INDIVIDUAL RECOGNITION IN BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*): FROM ACOUSTIC DISTINCTIVENESS IN SIGNATURE WHISTLES TO VISUAL SELF-RECOGNITION

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Individual recognition in bottlenose dolphins (*Tursiops truncatus*):

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It seems to me that the natural world is the greatest source of excitement;
the greatest source of visual beauty; the greatest source of intellectual interest.
It is the greatest source of so much in life that makes life worth living.

(David Attenborough)

Abstract

Recognition is a crucial process in animal social interactions and communication. Despite numerous contributions on recognition processes in a wide variety of species, the field lacks a comprehensive review, as well as an ordering structure and clear definitions. I introduce the ordering principles of signal modality and social level to increase comparability of studies, avoid confusion within the field, and guide future research. Careful consideration of these principles may be revealing: For example, recognition on a group level (e.g. kin-recognition) might be based on individual recognition, where the receiver recognises a sender based on individually distinctive cues. While individual recognition has been demonstrated in many species, little is known about the development of individual recognition signals and the roles genetics, maturation and learning play. Here, I focus on signature whistles, an acoustic signal for individual recognition in bottlenose dolphins. I analyse the whistle development of dolphin calves during ontogeny to calculate the time when the signal stabilises enough to function as a reliable recognition signal. Other means of individual recognition are explored by considering variation and changes in acoustic parameters. Previous studies suggested that vocal production learning might matter in signature whistle development. I show that dolphins use model-sounds from their environment, which provides evidence for vocal production learning.

Self-recognition is a special form of individual recognition, where the same individual is both the signaller and receiver. Successful self-recognition has been suspected to be an important evolutionary step towards consciousness, but was long thought to be absent in animals other than great apes. While dolphins were considered promising candidates, the established method was not suitable to test marine mammals. I introduce an adjusted method, discuss the pitfalls of the mark test, and present first evidence for mirror-guided self-inspection in bottlenose dolphins.

Declaration

1. Candidate's declarations:

I, Alina Loth, hereby certify that this thesis, which is approximately 46,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in January 2014 and as a candidate for the degree of PhD in April 2015; the higher study for which this is a record was carried out in the University of St Andrews between 2014 and 2017.

2. Supervisor's declaration:

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD in the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Acknowledgements

This is it, it's done! 3 year, 3 months and 33 days after I arrived in St Andrews and lost my heart to Scotland (and my liver to Talisker Whisky), I finally finish this long-term project writing these Acknowledgements. As I am painfully aware that this section will probably have by far the most readers, I would like to first of all shamelessly use this opportunity for some cliff-hangers to maybe lure one or two of you into reading further, because your interest is what makes science matter!
Have you ever asked yourself if you chose the right partner, if you have a cuckoo child, or if there are parasites living in your body that you should be aware of? All of these life-changing questions will be addressed in one way or another in chapter 1! Even more exciting is chapter 2, where you can gain exclusive insights into what happens when offspring names itself. And while you are on it, just continue with chapter 3 and find out how the environment might influence the development of names. Not convinced yet whether you should continue reading after you (hopefully) found your name in the acknowledgments? In chapter 4 you can finally find out who the person with the messy hair is that appears every morning in your bathroom mirror. Here you can also hear the story of the Darwin, the dolphin that decided that spending € 300 on research equipment is definitely a waste of money. And for those of you who just cannot be bothered to read, there are visual abstracts at the end of each chapter!

Now that I at least tried everything within my power to increase the readership of my scientific opus magnum to 4+, it is time to thank the people who made this thesis possible. First of all, here`s to the confirmed 4 in my 4+ audience: I thank my supervisor Prof Vincent M. Janik for giving me the great opportunity to work on this amazing project, and for supporting me throughout my academic journey. I am also very grateful to my internal examiner, Prof Peter Tyack, and my external examiner, Prof Thomas Bugnyar, for their time and for their invaluable feedback on this thesis.
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I thank all the dedicated staff from the Duisburg and Nuremberg dolphinaria for their support and their incredible passion for the dolphins in their care. It was a pleasure being part of your teams! I also thank the staff at the field station in Belize for making my stay there both successful as well as very enjoyable. I thank Dr Livio Favaro and the involved staff from the facilities Acquario di Genova and Oltremare for collecting the data of some dolphins analysed in chapter 2 and 3. And I thank Dr Thomas Götz for helping with the data collection in Duisburg (I blame you for getting me excited about acoustics in the first place). Acoustic recordings from Sarasota dolphins were provided courtesy of the Sarasota Dolphin Research Program and were pre-processed by Dr Braulio Leon-Lopez. I thank Diego Rita Espada and Arielle McDermott-Amos for re-coding some of my data to check for inter-rater reliability.
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Recognition in animals

1.1 General Introduction

Recognition is the ability to identify someone or something from previous experience or knowledge. While the term recognition is used in a multitude of interactions and levels ranging from molecular, to cellular, to organismic, in this thesis I purely focus on recognition on the organismic level. Recognition allows individuals to adjust their behaviour based on direct or indirect information (e.g. eavesdropping) (Penn 2010). This is beneficial in a wide variety of different challenges animals face, e.g. avoiding predators, finding prey, avoiding agonistic encounters with previous opponents in competitive or territorial species, identifying long-term mating partners, or rearing offspring (Thom and Hurst 2004). Many of these interactions are energetically costly. In general, it should be beneficial for an individual to allocate behaviours and the investment of resources specifically to adequate receivers to minimise energy investment: The less energy animals have to invest in inadequate receivers, the better for the individual's overall fitness (Darwin and Beer 1951; Hamilton 1964). Recognition is then a cognitive process that can help animals mediate energy investment and allocation of behaviours to other individuals or groups of individuals. The resulting differentiation in behavioural treatment can be understood as the "action component" of recognition (Mateo 2004, p. 730). As per Tinbergen (1963), this functional explanation of recognition can be complemented with a mechanistic explanation: The action component is the result of intricate recognition mechanisms based on a variety of perceptual cognitive abilities, which permit the initial perception and analysis of difference necessary to allow for differentiated treatment in the first place (although they may have evolved unrelated to recognition per se, e.g. perceptual abilities can also serve some other purpose; Mateo 2004, p. 730). Understanding these precise processes involved in and allowing for recognition provides a more comprehensive picture of animal behaviour and interactions. This may also include a description and analysis of dynamic processes of recognition ability development or even learning within individuals.

The aim of this thesis is to explore the mechanisms and development of recognition processes in bottlenose dolphins. To that end, I focus on the development of acoustic signals for individual recognition, and the ability of the species for visual self-recognition. As I further detail below, bottlenose dolphins are particularly suited to such research for a variety of reasons: They live in complex fission-fusion societies, make use of a wide range of different potential recognition modalities, and have previously demonstrated a high level of cognitive processing. Ability for visual self-recognition in bottlenose dolphins would also provide additional evidence for convergent evolution of this trait, as will be further discussed below. In this chapter, I provide an overview of the current literature regarding social recognition in the animal kingdom. I propose a new approach to sorting the extensive amount of studies on social recognition by introducing a categorisation based on the level of recognition (ranging from inter-species to individual) and modality (acoustic, chemosensory, visual) used in the recognition process. I proceed to discuss these categories and their intersection in a wide range of species based on relevant literature. I then focus on recognition in bottlenose dolphins, demonstrate how existing literature on this species can be placed within the two categories, and point out gaps in existing research which provide the rationale for this thesis. This links to the thesis overview provided in the final section of this chapter.

1.2 Definition and mechanisms of animal recognition

Recognition derives from Latin “recognoscere” (to know again) and can be defined as a mental process that relies on the internal evaluation of identity signals from the environment, which can be matched with or analysed based on previous experiences and combined with spatial or contextual information, to identify another individual (Beecher 1982; Holmes and Sherman 1982; Mateo 2004; Tsutsui 2004; Penn 2010). The recognition process involves several potential components: a sender producing identity cues, spatial or contextual information, a signal receiver, and potential decisions or actions by the receiver as a result of the recognition process (Figure 1)(Sherman et al. 1984, Waldman et al. 1988, Penn 2010).

There is an ongoing debate about which mechanisms are involved in the recognition process: Tang-Martinez (2001) argues that it might be a question of different cues rather than of different mechanisms, and that associative learning and habituation are the most likely explanations for most forms of recognition. Neff and Sherman (2002) describe the decision-making process underlying recognition as a combination of proximate cues that are evaluated and mentally weighted against previous information (predisposition). Throughout this thesis, I refer to recognition as a mental process without implying any cognitive awareness or a conscious decision.

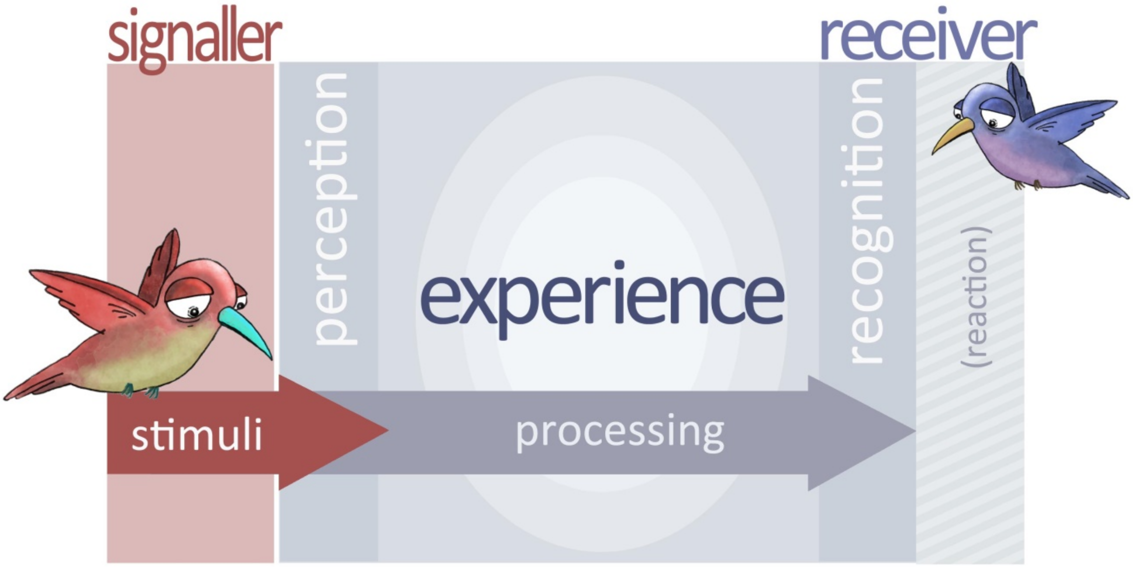


Figure 1: **Recognition process between a signaller and a receiver.** A stimulus or identity cue produced by a signaller in one or several modalities (e.g. acoustic, visual, olfactory) is perceived by the sensory system of a receiver. The receiver processes the information mentally (taking previous information and experience into account) which leads to a recognition result in a specific recognition level (e.g. species-recognition, kin-recognition, and individual-recognition).

Recognition often involves a trade-off between the costs and benefits for both the sender as well as the receiver. To avoid these costs, it can be beneficial for individuals to (attempt to) conceal their own identities (Beecher 1991; Kempenaers 1996; Pagel 1997). The adaptive value of recognition should be particularly high if the costs of a behaviour are high, if individuals or groups of individuals encounter each other repeatedly, or if complex social interactions take place (e.g. long-term associations between individuals)(Thom and Hurst 2004; Tibbetts 2004; Tibbetts and Dale 2007).

Animals use a variety of different signal modalities for recognition including visual, olfactory, chemosensory, or acoustic signals. These modalities are not mutually exclusive and can be combined in a crossmodal recognition process (e.g. Kulahci et al. 2014, Mateo 2004). The spectrum of levels or contexts of recognition is as diverse as the species using it: Recognition can take place between different species on an inter-species level (e.g. prey, predators) or within species as a form of intra-species recognition (e.g. neighbour, mate, kin). Generally, recognition can be either based on group characteristics (e.g. sex, reproductive status, dominance rank, kinship), or specific individuals can be recognised by distinctive recognition signals.

1.3 Research framework of animal social recognition

There is a substantial body of literature within the field of animal recognition. Sorting the contributions to the field by level and modality provides helpful guidance to compare studies across species as well as to identify gaps within a specific taxon, modality or level of interaction. I discuss the different levels of recognition in decreasing order of scope, i.e. with regards to the number of individuals that are involved in particular interactions: Starting with inter-species recognition, I discuss the mechanisms involved in parasite, predator and prey recognition. Moving on to intra-species recognition, I present examples for species-, sex-, group-, neighbour-, kin-, and parent-offspring-recognition. Next, I discuss recognition based on an individual level. Last, I focus on the special case of recognition where one individual is both the signal sender as well as receiver, namely self-perception and self-recognition. I outline the sensory modalities employed within each level of recognition, which defines the mode in which the recognition signal is produced and received, ranging from sound or chemicals to visual body movements or colouration. Table 1 presents some examples of recognition from a variety of species within the ordering framework of level and modality, demonstrating the use and utility of my ordering categories.

The study examples discussed in this chapter were picked to provide an overview of contributions ranging different modalities, levels as well as the variety of taxa, and do not represent an exhaustive review of the study field. The studies are discussed in the following sections, which are sorted by level of recognition. It must be stressed that many studies find evidence for recognition without addressing the question of either level or modality, and many recognition processes studied on a higher level might indeed be based on lower-level recognition. Where appropriate, this will be highlighted in the subsequent discussion.

1.3.1 Inter-species-recognition

Inter-species recognition refers to the process involved in identifying heterospecifics in contrast to conspecifics. Inter-species recognition goes beyond discrimination based on intra-species recognition abilities (which will be discussed in section 1.3.2.): Identifying the absence of intra-species cues does not qualify as inter-species recognition. Instead, it requires the active identification of heterospecific cues which may then mediate allocation of behaviours. Such recognition of heterospecifics can also occur at the more detailed level of individual-recognition, which will be discussed in more detail in the respective subsection (section 1.3.3). Nevertheless, even in these cases heterospecifics often rely on the same cues and mechanisms for recognition as for within-species recognition (e.g. Herzner et al. 2005). Inter-species recognition most often occurs in interactions such as predation or parasitism, but can also be beneficial to identify suitable resources (e.g. habitats)(Matyjasiak 2005), and will be discussed in this order below. Parasite-host as well as predator-prey interactions usually involve high potential costs as well as high potential benefits. While for the prey and host species imminent survival is at risk, high costs can also be incurred for predators, e.g. when becoming exhausted or injured during the hunt, or for parasites when ending up in a dead-end host. Therefore, effective recognition on one side and avoidance of identification on the other should have a selective value resulting in an evolutionary arms race between species. This reciprocal evolutionary relationship is weakened by the fact that species often interact with a multitude of different species resulting in more general defence mechanisms (Rothstein 1990).

Table 1: Cited animal recognition studies sorted by recognition level and signal modality.

			signal modality					
			acoustic	**olfactory/chemosensory**	**Visual**	**contextual spatial**	**crossmodal**	**unspecific**
recognition level	**inter-species recognition**	**(competitive) species**					Matyjasiak 2005	
		parasite-host		Martin et al. 2012 Kavaliers et al. 2005 Lewis et al. 1996	Williams 2008 Kacsoh et al. 2013			
		predator	Deecke et al. 2002 Mann et al. 1998 Billings et al. 2015 Hristov & Conner 2005	Brown & Godin 1999 Mathis & Vincent 2000 Gerlai 1993 Magurran 1989 Ferrari et al. 2007	Mathis & Vincent 2000 Gerlai 1993 Blumstein et al. 2000			
		prey	Hristov & Conner 2005	Apfelbach 1986 Herzner et al. 2005	Darmaillacq et al. 2008 Garcia & Drummond 1995		Cunningham et al. 2009	
	intra-species recognition	**species**	Rafferty & Boughman 2006		Detto et al. 2006			
		sex and mate	Wade & Arnold 2004 Mann et al. 2003 VonHelversen & vonHelversen 1997 Ryan & Rand 1993	Ameyaw-Akumfi & Hazlett 1975 Bekoff 2001 Herzner et al. 2005 Ferkin & Johnston 1995 Mason &Gutzke 1990	Sætre & Slagsvold 1992 Cooper 1984		Acquistapace et al. 2002 Marco et al. 1998	
		social group	Boughman 1997 Rendell & Whitehead 2003 Ford 1991 Deecke et al. 2000 Deecke et al. 2010	Dani et al. 2001				
		neighbour	Myrberg & Riggio 1985 Davis 1987 Godard 1991 Bee & Gerhardt 2000	Müller & Manser 2007 Jutsum et al. 1979 Rosellf & Bjørkøylif 2002	Detto et al. 2006 Leiser 20			Tierney et al. 2013 Qualls & Jaeger 1991 Bishop et al. 2015 Leiser & Itzkowitz 1999 Husak & Fox 2003
		kin	Hauser 1991 Pfefferle et al. 2016	Yamazaki et al. 1988 Holmes 1986 Holmes & Sherman 1982 Mateo & Johnston 2000 Mateo 2002 Krause et al. 2012 Gamboa et al. 1996	Parr & deWaal 1999	Elwood & Ostermeyer 1984 Shugart 1978		Frommen et al. 2007 Porter et al. 1981 Kuester et al. 1994 Rantala & Marcinkowska

			Espelie et al. 1994 Coffin et al., 2011		2011 Mateo & Johnston 2000 Woolfenden & Fitzpatrick 1984 Emlen & Wrege 1988 Kinnaird & Grant 1982 Coeckelberghs 1975 Wong & Balshine 2011 Burda 1995 Petrie et al. 1999
individual recognition	**Individual**	Townsend et al. 2012 Bergman et al. 2003 Boeckle et al. 2012 Wanker et al. 1998 Clark et al. 2006 Cheney & Seyfarth 1988 Blumstein et al. 2004 Aubin & Jouventin 1998 Searby & Jouventin 2003 Draganoiu et al. 2006 Charrier et al. 2002, 2003 Insley 2000 Sayigh et al. 1999	D'Ettorre &Heinze 2005 Gherardi et al. 2005 Hurst et al. 2002	Dale et al. 2001 Tibbetts 2004 Carey 1992 Kendrick & Baldwin 1987 Kendrick et al. 2001 Eakley & Houde 2004 Marzluff et al. 2010, 2012 Newport et al. 2016	Kondo et al. 2012
	self-perception	McArthur 1986	Bekoff 2001 Bonadonna & Nevitt 2004 Mardon & Bonadonna 2009 Thünken et al. 2009	Salzen & Cornell 1968	Burley & Foster 2006 Lerch et al. 2013
	self-recognition			Gallup 1970 Amsterdam 1972 Suddendorf & Collier-Baker 2009 Anderson & Gallup 2011 Plotnik et al. 2006 Prior et al. 2008	

Predator-prey

Predator interactions are often lethal for the prey, leaving only very limited opportunity for learning experiences especially in species without parental care. Therefore, several species are able to recognise predators without previous encounters (Veen et al. 2000; Hawkins et al. 2004), leading some researchers to assume that predator-recognition cannot require learning (Tinbergen 1948). However, many social species (e.g. with parental care) show a gradual development of predator recognition, suggesting that learning and particularly social learning might in fact play an important role (Griffin et al. 2000; Hollén and Radford 2009). In addition, alarm cues emitted by another individual as a response to a predator can be used for associative learning and predator recognition (e.g. Mirza & Chivers 2001). These alarm cues can either be emitted by a conspecific (Manser 2001) or by a heterospecific (Bilá et al. 2017; Mirza and Chivers 2001), and will only be discussed here briefly as a case of indirect predator recognition through the recognition of another individual. Bergstrom and Lachmann (2001) argue that alarm cues in general might be a signal to the predator that it has been detected rather than an alarm for conspecifics. African green monkeys (*Chlorocebus aethiops*)(Seyfarth et al. 1980) and meerkats (*Suricata suricatta)*(Manser 2001) emit different types of alarm calls as a response to specific predators. Young meerkats learn during ontogeny to show appropriate predator avoidance behaviour in response to a conspecific's alarm call (Hollén and Manser 2006). One example for heterospecific predator alarm cues can be found in fathead minnows (*Pimephales promelas*), which learn to recognise predator fish (*Perca avescens*) by associating the alarm cues from predated conspecifics in the predator's diet with alarm cues from brook sticklebacks (*Culaea inconstans*)(Mirza and Chivers 2001).

Many fish species use chemical alarm cues when confronted with predators (see Kelley et al. 2003 for a review). When European minnows (*Phoxznus phoxtnus*) encounter a predator in a potentially dangerous situation, they associate its odour with the situation and learn to avoid it (Magurran 1989). Glowlight tetras (*Hemigrammus erythrozonus*) recognise predators from chemical cues in their diet (Brown and Godin 1999). Fathead minnows (*Pimephales promelas*) are not only able to learn to recognise the odour of a predator, but can also generalise this recognition signal to closely related predator species (Ferrari et al. 2007). Females of the European beewolf (*Philanthus Triangulum*) use chemosensory recognition when they hunt honeybees (*Apis mellifera*) to deposit their eggs (Herzner et al. 2005). Larval newts (*Notophthalmus viridescens*) can recognise heterospecifics visually, but are dependent on chemical cues to differentiate between predatory and non-predatory species (Mathis and Vincent 2000). Predators can in turn use the same modality to recognise prey: European polecats (*Mustela putorius*) learn to recognise prey odours during a sensitive phase between

60 and 90 days of life and develop a preference for these prey species (Apfelbach 1986). The prey-recognition abilities of North Island brown kiwis (*Apteryx mantelli*) were tested in a crossmodal approach showing that while the animals are using a range of modalities, they are most efficient when confronted with olfactory cues (Cunningham et al. 2009).

Similarly, acoustic cues can function as predator recognition signals that lead to avoidance behaviour by potential prey: Harbour seals (*Phoca vitulina*) can recognise calls from killer whales (*Orcinus orca*) and differentiate between the sounds of familiar fish-eating (non-predatory) and unfamiliar mammal-eating (predatory) populations (Deecke et al. 2002). The American shad (*Alosa sapidissima*) can detect the ultrasonic sounds that cetacean predators (e.g. *Tursiops truncatus*) emit during echolocation (Mann et al. 1998). Black-capped chickadees (*Poecile atricapillus*) and mountain chickadees (*Poecile gambeli*) can recognise the calls of several raptors (low-threat and high-threat) and respond with different alarm calls (Billings et al. 2015). Milkweed tiger moths (*Euchaetes egle*) can detect the echolocation sounds of big brown bats (*Eptesicus fuscus*) and emit an ultrasonic pulse in response, which is in turn recognised by the bats and often leads to prey avoidance due to previous experience with the distasteful moth species (Hristov and Conner 2005).

The visual modality seems to play an important role in the recognition of unfamiliar predators by paradise fish (*Channa micropeltes*), but olfactory cues alone are sufficient for sympatric and most likely more familiar predators (Gerlai 1993). Predator naïve tammar wallabies (*Macropus eugenii*) respond to visual cues of potential predators with cautious behaviour (Blumstein et al. 2000). These recognition abilities are even used by juvenile or embryonic developmental stages of animals: While still in their transparent egg envelope, prenatal cuttlefish embryos (*Sepia officinalis*) that were visually familiarised with crabs (*Carcinus sp.*) developed a strong priority for this prey source later in life (Darmaillacq et al. 2008). While Mexican garter snakes (*Tbamnopbis melanogaster*), mainly use olfactory cues for prey recognition, they also show a preference for moving objects with specific sizes and shapes when experimentally confronted with visual cues only (Garcia and Drummond 1995).

Parasite-host

In contrast to predators and prey, parasite-host interactions often take place between a smaller number of potential species as parasites are often highly specialised, sometimes to only one host species. This makes suitable recognition mechanisms for both the parasite as well as the host much more specific and increases the selective pressure on this recognition arms-race. Here, I focus on examples of parasite-host interactions where both species are animals. Recognition systems involving microparasites (e.g. viruses, bacteria, protozoa, and fungi) are discussed elsewhere (e.g. Schmid-Hempel 2011).

Bumblebees (*Bombus*) for example use a sophisticated olfactory system (based on hydrocarbons) for intra-specific recognition within colonies, but these cues are also identified and mimicked by other bumblebee species that live as social parasites within the colonies, so called cuckoo bumblebees (subgenus *Psithyrus*). While some of these parasitic species mimic the recognition cues of the host, others use an olfactory repellent to avoid being recognised as intruders by the host colony (Martin et al. 2010). The parasites not only highjack the olfactory recognition system of their hosts, they also mimic their body colour patterns to avoid visual recognition (Williams 2008). In contrast, fruit flies (*Drosophila melanogaster*) are able to visually recognise an endoparasitoid wasp (*Leptopilina heterotoma*) and respond with a behavioural change by laying their eggs on ethanol-laden food sources that can protect the larvae from an infection by the parasite (Kacsoh et al. 2013). The nematode *Steinernema carpocapsae* seems to be capable of detecting volatiles from the cuticle of insects to recognise the suitability of potential host species (e.g. *Agrotis ipsilo*)(Lewis et al. 1996).

Some rodents use olfactory recognition to detect parasite infections in conspecifics and respond with avoidance behaviour (Kavaliers et al. 2005), but it remains to be investigated whether these recognition signals are related to the parasite itself or are a mere side effect caused by the infection.

Resources

Finally, many species have overlapping or even very similar requirements for resources (e.g. food or breeding spot) and inter-species-recognition becomes crucial in the competition for these resources with heterospecifics: Blackcaps (*Sylvia atricapilla*) for example defend their breeding territories not only against conspecifics but also against closely related garden warblers (*Sylvia borin*)(Garcia 1983; Blondel et al. 1996). Male blackcaps associate the visual cue of the plumage with the acoustic cue of the song type and recognise garden warblers based on both modalities (Matyjasiak 2005). Even though studying inter-species recognition between competing species sheds light on the many diverse interactions within an ecosystem, research on the phenomenon is surprisingly scarce. This may be because isolating these processes from other interaction processes is inherently difficult. Further studies probing the linkage between resource competition and inter-species recognition would be highly desirable.

1.3.2 Intra-species-recognition

Intra-species-recognition comes in many forms, ranging from species to individual recognition. While these sub-categories differ in their recognition level, the employed recognition modality and mechanisms can be identical. Efforts to define the precise recognition level are often challenged by the overlap between the different sub-categories, which makes careful differentiation crucial to prevent confusion and misleading uses of terminology.

Species-, sex-, and mate-recognition

The definition of species-recognition in particular has caused much discussion, which was mainly fuelled by the different authors' understandings of whether or not the term "species" itself can be defined in an adequate way (Mendelson and Shaw 2012; Mendelson and Shaw 2013; Padian and Horner 2013). Of equal or greater importance, however, is a definition of different levels of recognition to avoid confusion in the interpretation of results between scientific publications. Here, I propose an ordering system within intra-species recognition following the same level-of-recognition logic introduced above, which allows the establishment of criteria and should clarify some of the ongoing misleading use of terms and spectra of intra-specific-recognition in the literature.

Species-recognition, as the level of intra-species-recognition with the broadest scope of potentially involved individuals, refers to the processes involved in distinguishing conspecifics from heterospecifics, and therefore focuses on the species as a whole rather than on subgroups within the species. Padian and Horner (2013) define species-recognition as "the ability of individuals to recognize conspecifics for all relevant social purposes (cooperation, competition for resources, group behavior including colony formation, defense, etc.), and the processes by which they do so" (p. 249)(Table 2). This contrasts species-recognition from inter-species recognition, but also from sex-, mate-, and group-recognition, which all enable recognition on a sublevel within the own species. Species-recognition has often been discussed as a process so entangled with sex- and mate-recognition that it has even been used synonymously (or just not teased apart) by some authors (e.g. Rafferty & Boughman 2006). However, conspecifics interact for many purposes besides mating and have to adjust their behaviour accordingly, so species-recognition clearly has its value outside of and in addition to sex- and mate-recognition (Padian and Horner 2013).

