorded at a duty cycle of 30 minutes per hour (cliplevel: 174 – 176 dB re 1 μ Pa; sampling rate: 96 kHz; 16-bit, flat (\pm 3 dB) frequency response from 0.02 – 60 kHz) for 23-37 days (Table 4.9.S4). For each SoundTrap, the masking noise level was calculated as the spectral noise density of background noise added to the auditory critical ratios measured for bottlenose dolphins (Johnson, 1968). Spectral noise density corresponds to the amount of power per 1 Hz band (dB re 1 μ Pa²/Hz) and was calculated using a FFT length of 1024, a window length of 512 and a 50% window overlap. The critical ratio is the difference between the sound pressure level of a pure tone just audible in the presence of continuous noise of constant spectral density and the sound pressure spectral density for that noise expressed in dB (American National Standards Institute, 2008). The appropriate masking noise level were derived by interpolating masking noise levels to the centroid frequency of pops (1.8 kHz) and ranged between 81 – 96 dB re 1 μ Pa (Table 4.9.S5).

4.6.4 Bathymetry data

The bathymetry data was produced following the workflow from Lebrech et al. (2021) using 673 Level 2a Sentinel 2 satellite images with a 10 x 10 meters resolution obtained between August – January of 2017 – 2020 from Sentinel Hub. These time periods represent the best

observation conditions, with cloud cover $< 1\%$ and low precipitation, turbidity, and wind. Following the removal of land areas using NDWI filter (McFeeters, 1996), the processing of the bathymetry was performed in three steps. First, an initial bathymetry was generated for each individual image using the equation from Stumpf et al. (2003) and calibration points (i.e., true depth measurements) from the Australian Hydrographic Office. The resulting bathymetry files were reviewed and 429 files presenting either a coefficient of correlation with the calibration points < 0.7 or significant temporal artefacts (e.g. sediments plumes, meteorologic event inprints vessels etc.) were discarded. Second, the remaining 244 files, with an average coefficient of correlation of ~ 0.85 , were corrected for regional image reflectivity changes using an error model based on the integration of the calibration points. Third, the final satellite-derived bathymetry data was calculated as the median value of all individual overlapping bathymetry files. The vertical accuracy of the data could not be precisely measured due to the lack of independent comparative datasets, however the median standard deviation of the overlapping bathymetry which is of 1.12 m can be regarded as an approximation. Such value is consistent with the vertical accuracy of the NWS SDB of 1.2 m, measured using nearly 16,000 lidar depth soundings (Lebrec et al., 2021).

4.6.5 Sound propagation modelling and two-dimensional active space reconstruction

High-resolution bathymetry data were used to model variations in sound propagation and resulting detection range across the eastern gulf of Shark Bay. To do this, sampling points (geographical locations from where active space would be estimated) were defined by a 1 x 1 km square grid throughout the study area (Figure 4.2). For each sampling point that had a depth of $> 1\text{m}$, we modelled sound propagation in 360 radials (1-degree resolution) extending 2 km out from each point using a 2-dimensional (distance vs depth) bellhop model implemented in Matlab (Acoustics Toolbox: <http://oalib.hlsresearch.com/AcousticsToolbox/>). Sound

propagation was modelled assuming a source depth of 0.5 m and a sound frequency of 1.8 kHz corresponding to the mean centroid frequency of pops. An average sound speed profile corresponding to October (peak mating season in Shark Bay) was used in models, and bottom properties were adjusted to reflect sandy silt (Sandy silt: density = 1.7 g/cm³; sound speed = 1567 m/s). While the model was implemented in two dimensions (distance vs depth: Figure 4.2C) to capture sound reflection and refraction, an average sound attenuation as a function of distance was extracted for a receiver at a depth of 0.5 m.

Each sampling point was assigned a median masking noise level by directly attributing the noise level from the acoustic recorder that best represented the general location of the given sampling point (Figure 4.2D; Table 4.9.S5). This was done based on consideration and discussions between authors dependent on where the habitat structure created natural barriers i.e. shallow flats, that would naturally prevent sound transmission from e.g. one deep channel to the other. The location-specific masking noise level and median apparent source level (both in dB re 1 µPa, rms) were then used to estimate the maximum communication range along each radial (Jensen et al., 2012); assuming sound detection when received level exceeded spectral noise density plus the frequency-specific auditory critical ratio. In the very rare event that received level still exceeded masking noise level at 2 km range, the average sound propagation coefficient along this radial was used to extrapolate to the maximum communication range. Finally, the estimated communication range was integrated across all radials to estimate the total two-dimensional estimate of active space (km²) for each sampling point (Figure 4.2E). This was done for each sampling point throughout the area to assess habitat variability in active space (Figure 4.2).

4.6.6 Active space as a driver of cooperation dynamics

For each focal male ($N = 102$), we calculated their individual home range using GPS coordinates from all surveys that each individual was seen in during the 2001 – 2006 period. Individual home range areas (km^2) were based on 50% Epanechnikov kernel density estimates (R package *adehabitatHR*) and a customised smoothing factor (as per (Wild et al., 2019)). For all males we estimated the mean active space of pops based on an average of all active space sampling points that fell within the given male's home range.

To control for the influence of animal density on first-order alliance size and consortship behaviour, we calculated the number of individuals per km^2 within each male's home range (total number of individuals within male A's core home range / male A's core home range in km^2). The total number of individuals per km^2 within each male's home range was estimated by extracting all surveys from June to December between 2001 to 2006. All sightings of individuals of less than 3 years of age were excluded as animals of this age are considered dependent calves. We controlled for survey effort within each male's home range by identifying the male with the fewest recorded surveys within his home range (male ID = TIT; 230 surveys) and then randomly chose 230 surveys from within each male's home range and extracted the total number of individuals seen in these surveys. In addition to animal density, we wanted to ensure that consortship behaviour was not driven by differences in the number of male rivals encountered in each male's home range. We therefore extracted all sightings with at least one adult male (male > 12 years of age) and based on the lowest number of surveys that contained at least one adult male within the home range of each of our focal males (male ID = TIT, $N = 97$), we randomly selected 97 surveys for each focal male from which the total number of unique adult males were extracted. Finally, to confirm that first-order alliance group size was not driven by variations in prey availability or foraging behaviour, we estimated the average foraging group size within each male's home range based on surveys collected from

January to July (outside the mating season) between 2001 and 2006 where the primary group activity was foraging.

4.6.7 Statistical analysis

All statistical procedures were conducted in R Studio (v. 2022.02.2). Using a mixed modelling framework, we investigated the influence of the active space of pops on (i) the proportion of consortships a male participated in as part of a first-order alliance trio, (ii) consortship rate and (iii) maximum consortship duration. In addition to active space, we also included second-order alliance size, a male's cumulative bond strength with his second-order allies, the number of individuals within a male's home range, the number of rival males within a male's home range, and average foraging group size within a male's home range, as fixed effects.

Prior to running all models, we tested for collinearity between the fixed effects by measuring the variance inflation factor (VIF) for all models, which is a measure of multicollinearity between multiple fixed effects within a model (*car* package in R). Only predictor variables with a $VIF < 3$ (Zuur et al., 2010) were retained in the model.

To investigate how the mean active space of pops predicted trio formation and a male's consortship rate, we built generalised linear mixed-effect models (*lme4* package in R) with a binomial family for proportional data. For the model examining how active space of pops predicted maximum consortship duration we built a linear mixed-effects model. For all three models, the fixed effects were the mean active space of pops, second-order alliance size, the number of individuals per km² within each male's home range and the total number of adult male rivals within each male's home range. Furthermore, mean foraging group size per km² within each male's home range was included as a fixed effect in our proportion of trios' model, and normalised cumulative bond strength with second-order allies was included as a fixed effect in our consortship rate and maximum consortship duration models. For all three models,

alliance ID was included as a random effect. Our proportion of trio's model was weighted by the total number of participated consortships and or consortship rate model was weighted by the total number days that a male was observed (See supplementary material Table 4.9.S1 for full model equations).

We present two analytical approaches. In the main text we use a traditional hypothesis testing approach where we used ANOVA (*stats* package in R) to test whether the full model (containing our fixed effect of interest i.e., active space) explained significantly more variance than the null model (without our fixed effect). In the supplemental material, we present results using a multi-model inference approach with model averaging, to consider all plausible models based on the fixed effect variables included in our models. First, we used the *standardize* function in R (package *arm*) to standardise our models' fixed variables, setting the mean to 0 and the standard deviation to 0.5, making them directly comparable. Secondly, all models were ranked based on their AIC value (Akaike Information Criterion) using the *dredge* package in R, followed by model averaging across the best supported models ($\Delta AIC \leq 2$ (Burnham and Anderson, 2002; Grueber et al., 2011)) using the *model.avg* function (R package *MuMIn*). Both approaches show strong agreement with regards to which predictor variables influence the response variable.

To explore whether forming trios has a reproductive benefit, we built two additional mixed-effect models to determine if trio formation predicted either consortship rate or maximum consortship duration. We used ANOVA (*stats* package in R) to test whether the full model (containing our fixed effect of interest i.e., trio formation) explained significantly more variance than the null model (intercept only).

For all models we used the *effects* (Fox and Weisberg, 2019) and *ggplot* (Wickham, 2016) packages in R to plot model estimates of the raw data, and the *DHARMa* package to assess

model fit (Hartig, 2022). The same methods and statistical models were used to investigate the influence of the active space of whistles on trio formation. These results are presented in the appendix.

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4.9 Supplemental material

Table 4.9.S1: Full model summary after model averaging investigating how a male's active space of pops impacts (a) trio formation, (b) consortship rate and (c) consortship duration. For (a) and (b) model averaging was performed across 10 and 3 top models, respectively with an $\Delta AIC < 2$. For (c) there was only one top model (same as the full model presented in the main manuscript), hence why model averaging is not shown for this model.