Fiddler crabs (*Uca mjoebergi*) show species-recognition based on visual cues: When the species-specific claw colouration patterns were experimentally altered, females continuously approached males that showed the species-specific claw colour regardless of whether they in fact belonged to a closely related but different species (*Uca signata*)(Detto et al. 2006). As fiddler crabs also appear to use the same recognition mechanism for sex-, mate-, as well as neighbour-recognition (Detto et al. 2006), this example illustrates nicely the overlap between modality and mechanisms while the level varies and should be addressed carefully. So in general, researchers should carefully consider which terminology is appropriate for the evidence they are presenting.

Table 2: Definitions of the different spectra of intra-specific-recognition in social interactions.

		definition	Source
Recognition level	**species-recognition**	*"The ability of individuals to recognize conspecifics for all relevant social purposes (cooperation, competition for resources, group behavior including colony formation, defense, etc.), and the processes by which they do so."*	Padian & Horner 2013, p. 249
	sex-recognition	*Sex-recognition is defined as the ability to distinguish between conspecifics from the same and the opposite sex.*	
	mate-recognition	*Mate-recognition is defined as a "behavioural response indicating that one individual considers another an appropriate mate, even if mistakenly. […] It does not imply preferences or comparison", contrasting it to mate-preference which implies a process of comparison between recognised mates.*	Ryan & Rand 1993, p. 648

Sex-recognition can be favoured by a range of signals in different modalities (Table 1). For example, many species show sexual dimorphisms where both sexes vary in morphology, physiology and/or behaviour: While some species show a visual sexual dimorphism, e.g. differences in plumage or fur colouration between sexes (Lande 1980; Cooper 1984; Sætre and Slagsvold 1992; Owens and Hartley 1998), other species use the acoustic modality for sex-recognition (or potentially mate-recognition), e.g. when only one sex can produce song or both sexes emit different songs or calls. While in zebra finches (*Taeniopygia guttata*) only the males sing (Wade and Arnold 2004), in plain wrens (*Thryothorus modestus zeledoni*) both males and females engage in sometimes complex duets with different song elements produced by each sex (Mann et al. 2003, see Mann et al. 2009 for a review). The same vocal dimorphism exists in male and female grasshoppers (*Chorthippus biguttulus*) which produce two sex-specific song types in their communication (von Helversen and von Helversen 1997). Domestic dogs (*Canis familiaris*) show behavioural differences when confronted with female versus male urine (Bekoff 2001). The aquatic crayfish (*Procambarus clarkii*) produces a pheromone that allows for sex-differentiation (Ameyaw-Akumfi and Hazlett 1975) but in a related species (*Austropotamobius pallipes*) it seems that additional visual cues play an important role in reliable sex-recognition (Acquistapace et al. 2002).

While sex-recognition describes the broader ability to differentiate between conspecifics based on their sex (which includes both individuals with the same as well with the opposite sex compared to the recogniser), mate-recognition aims at recognising conspecifics of the opposite sex and/or avoiding individuals of the own sex, for the purpose of mating (see Table 2). While thus always a sub-category of sex-recognition, mate-recognition should be used as a more specific term for recognition aimed at mating purposes. For example, males of the western toad (*Bufo boreas*) are able to use acoustic signals for mate-recognition, but in contrast to many other species they use the recognition signal for avoidance rather than for attraction: A male that is clasped by another male utters a release call which prompts a release (Marco et al. 1998). In addition to visual and acoustic cues, olfactory or chemosensory cues also aid in mate-recognition in a variety of species (Johansson and Jones 2007). The males of the European beewolf (*Philanthus Triangulum*) can create a sensory “trap” by attracting females with a pheromone that is remarkably similar to a chemosensory signal produced by the females’ main prey, the honeybees (*Apis mellifera*). The males are then able to court the female beewolfs that are attracted by the scent of the pheromone (Herzner et al. 2005). Meadow voles (*Microtus pennsylvanicus*) show strong preferences for odours of the opposite sex (Ferkin and Johnston 1995) and male leopard geckos (*Eublepharis macularius*) rely on chemical skin cues to recognise females for mating purposes (Mason and Gutzke 1990).

Ryan and Rand (1993) define mate-recognition as a “behavioural response indicating that one individual considers another an appropriate mate, even if mistakenly. […] it does not imply preferences or comparison” (p. 648). This definition additionally contrasts mate-recognition with mate-preference, which implies a process of comparison between recognised mates, and should not be discussed as an own form of recognition but rather in the light of sexual selection (Ryan and Rand 1993). Túngara frogs (*Physalaemus pustulosus*) provide an example for the separation between mate-recognition and mate-preference: Male túngara frogs produce two different types of mating calls to attract females: while one is a whine call, the other one is a whine call with an additional chuck sound. Female túngara frogs recognise males with both call types but prefer to mate with males emitting whine-chuck calls (Ryan and Rand 1993). This illustrates that sexual selection can favour an increase in signal variation while mate-recognition remains stable. Species-recognition and sexual selection through mate-preference have long been seen as antithetical in signal evolution as species recognition should decrease the variability of recognition signals within a species while sexual selection through mate-choice should increase it (e.g. Templeton 1979, Gerhardt 1982). Natural and sexual selection on sex- and/or mate-recognition signals can also potentially influence speciation (Higgie et al. 2000). It thus becomes crucial to consider both within-species and between-species variation to understand the evolution of recognition signals.

Besides serving as a subcategory to sex-recognition, mate-recognition has also been, somewhat misleadingly, used to describe interactions based on kin- or individual-recognition. Indeed, mate-recognition can involve both individual-recognition as well as avoidance based on kin-recognition. However, even though the outcome of the recognition process is the identification of a mate, the underlying recognition level is not necessarily mate-recognition, but rather individual-recognition or the avoidance of kin. These processes will be discussed in greater detail within the respective paragraphs below.

Neighbour-stranger discrimination - "dear enemy phenomenon"

Many animals defend territories (e.g. for breeding or feeding) against conspecifics. The recognition of neighbours in contrast to strangers or intruders can help mediate territorial interactions (Tibbetts and Dale 2007). Neighbours could potentially pose less of a threat to a territory defender as they already possess territories themselves, while strangers might be more likely to challenge for resources. Thus, aggression directed towards neighbours is often comparatively lower than aggression towards non-neighbours or strangers (Jaeger 1981). If neighbours and strangers in general cause different threat levels, discrimination on a group level (familiar, unfamiliar) should be sufficient to reduce the cost of defence, but in many cases recognition on an individual basis is also possible (which will be covered below).

The reduction of aggression towards conspecifics in neighbouring territories is known as "dear enemy" recognition (Fisher 1954). Many species are capable of recognising their territorial neighbours and adjust their behaviour to minimise the cost of a defence (Fisher 1954; Wilson 1975). The recognition of territorial neighbours has been described in a variety of taxa ranging from insects (Jutsum et al. 1979, Detto et al. 2006), fish (Myrberg and Riggio 1985; Leiser and Itzkowitz 1999), amphibians (Davis 1987), reptiles (Qualls and Jaeger 1991), birds (Godard 1991) and mammals (Müller and Manser 2007). When resident territorial convict cichlids (*Cichlasoma nigrofasciatum*) are simultaneously confronted with two intruders, they show significantly more defensive behaviour directed against the stranger compared to the territorial neighbour (Leiser and Itzkowitz 1999). Male collared lizards (*Crotaphytus collaris*) show lower levels of aggression towards neighbours compared to strangers within their territory as well as in an open arena. But there is no behavioural difference when the neighbour appears on the opposite side of the territory that is not the boundary to the territory it holds. This suggests that collared lizards are able to recognise neighbours and that a decrease in aggression is due to actual threat level caused by the opponent within the context

(Husak and Fox 2003). Fiddler crabs (*Uca capricornis*) use the visual modality for neighbour recognition by distinguishing between the colour pattern on the carapace of familiar neighbouring females and of unfamiliar females (Detto et al. 2006). Hooded warblers (*Wilsonia citrina*) can not only recognise the songs of territorial neighbours, but also know the location of the signaller's territory: Males ignore the song of a territorial neighbour that comes from the right direction but show strong defensive behaviour if a playback of the familiar song comes from the wrong side of the territory. They also retain this information for over eight months while migrating before returning to the same breeding territories (Godard 1991). Eurasian beavers (*Castor fiber*) use scent marks to distinguish between neighbours and strangers (Rosell and Bjørkøyli 2002).

Classic examples for "dear enemy" recognition come from males of the North American bullfrog (*Rana catesbeiana*)(Davis 1987) as well as bicolour damselfish (*Pomacentrus partitus*), which show a stronger response towards the playback of a stranger's call or sound than to one of their territorial neighbour (Myrberg and Riggio 1985). Gray seals (*Halichoerus grypus*) are breeding in close proximity, and the stability of spatial male identities reduces the aggression amongst males (Bishop et al. 2015). However, all three studies fail to control for the cue modality involved in the recognition process, which needs to be addressed by further studies.

Variegated pupfish (*Cyprinodon variegatus*) show a significant decrease in aggression towards males from neighbouring territories but show high levels of aggression as soon as a female enters the conspecific's territory. This behavioural difference suggests that the dear-enemy-phenomenon might be a flexible behavioural adjustment between territorial males (Leiser 2003).

The "dear enemy" effect has been explained either by different familiarity levels between individuals or by varying threat levels between neighbouring individuals and intruders. Both the relative-threat- and the familiarity-hypotheses predict a decrease of aggression towards neighbours in most species, but only the relative-threat-hypothesis would predict an increase in aggression between neighbours with increased competition (Ydenberg et al. 1988; Temeles 1994). Here, the relative threat of strangers versus neighbours would be inverted and aggression to neighbours becomes relatively more agonistic, leading to what has been described as the "nasty neighbour effect". This effect has been observed in banded mongoose (*Mungos mungo*)(Müller and Manser 2007) and in female crayfish (Tierney et al. 2013).

Group-recognition

Another potential sub-category within a species can be social groups. It can be crucial to recognise members of the own group versus intruders. While social groups are often kin-based and some more specific examples will be discussed below, some species also use recognition signals to identify group members independently of kin-relationships. Greater spear-nosed bats (*Phyllostomus hastatus*) produce foraging calls that differ between social groups (Boughman 1998) and sperm whales (*Physeter macrocephalus*) produce clan-specific click trains (Rendell and Whitehead 2003). Paper wasps (*Polistes dominulus*) use chemosensory cues to recognise kin and non-kin nest mates (Dani et al. 2001).

Kin-recognition

Kin-recognition is among the most diverse and well-studied sub-categories of intra-species-recognition. It is defined as "the ability to identify, distinguish or classify kin from non-kin, regardless of the mechanism or evolutionary functions" (Penn & Frommen 2010, p. 58). The ability to recognise kin is often measured as a behavioural difference towards other individuals based on kinship (Holmes and Sherman 1982), even though successful recognition does not necessarily need to lead to a behavioural action. These behavioural differences can be either investment or avoidance behaviour. The ability to recognise and distinguish kin from non-kin has been discussed in the literature as a key component of kin-selection theory and inclusive fitness (Hamilton 1964). The avoidance of mating with closely related individuals prevents inbreeding depression and therefore a loss of genetic variation (Bateson 1980; 1982; 1983; Crnokrak and Roff 1999). This avoidance behaviour does not necessarily involve kin-recognition as it could also be based on a sex-biased dispersal (Barnard and Burk 1979; Tang-Martinez 2001) but many species do show kin-avoidance (or kin-preference) that involves recognition. Even though kin- or offspring-recognition can be performed on a group-recognition level, individual recognition might take place in some interactions and both levels can be hard to distinguish experimentally. Furthermore, kin-recognition can be based purely on spatial or environmental cues which can function reliably when individuals stay within close proximity of only related individuals, or when dependent offspring stay in one location (e.g. Shugart 1978). A popular example where kin-recognition purely based on contextual information seems to fail is successful cheating by brood parasites. Some cuckoo species (family: Cuculidae) lay their eggs into other bird species' nests and the host pair feeds the cuckoo's chick in their own nest (Rothstein 1990). House mice (*Mus musculus*) use contextual cues when they do not show aggressive behaviour or infanticide towards neonates after mating with the mother (Elwood and Ostermeyer 1984).

Some authors argue that recognition based on parameters other than phenotypic cues could be seen as a pre-form of phenotypic recognition and might indicate the absence of true kin-recognition (Barnard and Aldhous 1991; Tang-Martinez 2001). However, in most species spatial and environmental cues are combined with or replaced by kin-recognition based on other modalities such as visual, olfactory/chemosensory, or acoustic cues: Caspian terns (*Sterna caspia*) seem to mainly rely on contextual information during early development of their chicks. When the chicks are experimentally swapped during the first week, they continue feeding but choose their own offspring later on when given a choice, suggesting that they employ kin-specific cues in addition to contextual ones after familiarisation (Shugart 1978). Even though spatial or contextual information might play an additional role, many cases of kin-recognition require some sort of phenotype matching where the individual recalls learned characteristics. This information can be matched in three different ways (see Penn & Frommen 2010 for a review):

1) Individuals raised together with their siblings often familiarise themselves with their phenotype during a sensitive time in their ontogeny. This so called direct familiarity enables individuals to recognise kin they grew up with. Three-spined sticklebacks (*Gasterosteus aculeatus*) show a preference for shoaling with familiar individuals independent of genetic relatedness (Frommen et al. 2007). Female spiny mice (*Acomys cahirinus*) prefer to cuddle and nest together with individuals they were raised with, even when they were experimentally raised with non-kin (Porter et al. 1981). Barbary macaques (*Macaca sylvanus*) avoid mating with individuals they became familiar with in early life (Kuester et al. 1994), and humans show a similar effect of negative imprinting (referred to as the "Westmarck effect") during early childhood (Rantala and Marcinkowska 2011).

2) Some species familiarise themselves with a kin-specific phenotype and are later able to recognise even unfamiliar kin by matching the phenotypes (Wyatt 2003). This process is described as indirect familiarity and also allows for recognition of more distantly related individuals that might not have been present during early development (e.g. cousins or half-siblings). Chimpanzees (*Pan troglodytes*) are not only able to match their own phenotypes to other individuals as an indicator of relatedness, in an experimental study they were also able to match the faces of unknown females with their male offspring, but failed to match mothers and daughters (Parr and de Waal 1999). This would hint at an ability to visually recognise the kin-status of unknown individuals independent of experience with these individuals based on phenotypic similarity.

3) During self-referent phenotype matching, individuals use their own phenotype to distinguish kin from non-kin ("armpit effect"; Dawkins 1976). Here, familiar is what has a high similarity to the animal's phenotype. Male inbred mice use olfactory cues for kin-recognition and mate-choice: They avoid mating with females that carry the same haplotype compared to their own, even when they were experimentally cross-fostered, allowing for inbreeding

avoidance even with distantly related females (Yamazaki 1988). Golden hamsters (*Mesocricetus auratus)* mate multiple times and have litters with both full and half-siblings which are raised in the same nest, yet they show behavioural differences depending on relatedness (Mateo and Johnston 2000). This holds true even if individuals are experimentally raised only with non-kin and therefore have no postnatal learning experience to familiarise themselves with a kin-specific phenotype. However, pre- and early post-partum familiarisation could not be ruled out as an alternative explanation (e.g. Hauber & Sherman 2001, Mateo & Johnston 2003). Belding's ground squirrels (*Spermophilus beldingi*) show higher levels of interest in the scent marks from unrelated individuals compared to unfamiliar kin, which indicates potential kin-recognition and mate-avoidance without prior experience (Holmes and Sherman 1982; Holmes 1986; Mateo and Johnston 2000; Mateo 2002). Peacocks (*Pavo cristatus*) display together with multiple males in leks to attract females and associate significantly with kin. This holds true even when males were artificially hatched in separation from kin, indicating an ability to recognise kin without social learning or environmental cues (Petrie et al. 1999).

The three described mechanisms for kin-recognition occur in a wide range of species and are not mutually exclusive. Combinations of the mechanisms can be used during different life stages or by different individuals from the same species (Neff and Sherman 2002; Mateo 2004). Rhesus macaques (*Macaca mulutta*) produce "coo" vocalisations that show higher similarity between closely related individuals, potentially allowing for kin-recognition (Hauser 1991) but it remains unclear if these similarities are caused by genetic relatedness or close association. For many studies showing kin-recognition, the underlying mechanisms are indeed unclear, and especially self-referent phenotype matching and indirect familiarity are sometimes challenging to tease apart (Pfefferle et al. 2016).

Zebra finches (*Taeniopygia guttata*) are able to distinguish between kin- and non-kin based on genetically determined olfactory cues (Krause et al. 2012). Humboldt penguins (*Spheniscus humboldti*) prefer the odours from unrelated individuals over the odour from unfamiliar kin (Coffin et al. 2011). Social paper wasps (*Polistes fuscatus*) produce olfactory cues that allow for both the recognition of individuals from the same colony as well as for kin-recognition of closely related individuals in sister-colonies (Espelie et al. 1994; Gamboa et al. 1996).

The recognition between parents and their own offspring can be seen as a more specific sub-category of kin-recognition. Examples where parent-offspring recognition has been shown to function on an individual basis will be discussed below as part of the section on individual-recognition. For many species, however, a more general recognition of "own offspring" as a distinct group (but without individually recognising all the group's members) might well be sufficient.

Many species invest in parental care (Doody et al. 2013) and offspring recognition can be crucial to prevent misplaced parental investment especially in species that breed in large colonies with only reduced spatial cues available (Aubin and Jouventin 1998; Aubin et al. 2000). While parent-offspring-recognition can be based on the same mechanisms as described above for kin-recognition, most cases of parent-offspring-recognition seem to be based on individually distinctive cues rather than on a group-recognition level (e.g. Aubin and Jouventin 2002) and examples will be discussed in more detail in the following section about individual recognition. Many species increase their indirect fitness by supporting closely related individuals or by avoiding resource competition with kin (Doody et al. 2013). If the benefit of an energy investment is an increase in direct or indirect fitness, it should be beneficial to recognise related individuals or offspring reliably to avoid misplaced investments.

Cooperative breeding is an especially well-studied case of investment in kin. While cooperative breeding is common in avian and mammalian societies (see Jennions & MacDonald 1994 for a review) as well as in social insects (Queller and Strassmann 1998), it has not yet been documented in any amphibian or reptile species (Doody et al. 2013). In fish it has been described in several cichlid species (Taborsky and Limberger 1981). Especially the African cichlid (*Neolamprologus pulcher*) has been well studied and established as a model species to investigate the evolution of cooperative breeding behaviour (Coeckelberghs 1975; Wong and Balshine 2011). In cooperatively breeding species, individuals help to raise the offspring of another pair in favour of raising their own offspring (see Komdeur and Hatchwell 1999 for a review). Helping can be defined as any costly behaviour (often decreasing the donor's direct fitness) that provides some benefit and increases the breeding success. It can be directed at the infants themselves or indirectly to the parents, and it can range from (but is not restricted to) feeding, protection, grooming, thermoregulation, or allosuckling (see Jennions & MacDonald 1994 for a review). Helping behaviour can be advantageous independently of a kin relationship as the helper gains experience and thereby increases its chance to successfully raise own offspring in the future, gains the right to stay in a colony, or might inherit a breeding territory (Clutton-Brock 2002). If helping evolved to increase indirect fitness by investing in genetically related individuals, helpers should be able to distinguish between related and unrelated breeding individuals, and should prefer to assist the most closely related pair. Indeed, this form of recognition seems to be established in most societies where cooperative breeding occurs and is most often observed between closely related individuals. Experimental studies have shown that helpers often decrease their helping investment with a decreasing genetic relatedness to the infants (see Clutton-Brock 2002 for a review). A strong preference to help the breeding pair the helper is genetically most closely related to and an adjusted helping effort in regards to relatedness has been described in many avian societies e.g. Florida scrub jays (*Aphelocoma coerulescens*)(Woolfenden and Fitzpatrick 1984), white-fronted bee-eaters (*Merops bullockoides*)(Emlen and Wrege 1988), or the Galapagos mockingbird (*Nesomimus parvulus*)(Kinnaird and Grant 1982).

1.3.3 Individual-recognition

This form of recognition refers to the processes involved in recognising individuals based on their individually distinctive identification cues. It cannot be excluded that individually distinctive cues are indeed underlying many levels of recognition, but studies often concentrate on a specific recognition level rather on the recognition process as such, so individual recognition can often neither be excluded nor confirmed based on the evidence provided. Here I focus on examples where it has been demonstrated that recognition takes place on an individual basis. Individual recognition should be especially beneficial if individuals interact repeatedly in complex social situations (Cheney and Seyfarth 1988). Such interactions may help to ensure stability and reciprocity in cooperative groups, decrease competition for resources and status, mitigate inbreeding, and decrease individual costs for territorial defence and anti-predator vigilance (Hamilton 1964; Trivers 1971; Tibbetts and Dale 2007).

Signals that facilitate individual recognition are called identity signals and can be encoded in a variety of modalities (e.g. olfactory, visual, and acoustic)(Beecher 1982; Dale et al. 2001). Individual recognition requires identity signals that are distinctive enough to distinguish reliably between individuals as well as more complex recognition and memory abilities from the receiver (Mateo 2004). In order to be distinctive and reliable as a recognition signal, identity signals should have a low variability within the individual and a high variability between individuals (Beecher 1982), and remain stable over time, only showing gradual changes to allow for continuous recognition by the receiver (Thom and Hurst 2004). For example, odours are widely used as an individual recognition signal. While they usually carry both genomic as well as metabolic information about the signaller, the genetic component is generally crucial to allow for temporal stability of the recognition signal (Thom and Hurst 2004).

A truly unique identification cue within a species is often unnecessary due to spatial distribution of populations and individuals within the population, which means that individuals usually only encounter a subset of individuals from their species and the identity signal only has to be unique within this subset (Thom and Hurst 2004). In general, the benefits associated with individual recognition should outweigh the costs (e.g. caused by confusion due to increased signal variation)(Dale et al. 2001). The increasing difficulty of differentiating between individuals within a large social group could be compensated by an increase in variability and signal complexity (Pollard and Blumstein 2011). The evolution of individuality in signals might therefore have been promoted by social group size: for example, Pollard & Blumstein (2011) find a strong link between group size and acoustic distinctiveness in the alarm calls of several sciurid rodent species. Additionally, sexual selection could favour individual identification if mating success is increased with successful recognition (Tibbetts and Dale 2007).

Traditional experimental approaches to test for individual recognition are the presentation of individual cues (Insley 2000) or the alteration of a signal and the observation of the receiver's response (Aubin et al. 2000; Hurst et al. 2001; Janik et al 2006). Townsend et al. (2012) tested meerkats (*Suricata suricatta*) for their ability to recognise individual conspecifics based on voice cues in their vocal signals. By playing back one individual's sounds from two different directions, they confronted the animals with a physically impossible setup, assuming they would recognise both playbacks were recorded from the same caller. Indeed the animals reacted more strongly to the impossible setups than to the possible control. In a crossmodal expectancy violation setup, large-billed crows (*Corvus macrorhynchos*) were simultaneously confronted with the visual and acoustic recognition signals of familiar group members. The crows reacted faster and looked longer when both stimuli were incongruent, indicating the ability of individual recognition in this species (Kondo et al. 2012).

Even though a recognition signal might be individually distinctive enough to potentially allow for individual recognition, it is crucial to also test whether the signal receiver makes use of this distinctiveness to recognise on an individual basis. A signal's individual distinctiveness does not necessarily indicate its recognition on an individual level by the receiver. With regards to alarm calls, for example, the individual identity of the signaller could be crucial to evaluate signal honesty and relevance (e.g. Cheney & Seyfarth 1988). However, while Meerkats produce alarm calls with individually distinctive acoustic parameters, receivers fail to recognise individual signallers based on these calls (Schibler and Manser 2007). In contrast, Vervet monkeys (*Chlorocebus pygerythrus*) start to ignore calls from repeatedly unreliable group members (Cheney and Seyfarth 1988). Yellow-bellied marmots (*Marmota flaviventris*) react differently to an alarm call depending on the identity of the caller, its distance, and the number of individuals calling, which suggests an ability to assess the relevance and reliability of alarm calls (Blumstein et al. 2004). Evidently, alarm calls are not the only category of acoustic signals that are used for individual recognition: Within a playback experiment, chacma baboons (*Papio hamadryas*) were able to recognise the dominance rank as well as the kinship of a caller (Bergman et al. 2003). Ravens (*Corvus corax*) not only show long-term memory when it comes to the distinction between the calls of familiar individuals, they also respond with a differently modulated call reflecting their previous relationship with the signaller (Boeckle and Bugnyar 2012).

Acoustic signals can encode identity in two main ways: 1) Voice cues, acoustic variations in vocalisations caused by variation in the morphology of the vocal apparatus, are the most common mechanism for acoustic individual recognition (Symmes et al. 1979). Voice cues are not signal-specific, which means they affect all vocalisations of an individual. It has been hypothesised that voice cues evolved as "by-product distinctiveness" under natural selection with variation being caused by body size and the morphology of the vocal tract (Boughman and Moss 2003). 2) Some species use distinctive signals to encode their identity within the modulation of a specific call type or within the combination of vocalisations (e.g. in songs) which are independent of vocal cues (Janik et al. 2006). These identity signals are rare and thought to be shaped by vocal production learning (Tyack and Sayigh 1997; Janik and Slater 1998; Janik 1999).

Not only recognising an individual, but also associating it with its dominance rank can reduce the costs of repeated aggressive interactions, such as agonistic competition, and aid in stabilising dominance hierarchies (Barnard and Burk 1979). Many social insects live in large colonies with strict hierarchical dominance structures where individual recognition helps to reduce the costs of repeated status assessment (Hölldobler and Wilson 1990). Ant queens (*Pachycondyla villosa*) use chemical cues to recognise individual queens they have previously interacted with and show lower levels of aggression towards such familiar queens (D'Ettorre and Heinze 2005). Hermit crabs (*Pagurus longicarpus*) can recognise the odour of familiar conspecifics on an individual basis and associate their identity signal with their agonistic behaviour as well as with the quality level of the shell the opponent inhabits (Gherardi et al. 2005).

Individual recognition based on the visual modality seems to play an important role in high-density social groups where the acoustic domain might be masked due to the large number of individuals vocalising: Ruff sandpipers (*Philomachus pugnax*) as well as red-billed queleas (*Quelea quelea*) are able to recognise individuals visually within their breeding colony (Dale et al. 2001). Guppy females (*Poecilia reticulata*) can visually recognise the males they have previously mated with (Eakley and Houde 2004) and paper wasps (Polistes) use distinctive facial colour patterns for individual recognition (Tibbetts 2004).

Individual recognition based on visual facial cues seems to require a neural specialisation (Haxby et al. 2002; Kanwisher and Yovel 2006; Tsao et al. 2006) and plays a crucial role in many primate species (Pascalis and Bachevalier 1998; Parr and de Waal 1999; Parr et al. 2000). Facial recognition is especially well studied in humans, which are able to recognise the faces of several hundred individuals based on general face characteristics even if facial expressions and/or gaze are changing (Haxby et al. 2002; Posamentier and Abdi 2003). After seeing 50 pictures of unfamiliar faces for 5 seconds, humans were able to pick up to 90% of these from a larger sample (Carey et al. 1992). Facial recognition has been also reported for sheep (*Ovis aries*), which can recognise the faces of up to 50 conspecifics, and also recognise humans based on static pictures of their faces (Kendrick and Baldwin 1987; Kendrick et al. 2001). American crows (*Corvus brachyrhynchos*) are able to recognise the faces of caring or threatening humans (Marzluff et al. 2010; Marzluff et al. 2012). While lacking a neocortex, archerfish (*Toxotes chatareus*) have shown to also be able to discriminate between human faces, hinting at a convergent evolution of this cognitive ability (Newport et al. 2016).

For species that invest in biparental care it can be crucial to recognise the individual partner in order to coordinate parental investment, and the same holds true for species that build long-term or even monogamous pair bonds (Reichard and Boesch 2003). Spectacled parrotlets (*Forpus conspicillatus*)(Wanker et al. 1998) and Magellanic penguins (*Spheniscus magellanicus*)(Clark et al. 2006) show a preference for responding to their mates but also discriminate between the contact calls of other individuals from their social group. And house mice (*Mus domesticus*) use the olfactory modality for the recognition of individual mates (Hurst et al. 2001).

Individual recognition can also take place between parents and their offspring, e.g. in order to avoid misplaced parental investment or to beg for food (Aubin and Jouventin 1998; Aubin et al. 2000). In colony-breeding king penguins (*Aptenodytes patagonicus*), parents and offspring have to find each other between hundreds of conspecifics based on distinctive calls (Aubin and Jouventin 1998). The ability to perceive and differentiate a relevant call from all other calls made by conspecifics in the noisy social environment has been labelled the “cocktail party effect” (Aubin and Jouventin 1998). Sheep ewes (*Ovis aries*) also use acoustic signals to recognise their lambs and to locate them within the flock (Searby and Jouventin 2003). Some species of seabirds have even been shown to demonstrate visual egg recognition (Buckley and Buckley 1972; Gaston et al. 1993). In black redstarts (*Phoenicurus ochruros*), both sexes invest in parental care, and based on acoustic individual recognition, they each develop a strong feeding preference for a specific chick (Draganoiu et al. 2006). In fur seals (*Arctocephalus tropicalis*), pups and their mothers have been shown to recognise each other’s calls (Charrier et al. 2002; Charrier et al. 2003b), and in a playback study, mothers were shown capable of recognising their pup’s call even as that call changed with developmental stages and even years later, providing evidence for long-term and adaptive recognition (Charrier et al. 2003a).

Mothers and pups of northern fur seals (*Callorhinus ursinus*) were similarly able to recognise each other's calls after four years of separation (Insley 2000). A similar long-term memory of recognition cues of conspecifics has been documented for sheep (*Ovis aries*)(Kendrick et al. 2001), ravens (*Corvus corax*)(Boeckle and Bugnyar 2012), cotton-top tamarins (*Saguinus oedipus*)(Matthews and Snowdon 2011), and bottlenose dolphins (*Tursiops truncatus*)(Bruck 2013).

1.3.4 Self-perception and self-recognition

Self-perception, self-inspection and self-recognition refer to the processes involved in receiving and processing recognition cues from oneself. Studies on the perception of recognition signals where signaller and receiver are the same individual have frequently led to debates in the relevant literature, fuelled by definitional problems (including for "self" and "other" (Catmur et al. 2016)), and a lack of conceptual differentiation between familiarity, awareness, and consciousness, especially when related to recognition. One clear distinction was proposed by Lewis (2006), who separated two levels of self-cue-perception: the machine self that "knows without knowing", and the "idea of me" where the individual "knows that it knows" (p. 17). Similarly, I suggest here a strict differentiation between the terms self-perception, self-inspection, and self-recognition: self-perception involves a reception and processing of own stimuli (e.g. olfactory or vocal cues) by means of the senses without a mental delineation (let alone awareness) of the origin of these cues as "self" or "other" respectively. While there is no differentiation between own cues and those of others necessary for self-perception, repeated self-perception can increase one's familiarity with the perceived cues and can lead to behavioral changes such as e.g. preferences or a decreased interest.

It can be helpful to understand the perception of self-stimuli to understand the neurological and behavioural mechanisms involved in receiving and processing cues from oneself more broadly. For this reason, individuals have been confronted with their own cues by presenting them their vocalisations, scent, or image in mainly within-modality experiments. Frequently, these experiments have been conducted to gain a better understanding of the animal's social communication rather than insights into self-perception, but they should still be discussed briefly here. An extensive amount of experimental studies have been conducted amongst oscine songbirds and employed playbacks of an individual's own song (see Derégnaucourt & Bovet 2016 for a review). When confronted with a series of playbacks with decreasing similarity to their own song, male song sparrows (*Melospiza melodic*) also show a gradual decrease in the strength of their territorial response (McArthur 1986). Individuals of most tested bird species show a much stronger reaction after hearing a playback of their own song compared to a neighbour or stranger (Falls 1985; Stoddard et al. 1992), but the reactions varies between species and can range from song matching to approaching the speaker.

This could be explained by "song matching" mechanisms. Krebs et al. (1981, p. 918) define song matching in birds as a signal receiver's response to a playback or rival consisting of "singing phrases from its repertoire which resemble the stimulus song", which has been suggested to play an important role in the vocal territorial defence of many oscine bird species and might be an efficient communication method to directly address a rival (Krebs et al. 1981; Falls et al. 1988; Janik 2000; Miller et al. 2004). Birds might perceive a playback of the own song as a fully matched version of the own song produced by a contestant, and therefore react aggressively (Bertram 1970). Additionally, the perceived playback version of the own song likely diverges from the distorted version the animal perceives of its own vocalisations via the transmission of sound waves through the bone structures of the head (Derégnaucourt and Bovet 2016). If the individual were to indeed recognise the playback as its own vocalisation (rather than simply perceive potentially irritating degrees of familiarity), both a stronger reaction driven by curiosity or irritation as well as a weaker one due to a less urgent need to react to one's own call compared to that of a potential competitor would be plausible. Acoustic playback studies in territorial singing birds might provide insight into the use and function of song matching rather than into acoustic self-perception. Bottlenose dolphins (*Tursiops truncatus*) also use vocal matching in their social communication when two individuals produce a whistle of the same frequency modulation with a gap of less than 3 seconds in between (Janik 2000). But other than in songbirds, mainly closely associated individuals match each other and matching is presumably used as a contact signal (Janik 2000; King et al. 2014; King 2016). In a playback study, King et al. (2014) played back either a computer-generated version of an individual's own signature whistle or a whistle of a conspecific as a control. The animals responded significantly more often with a vocalisation to the playback of their own whistle, without showing any signs of aggression.

Unfortunately, acoustic self-perception has not been addressed to the same extent in terrestrial mammal species: Mitani (1984) played back song recordings of self, neighbours and strangers to gibbons (*Hylobates muelleri*) but failed to find any behavioural differences between the conditions. To gain a better understanding of acoustic self-perception, further studies especially focusing on species that do not use vocal matching in their social communication would be highly desirable.

Salzen and Cornell (1967) tested chicken for visual self-perception by isolating and colouring chicks and then testing for later companion-choice-preference based on the own body colour.

Chicks that had access to a reflective water bowl, and therefore were able to perceive their own appearance, showed a preference for companions with the same body colour. Chicks without access to a reflective surface did not show a preference for the own colour. This hints at the possibility that the chicks developed a preference based on the perception of their own visual appearance. Self-evaluation has been tested by experimentally manipulating the body condition of female canaries (*Serinus canaria*) by cutting their flight feather (causing an inferior body condition). The birds were less selective when choosing a mate based on its song, which could hint at ability for self-evaluation and perception (Burley and Foster 2006; Lerch et al. 2013).

Bekoff (2001) tested a domestic dog (*Canis familiaris*) for its behavioural reactions towards own urine versus urine from other males or from females. The dog paid less attention (lower sniffing times) and urinated less often over the sample when it was its own urine. Considering the sample size (n=1), these results can only be seen as an indicator of potential self-perception abilities in dogs and further studies would be highly desirable. When confronted with both their own and a conspecific's odour, blue petrels (*Halobaena caerulea*) and Antarctic prions (*Pachyptila desolata*) also show a preference for the conspecific's scent compared to their own (Bonadonna and Nevitt 2004; Mardon and Bonadonna 2009). The opposite holds true for cave breeding cichlids (*Pelvicachromis taeniatus*), which preferably pick a cave with their own odour compared to one with the scent of either familiar kin or an unfamiliar individual (Thünken et al. 2009). In general, the use of the chemosensory modality in self-perception studies might be less likely to violate the individual's expectations: Individuals are more likely to be confronted with their own chemosensory cues within the natural environment than with playbacks of its own sound or visual appearance.

In contrast to self-perception, self-recognition involves an additional capacity to differentiate the self from others. This capacity may involve the existence of a "mental image of the self" (Mitchell 2002). However, while some of the discussed studies show a certain level of familiarity with own cues, it is challenging to determine whether the animals also have a mental concept of "self", which would indicate self-recognition. Some authors strongly argue for the importance of kinaesthetic-visual matching to distinguish self-perception from self-recognition (Mitchell 1997; Mitchell 2002). Mitchell (2002, p. 346) argues that "kinesthetic-visual matching […] is the recognition of similarity between the feeling of one's own body's extent and movement (variously called kinesthesis, somasthesis, or proprioception) and how it looks (vision)". While kinaesthetic matching is unlikely isolated from matching within or between other modalities (Marten and Psarakos 1994), vision remains the only modality used to test for self-recognition across species. Bar convincing test methods making use of alternative modalities, successful kinaesthetic-visual matching will remain the only evidence suggestive of self-recognition in non-human animals. Currently the only comparative test to distinguish self-recognition from self-perception in species without language abilities is the "mirror mark test" developed by Gallup (1970). Morin defines mirror self-recognition as a "kinaesthetic representation of the body with the image seen in the mirror [where the animal] infers that 'it's me'" (Morin et al 2011, p.370). This, of course, narrows the number of promising species to test for self-recognition to those that use vision for recognition and are also able to perform the body movements associated with passing the test (e.g. touching a mark on the own body). Therefore, it has to be stressed that the absence of evidence for self-recognition in a species might be due to limitations of both definitions as well as tests rather than an actual lack of abilities. I here use "self-inspection", i.e. the active inspection of own cues measured through a behavioural response, to help remedy this definitional problem and break down the binary distinction between self-perception (i.e. the processing of own cues whilst lacking a mental image of self) and self-recognition (with the assumed mental capacity of differentiating between self and other based on previous experience). Whilst not suggestive of full self-recognition, then, self-inspection (e.g. of the own mirror image) may point towards latent neurological capacities necessary for fuller forms of recognition and differentiation of the self. Indeed, the concept of mirror guided self-inspection can be useful in studies on animals whose behavioural response to the own mirror image (e.g. self-directed behaviours towards marks on the own body) point towards a possible capacity of self-recognition, but fail to provide conclusive evidence for a cognitive differentiation between self and other.

More generally, then, a species' or individual's failure in passing the mirror mark test is challenging to interpret, and does not allow conclusions about the absence of self-recognition (Povinelli 1987). And even if a species generally passes the mirror mark test, a proportion of the tested individuals always fails to pass (e.g. Gallup 1970, Povinelli et al. 1993, Plotnik et al. 2006, Prior et al. 2008). The interpretation of self-recognition studies is an ongoing debate in the literature, with some authors arguing that mirror self-recognition might be suggestive of self-awareness or consciousness (e.g. Gallup 1970, 1983, 1985, Povinelli et al. 1993). Self-awareness has been defined as a state in which an individual actively identifies and processes information about its own identity, including information about its mental state (Morin 2006, Morin 2011). This hints at a capacity of introspection and reflection on the self. Morin (2011) describes the strong cognitive connection between self-awareness and self-recognition but concludes that both can be independent cognitive entities. Other authors see mirror self-recognition merely as a form of social mirroring without any form of self-concept (Heyes 1994). Most authors agree that self-directed behaviour in front of a mirror provides evidence for some degree of self-recognition (de Veer and van den Bos 1999) or at least for an ability to collate representations (Suddendorf and Butler 2013).

Despite immense research efforts (for a review see Gallup et al. 2002), mirror self-recognition has so far only been convincingly documented in great apes (Gallup 1970; Amsterdam 1972; Suddendorf and Collier-Baker 2009; Anderson and Gallup 2011), Asian elephants (*Elephas maximus*)(Plotnik et al. 2006), and magpies (*Pica pica*)(Prior et al. 2008). Previous studies on mirror self-recognition in bottlenose dolphins (*T. truncatus*)(Marino et al. 1994; Marten and Psarakos 1994; Marten and Psarakos 1995a; Marten and Psarakos 1995b; Reiss and Marino 2001) have been severely criticised for their methodological flaws, and remain inconclusive (Gregg 2013; Harley 2013; Manger 2013; Güntürkün 2014). Besides this small number of species passing the test, many species show middle stages between passing and failing the test (such as active inspection of the own mirror image, see above). In addition, male African cichlid fish (*Astatotilapia burtoni*)(Desjardins and Fernald 2010) as well as capuchin monkeys (*Cebus apella*)(de Waal et al. 2005) show different behaviour towards their mirror reflection than would be expected in interactions with a conspecific. The African cichlids do show aggressive behaviour similar to the territorial defence displayed when interacting with a rival, but show a substantially different brain gene expression during the interaction with the mirror (Desjardins and Fernald 2010). Several species can be trained to use their mirror reflection to locate hidden food (Heschl and Burkart 2006; Broom et al. 2009; Medina et al. 2011), and African Grey Parrots (*Psittacus erithacus*) are capable of mirror-guided object discrimination (Pepperberg et al. 1995). It has been demonstrated that rhesus macaques (*Macaca mulatta*)(Chang et al. 2017) and pigeons (*Columba livia domestica*)(Epstein et al. 1981) can reach the passing criteria of the test after extensive operant condition training even though they fail to pass the test spontaneously. Both examples do not demonstrate self-recognition due to the lack of spontaneous self-directed behaviour, but all these degrees between self-perception and passing the mirror mark test could indicate a cognitive continuum rather than a binary approach between failed and successful self-recognition (Plotnik et al. 2010)(for a more detailed summary of the study field of mirror self-recognition see chapter 4.2).

1.4 Recognition in bottlenose dolphins

In the preceding sections, I introduced an ordering framework for the field of recognition in animals more broadly, and have subsequently categorised previous research in the field to demonstrate the framework’s utility. I have also pointed out the challenges and promises inherent in such research. In the next paragraphs, I focus on a particular species at the core of this thesis, namely bottlenose dolphins, to introduce their importance to the field of animal recognition studies (see Table 3 for cited studies on dolphin recognition). Using the framework introduced above, I position this thesis and its contributions within the field, and show how the study of bottlenose dolphins has led to many exciting findings in the field of recognition.

1.4.1 Inter-species and object-recognition

The majority of studies addressing some facet of inter-species recognition dynamics in bottlenose dolphins have actually been conducted on acoustic object-recognition through echolocation. Bottlenose dolphins are able to discriminate between objects by using broadband frequency click sounds and listening to the sound echo that is reflected by the object (Dewsbury 1980). In a match-to-sample (Roitblat et al. 1990; DeLong et al. 2006) or crossmodal match-to-sample scheme (Herman et al. 1998; Pack et al. 2002), they are able to identify an object they previously echolocated on and can distinguish object characteristics (Harley et al. 2003). This even works when the dolphin is not echolocating itself but is eavesdropping on the echo clicks produced by conspecifics (Xitco and Roitblat 1996).

Dolphins are also able to use tonal sounds, rather than echo clicks, for object-recognition: Reiss and McCowan (1993) used symbols on an underwater keyboard and computer-generated model sounds as a stimulus for an object in order to determine the range of vocal mimicry and object labelling. After operant conditioning in identification and vocal labelling of five different objects visible over the water surface, a dolphin was able to mimic the associated sound when seeing but not hearing the object (Richards et al. 1984). Bottlenose dolphins use echolocation not only for orientation but also for hunting (Norris et al. 1961; Dewsbury 1980). The recognition of prey-species rather than objects might rely on the same mechanisms of echolocation: similar to the tested objects, different fish species also show distinctive echoes that may allow for acoustic species recognition (Au et al. 2009; Yovel and Au 2010). In addition to the recognition of prey by actively producing echo clicks, dolphins also seem to be able to recognise prey species by listening to sounds the prey species produce (Gannon et al. 2005).

While dolphins seem to be fully capable of visual object recognition, association training has been reported to be significantly slower compared to acoustic discrimination tasks, and the visual differences between objects have to be faded out more slowly (Terrace 1963; Herman 1980). However, visual signals like hand signs play an important role in dolphin training within managed facilities: Even though these cues are often paired with acoustic signals, dolphins are capable of recognising and interpreting a range of visual signals, and even gestures and referential pointing (Shyan and Herman 1987; Herman et al. 2001; Tschudin et al. 2001). In a crossmodal approach, dolphins were trained to interpret the dynamic visual actions of humans and were able to spontaneously interpret them via echolocation when the human trainer was located behind an opaque screen under water (Kuczaj et al. 2008). Dolphins also appear to be capable of visually discriminating familiar human trainers based on their clothing (Tomonaga et al. 2015).

Even though dolphins have generally good visual capabilities (Supin et al. 2001; Cozzi et al. 2016) and are able to detect chemosensory cues (Nachtigall 1986; Kuznetsov 1992), the literature is lacking experimental evidence for inter-species recognition in these modalities. Bottlenose dolphins are also known to school in mixed species groups with other dolphin species (e.g. Connor 2000, Herzing and Johnson 1997). While little is known about inter-species-recognition in this social context, two experimental studies on captive dolphins provided evidence that bottlenose dolphins might be capable of discriminating the whistles of short-beaked common dolphin (*Delphinus delphis*) and Atlantic spotted dolphins (*Stenella frontalis*)(Caldwell M.C. 1973). This could hint at the potential for inter-species recognition in bottlenose dolphins on an individual level but further investigation is required.

Compared to other species, predator interaction in bottlenose dolphins might be rather limited due to the small number of predator species. Killer whales (*Orcinus orca*) are known to predate on bottlenose dolphins (Jefferson et al. 1991) and it has been described that mammal-eating killer whales eavesdrop on their prey's communication for recognition and detection (Deecke et al. 2005). This might explain why predator alarm calls seem to be absent in dolphins (Janik 2006; Connor 2007), and it is unclear whether dolphins use any other modality for predator recognition.

1.4.2 Intra-species-recognition/Individual-recognition

It has been argued that complex societies and large social group size are driving factors in the evolution of complex communication systems, cognitive abilities and individual recognition signals (Sayigh et al. 1999; Pollard and Blumstein 2011; Janik 2014). This makes dolphins a particularly interesting study species for intra-species-recognition. Similar to some corvids (Heinrich 1988) and many primates (Mc Farland Symington 1990; Amici et al. 2008), dolphins live in so-called fission-fusion societies, where individuals maintain long-lasting social bonds despite flexible association patterns and constantly changing group compositions with individuals leaving and reuniting with their associates (Wells et al. 1987; Smolker et al. 1993; Connor et al. 1998). Group sizes can reach up to a thousand individuals and subgroups generally tend to be formed by females with their dependent offspring, by adult males, or by juveniles (Wells et al. 1987; Wells 1991; Wells 2009). Social bonds are especially strong between adult males, which build and maintain strong alliances (Connor et al. 2011), and between females and their offspring (Connor et al. 1998; Connor et al. 2011). This variety of long-lasting social bonds within a complex social network is based on individual recognition (e.g. Janik et al. 2006, Sayigh et al. 1999).

Bottlenose dolphins produce whistles with individually distinctive frequency modulation patterns to broadcast their identity. These so-called “signature whistles” were first described by Caldwell and Caldwell (1965) as the primary whistle a dolphin would produce in isolation. Signature whistles are one of the few, and probably the best studied, examples of a true identity signal. Some bird species also use individually specific acoustic signals or song types for individual identification (Eens 1997; Wanker et al. 2005; Balsby et al. 2012), and humans use names to address each other. This type of acoustic individual recognition in dolphins appears to be independent of voice cues (Janik et al. 2006). Voice cues are individually distinctive acoustic variation within all vocalisations of an animal caused by morphological differences of the vocal tract. Many terrestrial animals mainly or solely rely on voice cues for individual acoustic recognition (e.g. Symmes et al. 1979, Candiotti et al. 2013). But air-filled cavities within the vocal tract are again highly affected by pressure changes during dives, making voice cues unreliable for individual recognition in dolphins (Tyack and Sayigh 1997). In contrast to voice cues the frequency modulation pattern of signature whistles seems to not be affected by changing water pressures during diving (Madsen et al. 2012).

Dolphins are capable of recognising the signature whistles of known individuals (Sayigh et al. 1999; Janik et al. 2006) and they produce copies to address each other (Tyack 1986; Janik 2000; Tyack 2000; King and Janik 2013; King et al. 2013). Bruck (2013) demonstrated that some individuals could still recognise the whistles of familiar individuals after more than 20 years of separation, thus showing long-term memory for social recognition. Calves develop their own distinctive signature whistle at some point within the first year of life (Caldwell and Caldwell 1979; Sayigh et al. 1990; Tyack 1997), and vocal learning is suspected to play a crucial role in the development of individually distinctive identity calls (Tyack and Sayigh 1997; Miksis et al. 2002; Boughman and Moss 2003; Fripp et al. 2005). But surprisingly little is known so far about the process and mechanisms involved in the development of these individual recognition signals. Bottlenose dolphin calves are born fully developed, yet also highly dependent on their mothers for the first years of their lives, and the maintenance of contact between the mother-calf pair is crucial for the infant’s survival (Janik 2009). Dolphin calves are usually nursed up to an age of between 3 to 6 years (Mann and Smuts 1999). Without the mother’s protection, they are easy prey for marine predators (Fearnbach et al. 2012). This long period of nursing and the close association between mother and calf might favour social learning (Connor et al. 2000). It has been argued that dolphin calves acoustically (Mello and Amundin 2005; Fripp and Tyack

2008; King et al. 2016a) as well as visually (Mann and Smuts 1998; Connor et al. 2000) familiarise themselves with their mothers to enable recognition and to decrease the likelihood of being separated.

In contrast to other species, there is no evidence for any group-specific or kin-specific modulation pattern in bottlenose dolphins signature whistles (Sayigh et al. 1999; Janik et al. 2006). Killer whales (*Orcinus orca*), for example, live in matrilineal groups and share a call that is correlated with relatedness to the matriarch, allowing for kin-recognition by means of shared kin-specific features within the calls (Ford 1991; Deecke et al. 2000; Deecke et al. 2010). This could be explained by the difference in social structure between the two species: Highly stable social groups or families like the matrilineal units in Orcas might favour the recognition on a group level, while the fission-fusion society of dolphins likely requires recognition on an individual level (Tyack 1986).

As discussed earlier, dolphins have a sophisticated sonar system for orientation and prey recognition so the question arises whether echolocation also plays a role in individual recognition. While tonal sounds, such as signature whistles, travel multi-directionally and over greater distances within the water column (Quintana-Rizzo et al. 2006), echolocation clicks are produced in a narrow beam and therefore very directional (Dewsbury 1980). Similar to vision, then, echolocation clicks seem to be only suitable for recognition over short distances. However, while dolphins show a range of potentially reliable visual marks (e.g. scratches, scars) making visual recognition possible, their bodies seem to be unsuitable for individual echo-based recognition for two main reasons: Firstly, in contrast to fish, the skin and blubber of the dolphins' bodies have anechoic properties, which means that they are acoustically less reflective (Au 1996) especially at those high frequencies that are necessary for the high resolution echolocation required in individual recognition (Janik 1999). Secondly, the best echo from the dolphin's body is produced by air-filled cavities, but these are highly variable due to compression at different water depths (Janik 1999), which makes the echo a highly unreliable signal for individual recognition.

Dolphins seem to be able to detect chemical cues within the water (Nachtigall 1986) but very little is known so far about the olfactory and chemosensory senses in dolphins. Similar to vision, olfaction is likely limited to a range of a few meters within the aquatic environment. This makes (tonal) sound the most likely modality for individual recognition over greater distances. However, it might be possible that dolphins use vision, echolocation and gustation as additional recognition modalities in short distances either independently or crossmodally. By using crossmodal experiments during which the animals are confronted with stimuli match and miss-match situations, a better understanding could be gained of modality usage and cross-modality dynamics in bottlenose dolphin individual recognition. It might be especially interesting to consider the visual and chemosensory senses of dolphins, which both have been relatively neglected in recognition studies. In order to test for a representational function of signature whistles, Bruck and Janik (in preparation) use a cross-modality approach which presents dolphins with playbacks of signature whistles of familiar individuals paired with urine samples of either the same individual, an unfamiliar one, or water as an control. If the animals are capable of perceiving the differences in the chemosensory stimuli, it would be fascinating to test the animals for gustatory individual recognition and potentially even self-perception.

1.4.3 Self-recognition and self-inspection

Dolphins have been identified as promising candidates for visual self-recognition: They are capable of understanding referential pointing (Herman et al. 1999) as well as the syntactical rules in gestures (Herman and Forestell 1985), both indicating a high level of visual and cognitive processing. They also show high accuracy in motor synchrony, where one individual closely matches the movements of another (Herman 2002; Sakai et al. 2010). This form of kinaesthetic imitation requires the internal mapping of the conspecific's actions and a transfer into their own movements (Tsakiris et al. 2007). This ability could hint at potential perspective-taking and empathy, which are thought to co-evolve with self-recognition (Plotnik et al. 2006; de Waal 2008).

When applying Gallup's (1970) self-directed dependent measurements in primate mirror self-recognition studies to dolphins, the most prominent challenge lies in the absence of extended limbs: Dolphins are not physically capable of touching or manipulating a marked spot on their body while observing their mirror image. Hence, the established criterion for passing the mirror mark test cannot be reached, and discrimination between social and self-directed behaviour is challenging. In attempts to avoid this problem, researchers (Marino et al. 1994; Marten and Psarakos 1994; Marten and Psarakos 1995a; Marten and Psarakos 1995b; Reiss and Marino 2001) have used mark-oriented behaviours, latencies, and movements as dependent variables and indicators for mirror self-recognition. However, all previous studies on mirror self-recognition remain inconclusive due to severe methodological flaws, particularly the lack of controls (Gregg 2013; Harley 2013; Manger 2013; Güntürkün 2014)(for a detailed discussion of previous mirror mark studies see chapter 4.2). It also remains to be thoroughly discussed whether the available evidence is indicative of self-recognition or rather self-inspection as per the definitions suggested above.

Acoustic self-recognition or self-perception (as discussed in section 1.3.4) is methodologically challenging to study, as it cannot be tested outside the dolphins' natural communication system. Similar to song in many oscine birds, the production of signature whistle copies has an important communicational meaning, especially when closely associated individuals produce signature whistle copies to address each other and engage in vocal matching interaction (Janik 2000; King et al. 2013; King et al. 2014). Playback studies with signature whistles often initiate vocal matching (King et al. 2014) and are therefore a fascinating experimental design to understand this communicational function, but of very limited use when it comes to self-stimuli perception or acoustic self-recognition.

Table 3: Cited studies in the field of dolphin recognition sorted by recognition level and signal modality.

			signal modality						
			Acoustic				chemosensory	visual	crossmodal
			passive (listening)	tonal	Echolocation	eavesdropping			
recognition level	inter-species & object	object			Roitblat et al. 1990 DeLong et al. 2006 Harley et al. 2003 Herman et al. 1998 Houser et al. 2005 Roitblat et al. 1995	Xitco & Roitblat 1996			Harley et al. 1996 Pack & Herman 1995 Pack et al. 2002 Richards et al. 1984
		gestures, signs						Herman et al. 2001, Tschudin et al. 2001, Shyan & Herman 1987	
		human						Tomonaga et al. 2015	
		other species		Caldwell et al. 1973					
		predator							
		Prey	Gannon et al. 2005		Au et al. 2009 Yovel & Au 2012				
		parasite							
	intra-species	sex-, mate-, group							
		Kin		* Janik et al. 2006, Sayigh et al. 1999					
		offspring	Based on individual recognition						
	individual	individual		Sayigh et al. 1999 Bruck (2013) Janik et al. 2006					Bruck (unpublished)
		self-perception							
		self-recognition		-	-	-	-	(Marino et al. 1994, Marten & Psarakos 1994, Reiss & Marino 2001)	

*Providing evidence for absence of this level of recognition e.g. by showing evidence for other level

1.5 Thesis Overview

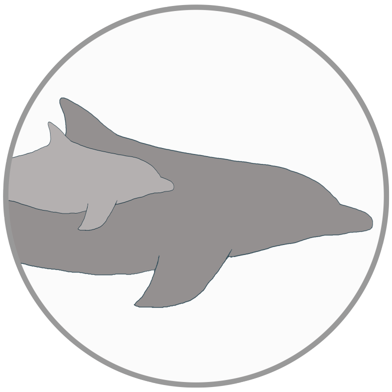
In this thesis, I focus on recognition in bottlenose dolphins. I tackle two of the gaps within the field identified in the preceding sections of this chapter, namely the development of acoustic identity signals and the capacity for self-recognition in this species.