(a) full model = *glmer(prop.trios ~ 2nd order alliance size + animal density + foraging group size + rival males + active space of pops + (1/2nd order alliance affiliation)*, weights = Number of consortships, family = binomial)

Full average	Estimate	Std. error	Adjusted SE	z-value	Pr (> z)	CI (2.5 %)	CI (97.5 %)
Intercept	3.913	1.007	1.020	3.837	0.0001 ***	1.914	5.912
Active space	5.898	1.732	1.752	3.366	0.0008 ***	2.463	9.332
Animal density	-0.345	0.677	0.681	0.506	0.613	-1.680	0.991
Rival males	0.475	0.533	0.537	0.885	0.376	-0.577	1.527
Second-order alliance size	0.113	0.760	0.768	0.147	0.883	-1.392	1.618
Foraging group size	-0.384	0.564	0.568	0.676	0.499	-1.496	0.729

(b) full model = *glmer(Consortship rate ~ 2nd order alliance size + Cumulative bond strength + animal density + rival males + active space of pops + (1/2nd order alliance affiliation)*, weights = Days, family = binomial)

Full average	Estimate	Std. error	Adjusted SE	z-value	Pr (> z)	CI (2.5 %)	CI (97.5 %)
Intercept	-0.4784	0.1130	0.1144	4.181	< 0.0001 ***	-0.7027	-0.2541
Active space	0.7121	0.2223	0.2251	3.164	0.0016 **	0.2709	1.1532
Animal density	-0.3078	0.1188	0.1203	2.558	0.0105 *	-0.5436	-0.0719
Rival males	0.0054	0.0434	0.0439	0.123	0.9021	-0.0807	0.0915
Second-order alliance size	0.1174	0.2182	0.2196	0.534	0.5931	-0.3131	0.5478
Cumulative bond strength	0.2321	0.0778	0.0788	2.946	0.0032 **	0.0777	0.3865

(c) full model = *lmer(Consortship duration ~ 2nd order alliance size + Cumulative bond strength + animal density + rival males + active space of pops + (1/2nd order alliance affiliation))*

4.9.1 Whistle acoustic parameters

While whistles were not the focus of this study (for reasons we highlight in the introduction of the main text), we present the results for whistle active space and trio formation here. A total of 24 whistles with a signal-to-noise ratio (SNR) of > 6 dB were recorded with a confirmed distance estimate (using a laser range finder). The mean apparent output source level (ASL) of whistles was 140.5 ± 5.5 dB re 1 μ Pa (rms) and the mean centroid frequency of whistles was 9.1 ± 4.3 kHz. Finally, the median ambient NL (spectral noise density + critical ratio) at the centroid frequency of whistles ranged between 75 – 96 dB re 1 μ Pa. These values were used as input in the sound propagation model. Like for the model investigating the active space of pops on trio formation, we built a generalised linear mixed-effects model to examine the influence of whistle active space, with a binomial family for proportion data. We included proportion of trio formation as the response variable and the mean active space of whistles, second-order alliance size, the number of individuals per km² within each male's home range (animal density), foraging group size per km² within a male's home range and the total number of adult male rivals within each male's home range as the fixed effects. Alliance ID was included as a random effect.

Table 4.9.S2. Full model summary before model averaging investigating how a male's active space of whistles impacts trio formation.

<i>Response:</i>				
<i>Proportion of trios</i>	<i>Estimate</i>	<i>Std. error</i>	<i>z-value</i>	<i>Pr (> z)</i>
<i>Intercept</i>	-0.668	5.334	-0.125	0.900
Active space	0.288	0.384	0.750	0.454
Animal density	-0.055	0.034	-1.617	0.106
Rival males	0.029	0.027	1.071	0.284
Second-order alliance size	0.457	0.510	0.897	0.370
Foraging group size	-0.410	0.351	-1.171	0.242

Table 4.9.S3. Full model summary after model averaging investigating how a male's active space of whistles impacts trio formation.

*full model = glmer(prop.trios ~ 2nd order alliance size + animal density + foraging group size + rival males + **active space whistles** + (1/2nd order alliance affiliation), weights = Number of consortships, family = binomial)*

Full average	Estimate	Std. error	Adjusted SE	z-value	Pr (> z)	CI (2.5 %)	CI (97.5 %)
Intercept	3.832	1.551	1.570	2.440	0.015 *	0.754	6.909
Active space	0.163	0.896	0.904	0.181	0.857	-1.608	1.935
Animal density	-1.621	0.830	0.840	1.930	0.054	-3.266	0.025
Rival males	0.106	0.307	0.310	0.342	0.732	-0.501	0.713
Second-order alliance size	0.542	1.724	1.738	0.312	0.755	-2.865	3.949
Foraging group size	-0.262	0.490	0.493	0.531	0.596	-1.228	0.705

Table 4.9.S4. SoundTrap deployment details. Six acoustic recorders (ST300; Oceaninstruments.co.nz) were deployed at six different locations within the eastern gulf of Shark Bay. Shown in the table is logger ID, deployment location (latitude and longitude), deployment date and depth (m) and retrieval date and depth at retrieval.

Logger ID	Latitude	Longitude	Deployment date	Deployment depth (meters)	Retrieval date	Retrieval depth
5153	S25°41'18.5"	E113°37' 49.3"	30.10.2019	11.7	26.11.2019	11.7
5154	S25°38'31.2"	E113°41'09.7"	30.10.2019	13.3	26.11.2019	13.2
5155	S25°44'29.5"	E113°41'26.2"	02.11.2019	7.8	26.11.2019	8.1
5156	S25°46'32.9"	E113°43'56.9"	04.11.2019	9.2	27.11.2019	9.1
5158	S25°46'57.5"	E113°46'10.7"	04.11.2019	9.4	27.11.2019	9.7
5159	S25°43'30.1"	E113°45'36.6"	04.11.2019	9.2	27.11.2019	9.8

Table 4.9.S5. Median ambient noise level (Spectral noise density (dB re 1 $\mu\text{Pa}^2/\text{Hz}$) + critical ratio (dB re 1 Hz) (Johnson, 1968) at the centroid frequency of pops (~ 2 kHz) and whistles (~9 kHz)) and 5th and 95th percentiles as recorded on six acoustic recorders (SoundTraps) deployed within the eastern gulf of Shark Bay, Western Australia. The six loggers were all deployed for one month in November 2019 recording at a duty cycle of 30 minutes per hour. SoundTrap 1 and 2 were deployed in the northern, more uniform habitat, whereas 5 and 6 were deployed in the southern, subdivided habitat. SoundTrap 3 and 4 were deployed between the two northern recorders and the two southern recorders.

Soundtrap ID	Ambient noise level \pm S.D. (2 kHz)	$P_5:P_{95}$ (2 kHz)	Ambient noise level \pm S.D. (9 kHz)	$P_5:P_{95}$ (9 kHz)
1	81.0 \pm 4.9	[71.4:87.1]	75.3 \pm 2.6	[72.0:80.0]
2	85.9 \pm 2.6	[82.8:90.0]	83.4 \pm 2.4	[81.1:88.6]
3	84.3 \pm 2.0	[81.9:87.4]	80.0 \pm 1.8	[79.2:83.3]
4	85.7 \pm 3.1	[82.7:92.4]	81.2 \pm 7.0	[78.6:98.3]
5	95.8 \pm 2.6	[92.9:101.5]	96.1 \pm 1.9	[94.1:100.3]
6	92.3 \pm 1.8	[89.8:95.2]	87.3 \pm 2.0	[85.3:91.8]

4.10 References

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Chapter 5 | The function of acoustic synchrony in multilevel dolphin alliances

5.1 Summary

Male synchronous behaviours are hallmarks of many animal species, with well-known examples including claw waving in male fiddler crabs and chorusing in male katydids. In most species, competition is the primary driver of behavioural synchrony. In contrast, cooperation drives synchrony in humans, where it has been shown to promote bonding, reduce the perceived formidability of opponents and enhance the success of future joint actions. A non-human species in which synchrony is also strongly linked to cooperative behaviour is the bottlenose dolphin. In a population of Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia, unrelated male dolphins cooperate in a multilevel alliance system where motor synchrony has been shown to play an important role in strengthening social bonds between allies. At the first-order alliance level, male dolphins cooperate to herd oestrus females and defend them from rival alliances in events termed ‘consortships’. When consorting a female, males produce a threat vocalisation called a “pop” in repetitive trains to induce the female to remain close. Allied males will sometimes engage in acoustic synchrony, matching each other’s tempo and synchronising pop train production. Here, I use an experimental playback design to test three leading hypotheses on the function of acoustic synchrony in male bottlenose dolphins: to intimidate rivals or female consorts, to impress female consorts, or to promote social bonding among allies. I show that females respond by avoiding the sound source, whereas males were more likely to orient towards and approach the source or not respond at all. However, I observed no difference in the response to synchronous versus asynchronous pop trains. These results suggest the general function of pops is to intimidate females, but that pop synchrony may have evolved to promote social bonding among allies.

5.2 Introduction

The use of synchrony in behavioural displays or in the precise coordination of acoustic signals are features of many animal species. Well-known examples include claw waving in male fiddler crabs (Backwell, 2018), chorusing in male bush crickets (Greenfield and Roizen, 1993), and flashing in male fireflies (Buck, 1938; Buck, 1988; Moiseff and Copeland, 2010). These are all examples of competitive synchrony where males compete to be the leading male (i.e. produce their signal first) to attract females and synchrony is therefore a by-product of male-male competition for mate attraction (Greenfield et al., 2017). While competition appears to drive synchrony in many animal displays, recent experimental research has shown the importance of human synchrony for promoting cooperation and in-group bonding (Launay et al., 2016; von Zimmermann and Richardson, 2016). Human synchrony may also function to reduce the perceived size and strength of rivals through the transmission of information about coalitionary strength to both participants and observers (Fessler and Holbrook, 2014). Examples of human synchrony include soldiers marching in synchronised steps, and the traditional Maori haka “Ka Mate” famously performed by the national rugby team of New Zealand to promote team-bonding and to intimidate rival teams (Savage et al., 2020). In addition to the immediate effect of inducing a collective feeling of unity and social bonding (Launay et al., 2016), synchrony in one context may also enhance performance in future separate collective acts (Valdesolo et al., 2010).

While cooperative synchrony has been extensively studied in humans, it has also been demonstrated in bottlenose dolphins. In Shark Bay, Western Australia male Indo-Pacific bottlenose dolphins cooperate in multilevel alliances to compete against rival alliances for access to oestrus females (Connor and Krützen, 2015; Connor et al., 1992; Connor et al., 2022). The core social unit of alliance formation is the second-order alliance consisting of 4-14 males

(Randić et al., 2012). Within the second-order alliance, males form first-order alliances, in which pairs or trios of males cooperate in herding receptive females in consortships (Connor and Krützen, 2015; Connor et al., 1992). Males from the same second-order alliance work together to defend their females from thefts by rival second-order alliances or cooperate to steal females (Connor and Krützen, 2015). Previous research suggests that synchrony promotes cooperation and signals social unity between males (Connor et al., 2006); allied males consorting females have been shown to perform synchronous displays, aerial leaps and synchronised surfacings with extreme precision (Connor et al., 2006). This affiliative behaviour has been suggested to reduce tension and promote cooperation between males interested in the same indivisible resource (i.e. the consorted female) (Connor et al., 2006). However, synchrony is not limited to males' movements in relation to each other. While consorting a female, males produce "pops", a low frequency, narrowband, pulsed signal, usually produced in repetitive trains, on average consisting of 9.6 individual pops per train (Connor and Smolker, 1996; Moore et al., 2020). Pops are only produced by male dolphins and almost exclusively in the context of consortships; acting as an agonistic signal prompting the female to stay close (Connor and Smolker, 1996; Vollmer et al., 2015). Males will also produce pops in synchrony, actively matching the emission and tempo of individual pops, as well as the length and timing of pop trains (Moore et al., 2020). This demonstrates that male dolphins are capable of acoustic coordination in a cooperative context (Moore et al., 2020), yet the function of pop acoustic synchrony remains unexplored.