Individual recognition is often an essential part of social communication. Bottlenose dolphins produce signature whistles with individually distinctive frequency modulation to broadcast their identity (Tyack 1997; Sayigh et al. 1999; Janik et al. 2006) but very little is known so far about the development of these identity signals. In chapter 2, I examine the process of signature whistle stabilisation during ontogeny. I conduct an analysis of fine scale recordings from seven bottlenose dolphin calves between birth and the stabilisation of their identity signal. This allows me to examine the acoustic potential for individual recognition within the calves' signals, describe the process of acoustic signal stabilisation, establish a general criterion for signature whistle stability, and predict a day of crystallisation during ontogeny.

In chapter 3, I examine the role vocal production learning plays in the development of signature whistles by comparing crystallised whistles to whistles of conspecifics present during the developmental phase. I also investigate whether sounds produced by heterospecifics (e.g. whistles produced by trainers in managed facilities) might influence signature whistle development through vocal production learning.

For a long time, bottlenose dolphins have been suspected to be capable of self-recognition however every experimental approach so far has failed to present conclusive evidence. The establishment of a mirror mark test suitable for marine mammals would not only increase our understanding about dolphin cognition, but about the evolution of these abilities more broadly. Therefore, in chapter 4, I focus on visual self-recognition in bottlenose dolphins. Previous attempts to test dolphins for self-recognition (Marino et al. 1994, Marten & Psarakos 1994, Reiss & Marino 2001) failed to provide conclusive evidence due to a lack of a suitable methodology as well as of adequate controls (Gregg 2013; Harley 2013; Manger 2013; Güntürkün 2014). I establish a new paradigm to test marine mammals for self-recognition by adjusting the mirror mark test methodology. I test dolphins and measure changes in their body orientation while in front of a mirror in response to markings painted around their eyes.

In chapter 5, I conclude by situating the results from chapters 2, 3 and 4 in the wider context of the animal recognition field. I discuss the development of individual recognition signals as well as the ability of self-recognition in bottlenose dolphins within the research framework and point out directions for future research.



2

Acoustic development of signature whistles in bottlenose dolphins

2.1 Summary

Across taxa, individual recognition plays an important role in caregiver-infant interactions and is often based on voice cues. Bottlenose dolphin calves are highly dependent on their mothers for nursing and protection and the maintenance of contact is crucial for their survival. Bottlenose dolphins produce signature whistles, a tonal call with a distinctive frequency modulation, to broadcast their identity. To date very little is known about the acoustic development from the first vocalisations after birth to a crystallised signature whistle. In this chapter I focus on the fine scale development and crystallisation process of signature whistles from seven dolphin calves to adulthood. A quantitative analysis using a threshold for signature whistle stability based on adult signature whistles, estimated the day of crystallisation between 19 and 23 days after birth. Even before the signature whistle crystallises, parameters in the calves' fundamental frequency are individually distinctive and potentially allow for reliable kin-recognition. The vocalisations of newborn calves show a high number of biphonations and potential nonlinear phenomena (e.g. overlapping contours, sidebands, chaos), which decrease during the first months. These nonlinear effects could trigger a caregiver response and additionally facilitate kin recognition.

2.2 Introduction

This chapter focuses on acoustic development in bottlenose dolphin calves in the context of kin recognition. As discussed in chapter 1, kin recognition plays an important role in many taxa, from reptiles to birds and mammals and can rely on a multitude of different modalities ranging from visual, tactile, olfactory, chemosensory, to acoustic recognition (e.g. Hauser 1991, Mateo & Johnston 2000, Parr & deWaal 1999). Reliable kin recognition is especially important when dependent offspring either have a certain amount of mobility after birth (Sayigh et al. 1990; Smolker et al. 1993) or if parents and neonates are regularly separated e.g. during foraging trips (Aubin and Jouventin 2002). The latter is particularly significant in species that leave their offspring during foraging trips in colonies with high numbers of individuals. For example, in most penguin species where breeding colonies can reach large group sizes, both parents take turns in foraging and are challenged by finding their chicks after returning from sea: little penguins (*Eudyptula minor*), banded penguins (*Spheniscus* spp.), Adélie penguins (*Pygoscelis adeliae*), emperor penguins (*Aptenodytes forsteri*), king pinguins (*Aptenodytes patagonicus*), macaroni penguins (*Eudyptes chrysolophus*), and gentoo penguins (*Pygoscelis papua*) use voice cues in their chicks' calls to reliably navigate back to their offspring (Aubin and Jouventin 2002; Clark et al. 2006). While some penguin species build nests within the colony (e.g. Gentoo and Adélie) and can therefore additionally rely on spatial cues when navigating back towards their partner or offspring, other species (e.g. emperor or king penguins) do not nest and have to rely mainly on vocal cues. And interestingly, especially these non-nesting species seem to have developed a sophisticated "two-voice" system that could enhance variation within the acoustic signal making the signal more distinct within the high background noise of the colony (Jouventin and Aubin 2002; Searby et al. 2004). Subantarctic fur seals (*Arctocephalus tropicalis*) are faced with a similar challenge: Mothers use call features in the pup's "female attraction call" to find their offspring within the colony (Charrier et al. 2002).

2.2.1 Acoustic recognition in bottlenose dolphins

Bottlenose dolphin calves are born fully developed but highly dependent on their mothers for nursing and protection (Mann and Smuts 1998; Mann and Barnett 1999; Fearnbach et al. 2012). The maintenance of contact between the mother-calf pair is crucial for the infant's survival (Mann and Smuts 1998; Mann et al. 2000) and contact can only be re-established reliably after physical separation if there is a form of recognition.

Bottlenose dolphin calves are highly mobile and swim independently immediately after birth (McBride and Kritzler 1951) and the physical separation from their mothers is a constant threat to their survival. Living in an aquatic environment where visual and chemosensory recognition is likely limited to a range of a few meters, and without an olfactory sense (Berta et al. 2014), dolphins mainly rely on acoustic signals to remain in contact and for recognition (Tyack 1997; Janik and Sayigh 2013). Specifically, bottlenose dolphins employ signature whistles for such recognition. These whistles are not fully formed until sometime after birth. The process of signature whistle crystallisation, during which the frequency modulation of the acoustic signal becomes stable, remains under-researched, however.

Most terrestrial species depend to a large extent on voice cues as by-product of physiological and anatomical differences for individual acoustic recognition (Clutton-Brock & Albon 1979, review for source-filtering: Taylor & Reby 2010). Constant pressure changes during dives affect the air volume within the vocal tract, making voice cues unreliable for marine mammals (Tyack and Sayigh 1997). Bottlenose dolphins overcome this obstacle by using distinctive frequency modulations (signature whistles), for individual recognition (see chapter 1.4 for more details regarding the mechanism and function of signature whistles). In contrast to voice cues, which affect all vocalisations of an individual, a signature vocalisation encodes the identity information within a specific call from the vocal repertoire (Janik et al. 2006). The identity information in signature whistles is encoded in the modulation pattern of the fundamental frequency, and individuals can still be recognised even if all voice cues are removed in a computer-generated whistle (Janik et al. 2006). This form of identity encoding appears to require vocal production learning and is rare within the animal kingdom (Tyack 1997; Fripp et al. 2005; Janik et al. 2006).

2.2.2 Signature whistle development during ontogeny

Dolphin calves are thought to develop their own signature whistles within the first year of life (Sayigh et al. 1990). Some authors report whistle crystallisation already within the first three months (Caldwell and Caldwell 1979), or even within the first week (Caldwell and Caldwell 1979; Tyack 1997).

To form a social bond and to avoid separation after birth, it would be highly advantageous for mother-calf pairs to recognise each other quickly and reliably. Dolphin mothers increase their whistle rates by a factor of ten before and after giving birth, which has been suggested to enhance the familiarisation of the calf with its mother's signature whistle (Mello and Amundin 2005; Fripp and Tyack 2008; King et al. 2016a; King et al. 2016b). Shortly after birth, the pair usually starts to engage in synchronous behaviours and body contact, which might additionally facilitate the social bond (Mann and Smuts 1999; Fellner et al. 2006; Sakai et al. 2006; Fellner et al. 2013). During the first weeks of life, mother and calf usually stay in very close proximity which potentially enables the pair to bond and to recognise each other reliably. But it remains unclear how and when mothers start to acoustically recognise their calves and how they bridge the crucial period before the calf develops a stable signature whistle.

A focus in research on the development of signature whistles over time has been on the changes after crystallisation and throughout a dolphin's life. Especially adult males form close social alliances and it has been reported that their signature whistles become more similar over time (Smolker and Pepper 1999; Watwood et al. 2004). In case the shared whistle was not part of the initial repertoire of both individuals, this increase in similarity could be explained by whistle convergence where the individuals adjust their whistles through vocal production learning (Smolker and Pepper 1999; Watwood et al. 2004). For mothers and calves it has been described, that signature whistles remained stable for ten to 30 years (Sayigh et al. 1990; Leon-

Lopez 2016). Bruck (2013) showed that individuals were able to remember signature whistles from familiar individuals for as long as 20 years, suggesting that long-term stability in signature whistles might be important for long-term recognition.

Dolphin calves start to whistle and echolocate immediately after birth (McBride and Kritzler 1951; Caldwell and Caldwell 1979; Caldwell 1990; Favaro et al. 2013) and seem to mainly whistle when they are separated from their mothers, indicating the importance of the calf's whistles as a contact signal (McBride and Kritzler 1951; Caldwell and Caldwell 1965). Early whistles are often described as irregular and chaotic in their frequency modulation but seem to gradually become modulated in a more stable way within the first 6 or 12 months of life (Caldwell 1990; Sayigh 1992; Gnone et al. 1996). Even though several authors described the vocal changes in dolphin calves during ontogeny (McBride and Kritzler 1951; Caldwell 1990; Sayigh 1992; Gnone and Moriconi 2010), these studies remained mainly descriptive and did not analyse any fine scale changes within the development of signature whistles. Furthermore they often used purely the occurrence of bubble streams to localise the signaller (McBride and Kritzler 1951; Gnone et al. 1996) a method that has been pointed out to be unreliable for localisation (Fripp 2005). Here I present the first acoustic fine scale analysis of dolphin calf whistles during ontogeny based on suction cup recordings which enable reliable identification of the calf as a signaller.

2.2.3 Factors influencing signature whistle development

Changes in the produced sound during ontogeny can be caused by several, non-exclusive causalities: the physical growth of the body and vocal apparatus, mechanical production control, neural production control, and potential vocal production learning. The dolphin's sound production apparatus is located in the nose and consists of two independent sets of phonic lips rather than the vocal cords in the larynx of other mammals or in the syrinx in birds (Cranford et al. 1996). The two pairs of phonic lips allow dolphins to potentially produce two independent sounds, one in each nasal passage. This enables dolphins to simultaneously use echolocation (e.g. for orientation) and to whistle (e.g. for communication)(Cranford et al. 2000). Whistles are produced by vibrations of the tissue and stabilised by the nasal air volume (Madsen et al. 2012).

Three different systems within the sound production apparatus that can influence changes in sound have been identified (Janik and Slater 2000; Fitch 2006): the respiratory system (influences duration and amplitude), the phonatory system (influences parameters of the fundamental frequency), and the filter system (determines the resonant frequencies and thus the energy distribution).

Voice cues are influenced by body growth during an individual's ontogeny in many species. Little brown bats (*Myotis lucifugus*) show a change in their sound structure during ontogeny with an increase in fundamental frequency and repetition rate as well as a decrease in duration over time (Moss et al. 1997). An increasing fundamental frequency in echolocation clicks in juveniles compared to adults is also found in recordings from sperm whale neonates (*Physeter macrocephalus*)(Watkins et al. 1988; Madsen et al. 2003) and bottlenose dolphins (Favaro et al. 2013). In contrast, in most mammalian species the fundamental frequency of calls decreases during body growth: Chacma baboons (*Papio ursinus*) for example show changes in their call duration, fundamental frequency, and energy distribution that vary with age and sex (Ey et al. 2007). Bottlenose dolphin calves grow extensively during the first months of their life, and the vocal tract is also constantly growing during this process. It is likely that these changes in size are affecting the sounds that a calf produces as it grows. In addition to ontogenetic changes on sound production, infants learn how to control their vocal apparatus effectively, testing the physiological and physical constraints. In order to produce a signature whistle in a stable and predictable way, some level of mechanical control of the vocal apparatus and the coordination between both pairs of phonic lips is necessary. This is likely to be challenging for a dolphin infant.

While the potential role of vocal production learning in the development of signature whistles will be discussed in more depth in chapter 3, this chapter is focused on the acoustic changes from the first vocalisations to a stable signature whistle due to maturing and increasing control of the vocal apparatus. In terrestrial mammals (Fitch et al. 2002; Townsend and Manser 2011; Briefer et al. 2015; Reby et al. 2016) and birds (Fee et al. 1998), nonlinear phenomena within vocalisations have been described (e.g. biphonations, sidebands, or chaos). In contrast to terrestrial mammals, dolphins are able to produce two vocalisations independently in each nasal passage. Biphonations can therefore be either caused by two simultaneous vocalisations or by a nonlinear phenomenon (different oscillations of the phonic lips within one nasal passage). Here I distinguish between the terms biphonations and nonlinear phenomena to stress that in dolphin vocalisations we do not know whether biphonations are a nonlinear phenomenon or produced in both nasal passages simultaneously. Nonlinear phenomena and biphonations are suspected to additionally facilitate kin recognition and to make infant vocalisations harder to ignore by increasing their variability (Fitch et al. 2002; Lingle et al. 2012). Very little is known so far about the occurrence or function of nonlinear phenomena in dolphin infants and their potential role for kin recognition. The acoustic development before crystallisation of signature whistles (when the frequency modulation of the acoustic signal becomes stable) is still uncertain.

2.3.4 Research questions

Three main questions arise out of the preceding overview: 1) How long does the signature whistle take to crystallise and how can stability be measured, 2) how does the acoustic development during ontogeny progress and 3) do vocalisations of new-born calves already allow for individual recognition even though the fundamental frequency modulation of the signature whistle might not be crystallised?

To better quantify the acoustic development in dolphin vocalisations during early ontogeny, the goal of this study is to first determine a metric drawn from the fundamental frequency modulation pattern that is characteristic for crystallised whistles in adults. For this reason, I analyse the signature whistles of adult bottlenose dolphins from two wild populations as well as from 4 captive facilities and with varying recording setups (e.g. during capture and free ranging) to control that none of these variables is affecting the stability threshold. Based on this analysis, I introduce the coefficient of variation of the similarity score as a metric for crystallisation, which is then used to predict when a calf's whistle crystallised. To test for distinctiveness and potential individual recognition, I also examine how vocalisations change in distinctiveness before and after crystallisation. Finally, changes in additional sound parameters (e.g. durations, biphonations, nonlinear phenomena like subharmonics or chaos) and whistle rates are described during the developmental phase.

2.3 Methods

2.3.1 Subjects

Calves

Vocalisations from seven bottlenose dolphin calves (4 males, 3 females) were recorded in four dolphin facilities (Germany: Duisburg and Nuremberg; Italy: Genoa and Oltremare) between 2011 and 2015 (Appendix Figure I). Recordings were collected on the calfs' first day of life up to an age of 204 days. Dates of birth, sex, parent's ID, facilities, and recording days of the calves are listed in the supplemental material (see Appendix Table I). All calves were housed in multi-pool-systems with their parents and between one and nine other adults present. Shortly before birth, mothers were separated from the group by meshed gates. After birth and during the recording period, mothers and calves were kept physically separated by net gates or fences from the rest of the group. However, these gates allowed acoustic contact with all animals in the pool system.

Adults

Adults were recorded in 4 managed facilities (Germany: Duisburg and Nuremberg; Italy: Genoa and Oltremare) and two wild populations (Belize and Florida). Information about dolphin identities, ages, sex as well as a detailed description of the captive group compositions can be found in Appendix Figure I and in section 3.3.1. Data from wild populations was collected in the Turneffe Atoll (Belize) and in Sarasota Bay on the west coast of Florida (USA). The population in Turneffe Atoll has been monitored as part of a long-term conservation project managed by the Oceanic Society. Since 2012 the field site on Blackbird Caye is protected as part of the "Turneffe Atoll Marine Reserve" (Turneffe Atoll Management Plan 2012-2017). The Atoll is located 50 km off the coast from Belize City and is divided by channels and islands into many small lagoons. The largest lagoon (average depth ~ 4 m) had generally high underwater visibility, facilitating visual observations of dolphins during the survey. During the recordings in January 2015, the resident dolphin population at Turneffe was estimated to consist of 160 individuals (Turneffe Atoll Management Plan 2012-2017), most of which were catalogued in a photo-identification database and monitored for the last 20 years. A sample of 10 signature whistles from the Belize population was included into the analysis.

The population in Sarasota Bay was recorded in 2013. Sarasota Bay is a shallow bay (average depth of 5 m) connected to the Gulf of Mexico. The population is monitored as part of a long-term study by the Sarasota Dolphin Research Program for the last 30 years (starting in 1970) and includes approximately 160 individuals (Allen 2014). A total of ten individuals (4 males and

6 females), were randomly selected from the 2013 recordings. Animal identity, sex and year of birth are listed in Appendix Table I.

2.3.2 Acoustic recordings

Calves

Acoustic recordings of calf whistles were taken during regular husbandry check-ups when the mother and calf pair was lifted by an elevator platform to more shallow waters to limit their mobility. As part of a training routine the mothers were slowly habituated to this procedure prior to giving birth. The calf was lifted above the water surface by familiar trainers, either onto the pool edge or right by the mother's side, and examined by a veterinarian. While body measurements and blood samples were taken, a suction-cup hydrophone was placed on the calf's melon (Duisburg and Nuremberg) or a hydrophone was put right behind the animal's blowhole (Genoa and Oltremare). The suction-cup hydrophone (HTI 96-min hydrophone; frequency response 2 Hz to 30 kHz, sensitivity -201 dB re: 1V/µPa, High Tech Inc., USA) was incorporated into a custom build silicon suction-cup and connected to a portable digital recorder (Tascam DR-40: frequency response 20 Hz to 20 kHz ± 3 dB, sampling rate 96 kHz, 24 bit, TEAC Corporation, USA or Edirol R44: sampling rate 96 kHz, 24 bit, Roland, USA) in Germany. In Italy the same hydrophone connected to a (TASCAM DR-80) recorder was used. An array of three additional hydrophones was placed around the pool in Duisburg and Nuremberg for additional recordings of the mother. As the frequency and duration of the husbandry check-ups were limited to a necessary minimum to minimize stress the recordings were spaced unevenly in time. The total number of recording days for each calf can be found in Appendix Table I (included in the supplemental material).

Adults

Signature whistles of the 28 captive individuals (six years or older) were recorded using an array of four hydrophones (HTI 96-min hydrophone; frequency response 2 Hz to 30 kHz, sensitivity -201 dB re: 1V/µPa, High Tech Inc., USA) around the pool. The array set-up was used to match whistle recordings to individuals by triangulation using the time of arrival differences on different recording channels of an Edirol R44 digital recorder (sampling rate 96 kHz, 24 bit). In four cases, adult individuals were recorded with a suction-cup hydrophone while temporarily restrained during medical treatment or before transport. Signature whistles from the mothers (in Duisburg and Nuremberg) were recorded with hydrophone arrays during husbandry checks of their calves as described above.

In Belize, 25 hours of recordings were collected during boat surveys using two hydrophones (HTI 96-min hydrophone; frequency response 2 Hz to 30 kHz, sensitivity -201 dB re: 1V/µPa, High Tech Inc., USA) towed on 2 m metal chains on both sides of the boat. The hydrophones were connected to a digital handheld recorder (Tascam DR-40: frequency response 20 Hz to 20 kHz ± 3 dB, sampling rate 96 kHz, 24 bit, TEAC Corporation, USA). When dolphins were in sight, recordings were collected continuously and pictures were taken for photo identification. Whistles could not be assigned to specific individuals but were considered to be signature whistles from unknown individuals of the population if several criteria were met: 1) criteria outlined in the SIGnature Identification (SIGID) method (Janik et al. 2013), 2) the whistle was found in at least two different encounters when at least one of the identified individuals was identified in all sightings and 3) only when no calf or sub adult was seen in the group. The SIGID method is a useful tool to identify signature whistles of unrestrained individuals and without an array of hydrophones. Within a recording, whistles had to occur in a typical bout pattern with repetitions of the same frequency modulation pattern and a minimum of 75% of all whistles of this type had to occur with inter-whistle gaps of 1-10s (Janik et al. 2013). A total of 10 individual signature whistles could be identified.

The recordings from the Sarasota populations were collected during brief capture-release events and health assessments in Sarasota Bay (Florida, USA) in 2013 as part of a long-term study by the Sarasota Dolphin Research Program. The whistles from 10 individuals were recorded using a suction-cup hydrophone (High Tech Inc. SSQ94 frequency response 2 Hz to 50 kHz ± 1 dB recorded on Sound Devices 744T digital recorder, frequency response: 10 Hz to 48 kHz ± 1 dB) on the melon while the animals were temporarily restrained in the water or lifted onto a research vessel.

2.3.3 Sound analysis

The sound recordings from all capture events were visualised using spectrograms in Adobe Premiere 2.0 (FFT size: 1024, frequency resolution: 48 kHz, weighting function: Hamming, window width: 100%).

From all calf signals with a high signal-to-noise ratio and a clear fundamental frequency, up to 20 whistles were randomly selected for each capture event, resulting in a total of 1542 extracted whistles from 88 capture events for n_C=7 calves. For adults, a sample of 20 signature whistles was randomly chosen. All sampled whistles were cut from the original recording file, saved as separate .wav-files, and transferred into Luscinia software database (Lachlan 2016) for further signal processing. For each signal, the fundamental frequency (f_0) was extracted from the spectrogram by marking it manually and using the algorithm provided by the program to extract the fundamental frequency (f_0) within the frequency band. A Dynamic Time Warping analysis (DTW) was performed in Luscinia to compare fundamental frequency modulations. The DTW analysis two signals are transformed along the time axis in order to find the best alignment with minimum distances between the two signals. The DTW generates a dissimilarity score ranging from 0 to 1 with 0 indicating that the signals are identical (Buck and Tyack 1993; Deecke and Janik 2006; Lachlan 2016). The initial point of alignment in Luscinia was set to start, 25 %, 50 %, 75% and the end (with the ends and not the start of the signals being aligned) of the two signals and then the best alignment for the comparison was chosen based on the Euclidean distance between the two time series. All parameter settings (compression factor: 0.001; minimum element length: 10; time SD weighting: 0.5; maximum warp: 100) were kept constant in Luscinia during all comparisons. For the statistical analysis dissimilarity scores were converted into similarity scores by subtracting them from 1. By performing pairwise comparisons a similarity score was calculated based on cross-correlation of whistle contours within the dataset.

Each whistle contour with a duration of more than 100 ms and a gap of more than 250 ms to the next whistle was treated as a single whistle (Esch et al. 2009; Janik et al. 2013). Signature whistles often occur in several repetitions as a multi-loop structure. These structures consist of varying repetitions of the signature whistle element often with a slightly different introductory and terminal element (Caldwell et al. 1990). If multi-loop whistles are included into a dynamic time warping analysis, the varying number of loops can change the results of inter-individual and within-individual comparisons making comparisons for similarity of fundamental frequency modulation patterns less reliable. If the central elements of a loop structure were acoustically so similar that they appeared as one cluster in non-metric multidimensional scaling (based on a distance matrix and principal component analysis)(Lachlan 2016), and if the central element also occurred outside of a loop structure, only one repetition per multi-loop was chosen randomly and included into the analysis. If these criteria were not fulfilled and a signature whistle consisted constantly of more than one element, all elements were connected for the DTW to enable a comparison of the complete whistle structure. For this, the fundamental frequencies (f_0) were aligned and the gap between them was deleted. This procedure was only necessary for the signature whistles of 5 adults out of 48 individuals. Two examples of the principal component analysis of multi-loop whistles that where similar enough to measure only one element (c and d) and that were so different that they were stitched (a and b) are shown in Figure 2.

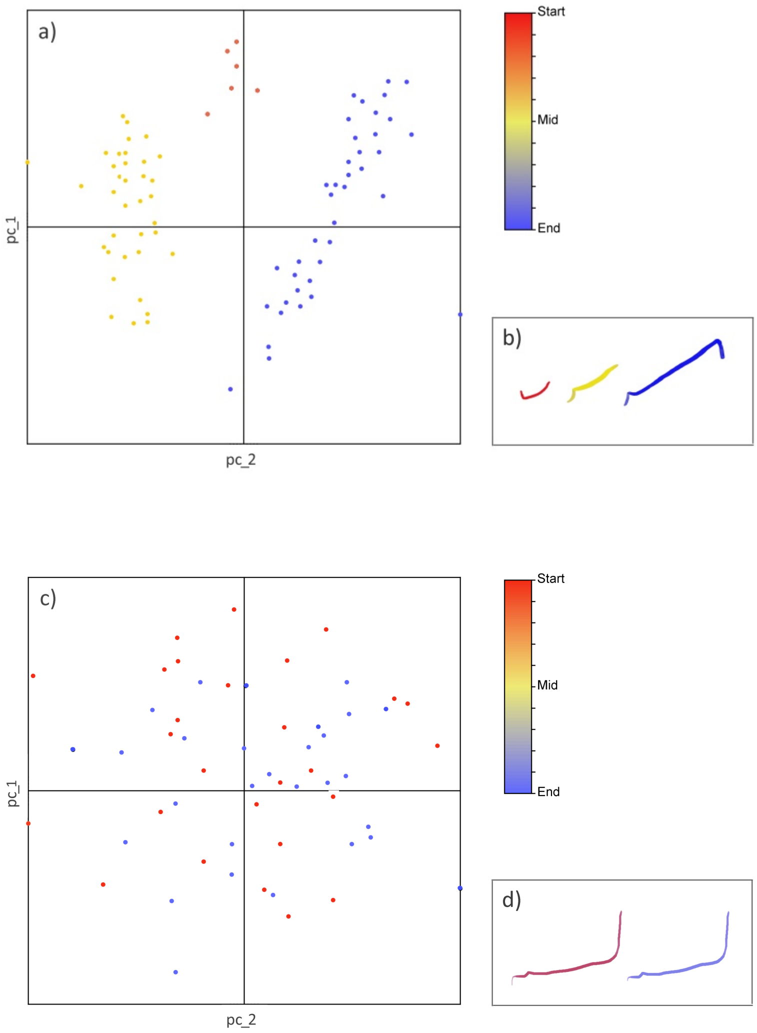


Figure 2: **Non-metric multidimensional scaling for two individuals** with a) un-similar loops that were never recorded in a single loop structure and were stitched for further analysis (frequency modulation illustrated in b), c) similar loops that did occur as a single loop and where only one loop was randomly picked for further analysis (frequency modulation illustrated in d). Colours indicate the position of the loop within the whistle with red being at the start, yellow being in the middle (or at the start in case of a whistle with only two loops), and blue being at the end of a multi-loop whistle.

Biphonations and nonlinear phenomena

All tonal vocalisations recorded from birth up to 228 days of age were manually scored from the spectrograms in Adobe Audition version 2.0 for the following acoustic features: biphonations (the occurrence of two independent frequency contours in the same signal or overlapping broadband sounds/clicks) or nonlinear phenomena (sidebands or deterministic chaos). The identification of these features followed the definitions given in Fitch et al. (2002) with the exception that biphonations (overlapping contours or clicks) are differentiated from nonlinear phenomena due to the differences in sound production in dolphins compared to primates. All vocalisations included in this analysis were recorded with a suction-cup hydrophone to avoid potential vocalisations by a second individual. A total of 1611 whistles were scored and 10 % were randomly selected and re-scored by a second rater who was naïve to the research question, the signaller ID, and the day of the recording during development. Between both raters a high level of agreement was achieved (Spearman's rho correlation: correlation coefficient= 0.962, P≤0.005).

2.3.4 Statistical analysis

Adults – threshold for signature whistle stability

A signal type can be described as stable when it is produced in a stereotypic way and with limited variation between repetitions. The signature whistles of adult bottlenose dolphins are used to broadcast the signaller's identity (Sayigh et al. 1999; Janik et al. 2006) and stability and repeatability within the signal is crucial. Therefore, it is reasonable to expect that the similarity within recordings of the same signature whistle should be higher than between different signals. To calculate the similarity score between two signals, dynamic time warping is used and the resulting dissimilarity score between the two vocalisations is subtracted from 1. To establish an average individual-specific similarity score for adult bottlenose dolphins, a pairwise comparison on all adult signature whistles was performed. Within each sample from an adult dolphin, each signature whistle was compared to all others within the sample (n_W=920).