Acoustic synchrony in male dolphins, like in humans, may have evolved to promote within-alliance social bonding. However, if synchrony encodes honest information on the quality, strength, or social unity of allied males, it may have been selected for as an honest signal to impress or to intimidate females or rival males. Given the coercive nature of pop

vocalisations, I predict that adult males and females will respond differently to playbacks of pop trains, with females more likely to show an avoidance response as females tend to avoid males due to intersexual aggression (Galezo et al., 2018). However, if synchronised pop trains evolved to impress females, I predict that females will show a weaker avoidance response to synchronised pop trains compared to asynchronised pop trains, whereas I would expect no difference in the response by males. If pop synchrony evolved to intimidate rival males or females, I would predict a stronger avoidance response to synchronised pop trains, compared to asynchronised pop trains for both sexes. Finally, if synchronised pop production evolved exclusively to promote social bonding and/or to reduce tension between allied males, I predict no difference in the response to synchronised and asynchronised pop trains for either sex. To explore these non-exclusive predictions, I used a within-subject paired playback design and drone-mounted video to test the response of adult male and female dolphins to playbacks of synchronised (treatment) and asynchronised pop trains (control). Not only does this experiment allow me to test the function of pop acoustic synchrony, it also provides an opportunity to test for general differences in responses by males and females to pops, which has not previously been tested.

5.3 Methods

Playback experiments were conducted in August 2021 in the eastern gulf of Shark Bay, Western Australia, on wild Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). Research on this population of bottlenose dolphins have been carried out on a near-annual and seasonal basis (usually austral winter and spring) since 1982 (Shark Bay Dolphin Research; www.sharkbaydolphins.org). The focal subjects of this study were adult males (either with their allies or on their own), adult females that were known to be reproductively active (i.e., they have previously been consorted by allied males or observed with a calf, either in a group

or on their own), or consorting groups consisting of allied males with a female consort. The playback protocol followed a within-subject paired experimental design, where each focal individual or group were exposed to two stimulus types; a treatment (synchronised pops produced by two males) and a control (asynchronised pops produced by two males i.e. two males popping independently of each other). The study was conducted in compliance with the ethics policies of the University of Bristol. Scientific permits for the study of animals were obtained from the Department of Biodiversity, Conservation and Attractions (DBCA), Western Australia.

5.3.1 Playback stimuli

Pop playback stimuli were created with a custom-written Matlab script using naturally recorded pops previously localised to adult males from three different second-order alliances (KS, RR and PD alliances). For both the treatment (T) and the control (C) stimuli, two pop trains from two different males (e.g. SMO and COO) from within the same second-order alliance were combined to create three repetitions of either synchronised or asynchronised trains, with each train consisting of 6-8 pops per male and each train separated by an inter-train-interval of 0.5 seconds, similar to naturally produced pop trains (Moore et al., 2020). The inter-pop-interval between one male's pops when produced in a synchronised train (i.e. SMO pop 1 and SMO pop 2) was randomly chosen from a normal distribution ranging from the \pm S.D. around the mean of inter-pop-intervals patterns of individual males in synchronised pop trains (Moore et al., 2020). Likewise, the interval between two males' pops were randomly chosen based on the distribution of inter-pop-intervals between two different males in synchronised pop trains (Moore et al., 2020). For the asynchronised stimuli the same distribution of inter-pop-intervals were used as described for the synchronised train, but the pop trains from the two males (e.g. SMO and COO) were further offset by a maximum overlap of 30%. Thus, each paired stimulus

(treatment versus control) used the same pops from the same two males but differed only in their temporal organisation (Figure 5.1). Pops from each individual male were always combined in the same sequential order as that of the original recorded pop sequence. Each stimulus was bandpass filtered using a 0.2 – 20 kHz 4th pole Butterworth filter, which adequately captures the energy of pops while excluding noise of lower and higher frequency. Pops within each stimulus were normalised to -6 dB to amplify the sound without clipping. Playback stimuli were played back through a Lubell underwater speaker (Lubell Labs Inc., Columbus, OH, USA; frequency response: 0.200 – 23 kHz (0.500 – 21 kHz \pm 10 dB)) in line with a Lubell modified amplifier (TOA CA160), connected to a TASCAM DR-44WL digital recorder. Prior to experimental trials, the source level of playback stimuli was estimated by playback of the stimuli to a calibrated, autonomous acoustic recorder (Soundtrap ST300-LF; oceaninstruments.co.nz; sample rate: 96 kHz; clip level: 176 dB re 1 μ Pa; flat frequency response: 0.02 – 60 kHz \pm 3 dB).

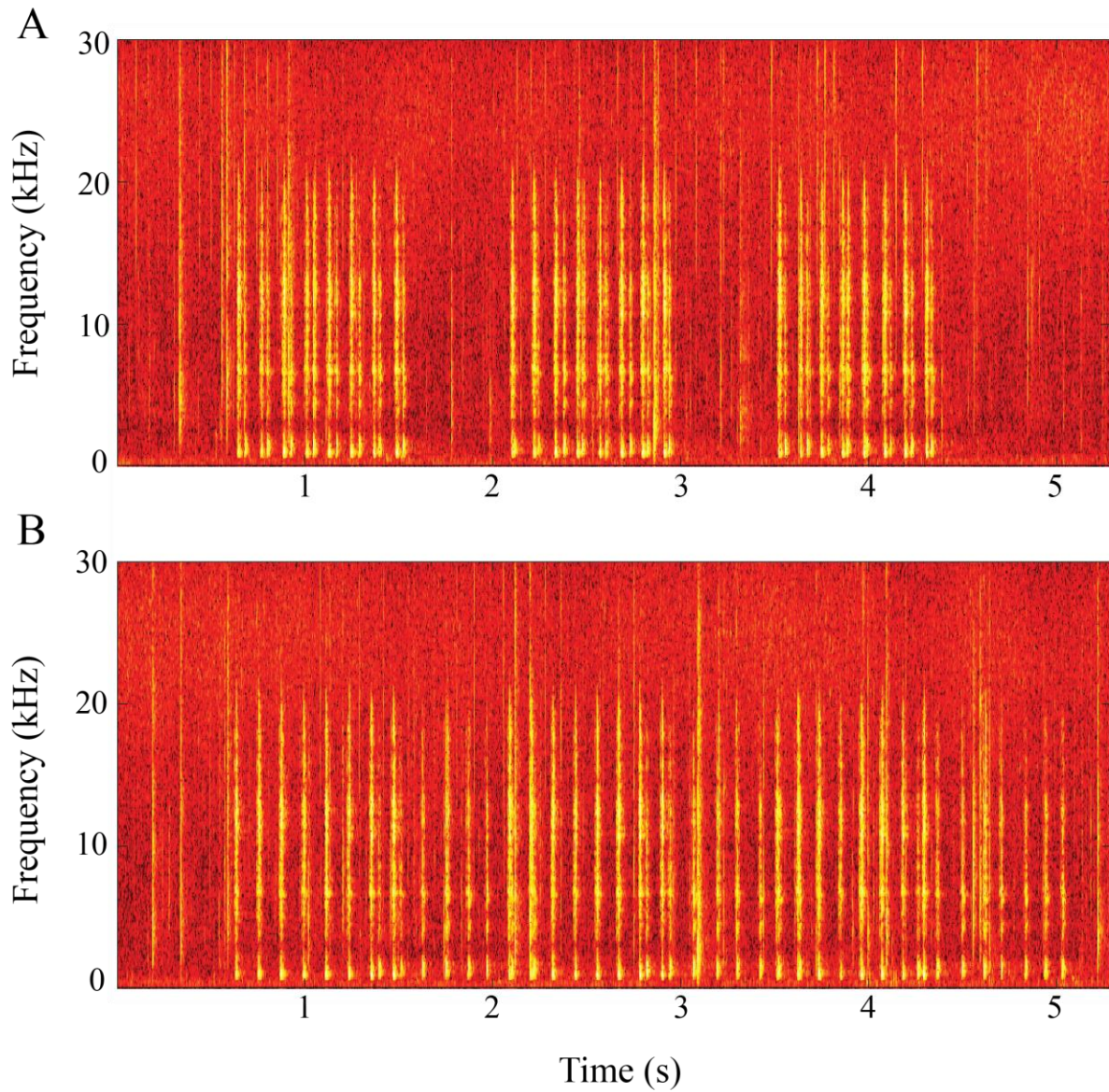


Figure 5.1. Example pop stimuli. Recorded spectrogram of the pop playback stimuli, showing an example of (A) a synchronous pop stimulus (Treatment) and (B) an asynchronous pop stimulus (Control). The examples are created using pops emitted by individuals DEE and CEB, two members of the same second-order alliance. Both spectrograms were created in Matlab (R2022a) (hamming window, FFT-size = 1024 and 50% overlap).

5.3.2 *Playback experiment*

Playback experiments were conducted only in conditions optimal for observation and recording (i.e. sea state ≤ 3 , light winds, no rain) from a 6.15 m research vessel, following a similar protocol to that of King et al. (2021). When a group of dolphins was encountered, the dolphins were approached to within 30 meters for photo-identification and 5-minute behavioural surveys. When the group consisted of potential subjects for playback experiments, we initiated a focal follow once the survey was completed. We deployed a hydrophone array consisting of four HTI-96 MIN series hydrophones (flat frequency response: 0.002 – 30 kHz ± 1 dB) towed at 1 meter depth in a rectangular formation ($\sim 2.3 \times 3.5$ m). The array was connected to a TASCAM DR-680MKII multi-track recorder recording audio at a sample rate of 96 kHz. A spoken track synchronised with the audio recordings was used to note the bearing, distance, behaviour, and individual ID of the focal subject(s) prior to and after each playback. The formation of the array around the research vessel allowed for the localisation of any vocal responses to the playback.

Following deployment of the hydrophones, we awaited suitable conditions for the playback (i.e. group composition, behaviour, visibility, position of individuals relative to each other). Playbacks were not conducted to groups of dolphins engaged in social behaviour and/or who were vocalising, even if the group composition was suitable. When suitable conditions were met the focal individual/group was allowed to move on average 77 meters (Range: 50-130 m) away from the research vessel. The research vessel was always attempted to be positioned in a way so that the focal individual(s) were heading away, and a playback was never conducted to focal subject(s) approaching the research vessel, as any behavioural approach response would be impossible to quantify (Figure 5.2). Prior to playback, a drone (Unmanned Aerial Vehicle (UAV): DJI Phantom 4 Pro+) with an integrated, gimbal-controlled camera (focal length: 8.8 mm; maximum resolution: 3840 x 2160 pixels; sample rate: 23 frames/s) was launched to

record high-quality video of the focal subject(s) response to each playback. Immediately after launching the drone, the drone and audio were synchronised using a spoken track. The drone was then flown to a position just above the focal group or individual. The drone was flown at altitudes (\bar{x} : 31 m, range: 28 – 40 m) that balanced the demand for maximising the ability to detect behavioural changes, while also maintaining a relatively broad field of view. Propeller noise at this altitude was unlikely to impact the animals as it is below the low-frequency hearing threshold of toothed whales and is completely masked by underwater ambient noise if the drone is flown at an altitude ≥ 10 m (Christiansen et al., 2016). At playback, every effort was made to keep the drone stationary to allow for correct assessment of behavioural responses. With the drone directly above the focal subject(s) we deployed the underwater speaker to a depth of 1 meter or to the middle of the water column in very shallow water (< 1.5 m). During the playback the underwater speaker was oriented directly towards the focal subject(s) and playback order (treatment versus control) was counterbalanced, with a minimum of 30 minutes between playbacks and a maximum of two playbacks conducted per focal subject(s) per day. Visual responses to playback, including changes in orientation and approach or avoidance distances to the focal individual(s), were estimated and annotated to the spoken track in the field and corroborated with a Bushnell laser range finder (± 1 meter accuracy) and the drone-mounted GPS.

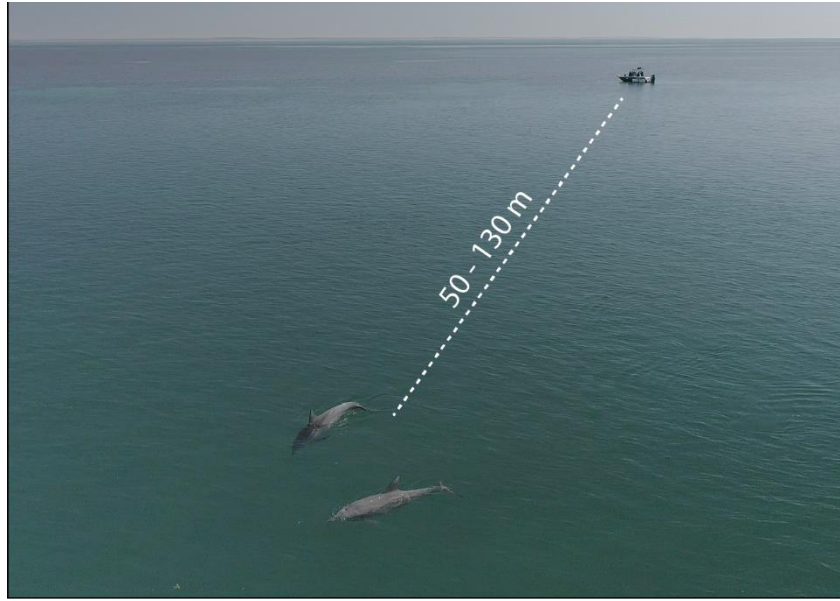


Figure 5.2. Drone point of view. When conditions were suitable for a playback (i.e. group composition, animal/group behaviour, animal group/heading) the drone was launched, synched with audio, and positioned above the focal animal(s). Distance estimates were noted based on a combination of Laser range measurements from the boat to the animals of interest, drone distance from the controller and based on experience. For all playbacks the research vessel's engine was turned off and the playback was conducted at a distance of 50-130 m to the focal animal(s). Photo credit: Simon J. Allen.

5.3.3 Video and acoustic analysis

Behavioural responses to playback, as recorded on the drone video, were analysed by scoring the following variables in Windows or Quicktime Media Player: (i) *time to response (seconds)* defined as the time from the start of the pop playback stimulus to the time of any visual response by the focal animal(s) to the playback; (ii) *response duration (seconds)* defined as the time the focal animal(s) starts responding to the playback to the time they have returned to pre-playback behaviour (i.e. turned back to original heading or reduced swimming speed to pre-playback speed) or to the time at which they disappear from view (i.e. dived beneath the surface) but had returned to pre-playback behaviour when they re-surfaced; (iii) *approach distance (meters)*

which is the distance from where the focal animal(s) first respond to the distance where the individual(s) return to pre-playback behaviour (negative values indicate an avoidance response where the focal subject(s) move away from the source). The distance was estimated on the video using an adult dolphin body length of 2 meters and corroborated with notes taken in real time from the research vessel during the experiment; (iv) *delta orientation (degrees)* which is the focal animal(s) relative change in orientation upon response to playback and (v) *orient to source (yes/no)* defined as a binary measure of whether the focal animal(s) oriented towards the playback source (the research vessel) upon playback.

All 24 drone playback videos and associated acoustic recordings and voice notes were first processed by one observer (P.M.S) using Adobe Audition CS6 (version 5.0). All videos were scored according to the defined behaviours. A second observer (S.L.K) blind to experimental playback treatments and the scores of the first observer then coded all drone videos. The second observer did not score the acoustic recordings as no focal animal(s) responded acoustically to the playbacks. Following data processing we conducted an inter-observer reliability analysis using the *irr* package in R studio (version 2022.02.2) to calculate the intraclass correlation coefficients (ICC) for two-way model for behaviours (i) to (v). We found excellent agreement between the two observers (ICC = 0.962, $p < 0.0001$, C.I. = 0.945 – 0.974), and for further analyses the scores given by observer one was used (P.M.S).

5.3.4 Statistical analysis

All statistical analyses were conducted in R studio version 2022.02.2 (R core team, 2020). To determine how (i) the general response to playbacks varied between sexes and (ii) how subjects responded to the synchronous versus asynchronous stimuli, I built three linear mixed-effects models for three of the behavioural responses (LMM; R package *lme4*) with ‘*approach*

distance, *response duration* and *delta orientation* as the response variables. Playback type (treatment = synchronous pop train; control = asynchronous pop train) and sex (male = A; B = female) were included as fixed effects. Caller ID and Subject ID were included as random effects to account for repeated measures where Caller ID is based on the ID code of the two adult males used to create the pop stimuli, and Subject ID represents each focal group/individual (See raw data in Appendix 5.8.1). For the linear mixed-effects model with *approach distance* as the response variable, the raw data were successfully log transformed to meet model assumptions. As the data was scaled over positive (approach) and negative (avoidance) values, the transformation was done by first removing the negative sign of all avoidance responses, then log-transforming the values, before finally adding the negative sign back again. When investigating the influence of playback type on response duration, I also log transformed the raw data to avoid violating the model assumption (after adding a value of 1^{-8} to all raw data values to allow for log transformation of response durations of 0).

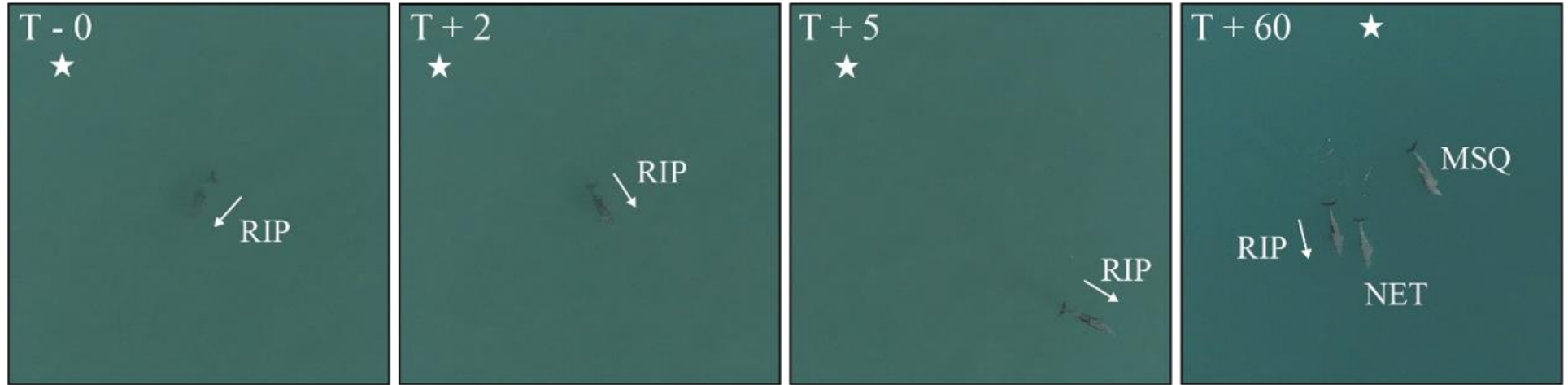
To investigate whether the focal subject(s) responded more often to one of the two playback types (visual response; yes = 1, no = 0) or whether they oriented towards the source in response to the playback types (yes = 1, no = 0), I built two generalised linear mixed-effects models (GLMM; R package *lme4*) with binomial families. Like in the previously described models, playback type (synchronous or asynchronous pop train) and sex (male or female) were included as fixed effects and Caller ID and subject ID were included as random effects.

A traditional hypothesis testing approach using anova (R package *stats*) was applied to determine whether all the full models, with playback type as the fixed effect of interest, and sex as the second fixed effect, explained significantly more variance compared to the null model, without the fixed effect of interest (playback type). Model fits were examined using the function *SimulateResiduals* (R package *DHARMA* (Hartig, 2022)), which allows visual

inspection of residual deviations from the expected distribution and model residuals versus the predicted values. *SimulateResiduals* checks for normality, overdispersion and homogeneity of variance. The raw data was plotted using the R package *ggplot*. I also explored whether the inclusion of an interaction between playback type and sex in the models explained any variance, but as the interaction was non-significant, it was removed from the models.

A

Focal subject: RIP ♀



B

Focal subject: BIG RID NAT w/ SUP ♂

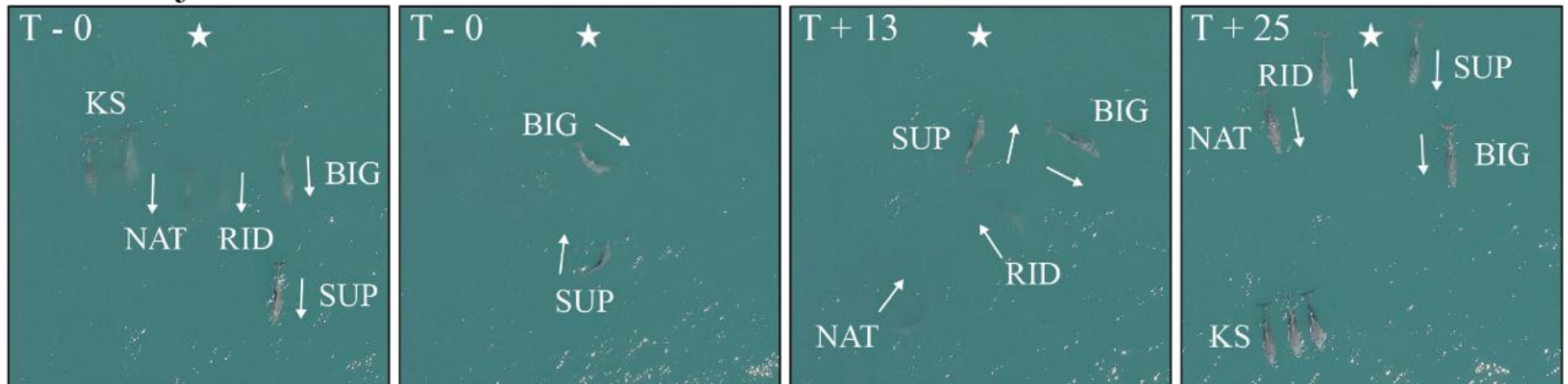


Figure 5.3. Behavioural responses to pop playback. Still photos from drone video recordings showing the behavioural responses of a female subject (A) and a group of male subjects (B). In both (A) and (B) the arrows indicate the animals' orientation, and the star indicates the direction of the research vessel at playback in relation to the animals. (A) shows the adult female dolphin RIP at the time of playback (T-0) and at 2 s (T+2), 5 s (T+5) and 60 s after the start of playback. (B) shows two trios from two second-order alliances (first-order trio NAT BIG RID from the PD and PAS PON DEE from the KS). The PD were consorting the female SUP and were our focal subjects. The still images represent their behaviour and orientation at the time of playback (T-0) and at 5 s (T+5), 13 s (T+13) and 25 s (T+25) after start of pop playback. RIP (A) responded to the playback by turning (90°) and swimming away. After 60 s she had joined with two younger females that had been foraging nearby (NET and MSQ) and had moved approximately 64 meters. (B) At playback (T-0) KS and RID and NAT had just dived. BIG and SUP responded by turning towards the source (180°) within 1 s of playback start. As they turned around RID and NAT returned to the surface at a changed orientation (T+13) before they all turned again (180°) and continued on the same heading catching up with the three KS that had moved ahead (T+25).