Since the standard deviation of the individual-specific mean similarity scores were different between individuals, the coefficient of variation (CV_{SI}, Eq 2.1) was used as a stability metric.

$$CV_{SI} = \frac{\sigma}{\mu} \tag{Eq 2.1}$$

Where σ is the standard deviation and μ is the mean. The coefficient of variation was used as a standardised measure of dispersion of the distribution and preferred over the standard deviation and the mean as it is more robust when comparing different datasets with varying means. As repeated measurements were performed in the pairwise comparisons and the data was auto-correlated, by incorporating the variation within the day in the CV_{SI}, the time evolution of the variance is accounted for. To calculate a similarity score between individuals, each whistle of an individual was compared to whistles from every other adult individual resulting in 112800 similarity scores between the 48 individuals. This is important to show that there is a difference in similarity within and between signature whistles types, so the within stability metric can indeed be used as a measure of stability. The 95% quantile of the adult CV_{SI}

distribution (CV_{Th}) was then estimated and represents the value expected for a dolphin that produces a repeatable, crystallised sound.

Calves

Least square linear regression model

To analyse the development of stability in the vocalisations of calves a pairwise comparison was performed based on DTW (Lachlan 2016) as described for adults. Only vocalisations within each individual and within a recording day were compared to each other. A total of 14766 similarity scores were calculated from 1542 whistles recorded from all seven calves in a total of 88 recording days. The coefficient of variation of all similarity scores was then calculated for each day. A regression model was fit with the day of life (t) as a response and the coefficient of variation of the similarity score for calves (CV_C) as the predictor variable (Eqn 2.2). All variables were log transformed to account for a non-normal distribution of the data (Anderson Darling test for normality, $P > 0.05$ for all transformed data).

$$\log(t) = a + b \log(CV_C) \qquad \text{Eq 2.2}$$

The model fit and the CV_{Th} from above was then used to estimate the expected day of crystallisation (D_c) for the seven calves. The regression analysis was performed in R Studio (Version 0.99.893 – © 2009-2016 RStudio, Inc.).

Discriminant Function Analysis

A cross-validated stepwise discriminant function analysis was performed to test for distinctive quantitative features within the fundamental frequency (f_0) of the calf vocalisations. The modulation of the fundamental frequency has been shown to be individually distinctive in adult bottlenose dolphins (Caldwell and Caldwell 1965; Tyack 1986; Sayigh et al. 1999; Janik et al. 2006), therefore only measurements from the fundamental contour (f_0) were used for this analysis. For n_W=1542 whistles from 7 calves, a total of 12 metrics from the fundamental contour were extracted from the Luscinia database (2016) and used as predictor variables (see Table 4 for definitions). The calf identities were used as a dependent variable with seven mutually exclusive levels. All statistical analyses were performed using SPSS software (IBM SPSS Statistics 23). Dependent variables were plotted to check for outliers, tested for multi-co-linearity (Pearson Correlation, $p>0.05$). Weights were incorporated to account for different sample sizes between individuals. In order to investigate developmental classification, the estimated day of crystallisation (D_C) from the regression model was used to separate the data into pre (day 1 to 18, n_W=816) and post (day 23 to 90, n_W=402) -crystallisation and the adult phase (two year or older, n_W=178) if available. Further splitting of the dataset into smaller time bins was prevented by the different recording days of the individuals and the irregular spacing within the dataset. Six of the seven calves were recorded in all three phases, only the calf from the Nuremberg facility could not be recorded during phase 3. The discriminant function analysis is based on 12 measurements from the fundamental frequency, defined in Table 4. The discriminant function analysis reports the percentage of correctly grouped whistles based on the metric from the fundamental frequency measurements. This percentage indicates the potential for individual recognition and was tested against a grouping by chance (χ^2 test).

Table 4: Descriptions for predictor variables included in discriminant function analysis, measured from fundamental frequency (f_0) of calf whistles.

Predictor variable	Description
Duration	Length of whistle (ms)
Fundamental frequency start	Frequency at the start of the whistle (Hz)
Fundamental frequency end	Frequency at the end of the whistle (Hz)
Fundamental frequency minimum	Lowest frequency along the fundamental (Hz)
Fundamental frequency time of minimum	Time with the lowest frequency (ms)
Fundamental frequency maximum	Highest frequency along the fundamental (Hz)
Fundamental frequency time of maximum	Time with the highest frequency (ms)
Fundamental frequency mean	Mean frequency of the fundamental frequency (Hz)
Fundamental frequency variance	Variance of the fundamental frequency (Hz)
Fundamental frequency mean change	Mean slope of fundamental frequency changes
Fundamental frequency change time of min	Slope at the time of minimal frequency, calculate as a linear regression within ± 10 spectrograph cells around the point of minimum
Fundamental frequency change time of max	Slope at the time of maximum frequency, calculate as a linear regression within ± 10 spectrograph cells around the point of maximum

Whistle rates

Whistle rates were calculated by dividing the total number of calf vocalisations by the duration of the recording. Most files from two of the calves (Indy and Goccia) where the hydrophone was held by hand rather than being incorporated into a suction-cup showed extensive clipping and could not be used as vocalisations may be masked resulting in inaccurate estimation of whistle rates. As data points are unevenly spaced throughout the recording period, a regression analysis would be heavily influenced by data points during the beginning of the developmental phase prohibiting a quantitative analysis. Descriptive statistics were preferred over a regression analysis due to the effect of outliers.

2.4 Results

2.4.1 Nonlinear phenomena

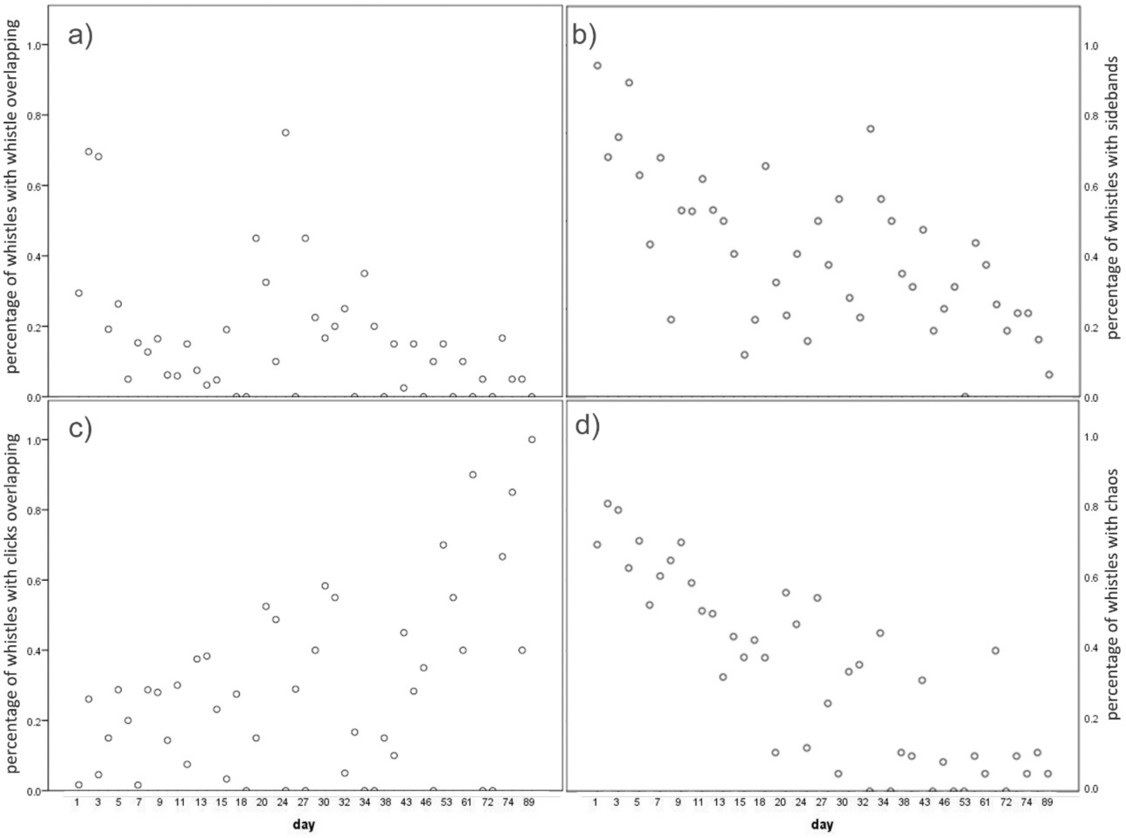


Figure 3: Proportion of nonlinear phenomena and biphonations over time during the developmental phase of seven calves: a) proportion of whistles with an overlapping or crossing fundamental frequency (f_0), b) proportion of whistles with sidebands, c) proportion of whistles with overlapping clicks, and d) proportion of whistles with chaos.

The scoring results are plotted in Figure 3. The proportion of whistles with overlapping and crossing contours, the proportion of whistles with sidebands and the proportion of whistles with chaos decreased over time (Figure 3a, b and d) while the mean number of whistles with overlapping clicks increased (Figure 3c). Generally, the highest energy of the vocalisation was in the fundamental frequency, but sometimes shifted to the first (or very rarely to the second) harmonic; no trend over time was visible (Appendix Figure III). An example of a spectrogram with the energy shifted to the first harmonic can be found in Appendix Figure IV.

2.4.2 Individual development in signature whistle crystallisation

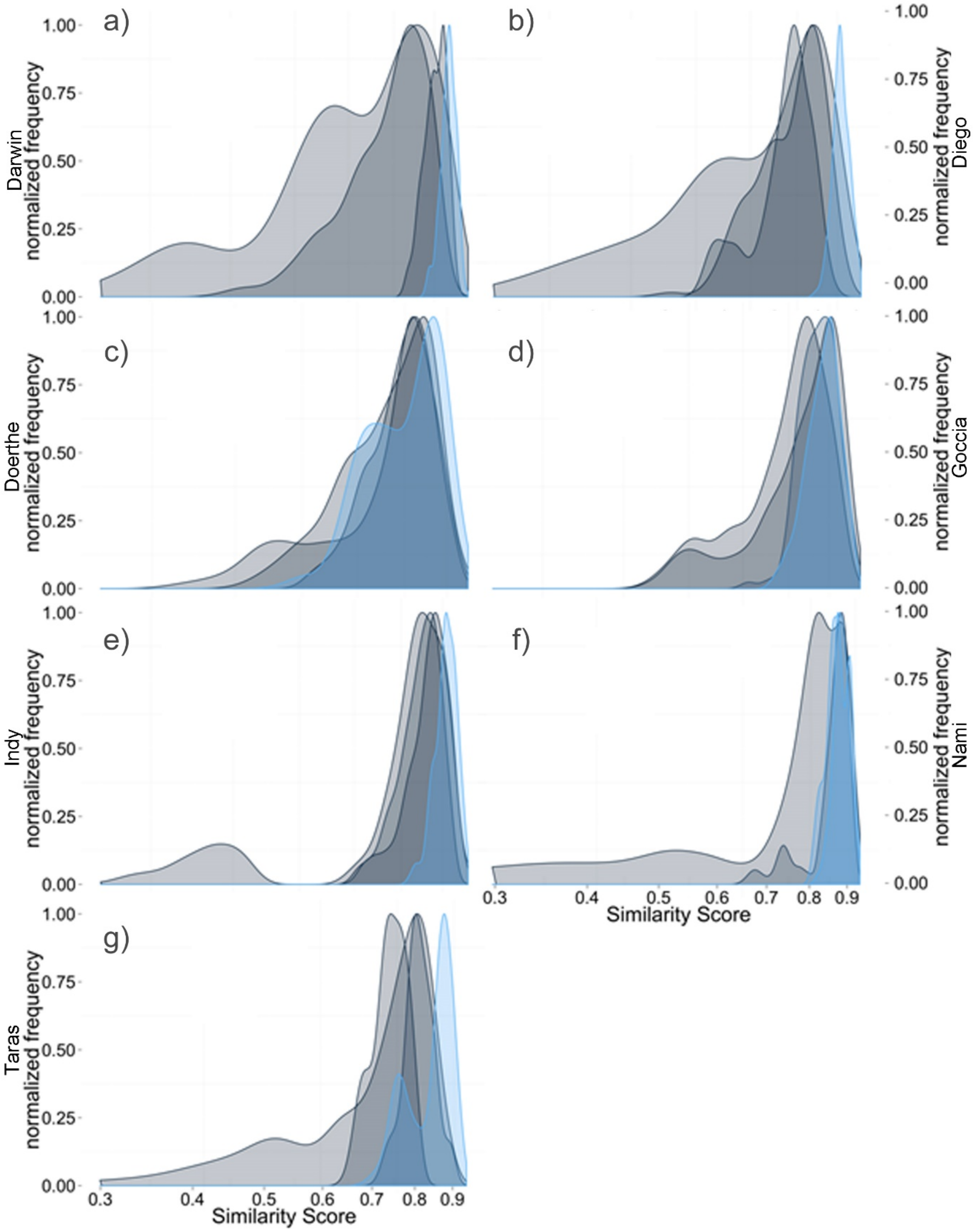


Figure 4: **Distributions of similarity scores for the seven calves during the developmental phase:** a) Darwin, b) Diego, c) Doerthe, d) Goccia, e) Indy, f) Nami, and g) Taras. For illustration purposes, only the first (light grey), two middle (increasing grey saturation), and the last (blue) recording day of each of the seven calves were plotted.

The acoustical variation within the vocalisation decreased between the first recordings of a calf right after birth and the last ones within the dataset. The mean of the similarity scores between whistles within one recording day increased with age ($SI_{meanfirst}$=0.71; $SI_{meanmiddle}$=0.77 ; $SI_{meanend}$=0.79) while its standard deviation decreased (sd_{first}=±0.14; sd_{middle}=±0.0.08; sd_{end}=±0.0.06)(Figure 4).

2.4.3 Measurement of stability in crystallised adult signature whistles

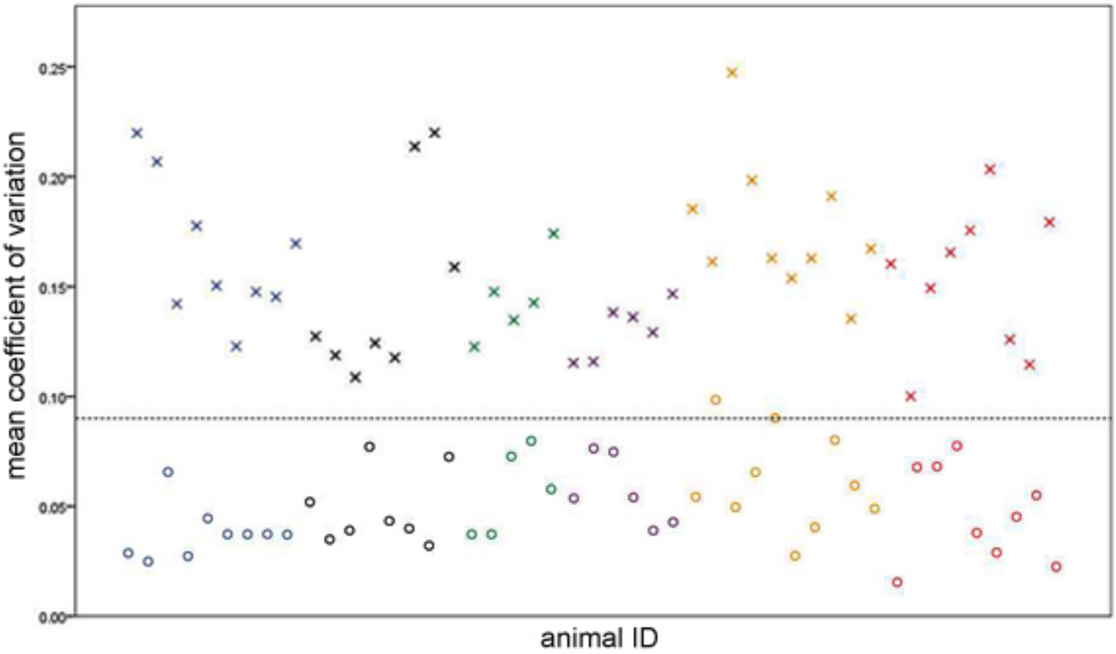


Figure 5: Similarity scores of signature whistles from adult bottlenose dolphins. Circles indicate within individual comparisons, crosses indicate between individual comparisons and the dotted line shows the 95th quantile of within individual comparisons (0.089). Colours are indicating the individual's population/facility (blue: Duisburg, black: Genoa, green: Nuremberg, purple: Oltremare, yellow: Belize, and red: Sarasota).

The signature whistles of captive (n_{AC}=28) and wild (n_{AW}=20) adult bottlenose dolphins were analysed to establish a threshold for the coefficient of variation which was assumed to indicate signature whistle stability. The mean coefficient of variation of signature whistle comparisons within adult individuals (n_A = 48) was 0.053 ± 0.022 and the 95th percentile was 0.089 (see Figure 5). Both the mean and 95% CV SI within individuals were significantly (Student's t-test, $P < 0.05$) lower than the average CV (0.58 ± 0.036) between individuals.

2.4.4 Crystallisation of signature whistles in calves

The results of the least-square linear regression analysis show a decrease in the coefficient of variance over time during the first 90 days ($log(t) = a + b\ log(CV_C)$, r^2 = 0.437). The within individual model equations are listed in Table 5. The individual plots for each calf can be found in Appendix Figure II. To test for potential interactions, the whistle rate was incorporated into the model but was not significant and did not improve the model fit (p>0.1, without whistle rate: r^2=0.437; with whistle rate: r^2=0.368).

Based on the model fit, the estimated day of crystallisation (D_C) was 20.8 [lower bound 19.2; upper bound 22.5]. The coefficients of variation of all calves over the whole recording period are shown in Figure 6. The developmental phase can be divided into four quadrants shown in Figure 7: I) vocalisations with a high coefficient of variation that is expected to be high, II) vocalisation with a low coefficient of variation that is expected to be high, III) vocalisations with a high coefficient of variation when is expected to be low IV) vocalisations with a low coefficient of variation that is expected to be low. Most vocalisations fall into quadrant I and IV and therefore show an expected coefficient of variation that is higher than the stability threshold of 0.089 before and below it after the day of crystallisation.

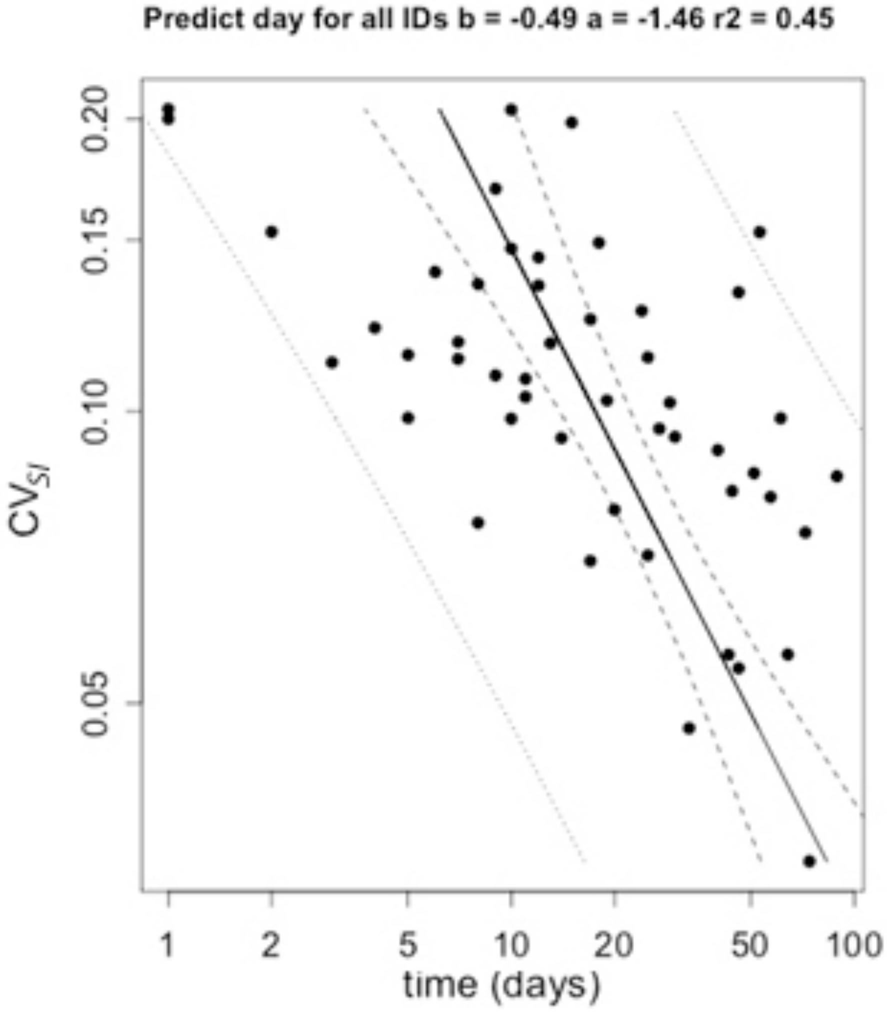


Figure 6: **Coefficient of variation of the similarity score (*CV$_{SI}$*)** over time to predict the day of calf signature whistle crystallisation (n_C=7; least-square regression model).

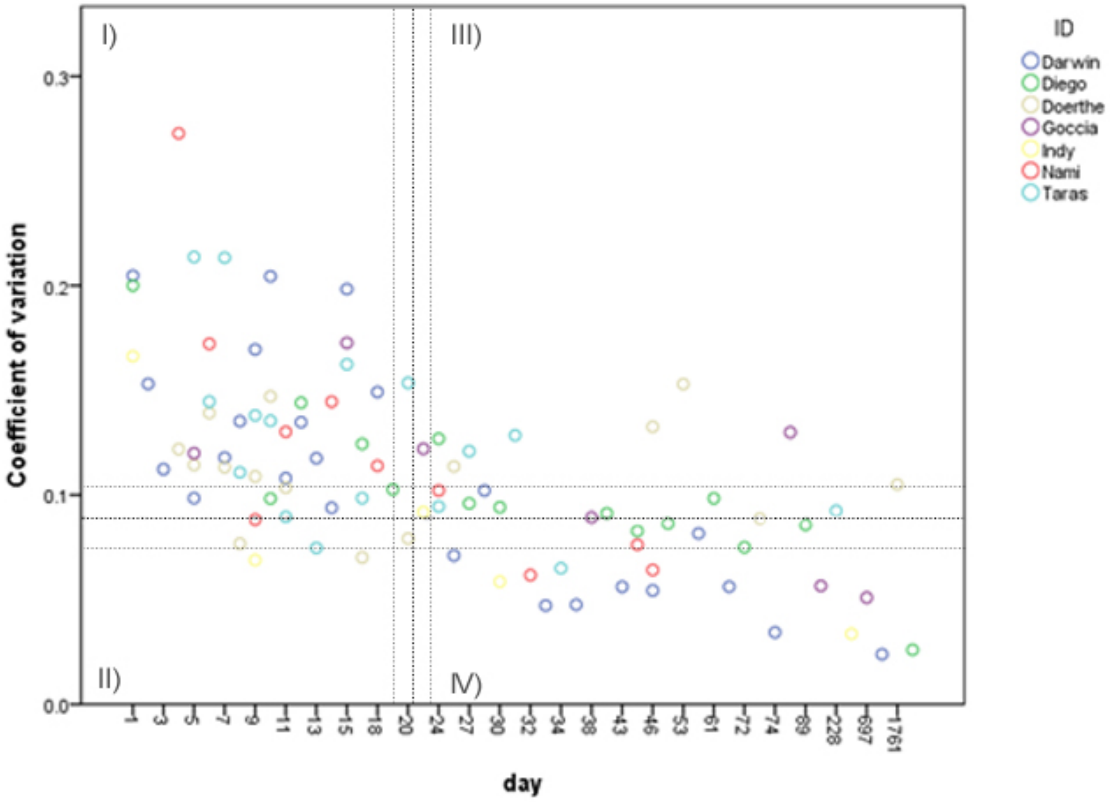


Figure 7: **Coefficient of variation of the similarity score (CV_{SI}) in signature whistles of all calves during the recording period.** The calculated stability threshold and the predicted day of crystallisation are included as dotted lines. The quartiles are indicating the four developmental states: I) High CV_{SI} before crystallisation, II) low CV_{SI} before crystallisation, III) high CV_{SI} after crystallisation, and IV) low CV_{SI} after crystallisation.

Table 5: Summary of the least square linear regression results based on similarity score (SI), day of recording (t) and whistle rate (wr). Significance between the dependent and independent variable is indicated by the p-values (p) where 95 % confidence intervals (CI), coefficient of determination (r^2) and sample size (n) are provided.

Model	Relation	logpredictor	95% CI for β	p	r^2 (adjusted)	n
All calves	log(*t*) α log(*CV*) $t = a\ CV_C^b$ log(t) = log(a) + b*log(CV_C)	-0.31(±)0.05	[-0.41;-0.21]	< 0.01	0.4372	48
Model with SI as predictor (to predict day for crystallisation)	log(*t*) α log(*CV*) $CV = a\ t^b$ log(CV) = log(a) + b*log(t)	-1.46(±)0.24	[-1.93;-0.98]	< 0.01	0.4372	48
Darwin (ID1)	log(*t*) α log(*CV*) $CV = a\ t^b$ log(CV) = log(a) + b*log(t)	-0.42(±)0.06	[-0.56;-0.29]	< 0.01	0.6785	21
Diego (ID2)	log(*t*) α log(*CV*) $CV = a\ t^b$ log(CV) = log(a) + b*log(t)	-0.19(±)0.04	[-0.28;-0.11]	< 0.01	0.6337	13
Doerthe (ID3)	log(*t*) α log(*CV*) $CV = a\ t^b$ log(CV) = log(a) + b*log(t)	-0.04(±)0.08	[-0.22;-0.14]	0.6321	-0.06197	13
Goccia (ID4)	log(*t*) α log(*CV*) $CV = a\ t^b$	-0.25(±)0.09	[-0.5;-0.00]	0.04946	0.5751	5

	log(CV) = log(a) + b*log(t)					
Indy (ID5)	log(*t*) α log(*CV*) $CV = a\ t^b$ log(CV) = log(a) + b*log(t)	-0.21(±)0.16	[-0.91;0.49]	0.3207	0.1923	3
Nami (ID6)	log(*t*) α log(*CV*) $CV = a\ t^b$ log(CV) = log(a) + b*log(t)	-0.41(±)0.13	[-0.72;-0.09]	<0.05	0.509	8
Taras (ID7)	log(*t*) α log(*CV*) $CV = a\ t^b$ log(CV) = log(a) + b*log(t)	-0.15(±)0.16	[-0.5;0.2]	0.3662	-0.009163	13
All calves vs whistle rates	log(*t*) α log(*t*) + log(*wr*) $CV = a\ t^b + wr^b$ log(t) = log(a) + b*(log(SI)+log(wr))	-0.22(±)0.03 -0.23(±)0.12	[-0.28;-0.16] [-0.47;-0.00]	< 0.01 0.05	0.3682	82
(interaction)	log(*t*) α log(*CV*) + log(*wr*) + log(*CV*) *log(*wr*) $CV = a\ t^b + wr^b + t*wr$ log(CV) = log(a) + b*(log(t)+log(wr))+ log(t)*log(wr)	-0.41(±)0.28 -0.37(±)0.22 0.06(±)0.08	[-0.96;0.14] [-0.81;0..8] [-0.1;0.22]	0.14 0.11 0.48	0.3644	82

2.4.5 Discriminant function analysis

The percentage of correctly categorised whistles within the three time bins (before crystallisation, after crystallisation, as adults) increased over time reaching almost 100 % for after calves became adults (Figure 8). A Chi-square test was performed to test the correct categorisation against chance level (Table 6). Even though the percentage of correct categorisation increased throughout the development, the correct categorisation was significantly above chance level in phase 1 before the whistle crystallised.