5.4 Results

A total of 12 paired pop playbacks (N = 24 playbacks in total) were conducted. Of these, five paired playbacks were conducted to females, three of which were on their own and two were in groups. The remaining seven paired playbacks were conducted to three males on their own and four in groups. There was no evidence of a difference in the approach response to treatment versus control stimuli for either sex (Figure 5.4), but there was a clear sex difference in the general approach response to pops (LMM, *approach distance* (sex); $\beta \pm \text{S.E.} = -2.57 \pm 0.71$, $t = -3.63$, $p = 0.01$; Fig. 5.5A; Table 5.1, (i)); females showed a significantly stronger avoidance response, moving away from the sound source, whereas males either did not respond or approached the sound source. There was no difference in response duration to the treatment versus control stimuli (Figure 5.4B) although females did show a tendency to respond for longer than males to playback, however not significantly (Figure 5.5B). Likewise, there was no evidence for a difference in the magnitude of change in orientation to treatment versus the control stimuli for either sex (Figure 5.4C) and no difference in the general change in orientation of either sex regardless of playback type (Figure 5.5B). There was also no difference in whether the focal subject would orient towards the source for the treatment versus the control stimuli and there was also no difference between sexes. Finally, there was no evidence of a difference in the visual response to the treatment versus the control stimuli for either sex, nor was either sex significantly more likely to respond. The full model results can be seen in Table 5.1. Most behavioural responses occurred almost immediately at an average of 1.6 s after playback onset; however, two different males did not respond until 11 and 19 s after the start of the playback, respectively, but both responded with a 180 degree turn towards the source (Appendix 5.8.1).

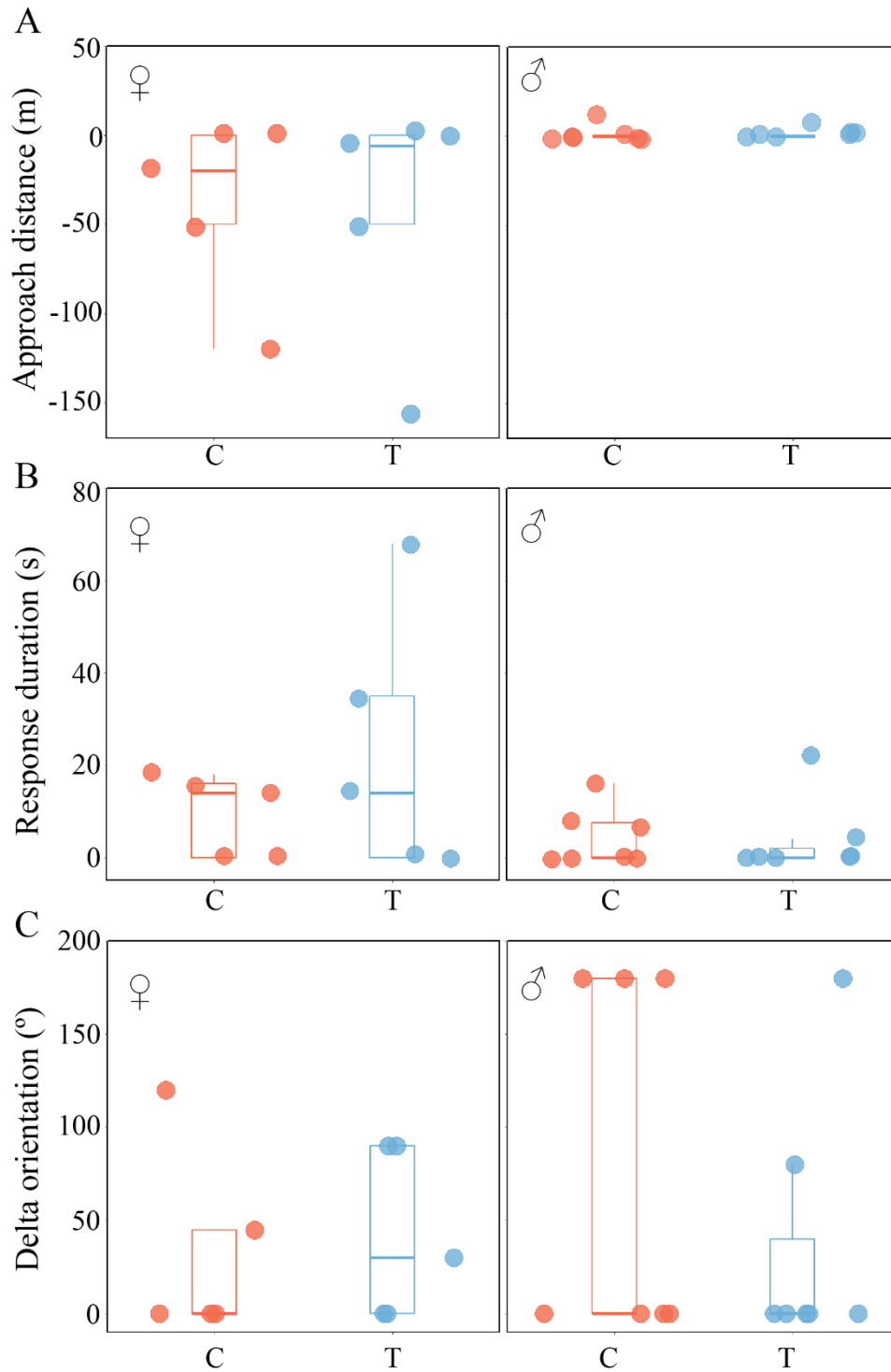


Figure 5.4. Behavioural responses of females and males to synchronous (treatment) and asynchronous (control) pop trains. (A) Approach distance (where a positive value corresponds to approach, and a negative value corresponds to avoidance), (B) response duration and (C) change in overall orientation as a function of dolphin playback category (C = control, $N_{\text{♀}} = 5$, $N_{\text{♂}} = 7$; T = treatment, $N_{\text{♀}} = 5$, $N_{\text{♂}} = 7$). Behavioural responses to the asynchronous pop train stimuli (C) are shown in red, while responses to synchronous pop train stimuli (T) are shown in blue.

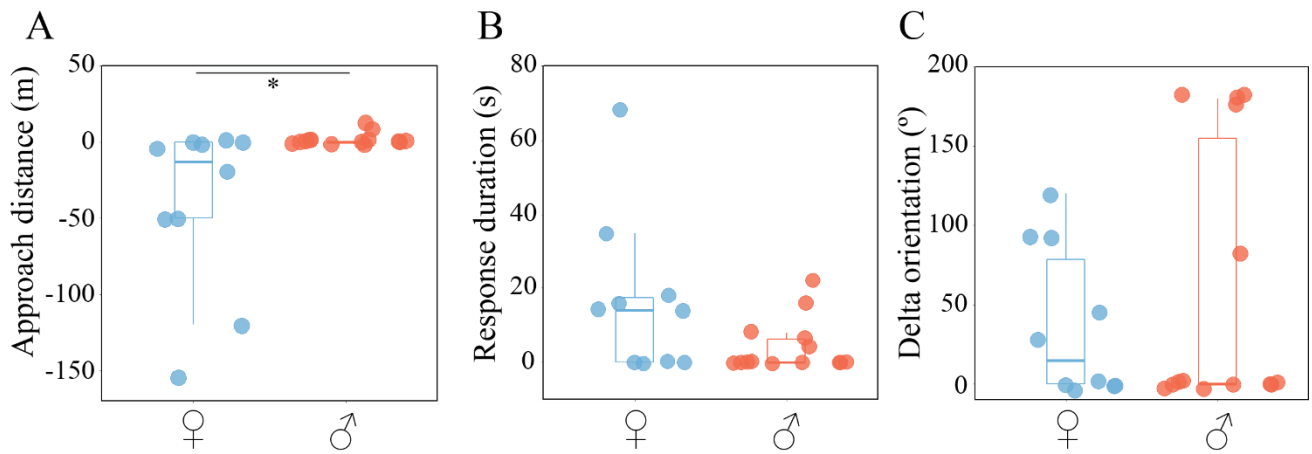


Figure 5.5. Behavioural responses of females and males to pop playback. (A) Approach distance (where a positive value corresponds to approach, and a negative value an avoidance), (B) response duration and (C) change in overall orientation as a function of dolphin sex ($N_{\text{♀}} = 10$; $N_{\text{♂}} = 14$). Female responses are shown in blue, and male responses are shown in red. Asterisk in (A) denotes statistical significance ($p = 0.01$; linear mixed-effects model).

Table 5.1. Model results. Parameters estimates of the linear mixed-effects models for (i) *approach distance*, (ii) *response duration* and (iii) *delta orientation* and parameter estimates of the general linear mixed-effects models (iv) *orient to source (yes or no)* and (v) *visual response (yes or no)* with playback type (treatment (T) = synchronised pop train; or control (C) = asynchronised pop train) and sex (male or female) as fixed effects. For all models, the baseline level (i.e., intercept) is ‘male’ for sex and ‘control’ for playback type. Subject and Caller ID were included as random effects for all models.

Statistically significant p-values are highlighted in bold.

<i>(i) full model = lmer(approach distance ~ playback type + sex + (1/Subject) + (1/Caller ID))</i>						
	Estimate (β)	SE	C.I. (2.5%)	C.I. (97.5%)	t value	p value
Intercept	0.31	0.58	-0.83	1.42	0.54	0.60
Playback type (Treatment)	0.03	0.42	-0.82	0.88	0.07	0.95
Sex (Female)	-2.57	0.71	-4.05	-1.15	-3.63	0.01
<i>(ii) full model = lmer(response duration ~ playback type + sex + (1/Subject) + (1/Caller ID))</i>						
	Estimate (β)	SE	C.I. (2.5%)	C.I. (97.5%)	t value	p value
Intercept	-10.3	3.76	-17.42	-3.10	-2.73	0.01
Playback type (Treatment)	-1.55	4.00	-9.70	6.60	-0.39	0.71
Sex (Female)	5.54	4.94	-4.05	15.13	1.12	0.29
<i>(iii) full model = lmer(delta orientation ~ playback type + sex + (1/Subject) + (1/Caller ID))</i>						
	Estimate (β)	SE	C.I. (2.5%)	C.I. (97.5%)	t value	p value
Intercept	66.93	24.06	-17.42	-3.10	2.78	0.01
Playback type (Treatment)	-19.58	29.20	-9.70	6.59	-0.67	0.51
Sex (Female)	-19.64	29.62	-4.05	15.13	-0.66	0.51
<i>(iv) full model = glmer(Orient to source ~ playback type + sex + (1/Subject) + (1/Caller ID))</i>						
	Estimate (β)	SE	C.I. (2.5%)	C.I. (97.5%)	z value	p value
Intercept	-0.50	0.72	-2.07	0.90	-0.69	0.49
Playback type (Treatment)	-0.93	0.99	-3.09	0.96	-0.93	0.35
Sex (Female)	0.49	1.01	-2.68	1.44	-0.49	0.36
<i>(v) full model = glmer(Visual response ~ playback type + sex + (1/Subject) + (1/Caller ID))</i>						
	Estimate (β)	SE	C.I. (2.5%)	C.I. (97.5%)	z value	p value
Intercept	-0.44	0.76	-1.93	1.04	-0.59	0.56
Playback type (Treatment)	-0.39	0.89	-2.12	1.35	-0.44	0.66
Sex (Female)	1.08	1.00	-0.88	3.04	1.08	0.28

5.5 Discussion

This study shows a clear difference in the general response to pops between the sexes. Females tended to show a strong avoidance response to pop playbacks compared to males. This is in line with the purported function of pops as an agonistic threat vocalisation used by males to control female movement and induce them to stay close (Connor and Smolker, 1996; Vollmer et al., 2015). In contrast, males showed no strong response to pop playbacks, but did tend to orient towards the playback source. However, I found no evidence for a difference in response by either sex to the synchronous versus asynchronous pop stimuli. While this suggests that pop synchrony *may* have evolved to promote social bonding among allied males, it should be noted that this study likely suffers from a lack of power to detect an effect, and further playbacks should be conducted to confirm the findings and to exclude the competing hypotheses.

In response to pop playbacks, female dolphins tended to exhibit very strong avoidance responses, where they would increase swim speed and move away from the sound source. Surprisingly, two female subjects, who were both on their own and foraging at the time, did not show any behavioural response to the playbacks. However, this may be explained by female reproductive state. One of these females (DOD) turned out to be pregnant at the time of the playback as she had a calf three months later. The other female (KIT) had been observed being consorted on several occasions that same year, but she is older and has not had a calf in seven years and it has been shown that bottlenose dolphins experience reproductive senescence i.e. age-related decline in reproductive output (Karniski et al., 2018). My results therefore suggest that reproductive state may directly influence female response, or lack thereof, to pops. Nonetheless, the clear avoidance response that the majority of female subjects exhibited (irrespective of playback type) confirms the function of pops as an agonistic signal to intimidate females.

In contrast to females, males showed no sign of an avoidance response to playbacks. If males did respond, they were more likely to change their orientation towards the source and in a few cases, males would approach the sound source by a few body lengths. However, there was no clear difference in males' response to synchronous versus asynchronous pop trains. If the function of pop synchrony was to intimidate rival males, a stronger avoidance response by males to the synchronous pop playback compared to the asynchronous control would have been expected. Allied males may also be more likely to engage in affiliative social interactions in the face of a potential threat, such as engaging in petting or rubbing (Connor et al., 2006), movement synchrony (Connor et al., 2006; McCue et al., 2020), or even vocal exchanges to reaffirm their social bonds (Chereskin et al., 2022) in response to synchronous pop playbacks. Although based on a limited sample size, the lack of male response observed here, suggests that acoustic pop synchrony is not used to intimidate rival males. Instead, pop synchrony may function as a coalitionary signal, promoting social unity between allies (Fessler and Holbrook, 2014; Wiltermuth and Heath, 2008), although further testing of this hypothesis is needed.

My results showed no difference in response duration between sexes or playback type. When assessing response duration, I would measure focal subjects' responses until they returned to pre-playback behaviour or until they were not visible on the drone video anymore i.e., they dived. For females, this led to reporting conservative measures of response duration as females would often dive down out of view while still swimming rapidly away, but then resurface even further away from the sound source. Thus, female responses are likely to have been even longer, which is in line with what we know about the function of pops as an agonistic signal that females associate with male herding. During consortships allied males sexually coerce oestrus females and may force them out of their core home range with potential ecological cost to the females i.e. to an area in which they cannot use their normal foraging

tactics (Wallen et al., 2016). Additionally, females are often observed trying to escape their male consorts. As such, females have a clear incentive to show a strong and sustained response when they hear pops (Connor and Smolker, 1996; Galezo et al., 2018).

The results presented here shows no response of males to either of the two stimuli. The lack of response differences between the treatment and control stimuli for both males and females, suggests pop synchrony between male dolphins may, like in humans, promote affiliation and reduce tension between allies engaged in a cooperative act, and enhance their general cooperative abilities and effort (Valdesolo et al., 2010; von Zimmermann and Richardson, 2016). This is highly likely given the known importance of motor synchrony for mediating social bonds between allied males in this population (Connor et al., 2006; King et al., 2022). The observations of both vocal and motor synchrony between male allies suggests synchrony may have evolved to advertise coalitionary quality or relationship strength of allies (King et al., 2022), which has also been suggested for humans (Hagen and Bryant, 2003). It has also been shown that there is a link between oxytocin release and synchrony in humans, and that oxytocin plays a role in promoting trust and cooperation (De Dreu et al., 2010; Kosfeld et al., 2005; Spengler et al., 2017). However, recent evidence has also shown that oxytocin is not always involved in promoting affiliative behaviour (Berendzen et al., 2023). Whether a hormonal mechanism plays a role here and synchrony is linked to oxytocin release in dolphins is yet to be determined.

As highlighted throughout, the low sample size may mean there is not enough power to detect differences between the synchronous and asynchronous pop stimuli. Further, focal subject(s) were classified as either adult females or males, but within the groups of males there were also female consorts (N = 2 paired playbacks). One of these groups responded by

orienting towards and approaching the source, whereas the other group did not respond. While the sample size here is too low to properly address this, it may be that males respond differently depending on whether they are in an only-males group or consorting a female with allies. Consorting males may, for example, perceive the threat of rival males producing synchronised pops as greater, as synchronised pops may reflect male quality. If that is the case, consorting males would be expected to pay more attention to synchronised pops. In humans it has been shown that men will find alleged criminals less physically threatening if they walk in synchrony, compared to men performing the same task but walking out of sync (Fessler and Holbrook, 2014). Similarly, pop synchrony may reduce the perceived formidability of rivals between males engaging in the synchronous act. Furthermore, male eavesdroppers may also use acoustic synchrony to assess the coalitionary strength of males herding a female, before deciding whether to attempt a theft of that female. Thus, pop synchrony may serve a dual function, communicating information to both the participating individuals as well as potential observers (Fessler and Holbrook, 2014). It would therefore be particularly interesting to conduct further playbacks to males; both to allied males in single sex groups and in consorting groups (males herding a female), to unravel any contextual differences in male response to synchronous versus non-synchronous pop trains, something that the current sample size does not allow me to assess.

5.6 Conclusion

In summary, I show that female dolphins exhibit a strong avoidance response to pop playbacks, compared to males who did not show a strong response to pops. This is the first experimental demonstration that pops function as an agonistic threat signal produced by males to induce females to stay close, which had not previously been shown. The results show no evidence of a difference in response of either sex to synchronous versus asynchronous pop trains. While this suggests, in line with the suggested function of dolphin motor synchrony, that pop synchrony may have evolved as a coalitionary signal to promote social unity and cooperation between male allies, a lack of response may be a result of the study lacking power to detect an effect.

5.7 Statement of future work:

During the final year of my PhD, I took two months out (September – August 2022) to conduct further pop playbacks for this project with the team. During this time, I was funded by an ASAB research grant awarded to my supervisor Stephanie King. Unfortunately, a requirement of the grant was that the work did not form part of a PhD thesis. However, we were able to double our sample size during this field season, conducting 26 playbacks of which 24 were paired (i.e. playback of both treatment and control). We conducted six paired playbacks to allied males in consortships (herding a female), four paired playbacks to female(s), and two paired playbacks to allied males in single sex groups. Two more playbacks (one treatment and one control) were conducted with two different groups of allied males in single sex groups but were not paired due to changes in weather conditions preventing us from staying with the group. We are planning to go back to the field this year to conduct further playbacks, focusing on males in consortships. We will then write the work up for publication.

5.8 Appendix

Table 5.8.1. Raw data overview. Overview of the 12 paired playbacks collected for this study. Values are based on the observations of one observer (P.M.S). *Focal ID*: The three-letter codes for individual focal subjects. *Sex*: F = Female, M = Male. *Playback type*: C = Control, T = Treatment. *Subject ID*: Unique subject ID. *Caller ID*: Unique ID for the two males, from which pop trains were combined to create the stimuli. *Visual response*: yes = 1, no = 0. Orient to source: yes = 1, no = 0.

<i>Focal ID</i>	<i>Sex</i>	<i>Playback type</i>	<i>Subject ID</i>	<i>Caller ID</i>	<i>Visual response</i> (yes = 1, no = 0)	<i>Time to response (s)</i>	<i>Response duration (s)</i>	<i>Orient to source</i> (yes = 1, no = 0)	<i>Delta orientation (°)</i>	<i>Avoid/Approach distance (m)</i>
LEN HUF	F	T	F1	D1C1	1	1	35	0	30	-50
LEN HUF	F	C	F1	D1C1	1	1	16	1	120	-50
DOD	F	C	F2	S2C2	0	NA	0	0	0	0
DOD	F	T	F2	S2C2	0	NA	0	0	0	0
RHO ZEP TNT	F	T	F3	S1C1	1	2	14	1	90	-6
RHO ZEP TNT	F	C	F3	S1C1	1	3	14	0	0	-120
SMO	M	T	M1	B1N1	0	NA	0	0	0	0
SMO	M	C	M1	B1N1	1	11	16	1	180	12
PLU RSP	M	C	M2	S1C1	0	0	0	0	0	0
PLU RSP	M	T	M2	S1C1	0	NA	0	0	0	0
DEE	M	C	M3	S2C2	1	19	8	1	180	0
DEE	M	T	M3	S2C2	0	NA	0	0	0	0
PAS PON CEB	M	T	M4	B2N2	1	1	4	0	80	0
PAS PON CEB	M	C	M4	B2N2	0	NA	0	0	0	0
KIT	F	C	F4	B1N1	0	NA	0	0	0	0
KIT	F	T	F4	B1N1	0	NA	0	0	0	0
BIG RID NAT w/ SUP	M	T	C1	S2C1	1	1	22	1	180	7
BIG RID NAT w/ SUP	M	C	C1	S2C1	0	NA	0	0	0	0
RIP	F	T	F5	D2C2	1	1	68	0	90	-156
RIP	F	C	F5	D2C2	1	1	18	0	45	-20
TTR SDG AGA w/ AMP	M	C	C2	D2C2	0	NA	0	0	0	0
TTR SDG AGA w/ AMP	M	T	C2	D2C2	0	NA	0	0	0	0
BUD	M	C	M5	D2C2	1	3	7	1	180	0
BUD	M	T	M5	D2C2	0	NA	0	0	0	0

5.9 References

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Chapter 6 | General discussion

In this thesis, I explored the importance of communication for facilitating cooperation in bottlenose dolphins, and how anthropogenic, ecological, and social factors influence vocal behaviour and, ultimately, social evolution. Bottlenose dolphins are well-known for their use of vocal communication to mediate a range of different cooperative behaviours, such as alliance mating behaviour, which is of particular interest in this thesis. However, while the use of vocalisations in this context is well-established, our understanding of how vocal communication facilitates cooperation, and how ecological factors may influence cooperative behaviour via an impact on sensory ecology, remains limited. In this thesis, I first explored how anthropogenic noise influences the acoustic communication strategies of a pair of bottlenose dolphins in human care performing a cooperative task (Chapter two). I then went on to quantify the acoustic properties of two social sounds important for cooperative behaviour in a population of wild Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia (Chapter three), and explored the impact of habitat heterogeneity on acoustic communication range (active space) and male social behaviour (Chapter four). Finally, I tested the function of acoustic synchrony between allied male dolphins in a cooperative context and hypothesised on why this vocal behaviour evolved (Chapter five). Here, I discuss these findings in more detail.