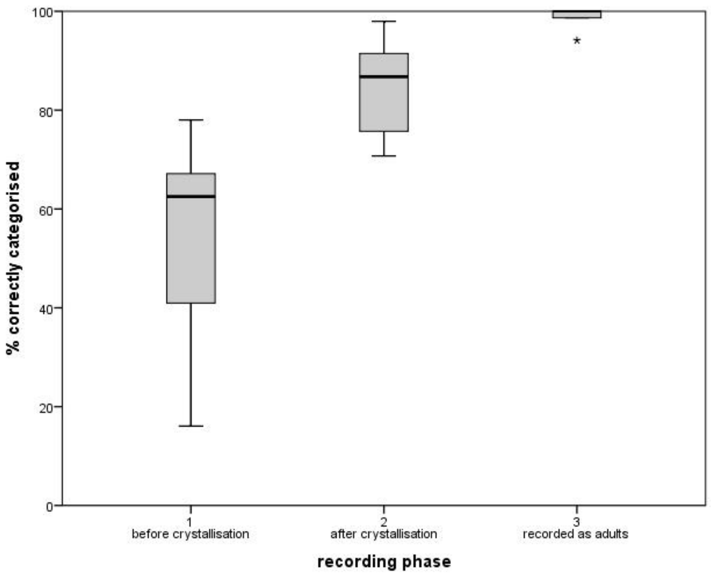


Figure 8: Percentage of correctly categorised calf signature whistles after discriminant function analysis. Dataset split into three time bins: 1) before crystallisation (day 1 to 18, n_W=835 whistles from n_C=7 individuals), 2) after crystallisation (day 24 to 46, n_W=359 whistles from n_C=7 individuals), and 3) recorded as adults (two years and older, n_W=178 whistles from n_C=6 individuals).

Table 6: Categorisation of whistles into predicted groups based on a discriminant function analysis. % correct indicates the percentage of whistles correctly categorised and χ^2 states the p-value of a test against chance.

		Predicted group membership									
	ID	Darwin	Diego	Doerthe	Goccia	Indy	Nami	Taras	Total	% correct	χ^2
Phase 1 Before crystallisation	Darwin	227	0	19	2	1	20	22	291	78.0	<0.001
	Diego	36	13	5	0	1	12	14	81	16.0	<0.05
	Doerthe	39	1	114	6	2	1	7	170	67.1	<0.001
	Goccia	7	0	5	10	3	0	0	25	40.0	<0.05
	Indy	0	0	4	10	25	1	0	40	62.5	<0.001
	Nami	22	4	0	3	0	78	9	116	67.2	<0.001
	Taras	16	4	14	0	1	19	39	93	41.9	<0.001
Phase 2 After crystallisation	Darwin	113	0	3	0	2	0	0	118	95.8	<0.001
	Diego	0	97	0	0	0	2	0	99	98.0	<0.001
	Doerthe	0	1	34	0	0	0	4	39	87.2	<0.001
	Goccia	2	0	0	14	2	0	0	18	77.8	<0.001
	Indy	4	0	0	1	14	0	0	19	73.7	<0.001
	Nami	0	7	0	0	0	59	2	68	86.8	<0.001
	Taras	0	6	4	0	0	2	29	41	70.7	<0.001
Phase 3 As adults	Darwin	22	0	0	0	0	-	0	22	100	<0.001
	Diego	0	18	0	0	0	-	0	18	100	<0.001
	Doerthe	0	0	16	0	1	-	0	17	94.1	<0.05
	Goccia	0	0	1	75	0	-	0	76	98.7	<0.001
	Indy	0	0	0	0	20	-	0	20	100	<0.001
	Taras	0	0	0	0	0	-	25	25	100	<0.001

2.4.6 Whistle rates

The whistle rates decreased slightly with time but no clear trend was visible across individuals (Figure 9). Descriptive statistic was chosen due to small sample size and the effect of outliers.

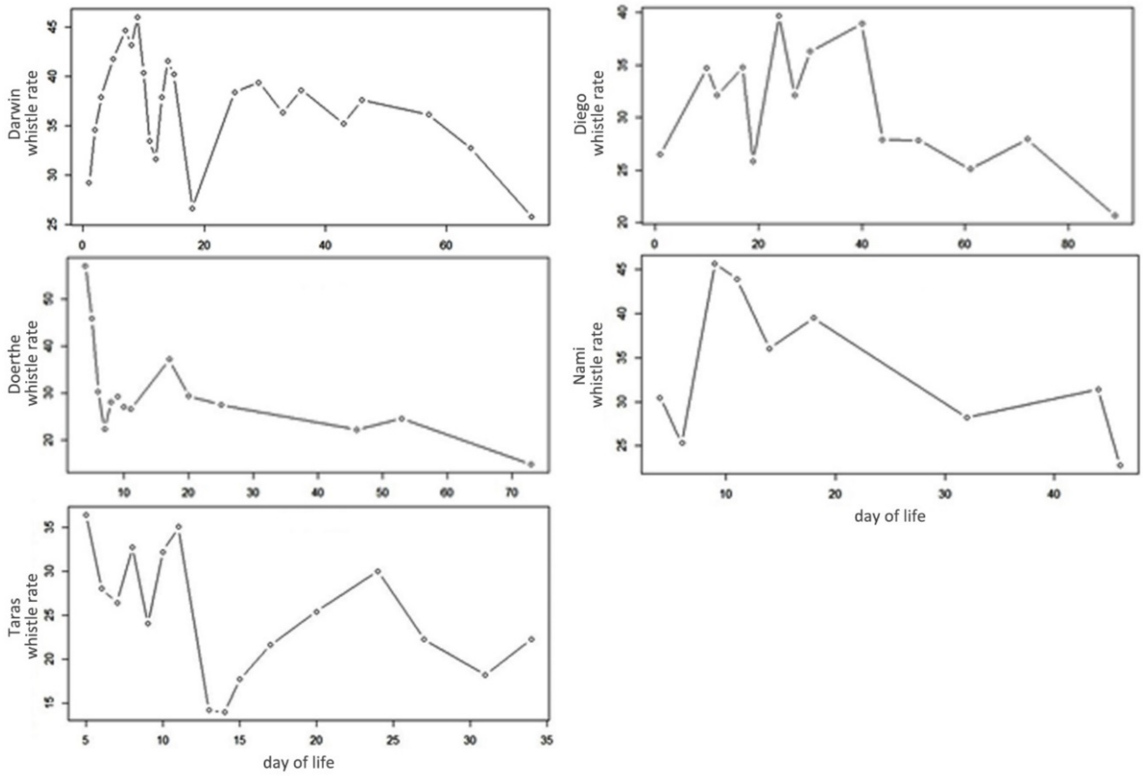


Figure 9: **Whistle rate as the number of whistles divided by recording duration in minutes per day of life for five calves.**

2.4.7 Development of fundamental frequency measurements over time

All measurements taken from the fundamental frequency (f_0) of the calves' vocalisations during the first 90 days of life are plotted in Figure 10. Data was grouped for all individuals to check for trends in the variation of fundamental frequency changes between individuals. Individual data sets of each calf were too small and recordings were too unevenly spread to interpret trends over time. With an exception of the fundamental frequency mean, there is a trend for an increased spread of data points over time so the variation increases. Note that the use of non-stratified data can decrease the representativeness of the sample by potentially increasing sampling error.

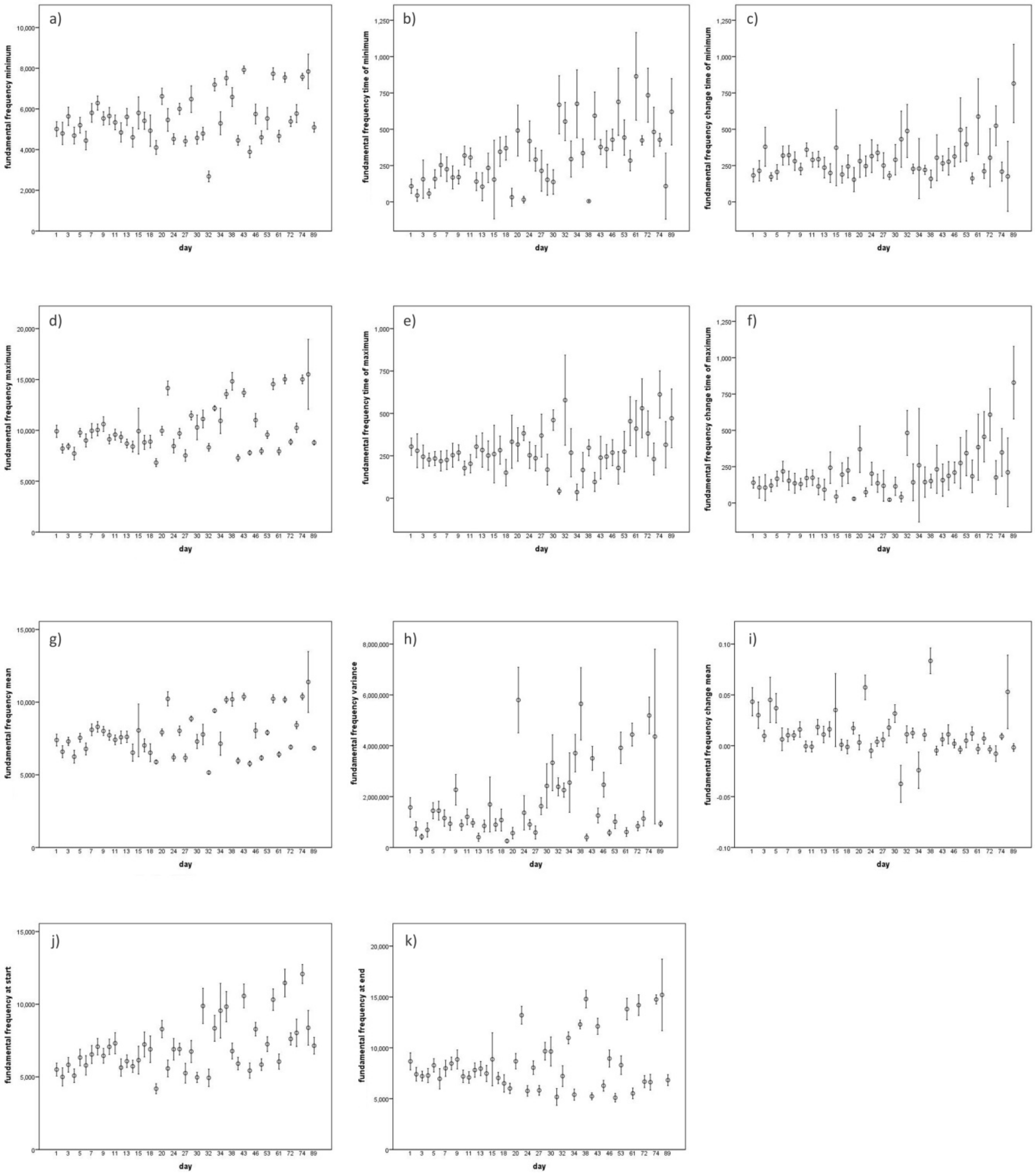


Figure 10: Means (± 95% CI) of fundamental frequency (f_0) measurements during the first 90 days of life (n_C=7). a) fundamental frequency minimum, b) fundamental frequency at time of minimum, c) fundamental frequency change at time of minimum, d) fundamental frequency at maximum, e) fundamental frequency at time of maximum, f) fundamental frequency change at time of maximum, g) fundamental frequency mean, h) fundamental frequency variance, i) fundamental frequency change mean, j) fundamental frequency at start, k) fundamental frequency at end.

2.4.8 Whistle duration

Average whistle duration increased reaching an asymptote at around the estimated day of crystallisation, D_C (Figure 11). After crystallisation, the mean duration continued to increase (Figure 11 and Figure 12).

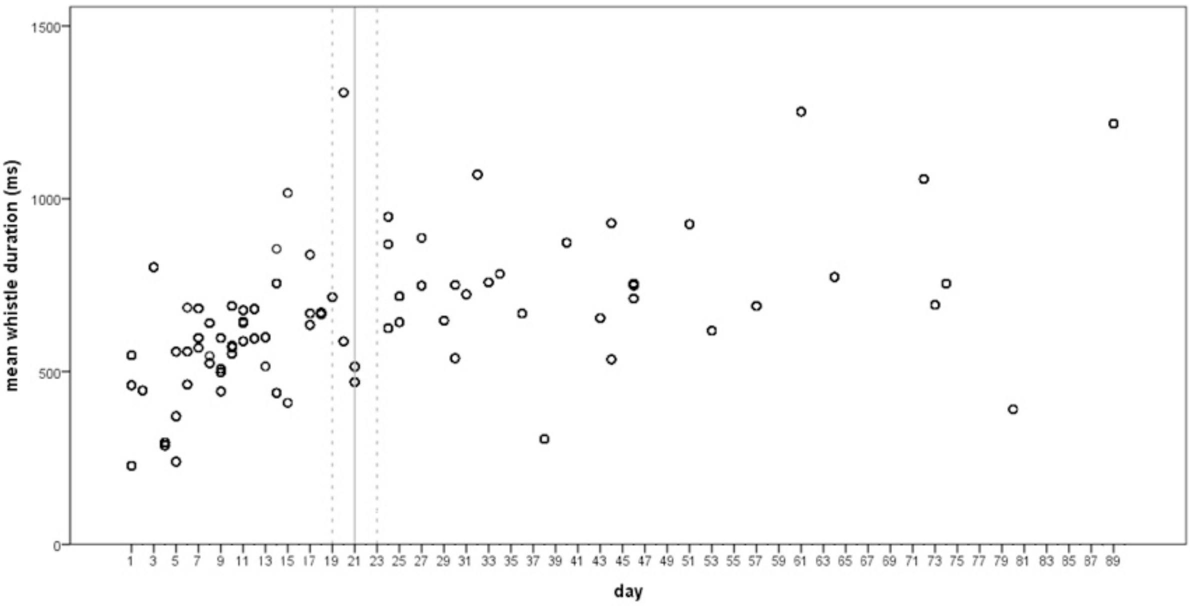


Figure 11: Mean whistle duration per day for each individual calf in milliseconds during the first 90 days of life (n_C=7). Vertical solid line indicates the predicted day of signature whistle crystallisation, dotted lines are indicating the upper and lower bound.

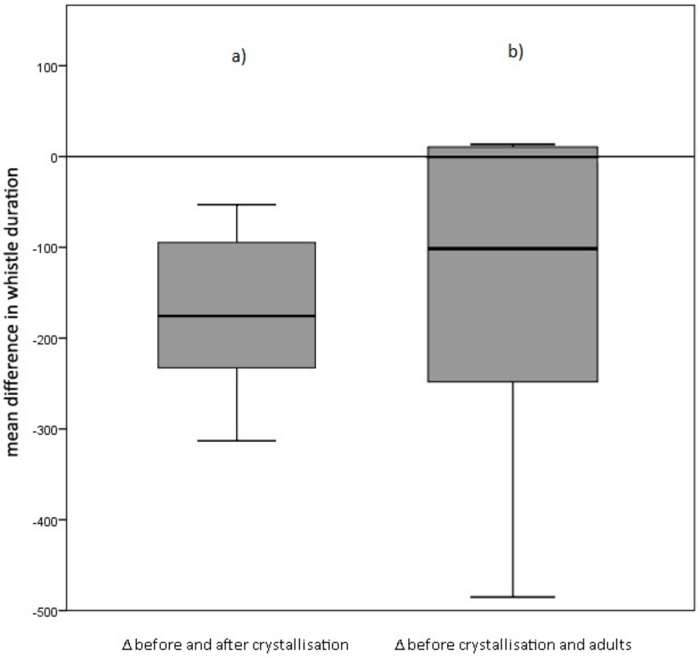


Figure 12: Differences in mean whistle duration of each individual (n_C=7) compared between a) before and after crystallisation and b) between before crystallisation and as adults.

2.5 Discussion

Whistles of bottlenose dolphin calves undergo a range of drastic acoustic changes in the first month of life. This process is likely driven by physical growth, increasing control over the sound production apparatus, and vocal production learning. While the influence of vocal learning is discussed in chapter 3, it is likely that all three go hand-in-hand and might not always be distinguishable. Here I present the first fine-scale analysis of the acoustical changes in the vocalisations of neonatal bottlenose dolphins during ontogeny. I describe the stabilisation process to crystallisation and beyond and establish a measurement for stability in signature vocalisations.

All seven dolphin calves produced whistles during the first capture event (between day one and day five after birth). Similar results have been reported by several other authors for whistles (Caldwell and Caldwell 1979; Morisaka et al. 2005; Gnone and Moriconi 2010) as well as for broadband clicks (Favaro et al. 2013). Compared to signature whistles of adult bottlenose dolphins, the occurrence of nonlinear phenomena and biphonations in calf whistles such as overlapping frequency contours and clicks, subharmonics and chaos are particularly noticeable at an early age (see Fitch et al. 2002 for a review on nonlinear phenomena in mammals).

Nonlinear acoustic phenomena are the occurrence of subharmonics and deterministic chaos within vocalisations (Glass and Mackey 1988; Fitch et al. 2002). Subharmonics are caused by periodic doubling when oscillators are coupled but vibrate at different frequencies, while chaos is caused by non-periodic, irregular vibrations (Fitch et al. 2002).

Biphonations with overlapping fundamental frequencies have been reported throughout the animal kingdom (terrestrial mammals: Fitch et al. 2005, fish: Rice at al. 2011, amphibians: Feng et al. 2009, and birds: Fee et al. 1998, Fletcher 2000). In humans, biphonations have been recorded in infant cries and patients with disorders of the vocal tract (e.g. asymmetrical growth of the vocal folds or paralysis of one side)(Mergell and Herzel 1997). Biphonations and nonlinear phenomena in general are common in a wide range of taxa but they are often ignored in acoustic analyses (Wilden et al. 1998; Lingle et al. 2012): In chacma baboons (*Papio cyncephalus*) nonlinear phenomena have been described in female barks (Fischer et al. 2001) and in rhesus macaques (*Macaca mulatta*) nonlinearities can be found in 30 % of all vocalisations (Fitch et al. 2002). They are a common element in the song of male zebra finches (*Taeniopygia guttata*)(Fee et al. 1998) and were described in 92.4% of killer whale (*Orcinus orca*) and 65.7% of North Atlantic right whale (*Eubalaena glacialis*) calls (Tyson et al. 2007). Mann and colleagues found nonlinearities in two different populations of west Indian manatees (*Trichechus manatus* spp.) 72 % of all calls showed nonlinearities in a population in Florida and 36 % in a manatee population in Belize (Mann et al. 2006). Nonlinearities are often found in "scream" and "bark" sounds (Tembrock 1976; Hauser 1992; Feddersen-Petersen 2000; Tokuda et al. 2002) and are prevalent especially in infant vocalisations e.g. in human infant cries (Robb and Saxman 1988; Fort and Manfredi 1998). Lingle and colleagues (2012) compared the acoustic features of infant distress calls amongst 18 vertebrate species and found a high degree of acoustic similarity adding to the hypothesis that nonlinear phenomena are highly-conserved system of social vocal behaviour in vertebrates. In meerkats (*Suricata suricatta*) nonlinearities are common in alarm calls, presumably making the calls less predictable and preventing receivers from habituation (Karp et al. 2014). Fitch and colleagues (2002) argued that even though nonlinearities might be by-products of vocal production, they could sub serve mother-infant recognition and their unpredictability, similar to the alarm calls in meerkats, makes infant cries hard to ignore.

In this study I describe the occurrence of biphonations and nonlinear phenomena (subharmonics, and chaos) in bottlenose dolphin calves during the first months of life. Bottlenose dolphin calves show a high percentage of biphonations right after birth (25 % of all whistles emitted during the first week of life had biphonations) and decrease over time (5 % biphonations within whistles produced after the second month)(Figure 3a) and after three months no biphonations are produced. While it seems to be a common phenomenon in young calves, it has been rarely described in adult bottlenose dolphins as no biphonations could be found in the 920 recorded signature whistles from 48 adult bottlenose dolphins in this study. Papale and colleagues (2015) described the occurrence of two independent fundamental frequencies in a signature whistle of one free-ranging adult dolphin in Italy. Unfortunately the authors could not rule out a dysfunction in the sound production apparatus as an alternative explanation for the production of biphonations in this individual. In recordings of free-ranging animals it can be challenging to allocate both fundamental frequencies of a biphonations without doubt to the same individual due to the often close proximity between individuals. This holds especially true for recordings of free-ranging mother-calf pairs which makes it very challenging to identify biphonations. The recording method, using a suction-cup hydrophone or a hydrophone placed behind the blowhole while the calf is lifted in the air, allows a clear identification of the signaller, excluding the possibility of two individuals whistling at the time and therefore causing a recording with an overlapping contour.

Biphonations are produced in the larynx of most mammals, by oscillations of the two vocal chords at different frequencies resulting in two independent fundamental frequencies (Fitch et al. 2002). In contrast to terrestrial mammals or the birds, biphonations in dolphins could either be caused by different oscillations of the two phonic lips in one nasal passage, which would be a nonlinear biphonation or, by a simultaneous whistle production by the phonic lips in each nasal passage, which is not a nonlinear phenomenon. Both pairs of phonic lips are known to be able to produce independent vocalisations (e.g. whistles or clicks) simultaneously. This ability is especially advantageous as it enables the animals to produce echolocation clicks for orientation while being able to communicate (Cranford et al. 2000). While the mean number of biphonations decreased during the first three months of the calves' lives, the mean number of overlapping broadband clicks increased (Figure 3a and c). Favaro et al. (2013) observed an increase in click trains produced independently from whistles with age in two male bottlenose dolphin calves recorded during the first three months of life. This could hint at the possibility that calves are initially producing two independent whistles in each nasal passage and that they learn how to mechanically produce a whistle and a click simultaneously with increasing age. There was no recording within the dataset that showed both a biphonation as well as an overlapping click.

While none of the 7 calves showed any sidebands or chaos in their signature whistles as adults, they were common during early vocalisations and decreased during the first 90 days of life (Figure 3b and d). Due to the apparent absence of nonlinear phenomena in adult signature whistles, they could enhance individual recognition before the calf develops a crystallised signature whistle and could serve as an urgency element to trigger a caregiver response. Nonlinearities could make it easier to identify the infant before the whistle crystallisation allows for reliable individual recognition. More detailed investigations into the actual production mechanism of biphonations in calves would be highly desirable to gain a better understanding about how nonlinear phenomena are produced in the claves vocal apparatus and whether they fulfil any communicative function.

Another acoustic parameter that has been discussed to underlie the changes during ontogeny has been the call duration. Morisaka et al. (2005) described an increase in whistle duration of neonatal dolphins over time and a correlation between whistle duration and respiration intervals. Sounds were recorded with one hydrophone and the signaller was identified using the occurrence of bubble streams from the calves' blowholes. It has been shown that not all vocalisations are associated with the production of visual bubble streams so the analysed whistles might not have been representative of the full vocal repertoire of the calves (Tyack 1986; Fripp 2005; Harley 2008). An increase in whistle duration during the signature development could be explained by growth of the respiratory system during ontogeny (Janik and Slater 2000) but it could also be linked to an increasing state of arousal as it has been shown in several species (Collins et al. 2011; Lingle et al. 2012). I found that the mean whistle duration of the calves increased in developmental phase 1 (until crystallisation, day 1 to day 19) but decreased after crystallisation. The duration of the calves' whistles during ontogeny might be limited by the growth of the respiratory system (Janik and Slater 2000). After crystallisation, the variation of signature whistle durations between individuals decreased while mean whistle duration increased. This suggests that duration might add to the variation and individual distinctiveness of signature whistles between individuals. Besides the difference in whistle duration, adult bottlenose dolphins often repeat their signature whistle in varying repetition numbers called multi-loop whistles where each element is called a loop (Caldwell 1990). The gap between individual loops within a multi-loop whistle is usually less than 250 ms (Esch et al. 2009). In a study on 81 wild bottlenose dolphins in Sarasota bay, 73% produced multi-loop whistles (Sayigh 1992). Multi-loop structures often consist of an introductory loop followed by repetitions of the signature whistle and a terminal element (Caldwell et al. 1990). The loop repetition rate has been linked to the animal's level of arousal and could have additional context related information (Caldwell et al. 1990; Esch et al. 2009). While adults produce multi-loop whistles often and with varying loop numbers, they seem to be less common in subadults (Caldwell 1990), and I found no evidence for multi-loop whistles produced by infants younger than 3 months. It remains contested whether each loop repetition should be considered as a separate whistle (e.g. McCowan and Reiss 2001) or if the whole multi-loop structure should be considered as one unit (e.g. Caldwell et al. 1990; Sayigh et al. 1990; 2007; Esch et al. 2009). This makes it plausible to use the whole structure if context-related or communicative research questions are considered. In this study, I decided to focus on the identity-related information in signature whistles, and therefore only used one stereotyped element or loop per whistle for the dynamic time warping comparison.

Variation in sound parameters can be affected by behavioural states like increasing stress (Lingle et al. 2012). Janik and colleagues (1994) compared whistle parameters from dolphins in a (rewarded or not rewarded) discrimination task and during temporary isolation. They found significant differences in 9 out of 14 fundamental frequency measurements from the animals' signature whistles, demonstrating that changing parameters within the frequency modulation encode contextual information. Calf whistles were recorded during highly standardised capture events, likely a stressful situation for the mother-calf pair. Acoustic changes (e.g. in duration) over time could potentially be caused by habituation to stress rather than growth, mechanical production control or learning. Especially whistle rates have been linked to and used as an indicator of stress. Esch et al. (2009) found a decrease in whistle rates during capture events and pointed out that this could be potentially linked to fatigue rather than habituation.

The whistle rates of five calves in our study did not show a decrease after repeated captures (Figure 9). There is a slight decrease in whistle rate with age, but no clear pattern can be seen across individuals. Additionally, calf whistle rates could be affected by the whistle rate of the present mother and a potential audience effect (Zuberbühler 2008; Coppinger et al. 2017) or even the individual's personality (Friel et al. 2016). Some variability in vocalisations I found during ontogeny could have been influenced by stress or habituation to the capture events: The occurrence of chaos and subharmonics in vocalisations are often linked to distress (Fitch et al. 2002; Lingle et al. 2012) and both appear to decrease over time in bottlenose dolphin calves and it remains unclear whether this might be linked to a habituation to the capture procedure. However, whistle rates are often used as an indicator of stress and the least square regression model did not improve when whistle rate was incorporated. However, it might be possible that the time window included in this analysis was too narrow to capture stress and habituation to captures over time. To get a better idea about the effects of capture induced stress on whistle development, cortisol measurements during ontogeny would be highly desirable.