6.1 Noise impairs cooperative behaviour

Communication is thought to be important for coordinating cooperative behaviour (King et al., 2021a; Mine et al., 2022). However, increasing levels of anthropogenic noise poses a significant problem for a wide range of animals because of its demonstrated impact on behaviour (Duarte et al., 2021; Pijanowski et al., 2011). Noise is of a particular concern for

marine animals due to their reliance on sound, as sound travels further and faster under water (Urick, 1983). Depending on the location of animals relative to the noise source, noise pollution has the potential to disturb, distract or even mask signals (i.e. prevent the detection and perception of signals; Erbe et al., 2016), and in some cases may even cause physiological harm, such as auditory damage or death (Barber et al., 2010; Morley et al., 2014; Tyack, 2008). While extensive previous research has documented several acoustic and other behavioural mitigation strategies that animals employ to compensate for noise (e.g. Ansmann et al., 2007; Brumm and Todt, 2002; Fuller et al., 2007; Kaiser and Hammers, 2009; Kragh et al., 2019; Tyack et al., 2011), it remained unknown whether these strategies were enough to overcome the effects of noise. In this thesis, I wanted to address that gap by investigating how increasing levels of noise impacted animals working together. It had previously been shown that pairs of bottlenose dolphins in human care were more successful in a cooperative task if whistles were used to coordinate their behaviour (King et al., 2021a). Using the same cooperative experimental design, but introducing various levels of anthropogenic noise, I found that dolphins actively adjusted their vocal behaviour, oriented more towards, and spent more time in close proximity to their partner. However, these partial compensation mechanisms were not enough to overcome the effects of noise as the dolphin's success rate in the cooperative task decreased with increasing noise levels. From a cognitive perspective, this study also provides evidence that dolphins can flexibly modify their vocalisations and behaviour to facilitate cooperative success (Sørensen et al., 2023). We showed that the dolphin dyad are capable of 'actively coordinated collaboration' (Duguid and Melis, 2020); providing further evidence that dolphins can use communication signals (i.e. whistles) to facilitate the successful execution of coordinated cooperative actions.

This study is to my knowledge the first to assess the impacts of noise on cooperative behaviour. I am confident this is not due to a lack of interest, but rather due to the difficulties

of conducting this type of experiment. These experiments require extensive knowledge of what the animals are trying to achieve when cooperating and which acoustic signals are used to facilitate the cooperative behaviour. Furthermore, they need to be conducted in a controlled setting, where both noise exposure levels and the use of acoustic signals can be closely monitored. Studies like this are, therefore, almost impossible to conduct in the wild, highlighting the importance of conducting experiments with animals in human care to aid our understanding of their wild counterparts.

While our sample size of one pair is indeed small, the study was conducted with two well-trained and highly motivated dolphins in human care, who were very experienced with the cooperative task and knew exactly what was expected of them. This is not the case for wild animals, where the initiation and coordination of cooperative behaviours may rely on cues or signals from either of the participating parties for coordination to be successful (Hamilton et al., 2022; Mine et al., 2022). If acoustic cues and signals are used by wild animals to coordinate cooperative behaviour, then it is likely that masking noise will not only lead to disturbance of ongoing cooperative behaviours but may also lead to missed opportunities for cooperation. In dolphins, sound facilitates cooperative foraging (Hamilton et al., 2022), group cohesion (Janik and Slater, 1998; King et al., 2021b), individual recognition (Bruck et al., 2022; King and Janik, 2013), multilevel alliance formation (Connor and Krützen, 2015; Connor et al., 2022; King et al., 2021b), and acoustic synchrony (Moore et al., 2020), with the latter likely promoting social bonding among allies (Chapter five). These behaviours are essential for individual fitness, and sustained noise disturbance may therefore directly influence individual health (Hotchkin and Parks, 2013; Southall et al., 2008), with implications for population health. The results I present in Chapter two are important in highlighting the need to account for the impact of noise on cooperation in wild animals, as the use of well-established compensatory mechanisms are insufficient to overcome the impacts of noise.

6.2 Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia

In the following chapters, my focus turned to explore different aspects of communication used for cooperation in wild bottlenose dolphins. For this purpose, I studied the population of Indo-Pacific bottlenose dolphins in Shark Bay, Western Australia. Long-term data has been collected on this population since 1982. Male dolphins in this population are well-known for their three levels of alliance formation, in which males compete over access to females (Connor and Krützen, 2015; Connor et al., 2022). At the first level, male pairs or trios will cooperate to herd oestrus females in events called consortships. The core social unit is the second-order alliance level, in which 4-14 males compete with other alliances over access to females (Connor and Krützen, 2015; Connor et al., 1992; Randić et al., 2012). Multiple second-order alliances will also cooperate in third-order alliances (Connor et al., 2022). The acoustic communication signals used by allied male dolphins in this population are well-studied, and include the use of whistles and pops (King et al., 2018; King et al., 2021b; Moore et al., 2020). Whistles are normally classified as non-signature and signature whistles. While our knowledge on the use of non-signature whistles to date remains limited, signature whistles are individually distinctive identity signals and function as vocal labels (Bruck et al., 2022; Caldwell and Caldwell, 1965; King and Janik, 2013; Sayigh et al., 1990), facilitating individual recognition (Janik et al., 2006; Sayigh et al., 1990) and group cohesion (Janik and Slater, 1998; King et al., 2021b). Pops function as an agonistic threat vocalisation used by males to induce females to stay close to the popping male (Connor and Smolker, 1996; Moore et al., 2020; Vollmer et al., 2015). Indeed, the long-term research project and the extensive existing data available on cooperative behaviour and communication, provided me with an unparalleled opportunity to build on our already existing knowledge to address research questions that requires such knowledge. Indeed, long-term research projects on wild populations have advanced the fields of animal behaviour, ecology and evolution (Clutton-Brock and Sheldon, 2010), allowing

observations of the same individuals across decades and providing researchers with a unique opportunity for investigating population-level impacts of anthropogenic activity, such as climate change (Wild et al., 2019). Chapters three to five in this thesis have all heavily relied on the existing knowledge and data collected on the Shark Bay dolphin population over the last four decades.

6.3 Acoustic communication range of whistles and pops

Quantifying the transmission properties of acoustic signals is important for understanding how variation in communication range may impact social behaviour and why certain signals are favoured for particular social functions. It also provides us with a better ability to interpret how anthropogenic noise pollution may impact a species' ability to communicate, which based on my results from Chapter two, is of high importance for understanding how noise pollution impacts functionally important group tasks.

The communication range, or active space (Marten and Marler, 1977), depends on the signal amplitude and frequency, the transmission loss, the auditory sensitivity of the receiver, and masking noise levels (Urick, 1983). In Chapter three, I quantified the communication range of pops and whistles using empirical measures of apparent source levels and frequency, transmission loss and masking noise levels collected in the eastern gulf of Shark Bay. I found that pops had a slightly greater communication range than whistles, but for both signals the communication range varied as a function of the habitat structure and ambient noise levels, varying from a couple of hundreds of meters in the southern, subdivided habitat to 1-2 km in the northern, open water habitat. However, using empirical measures to estimate the effective communication ranges of dolphin whistles and pops relies on a few assumptions. First, I collected measures of sound transmission loss at 18 locations within the study site. Based on these, I estimated the transmission loss coefficient (k) for both signals. While k was relatively

consistent for individual signals at a *single* location, transmission loss varied extensively between sites by up to 6 – 8 dB for stimuli at the frequencies of interest (i.e. frequencies comparable to the centroid frequency of pops and whistles). Such variation in k can lead to differences in the estimated communication ranges of several kilometres. This highlights the intricacies of quantifying acoustic communication ranges in complex, shallow water habitats characterised by large habitat heterogeneity. Habitat heterogeneity can indeed lead to large spatial variation in how sound is transmitted, through differences in how the signal is reflected, scattered and the impact of multipath arrivals. Other features of the habitat such as the current tide patterns, the presence of thermoclines, bottom bathymetry and type etc. may also play a role. For example, it has been shown that sound in areas with sea grass are attenuated quicker than in areas with different bottom types (Quintana-Rizzo et al., 2006).

Second, quantifying masking noise levels is not always straight forward. Here, I assumed that the effective communication range is when the received level of the signal (i.e. whistle or pop) falls below that of the masking noise level (Erbe et al., 2016; Fletcher, 1940). It should be highlighted that this represents the maximum, best-case communication range, as detection by a receiver also depends on the receiver's hearing sensitivity, orientation, and attention (i.e. they might be engaged with another behaviour) (Bradbury and Vehrencamp, 1998). Thus, the effective communication range for successful discrimination and recognition is likely shorter than estimated values (Erbe et al., 2016).

A typical approach is to estimate masking noise level as the sum of the spectral density and the critical ratio, which is a measure of when a pure-tone would be detected in white noise 50% of the time (Erbe et al., 2016; Fletcher, 1940). Measures of the critical ratio (CR) in bottlenose dolphins comes from a 1968 study (Johnson, 1968), in which the critical ratios of pure tones between 4 – 12 kHz were estimated in 1 kHz increments. In Chapter three (and four) I use the measures of critical ratio to assess masking noise levels. For whistles, which are tonal

sounds, the pure tone estimate of CR at 9 kHz was deemed appropriate (whistle centroid frequency, F_C : 9.1 kHz). However, pops are narrow-band, pulsed sounds produced at a F_C of 1.8 kHz, and the current estimates of CR used for pops in Chapter three and four may not represent the most appropriate measure for estimating masking noise level. Alternatively, I could have estimated masking noise levels based on 1/3rd octave band levels or the rms bandwidth of the noise in the same frequency band as the signal of interest. However, both of these measures would be unnecessarily conservative as previous research suggest the auditory bandwidth corresponding to CR at the frequencies of whistles are closer to 1/11th octave band, and would still only apply to whistles. For this reason, I used the best measure of masking noise level for whistles, and to allow comparison between whistles and pops, I used the same measure for pops. I would predict that a correct measure of CR for pops would be higher than the value currently used for pure tones at the same frequency, thereby reducing the estimated communication range of pops. Future work would benefit from studies on the auditory bandwidth of low-frequency pulsed sounds.

6.4 The impact of habitat heterogeneity on alliance behaviour

Using the empirical measures of pop apparent source levels and masking noise levels from Chapter three, I proceeded to investigate how habitat heterogeneity may impact dolphin alliance behaviour. Previous studies have mainly focused on the social processes driving social complexity. However, as highlighted in a recent study (He et al., 2019), research investigating the role of the physical configuration of the habitat on social complexity remains lacking. Habitat heterogeneity not only impacts animal movement, but also influences sound transmission. To my knowledge, the study presented in Chapter four, is the first to show that variation in sensory ecology, driven by habitat heterogeneity, plays a major role in shaping social evolution (i.e., cooperative group size and reproductive success). The population of

bottlenose dolphins in Shark Bay provided a unique opportunity to explore this question. First, the extensive data on male alliances collected over the last four decades allowed me to gain access to first-order alliance group size across years to explore variation in group size as a function of habitat structure (i.e., pairs in the south; trios in the north), highlighting the importance of long-term studies. Second, the population of dolphins in Shark Bay represent a single population living in an environment characterised by considerable variation in habitat structure, but where all individuals can freely move across the study area. As a result, this allowed me to investigate how habitat heterogeneity, and thus active space of pops, influences male social behaviour within one population. I found that variation in pop active space, mediated by habitat structure across the study area, predicted first-order alliance group size, driving the number of preferred alliance partners. In contrast, animal density, second-order alliance size, number of rival males, and foraging group size did not significantly influence first-order alliance size. For further analysis, I also want to include depth as an additional fixed effect in the models. It could be hypothesised that trios are favoured in the northern habitat, as females are more successful at escaping in the deeper water, compared to the shallower water in the south. While this is an important point to address, I predict this hypothesis to be unlikely; the southern area consists of flats and banks, but also deep channels, and the northern habitat similarly have shallower areas near the coast, yet males inhabiting these areas still form pairs and trios, respectively (Connor et al., 2017). An additional consideration for future analysis is accounting for substrate type in our noise propagation models. A previous study has shown that sea grass plays a significant role in sound transmission in shallow habitats, by significantly reducing the effective communication range of whistles (Quintana-Rizzo et al., 2006). Our applied bell hop model currently does not account for variation in substrate type, but depending on the availability, including this in our statistical models might be worth exploring further.

6.5 Limitations in using empirical measures versus a sound transmission model to estimate communication range

In both Chapter three and four I estimate the effective communication range of pops and whistles (communication ranges for whistles in Chapter four are presented in the supplemental material only, section 4.9). While the overall variation in communication ranges across habitat were similar, regardless of whether empirical or model estimates were used, with larger communication ranges in the northern habitat compared to the southern habitat for both signal types, the empirical measures showed slightly larger communication ranges for pops, and smaller ranges for whistles (Chapter three), whereas the modelling approach (Chapter four) suggested the opposite. However, it should be noted that the differences in absolute communication ranges of whistles and pops are minor compared to the 10-fold variation in communication ranges between the northern and southern habitat due to location, for both types of vocalisations. Thus, location has a much bigger influence on communication ranges than variation in the transmission coefficient k . Below, I will address the different assumptions underlying both methods, as well as the limitations that may have led to variations in the estimated communication ranges.

Empirical estimates provide as close to a true measure of sound transmission at a given location and at a given time as we can reasonably obtain. However, in complex habitats the transmission of sound at one location might be very different from the transmission of the same sound close by, or in a different direction. As such, collecting empirical measures representative of a given habitat can be extremely time-consuming. In contrast, in Chapter four my co-authors and I used a bell hop sound transmission model along with high-resolution bathymetry data to estimate the two-dimensional active space around sampling points spaced 1 km apart (1 x 1 km resolution), which allowed us to account for non-uniform spreading from a source. Indeed, using a model allows estimation of transmission loss across a whole area,

which is one of the great strengths of using a modelling approach. A disadvantage of the bell hop transmission model is that it is indeed just a model, though based on real data (i.e., bathymetry data, apparent source level measurements, signal frequency, masking noise level). It does not account for reflection in the horizontal plane; any reflections of sound from barriers such as banks into the sound channel are not modelled. (Bradbury and Vehrencamp, 1998). In contrast, empirical measurements account for these factors as this is directly reflected in the recorded received levels. However, even when using the empirical approach, we are provided with a transmission loss snapshot in time that may vary with tidal changes, temperature shifts, and wind- and weather conditions.

Finally, in Chapter three, I used empirical measures of k to estimate apparent source levels for whistles and pops and used these measures to estimate communication ranges. In Chapter four, I used measures of apparent source levels based on the assumption of spherical transmission loss (i.e., $20 \cdot \log(\text{range})$). The assumption of spherical spreading is often made when estimating apparent source levels from recordings of animals in the wild (Madsen et al., 2006; Urick, 1983). While this meant I used different measures of apparent source levels in Chapter three and Chapter four, it is important to note that the relative differences of estimated communication range across habitats for both signal types remained the same. Thus, the results presented in Chapter four that show how the active space of pops, driven by habitat heterogeneity, influence social evolution in a cooperative mating system, are robust.

6.6 The role of acoustic synchrony in male dolphins

Synchronous behaviour is strongly linked to cooperation in humans (Launay et al., 2016; von Zimmermann and Richardson, 2016); with examples including soldiers marching in synchronised steps and the famous traditional Maori haka “Ka Mate” performed by New Zealand’s rugby team to promote team bonding and to intimidate rival males (Savage et al., 2020). While the use of competitive synchrony is widespread in the animal kingdom (Backwell, 2018; Buck, 1938; Buck, 1988; Greenfield and Roizen, 1993; Moiseff and Copeland, 2010), dolphins represent the only non-human species in which a link between cooperation and synchrony has also been documented (Connor et al., 2006; Moore et al., 2020). While allied male dolphins in Shark Bay are well-known for their use of motor synchrony for promoting cooperation (Connor et al., 2006; King et al., 2022), the use of synchronous pop production was only recently discovered (Moore et al., 2020). In Chapter five, I set out to investigate the function of acoustic synchrony in male dolphins by testing three leading hypotheses. My results showed clear differences in the behavioural response between males and females to pop playbacks; females would show a strong avoidance response, whereas males would either approach the source or show no response. However, I found no effect of synchronous compared to asynchronous playback stimuli on response strength. These results confirm the previously purported function of pops as an agonistic threat vocalisation used by males to control female movement (Connor and Smolker, 1996; Vollmer et al., 2015).

Clearly, the major limiting factor of this study is the lack of power to detect any effect of pop synchrony on receiver response. Playback experiments are challenging to conduct, and require suitable playback conditions, such as the desired group composition, behaviour, distance to the focal subjects and position of individuals relative to each other. Given these challenges I was unable to conduct enough playbacks during my last field season, and further experimental playbacks are therefore underway to expand the sample size before publication.

While the results suggest pop synchrony *may* have evolved to promote social bonding among allies, more playbacks need to be conducted to unravel any contextual differences in the response of male and female dolphins to synchronous versus asynchronous pop trains. While outside the scope of my doctoral research, another very interesting aspect of this area of research, that we know very little about, is whether synchrony in dolphins is linked to oxytocin release, as it is in humans (De Dreu et al., 2010; Kosfeld et al., 2005; Spengler et al., 2017), or if dolphins exhibit a general link between oxytocin release and prosocial behaviour, as occurs in grooming in chimpanzees (Crockford et al., 2013) and alloparental care in meerkats (Madden and Clutton-Brock, 2011). It might also be possible that no link exists between oxytocin release and synchronous behaviour. For example, in prairie voles the presence of a oxytocin receptor is critical for pair-bonding, however, when this receptor is removed, prairie vole parents still perform parental behaviour, suggesting that more research is required for investigating the pathways supporting prosocial behaviours (Berendzen et al., 2023). Exploring this gap in our current knowledge would allow further insight into understanding the role of cooperative synchrony in dolphins.

6.7 Conclusion

The research I present in this thesis contributes to our knowledge of the importance of acoustic communication for cooperation in bottlenose dolphins. This work emphasizes the importance of acoustic signalling in dolphins for performing and promoting cooperative behaviour and highlights how non-social drivers (noise and habitat heterogeneity) may impact communication-mediated cooperative behaviours. By working in close collaboration with colleagues, and dolphins in human care, I was able to reveal novel insights into how noise pollution impacts dolphins working together and provide further evidence for dolphins' capability of actively coordinated collaboration. Then, as part of a long-term research project,

I was able to quantify the acoustic characteristics of two types of social sounds (i.e., pops and whistles), used to mediate cooperation between male dolphin allies. Using the acoustic parameters of pops, I show that habitat heterogeneity plays a key role in influencing cooperative group size and reproductive success and demonstrate the importance of habitat heterogeneity in shaping social evolution, something that until now has not been explored. Finally, I confirm the purported function of pops as an agonistic signal and suggest acoustic synchrony may, like in humans, have evolved to promote social bonding between allied male dolphins.

6.8 References

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Chapter 7 | Publications

In this section I present two papers in their published format. The first is the published format of chapter two, of which I am the lead author. The second paper is the result of a project I was fortunate to be involved with as a co-author. My specific contributions are highlighted below.

7.1 Anthropogenic noise impairs cooperation in bottlenose dolphins

Citation: Sørensen, P.M., Haddock, A., Guarino, E., Jaakkola, K., McMullen, C., Jensen, F. H., Tyack, P.L., and King, S. L. (2023). Anthropogenic noise impairs cooperation in bottlenose dolphins. *Current Biology*, 33, 1-6.

Author Contributions: Author contributions are highlighted in Chapter two.

7.2 Allied male dolphins use vocal exchanges to “bond at a distance”

Citation: Chereskin, E., Connor, R. C., Friedman, W. R., Jensen, F. H., Allen, S. J., Sørensen, P. M., Krützen, M., and King, S. L. 2022. Allied male dolphins use vocal exchanges to “bond at a distance”. *Current Biology*, 32, 1-7.

Author contributions: This paper was the output of the work done by E.C. during her time as a Master’s student. E.C., R.C.C., W.R.F., F.H.J., and S.L.K. designed the methodology and S.L.K., R.C.C., W.R.F., S.J.A., M.K and P.M.S. collected the data. E.C., S.L.K., W.R.F. and P.M.S. extracted and coded the data and E.C. processed and analysed the data with support from S.L.K., W.R.F., and F.H.J.. E.C. and S.L.K. wrote the manuscript, and all co-authors (R.C.C., W.R.F., F.H.J., S.J.A., M.K. and P.M.S) edited and provided comments to the manuscript.

Current Biology

Anthropogenic noise impairs cooperation in bottlenose dolphins

Highlights

- Anthropogenic noise impairs behavioral coordination in a cooperative context
- Dolphins modified their vocal signals to facilitate cooperative success
- Acoustic compensatory mechanisms are insufficient for overcoming noise impacts
- Critical to account for noise impacts on collective tasks in wild animals

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In brief

Anthropogenic noise impairs cooperative success in bottlenose dolphins. Sørensen et al. show that acoustic and other behavioral compensatory mechanisms are insufficient for overcoming the effects of noise on communication. This highlights the need to account for noise disturbance on functionally important group tasks in wild animal populations.

Current Biology

Allied male dolphins use vocal exchanges to “bond at a distance”

Highlights

- Allied males with weaker social bonds display higher whistle exchange rates
- Allied males with stronger bonds display higher rates of affiliative contact
- Whistle exchanges allow allies to maintain weaker yet vital social relationships
- Multiple mechanisms are needed to service bonds in complex animal societies

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In brief

Vocal exchanges are posited to function as a replacement for physical bonding. Chereskin et al. show that, within dolphin alliances, strongly bonded allies engage in more affiliative contact behavior, while weakly bonded allies engage in more whistle exchanges. This illustrates that vocal exchanges can be used to maintain key social relationships.