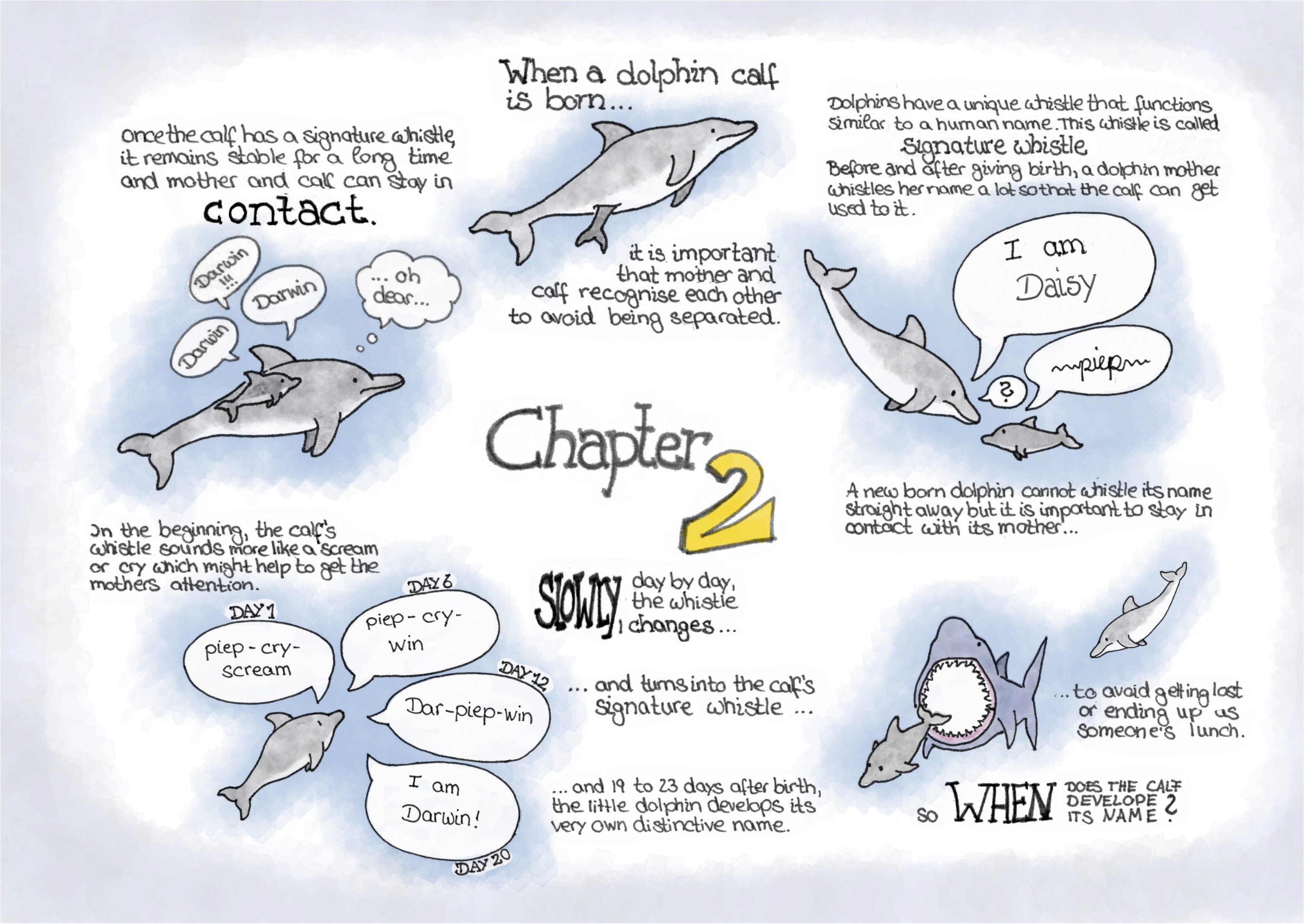
Besides changes in sound parameters during ontogeny, dolphins develop a distinctive frequency modulation pattern that allows for individual recognition. Two key aspects of individual recognition signals are their individually distinctive characteristics and certain stability over time. Regardless of the underlying frequency modulation, stability within an acoustic signal can be calculated by comparing vocalisations for their similarity. During the developmental process, all calves had a similar development pattern with an increasing mean similarity score and a decreasing standard deviation with age (Figure 4).

This shows that the vocalisations became more repeatable and stable during the first three months of life. Even though it has been shown that the whistles of closely associated individuals (especially males) can become gradually more similar to each other over time (Smolker and Pepper 1999; Watwood et al. 2004), signature whistles stay generally remarkably stable in their frequency modulation over time (Sayigh et al. 1990; Leon-Lopez 2016). This stability enables individuals to recognise each other's whistles even after long term separations (Bruck 2013). The ratio between inter-individual and intra-individual variability in signature calls seems to play a key role in effective recognition (Beecher 1991). By calculating the similarity score within the vocalisations of individual adults and in between different adults a metric of variability in signature whistles was established and stability in crystallised signature whistle can be evaluated. The mean coefficient of variation of the similarity scores within individuals was 0.089 which was significantly lower than between individuals. Using this adult stability metric as a threshold parameter, the mean day of crystallisation during the development of the calves was predicted to be 21 days after birth. In a study on 14 bottlenose dolphin calves, Caldwell and Caldwell (1979) observed that some individuals showed a signature whistle right after birth while one individual needed over 17 months. However, the majority developed a recognisable signature whistle modulation between 1.5 and 2.5 months. Tyack (1997) found that two of three calves already produced a distinctive modulation pattern within the first week after birth. These whistles showed high levels of correct classification in a discriminant function analysis. All seven dolphin calves in our study produced vocalisations before the day of crystallisation that looked similar to the frequency modulation of their final signature whistle. Even though first productions of the final frequency modulation pattern may occur very early in an individual's ontogeny, the modulation patterns still lack the repeatability crucial for reliable recognition of the signature whistle. This underlines the importance of a quantitative method to determine the time of signature whistle crystallisation. This has been absent in previous studies which mainly subjectively estimated a point of crystallisation by eye-balling spectrograms for a repeatable pattern which makes the results not comparable across studies.

During this early stage of development, the mean similarity score within the vocalisations is low and the standard deviation is high (Figure 4). The repeated captures of the calves for this study during health assessments could have influenced the time of signature whistle crystallisation but all seven calves showed similar crystallisation patterns even though the capture frequency varied immensely between individuals with a minimum of 5 and a maximum of 23 captures (see Appendix Table I for more details).

I suggest that the established stability threshold should be reached in order to classify a calf vocalisation as crystallised. The maintenance of contact between mother and calf is crucial for the infant's survival from day one after birth and voice cues that could bridge this crucial period are unreliable due to changing pressures during dives. The discriminant function analysis performed on 12 measurements from the fundamental frequency showed a correct classification of the calves' vocalisations before crystallisation that was already significantly above chance level. While this classification improves greatly after crystallisation and reaches 100% for adult signature whistles (Figure 8), it shows that the fundamental frequency modulation of the calves is already distinctive enough to potentially allow for individual recognition. In order to test whether dolphin mothers are actually able to recognise changing versions of their calf's vocalisations during this early period in ontogeny and whether they can also do so if nonlinear phenomenon are removed that might trigger an additional caregiver response, has to be further investigated.

2.6 Visual abstract chapter 2: Acoustic development of signature whistles



Chapter 2

When a dolphin calf is born...

it is important that mother and calf recognise each other to avoid being separated.

Dolphins have a unique whistle that functions similar to a human name. This whistle is called Signature whistle.

Before and after giving birth, a dolphin mother whistles her name a lot so that the calf can get used to it.

A new born dolphin cannot whistle its name straight away but it is important to stay in contact with its mother...

...to avoid getting lost or ending up as someone's lunch.

so WHEN DOES THE CALF DEVELOPE ITS NAME?

SLOWLY day by day, the whistle changes...

... and turns into the calf's signature whistle ...

... and 19 to 23 days after birth, the little dolphin develops its very own distinctive name.

In the beginning, the calf's whistle sounds more like a scream or cry which might help to get the mothers attention.

Once the calf has a signature whistle, it remains stable for a long time and mother and calf can stay in contact.

3

Vocal production learning in the development of bottlenose dolphin signature whistles

3.1 Summary

Vocal production learning occurs when a sound is modified through experience with perceived sounds (e.g. the vocalisations of other individuals). One potential example of vocal production learning within the context of animal communication is the development of signature whistles in bottlenose dolphins. Calves start to produce a stable and crystallised whistle that allows for reliable individual recognition between 19 and 23 days after birth. In this study, I found that seven out of nine calves, born and raised in different zoological facilities, develop a whistle that is significantly more similar to their mothers but not to their fathers. This provides evidence for the influence of vocal production learning on signature whistle development in this species. The identity of the mother seems to influence the likelihood that a calf is using her whistle as a model sound. While eight out of twelve calves showed high similarities with their mothers, the four calves of one specific female showed relatively low similarity scores to her whistle. I tested for a potential influence of human-produced whistles, which are part of the reinforcement training in dolphin facilities, on the development of signature whistles of captive calves. While there is no significantly higher similarity between the overall frequency modulation pattern of the whistle contours of captive calves to trainer whistles (compared to wild dolphins), I found higher similarities in start and end frequencies of the whistles and the overall frequency range (max-min) decreases in captive calves. A similar trend could be seen in dolphins that crystallised their whistles in the wild without exposure to trainer whistles but were brought into captivity as adults, providing evidence for plasticity in signature whistle production and whistle convergence through vocal production learning.

3.2 Introduction

While dolphin whistles have received considerable scientific attention throughout the last 50 years (see Janik and Sayigh 2013 for a review), the focus tended to be on types and usage of different whistles rather than the initial acquisition process in young dolphins. Particular attention was given to signature whistles because of their role for individual recognition, for their importance in social interactions and group cohesion (Smolker et al. 1993; Janik and Slater 1998; King and Janik 2013), and because they account for more than half of all emitted whistles (Cook et al. 2004), and in isolation for up to 90% (Janik and Slater 1998; Sayigh et al. 2007). Where the previous chapter focused on the acoustic development and stabilisation of signature whistles in new born dolphin calves, this chapter investigates the role of vocal production learning in the development of the signature whistle's specific and crystallised modulation pattern.

Vocal learning is defined as the modification of a signal based on the experience with sounds from the environment or with vocalisations of other individuals. This can affect the usage or comprehension of an existing signal via contextual learning, or it could affect production learning where the signal itself is modified (Janik and Slater 2000). While contextual learning appears to be quite common, production learning is rather rare in the animal kingdom (Janik and Slater 2000). Vocal production learning is thought to play a crucial role in the development of human language (Hauser et al. 2002; Fitch 2005), which has led to a research focus on the origins of vocal learning in our evolutionary ancestors. Non-human primates, our closest relatives, are conventionally thought to lack the neural capability for vocal learning (Lieberman 1968; Fitch 2000), although very recent findings indicate marmoset monkeys (*Callithrix jacchus*) might in fact exhibit vocal learning abilities (Takahashi et al. 2017). In any case, it seems to be rare in mammalian species in general: it could be demonstrated in infants of lesser spear-nosed bats (*Phyllostomus discolor*) and greater horseshoe bats (*Rhinolophus ferrumequinum*) that model their calls after their mothers (Boughman 1998; Jones and Ransome 1993; Esser 1994; see Knörnschild 2014 for a review) and pups of greater sac-winged bats (*Saccopteryx bilineata*) which learn to imitate the territorial song during ontogeny (Knörnschild et al. 2010). An Asian elephant (*Elephas maximus*) was reported to imitate human speech (Stoeger et al. 2012) and African elephants (*Loxodonta africana*) have been shown to imitate sounds emitted by trucks as well as chirping sounds produced by Asian elephants (Poole et al. 2005). Within the group of marine mammals evidence has been presented for seals (Ralls et al. 1985; Stansbury 2015) as well as for several cetaceans (see Janik & Slater 1997, Tyack & Sayigh 1997 for reviews). Vocal production learning seems to in fact be more prevalent in birds, where it has been studied widely (songbirds: Kroodsma 1982; hummingbirds: Baptista and Schuchmann 1990; parrots: Pepperberg 1981).

Three main driving factors for the evolution of vocal learning have been discussed: Firstly, vocal learning could be advantageous for species recognition in an acoustically diverse habitat with constantly changing sound transmission parameters or with a high density of species

(Nottebohm 1972; Hansen 1979). Secondly, by creating complexity within a communication system, vocal learning could be favoured by sexual selection if complexity is linked to an individual's fitness (Janik 1999). In many bird species the complexity of songs is an important part of mate choice (Catchpole 1980; Searcy and Andersson 1986). Finally, when voice cues are not sufficient or reliable enough, vocal learning could facilitate individual recognition (Janik and Slater 1997). Individual recognition based on acoustic signals is especially advantageous in complex social societies where other modes of recognition are limited or absent (see section 1.3.3 and 1.4 for more details). This holds true for bottlenose dolphins (*T. truncatus*): They live in complex fission-fusion societies and mainly depend on acoustic signals for recognition (Janik and Slater 1997). Signature whistles with an individually distinctive frequency modulation allow for such acoustic recognition (Tyack 1997; Sayigh et al. 1999; Janik et al. 2006), which plays an especially crucial role between mothers and their dependent offspring where it can facilitate contact (McBride and Kritzler 1951; Caldwell and Caldwell 1965; Tyack 1997; Janik and Sayigh 2013).

One trait that seems to play an important role in vocal production learning is the ability for vocal imitation where the vocalisation becomes more similar to a conspecific model sound (e.g. Catchpole & Slater 2008). Again, vocal imitation was long assumed to be absent in nonhuman mammals (Andrew 1962; Bloom et al. 1974). However, bottlenose dolphins are highly capable of vocal imitation and spontaneously mimic computer-generated sounds adequately even at the first attempt (Herman 1980; Richards et al. 1984; Reiss and McCowan 1993). Vocal imitation also plays a crucial role in the dolphins' natural communication system: as outlined in previous chapters, bottlenose dolphins produce signature whistles which encode the identity information in a specific frequency modulation pattern (Caldwell and Caldwell 1965; Tyack 1986; Janik et al. 2006; Janik 2009; Sayigh 2010), and even if all voice characteristics of the whistle are removed the signaller can still be identified by the distinctive modulation (Janik et al. 2006). Individuals produce imitations of the signature whistles of conspecifics in vocal interactions and to address each other (Tyack 1986; Janik and Slater 1998; King et al. 2013)(see section 1.4 for more details on the form and function of signature whistles). Even though signature whistles stay remarkably stable throughout a dolphin's life (Sayigh et al. 1990; Sayigh et al. 2007; Leon-Lopez 2016), it is known that the whistles of closely associated individuals, mainly allied males, do become more alike over time (Smolker and Pepper 1999; Watwood et al. 2004). The early vocalisations of dolphin neonates go through rapid acoustic changes before the signature whistle becomes stable. Calves develop their own individually distinctive frequency modulation and it crystallises between 19 and 23 days after birth. Parameters of the fundamental frequency of these whistles are still being refined until adulthood and the distinctiveness of the signal increases (see chapter 2 for more details).

Signature whistles could potentially be produced as an innovation, that is, as a modification based on model sounds, or they could be invented without any model (Marler and Peters 1982; Janik and Slater 2000). If vocalisations from the individual's environment are shown to affect signature whistle crystallisation, this suggests that vocal production learning plays a part in the development of these identification signals. Such sounds would then function as models for the shape of signature whistles in bottlenose dolphins (Miksis et al. 2002; Fripp et al. 2005), where the individual would develop a signature whistle that either contrasts or resembles the model. This would be evidence for vocal production learning under two conditions: first, the signal was not part of the individual's repertoire before, and second, genetic explanations can be ruled out as a sole explanation for the variation.

Fripp et al. (2005) found that calves developed signature whistles that were most similar to not closely associated community members, suggesting that whistles within the population might serve as model sounds. Sayigh (1992) described that two out of four calves developed signature whistles most similar to unrelated adult females within the population. When calves were raised in isolation with only their mothers' whistles as potential model sounds available, they developed a signature whistle similar to that of their mother (Caldwell and Caldwell 1979). In free-ranging individuals in Sarasota Bay (Florida, USA) calves had a signature whistle with higher similarity to their mothers' than to other individuals from the population (Leon-Lopez 2016). Sayigh et al. (1990; 1992; 1995b) compared mother-calf pairs of the same population and found that male calves developed whistles more similar to those of their mothers than female calves do.

For calves born and raised in human care, there is some discussion as to whether the bridge whistles used by trainers for positive reinforcement training might serve as model sounds, resulting in shorter and less modulated signature whistles in the captive calves (Tyack and Sayigh 1997; Tyack 1997; Miksis et al. 2002). However, the extent to which dolphins use vocal production learning in the development of their signature whistles remains to be comprehensively and systematically investigated. In this chapter, I will focus on the acoustic environment of bottlenose dolphin calves during the crystallisation of their signature whistles with a special focus on what role the mother's signature whistle as well as trainer whistles might play. Therefore, I compared the crystallised signature whistles of bottlenose dolphins to their pool mates as well as to the whistles of their trainers. Should calves be capable of vocal production learning, I would expect to see similarities between their crystallised signature whistles and sounds from their environment. As a control for a potential effect of the trainer's whistle as a model sound during ontogeny, I also checked the signature whistles of two control groups (individuals from wild populations and individuals that were born and raised in the wild but then transferred into captivity) for similarity to trainer whistles. The group not exposed to trainer whistles (wild dolphins) is not expected to show similarities. If the group born in the wild and transferred into managed facilities as adults showed similarities to trainer whistles, this could indicate ability for whistle convergence even after signature whistle crystallisation.

3.3 Methods

3.3.1 Subjects

Nine bottlenose dolphin calves (3 females, 6 males) born and housed in four facilities (Zoo Duisburg, Tiergarten Nuremberg, Acquario di Genova, Oltremare) were recorded between 2014 and 2016. Even though all individuals were recorded as sub-adults or adults (minimum age 2 years), they are referred to as offspring or calves in this chapter to distinguish them from adults which they are compared to and to stress that these individuals were born and raised within the facility and within a known group composition and acoustic environment. All individuals were housed in multi-pool systems together with both parents and several related and unrelated individuals. Between the four facilities, 24 adult bottlenose dolphins that were present during the developmental phase of the nine calves were recorded. Seven of these were caught from wild populations and brought into human care 20 or more years before the recording took place (in the following referred to as wild-caught dolphins). For names, sex, family, and life history of all recorded adults and calves included in this analysis, see Appendix Figure I and Appendix Table III and Appendix Table IV.

In addition to the adults from captive facilities, 20 individuals were recorded from two wild populations (Turneffe Atoll in Belize and Sarasota Bay in Florida, USA, for more details on the field sites see section 2.3.1).

Dolphins in all four facilities received positive reinforcement training on a daily basis. Human trainers use whistles (similar to dog whistles) from different fabrications and different brands (here referred to as trainer whistle). The staff composition of the facilities fluctuates seasonally but there is a constant core team of staff in all facilities that continuously works with the animals and takes the lead in training efforts. Whistles from a total of 20 trainers from this core-staff-team were included in the analysis of this chapter (4 Duisburg, 6 Genoa, 4 Nuremberg, 6 Oltremare).

3.3.2 Acoustic recording

Calves and adults in the dolphinaria

All individuals in human care were either recorded during short-term isolations from their social group or during spontaneously occurring short-term separations of small groups of 2 to 3 individuals. These short-term separations occur voluntarily when small groups of dolphins split from the main group and spend time alone in one pool of the multi-pool system. An array of 3 to 4 hydrophones (HTI 96-min hydrophone; frequency response 2 Hz to 30 kHz, sensitivity -201 dB re: 1V/µPa, High Tech Inc., USA) was placed around the pool to record simultaneously on a 4-channel recorder (Edirol R44: sampling rate 96 kHz, 24 bit, Roland, USA). Within the sound file, markers were set for all vocalisations visible in the spectrograms (FFT size: 1024, frequency resolution: 48 kHz, weighting function: Hamming, window width: 100%) in Adobe Audition. Using passive acoustic localisation based on the time of arrival differences on the 4 channels of the recording, it was identified whether the sound source was within the array of hydrophones (individual separated from the group) or outside (dolphin from the rest of the social group). Hydrophones were calibrated and positioned around the pool with the separated individual and within channels to bordering pools. To localise the sound source within the separation pool, the position of the hydrophones as well as the time delay were used (Knapp and Carter 1976; Schau and Robinson 1987; Freitag and Tyack 1993; Janik et al. 2000). In a few instances, the animals were not isolated from the group but could swim through the recording pool. In these cases, the position of the animals within the pool was either filmed, voice recorded or noted using the time code on the sound recorder for reference, and recordings were only used for localisation if the focal animal was alone within the hydrophone array. Based on this information, the sound source was localised within the recording pool and signals could be matched with the identity of the dolphin that was within the hydrophone array at the time. To distinguish signature from non-signature whistles, the SIGnature Identification (SIGID) method was used, where 75 % of all whistles must have the same frequency modulation and inter-whistle gaps of 1 to 10 seconds (Janik et al. 2013). Of the recorded and identified signature whistles, a sample of 20 whistles with a high signal to noise ratio was randomly selected for each individual and included into a Luscinia database (Lachlan 2016). Due to low whistle rates or high signal to noise ratio, the sample size for some individuals was less than 20 whistles (mean whistle number per individual= 18.8).

Adults from wild populations

Adults from Belize were recorded during boat surveys using two hydrophones towed on each side of the boat attached to 2m metal chains. The hydrophones (HTI 96-min hydrophone; frequency response 2 Hz to 30 kHz, sensitivity -201 dB re: 1V/µPa, High Tech Inc., USA) were connected to a digital recorder (Tascam DR-40: frequency response 20 Hz to 20 kHz ± 3 dB, sampling rate 96 kHz, 24 bit, TEAC Corporation, USA). Pictures of the dolphins' fins were taken during each survey with a digital camera (Canon SLR 550D, Tamron lens 55-350mm) for photo identification of individuals.

The dolphins from the second wild population in Sarasota Bay were recorded during brief capture events as part of a long-term study run by the Sarasota Dolphin Research Program (www.sarasotadolphin.org). From the estimated 160 individuals from this population (Allen

2014) a randomised sample of 10 individuals recorded in 2013 was picked. Details on the identity, age, and sex of the Sarasota animals can be found in Appendix Table IV.

Trainers

The manufactured whistle that dolphin trainers use to give a bridge signal for positive reinforcement training (Pryor 2002) was recorded during training sessions or visitor presentations using a Samsung Galaxy S3 smartphone (Duisburg), a hydrophone and a digital recorder (Nuremberg: HTI 96-min hydrophone; frequency response 2 Hz to 30 kHz, sensitivity -201 dB re: 1V/µPa, High Tech Inc., USA; TASCAM DR-80 recorder; Oltremare and Genoa: integrated microphones of the TASCAM DR-40 recorder, frequency response, 20Hz-20kHz +1dB/-3dB).

3.3.3 Selection of vocalisations

In a pool with 1 to 3 dolphins surrounded by hydrophones, triangulation based on the time of arrival was used to identify the individual signalling (Freitag and Tyack 1993; Janik et al. 2000). The SIGID method was used to identify signature from non-signature whistles (Janik et al. 2013). Only whistles that were identified as signature whistles and could be positively matched to a specific individual were included in the analysis.

Individuals from the two wild populations were included in the analysis as a reference to investigate differences between dolphins in the wild versus in human care. A distinct individual identification and life history data were not necessary for this comparison. Nevertheless a conservative approach was used to ensure that only signature whistles from adults were included and that no non-signature whistles were incorporated. For the Belize population only whistles were included that were 1) positively identified as signature whistles (SIGID method: Janik 2013), 2) recorded in at least two sightings on different days, 3) when the photo-ID-database showed only one individual overlapping between the groups, and 4) when no calves were seen in the group during the survey.

From all dolphin and trainer recordings a sample of 20 whistles per individual was randomly picked. The Luscinia database (Lachlan 2016) can only process recordings with a 16 bit resolution, so files were transformed where necessary before including them into the database. The fundamental frequency contour of a total of 688 whistles was marked in a spectrogram display using Luscinia.

3.3.4 Statistical Analysis

Test for crystallisation

To ensure that only crystallised whistles were included in the analysis, all dolphins of unknown age or with an age lower than three years were tested for stability within their signature whistles. Using the methodology established in chapter 2.3.4, a similarity score was calculated for each individual. The coefficient of variation within an individual had to be lower than the established stability metric of 0.089 (see chapter 2.4.3 for more details) to be included in the analysis of this chapter.

Similarity scores between individuals

Using the extracted contours of the fundamental frequencies of whistles, pair-wise comparisons with a Dynamic Time Warping (DTW) algorithm were performed in Luscinia (Lachlan 2016)(for more details on DTW analysis see section 2.3.3). A pairwise comparison between all whistles from one individual with all whistles from another resulted in a range of dissimilarity scores between all whistles of these two individuals. Dissimilarity scores were extracted from Luscinia and transferred to Excel, R and SPSS (IBM corp. version 19) for further analysis. Dissimilarity scores were subtracted from 1 to gain similarity scores. To test for group differences, a mean similarity score was used to account for repeated measurements and autocorrelation within the data. Due to the lack of change over time in crystallised signature whistles (only crystallised whistles were used) it was unnecessary to use the coefficient of variation.

Linear Mixed Effects Model

A linear mixed effects model was performed in R using the package lme4 (Bates 2015) to test for an effect of relatedness on similarity scores. In the full model, similarity score was used as a dependent variable, and relatedness between two individuals as the independent variable. To account for repeated measurements, calf-ID and adult-ID were incorporated as nested random effects within population. Relatedness was scored as a social category with one of 12 mutually exclusive values (mother, father, sister, brother, same mother, same father, grandmother, grandfather, aunt, unrelated female, unrelated male, trainer) this data was gathered from life-history information and genetic analysis from the dolphin facilities (see Appendix Figure I for relatedness within the four facilities). The mother-calf comparison was used as a reference level to test for significant differences between the similarity score of mother and calf and any other individual in the facility. Diagnostic plots were checked for violation of model assumptions.

Similarity to trainer whistles

To check whether the exposure to trainer whistles influenced signature whistle development, all dolphins were categorised in one of three groups depending on life history data: 1) born and raised in captivity (N=23; n_{CC}=604), 2) caught in the wild but lives in captivity (N=7; n_{WC}=141), or 3) born and lives in the wild (N=20; n_{W}=728). These were then compared to a sample of trainer whistles (N=20; n_{T}=199). The whistles of the trainers were present during vocal development for group 1, they were not present during vocal development but are familiar to group 2. All individuals that were held in captivity were exposed to trainer whistles for a minimum of 20 years. For group 3, trainer whistles were neither present during vocal development nor should be familiar. Pairwise comparisons (cross-correlation) based on DTW were calculated to test for an influence on similarity. In a second step, six measurements from the fundamental frequency (f_0) of each whistle were taken and compared between groups: minimum frequency ($f_{0\,\text{min}}$), maximum frequency ($f_{0\,\text{max}}$), frequency at the start of the whistle ($f_{0\,\text{start}}$), frequency at the end of the whistle ($f_{0\,\text{end}}$), frequency range ($f_{0\,\text{range}} = f_{0\,\text{max}} - f_{0\,\text{min}}$), and whistle duration ($f_{0\,\text{duraton}}$). Descriptions for the six parameters can be found in Table 7. Individuals from captive facilities (group 2 or 3) were compared to the whistles of their familiar trainers while wild individuals were compared to randomised trainer whistles. A two-way ANOVA and an unweighted mean post hoc analysis were used to investigate for statistically significant differences in whistle parameters between groups. Variables were log transformed where necessary to account for non-normality (Levene's test $p<0.001$) and non-equal homogeneity (shapiro-wilk test $p<0.001$). Additionally a conservative alpha level of 0.001 was used.

Table 7: Descriptions for acoustic parameters measured from the whistles fundamental frequency.

Symbol	Predictor variable	Description
$f_{0\,\text{duration}}$	Duration	Length of whistle (ms)
$f_{0\,\text{start}}$	Fundamental frequency start	Frequency at the start of the whistle (Hz)
$f_{0\,\text{end}}$	Fundamental frequency end	Frequency at the end of the whistle (Hz)
$f_{0\,\text{min}}$	Fundamental frequency minimum	Lowest frequency along the fundamental (Hz)
$f_{0\,\text{max}}$	Fundamental frequency maximum	Highest frequency along the fundamental (Hz)
$f_{0\,\text{range}}$	Fundamental frequency range ($f_{0\,\text{max}} - f_{0\,\text{min}}$)	Frequency bandwith in which the sound is modulated (Hz)

3.4 Results

3.4.1 Calf whistles and their possible models

The similarity scores were calculated in pairwise comparisons between each calf and all adults and trainers recorded from the same facility. All similarity scores for the 9 calves are shown in Figure 13. The comparisons were sorted by level of relatedness. Mothers, fathers and full siblings have 50% genetic relatedness with the calf, half-siblings, grandfather, grandmothers and aunts have 25% and all other dolphins as well as the trainer whistles were categorised as less than 25 %. Seven out of nine dolphin calves (with the exception of Diego and Dobbie, two sons of Pepina from the Duisburg facility) showed the highest similarity scores when compared to their mothers. The similarity scores between the calves' whistles and their fathers' whistles were not significantly higher than those of all other comparisons. Diego and Dobbie developed signature whistles that were most similar to the whistle of two unrelated females. The results from the linear mixed effects model are shown in Table 8. All comparisons were tested against the calf-mother similarity score as a reference level. The relatedness to the mother had a significantly higher effect on the similarity score than any other relatedness level.

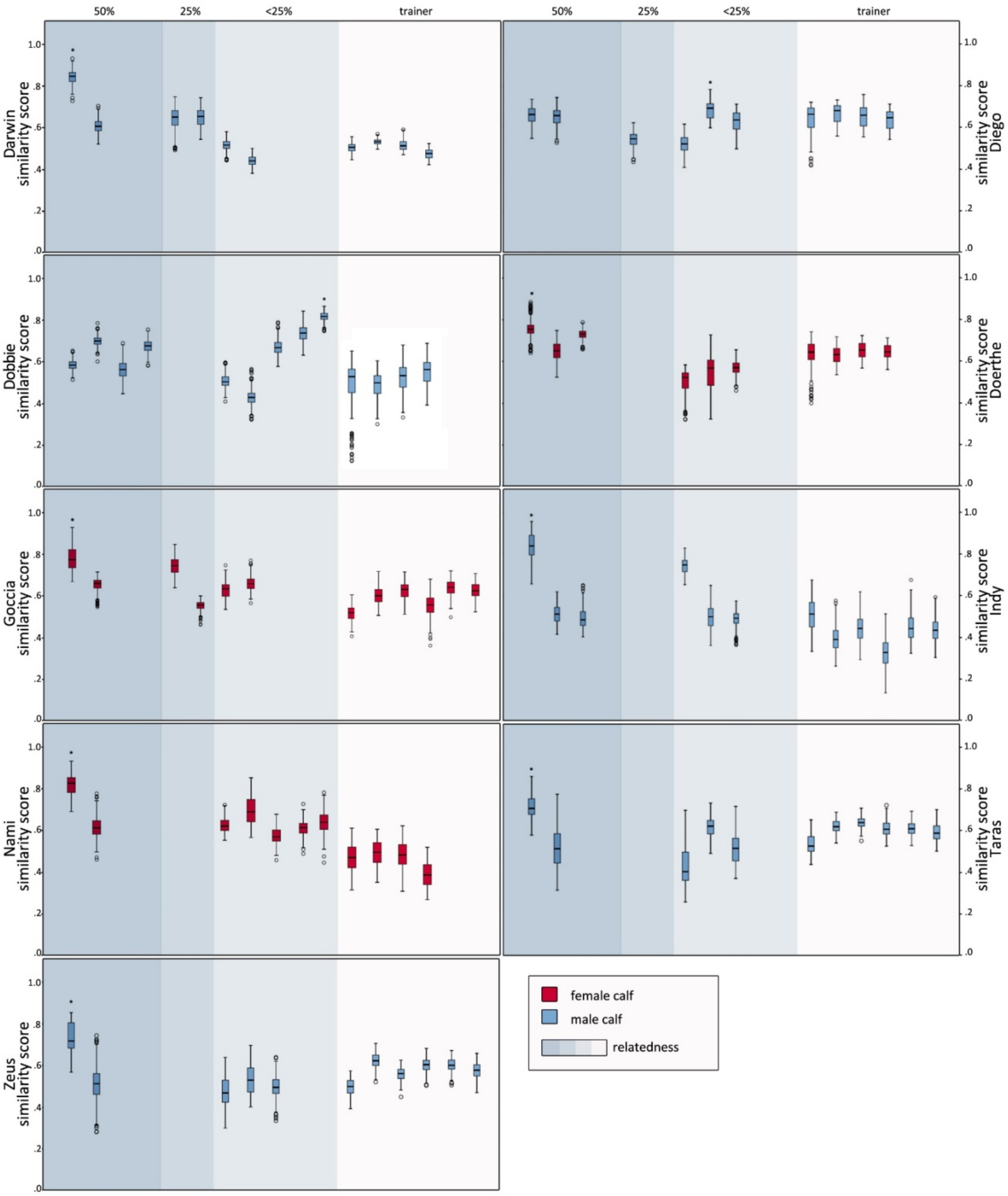


Figure 13: Similarity scores between whistles of the calf and of adults and trainers from the same facility. Comparisons are sorted by degree of relatedness with the first boxplot always comparing the calf and its mother and the second the calf and its father. Comparisons to human trainer whistles are shown on the far right. The first Tukey boxplot always resembles the comparison with the mother, the second one with the father. Female calves are plotted in red, males in blue. Asterisks indicate the comparison with the highest similarity score in each graph.

Table 8: Summary of linear mixed effects model predicting effect of relatedness on whistle similarity compared to mother. Coefficient $e^{ß}$ and confidence interval (CI) are provided. The p-value (P) indicates a significant difference between whistle similarity to the mother and each compared level of relatedness.

Social category	**coefficient e^{β}**	**CI**		**P**
		2.5%	**97.5%**	
Father	0.76	0.69	0.84	<0.000
Sister	0.61	0.60	0.62	<0.000
Brother	0.80	0.63	1.01	<0.05
Aunt	0.74	0.73	0.75	<0.000
Grandfather	0.73	0.66	0.80	<0.000
Grandmother	1.10	1.10	1.11	<0.000
Same father	0.59	0.58	0.60	<0.000
Same mother	0.71	0.70	0.71	<0.000
Unrelated female	0.83	0.83	0.84	<0.000
Unrelated male	0.76	0.70	0.84	<0.000
trainer	0.75	0.69	0.81	<0.000

3.4.2 Mother-calf comparisons

To investigate the degree of whistle similarity between mothers and their calves, all mother-calf comparisons were plotted in Figure 14. Seven different mothers were compared to up to four of their calves. Plotted in blue is a female from the Duisburg facility (Pepina), whose similarity scores with all four of her calves were much lower than that of any other mother-calf comparison. Examples of the fundamental frequency modulation of the signature whistles of mothers and calves with high similarity scores are plotted in Figure 15 and those with low similarity scores are shown in Figure 16.

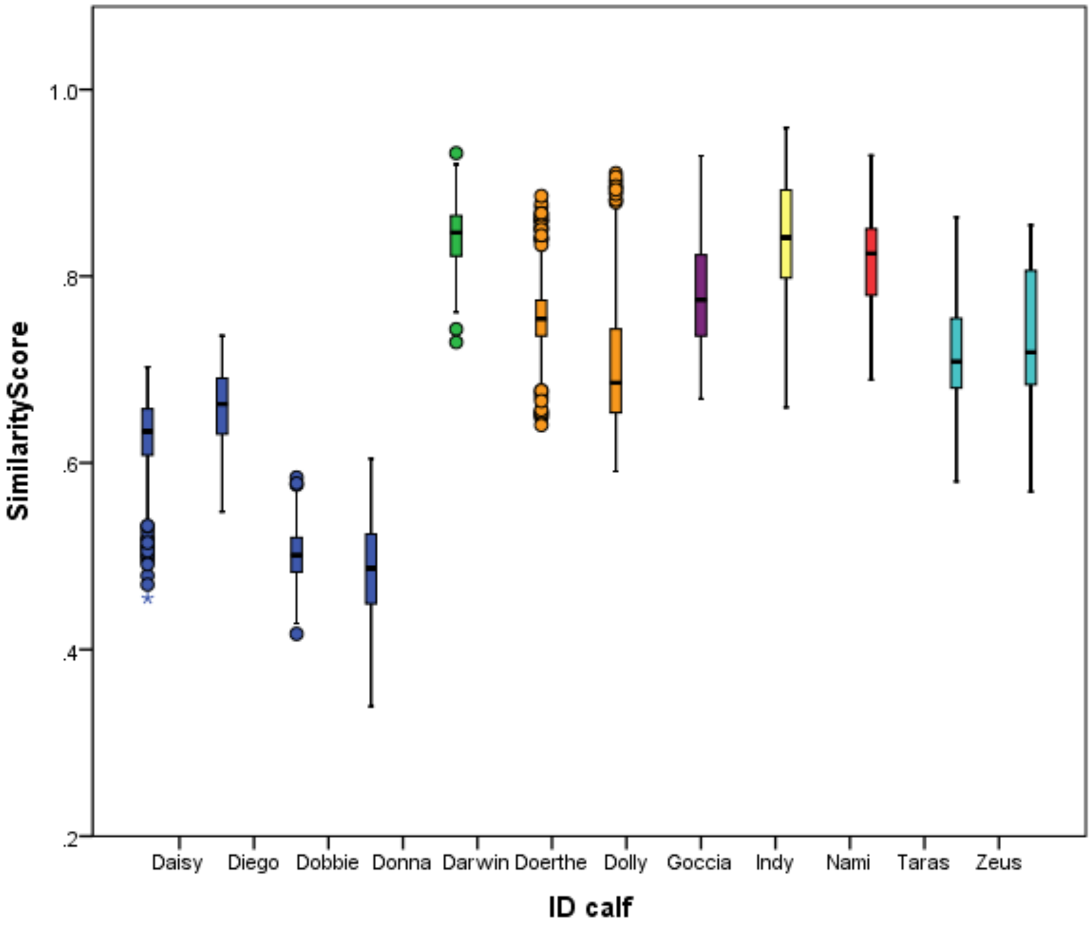


Figure 14: Similarity scores between mother-calf pairs. Each mother is indicated by a different colour. Mother identities are colour-coded as following: Dark blue: Pepina (four calves, Duisburg), green: Daisy (Duisburg), orange: Delphi (two calves, Duisburg), purple: Nau (Genoa), yellow: Luna (Genoa), red: Sunny (Nuremberg), light blue: Blue (Oltremare).

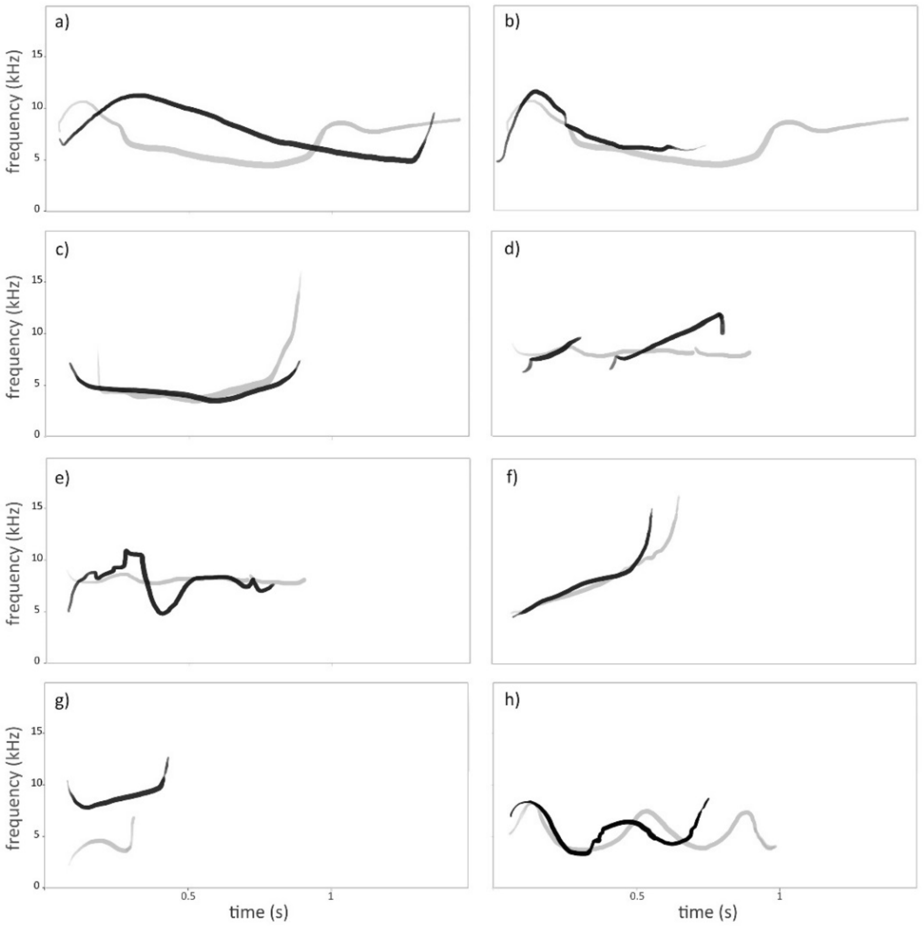


Figure 15: Fundamental frequencies (f_0) of the signature whistles of mother-calf pairs with high similarities. Whistle contours of mothers are coloured in grey, contours of calves are coloured in black and are aligned at the signal beginning: a) Blue and Taras, b) Blue and Zeus, c) Daisy and Darwin, d) Delphi and Dolly, e) Delphi and Doerthe, f) Luna and Indy, g) Nau and Goccia, and h) Sunny and Nami.

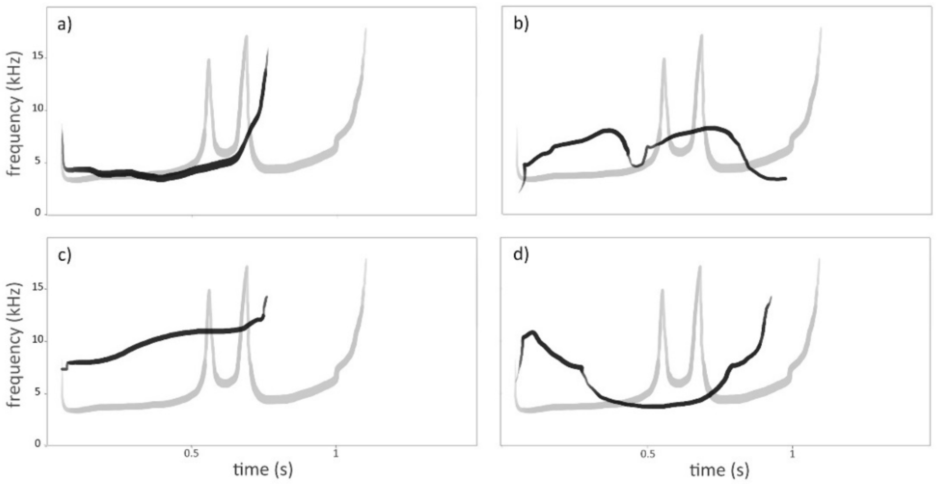


Figure 16: Fundamental frequency (f_0) of Pepina's signature whistles compared to her calves. Whistle contours of Pepina are coloured in grey, contours of her calves are coloured in black: a) Daisy, b) Diego, c) Dobbie, and d) Donna.

3.4.3 Captive and wild dolphins compared to trainer whistles

The similarity score of the overall frequency modulation between dolphin whistles and the bridge whistle of human trainers is shown in Figure 17 (for spectrogram examples of trainer whistles see Appendix Figure V). None of the three groups (born in captivity, caught in the wild but lives in captivity, wild) showed a higher mean similarity score to the trainer whistles compared to the other two groups. When specific acoustic parameters rather than the overall modulation pattern were compared, signature whistles of captive born calves were significantly more similar in start and end frequency to the trainer's whistles than those of wild or caught animals (Figure 18c and d). There was a clear increase in minimum and a decrease in maximum frequency from wild, to caught, to captive born dolphins to trainers but the four groups showed no statistically significant difference for these two parameters. Signature whistles of captive born calves and trainer whistles showed a significantly lower frequency modulation range (F_{max}-F_{min}) compared to wild and caught dolphins (Figure 18e). There was no significant difference in whistle duration between the four groups (Figure 18f).

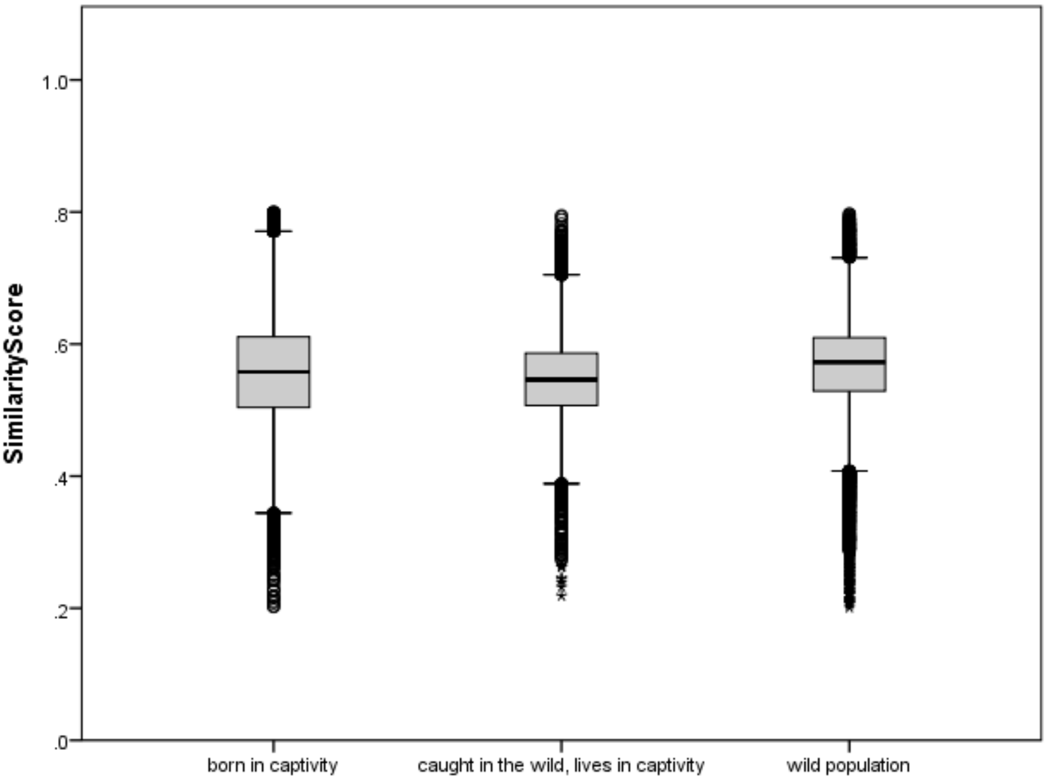


Figure 17: Similarity scores of adult signature whistles compared to trainer whistles based on dynamic time warping and pairwise comparisons. Dolphins were grouped into one of three categories based on life-history data and their exposure to trainer whistles: 1) born in captivity with trainer whistles present during signature whistle crystallisation (N=23; n_{CC}=604), 2) born in the wild with no trainer whistle present during signature whistle development but exposed to trainer whistles after being caught (lived in captivity for a minimum of 20 years) (N=7; n_{WC}=141), and 3) individuals from a wild population that was not familiar with trainer whistles (N=20; n_{W}=728).

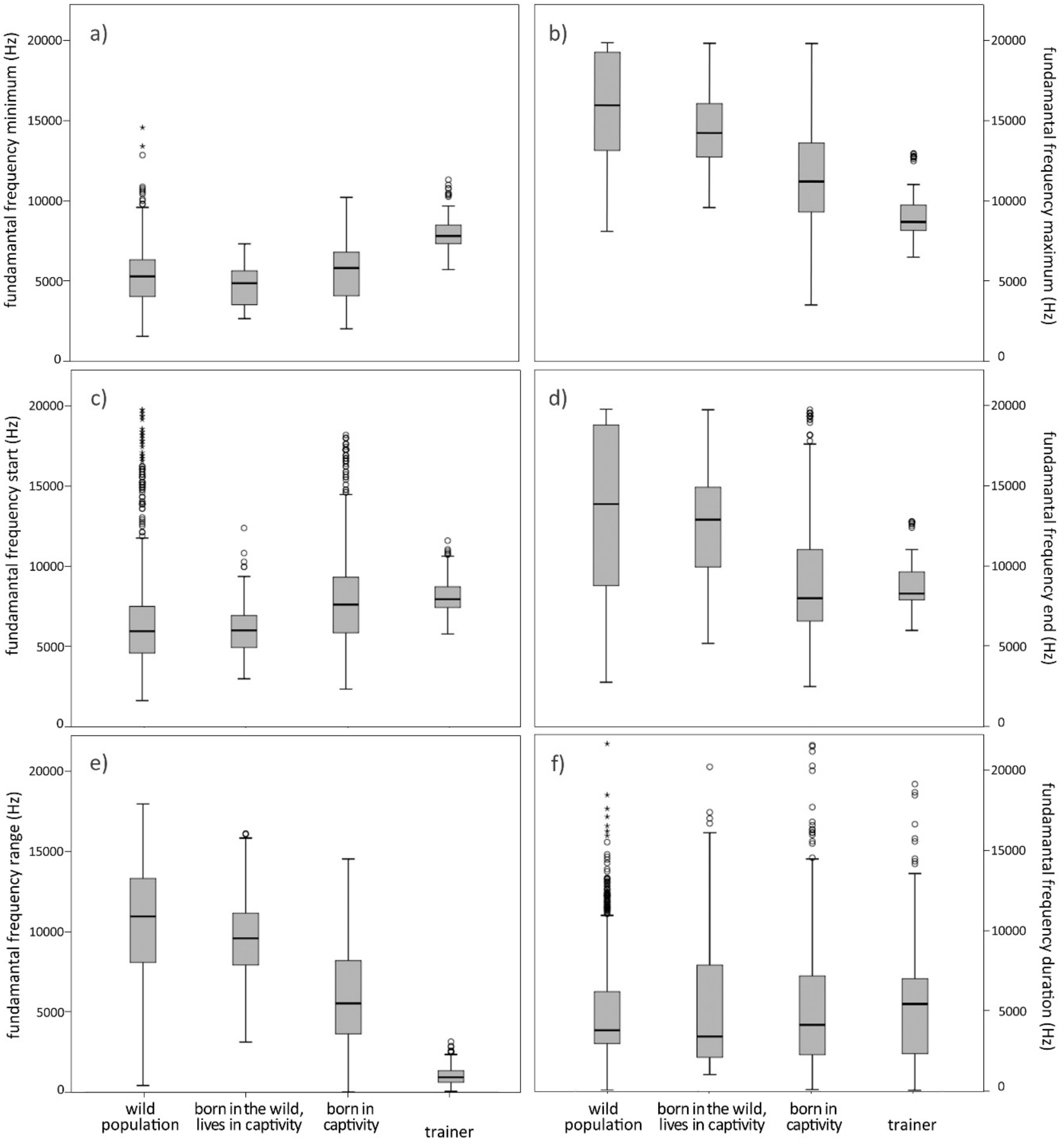


Figure 18: Whistle parameters measured from adult signature and trainer whistles. Individuals were categorised into one of four groups: 1) wild population (N=20; n_W=728), 2) born in the wild but brought into captivity (N=7; n_{WC}=141), 3) born and raised in captivity (N=23; n_{CC}=604), and 4) trainer whistles (N=20; n_T=199). Different measurements were taken from the fundamental frequency (f_0): a) minimum fundamental frequency ($f_{0\,min}$), b) maximum fundamental frequency ($f_{0\,max}$), c) fundamental frequency at the start of the whistle ($f_{0\,start}$), d) fundamental frequency at the end of the whistle ($f_{0\,end}$), e) fundamental frequency range ($f_{0\,range} = f_{0\,max} - f_{0\,min}$), and f) whistle duration ($f_{0\,duration}$). The statistical results are presented in Appendix Table II.

3.5 Discussion

This study provided strong support for vocal production learning during the development of signature whistles in bottlenose dolphins. I showed that seven out of nine dolphin calves developed signature whistles that were most similar to their mothers' whistles, but not to their fathers' whistles. Additionally, sounds from the environment, such as trainer whistles, can influence acoustic parameters both in captive-born calves as well as in wild-born dolphins that lived in captivity for more than 20 years. This confirms whistle parameter convergence and a lifelong ability for vocal learning in bottlenose dolphins.

Bottlenose dolphin calves develop a crystallised frequency modulation pattern in their signature whistles between 19 and 23 days of life (see chapter 2.4.4 for more details). The stable and distinct modulation encodes identity information in bottlenose dolphins and individuals can be recognised even if all voice cues are removed (Janik et al. 2006). When compared to other whistles from their environment, calves showed the highest similarities in their modulation pattern to their mothers, suggesting that her signature whistle was used as a model sound. This corresponds with findings from a long-term study in Sarasota Bay, where mother-calf pairs showed high contour similarities (Leon-Lopez 2016). In contrast, a study from the same population by Fripp et al. (2005) showed that wild calves developed signature whistles most similar to an unrelated and not closely associated individual. Tyack (1997a) suggested that isolation of a calf with only one other individual increases the likelihood that the calf uses this adult as a model sound, regardless of relatedness. In an old study on 14 dolphin infants, only one that was raised with its mother isolated from the group developed a whistle similar to hers (Caldwell and Caldwell 1979). Even though the calves in our study were never acoustically isolated from their social group during development, the regular physical separation of mother and calf for veterinary checks might have affected the likelihood that the mother's whistle functioned as a model sound.

Sayigh (1992) described that two mother-calf pairs with high levels of synchronous surfacing showed low whistle rates but high degrees of similarity in their signature whistle contours. This could indicate that additional factors like whistle rates, behavioural differences, or even parenting style could also affect the similarity between contours. If similarity is affected by synchrony in behaviour (or vice versa), the separation from the group as it took place in our study could have enhanced the similarity of the signature whistles by reducing interference from other dolphins.

Mother identity was a significant factor in the model, suggesting that some mothers are significantly less likely to function as a model sound than others. While six adult females had high similarity scores with all their calves, I showed that the signature whistle of one female did not function as a model sound for any of her four calves. The mechanism behind the influence of the mother's identity on whistle similarity remains to be investigated in further detail, but potential explanations could be found in the complexity of the mother's whistle or the exposure rate: The high complexity in the signature whistle frequency modulation of the female that was not used as a model sound by any of her calves was particularly noticeable (Figure 16). In a study with individuals from Sarasota Bay, Sayigh et al. (1995) also suspected an influence of mother identity on whistle similarity. From ten dolphin mothers with more than one calf, only two had calves with high as well as with low similarity to their own whistle, and eight mothers had calves with exclusively dissimilar or somewhat similar whistles. Both observations hint at a potential effect related to mother identity that might have been underestimated in studies so far. The differences between dolphin mothers could be based in different parenting styles or different whistle exposure (e.g. whistle rates). The exposure to potential model whistles could have been artificially altered in our study due to the separation of mother and calf from the group and their regular separation during veterinary health assessments. The pair was never acoustically isolated but dolphins increased their whistle rates during separations (Caldwell 1990; Janik and Slater 1998; Sayigh et al. 2007) and therefore the exposure rate might have been altered. In addition to whistle rate, the loudness of potential model sounds could affect the likelihood that a sound serves as a model for the calf's whistle. The physical distance between the calf and the source of other potential model whistles due to separation might have influenced the high similarity between mother and calf whistles found in our study. Even in a context without any artificial separation of mother and calf, whistle rate and loudness could be influenced by different association levels between the mother-calf pair and other individuals from a population. Even though separation might have affected the similarity between the calves and the mothers whistles, all mother-calf pairs in this study were separated in the same way and therefore separation cannot be the only explanation for individual differences between mothers. A study on infant marmoset monkeys (*Callithrix jacchus*) demonstrated that the transition from immature to mature calls was significantly influenced by the level of parental contingent feedback (Takahashi et al. 2017). The influence of contingent feedback, of mother identity, and of exposure should be investigated in greater detail in future studies.

The trend to use the mother's whistle as a model sound was consistent across different facilities and across calf sexes. When human raters were used to judge the similarity between signature whistle contours of free-ranging dolphins, earlier studies found that male calves seemed to be more likely to copy their mother's whistle than females (Sayigh et al. 1990;

Sayigh 1992; Sayigh et al. 1995a). Sayigh et al. (1995) argued that female calves could be under additional selective pressure to develop a signature whistle distinctive to their mother's to allow for reliable individual recognition due to the matrilineal structure of dolphin societies, where females tend to stay in close contact with their mothers while males disperse. However, when contour similarity was calculated based on a bigger sample size and with dynamic time warping, Leon-Lopez (2016) found no significant sex difference in contour similarity between mothers and calves from the same population. As discussed earlier, the potential effects of mother identity and whistle exposure could create a sex bias especially within a small sample. Therefore it is also likely that the described sex bias in the study by Sayigh et al (1995) might have been strongly influenced by a few mothers with many male or female calves rather than by an actual difference between the calf sexes. To further investigate a potential sex bias in similarity between mothers and calves, a bigger sample size would be necessary.

Previous research has indicated that dolphin calves born and raised in human care might use the whistles of human trainers as model sounds (or are at least influenced by them) and therefore produce less modulated whistles (Miksis et al. 2002), for which my research provides additional support. Tyack and Sayigh (1997) calculated that only 4% of all whistles in a pool are emitted by trainers. This ratio might vary highly between facilities depending on training routines and the dolphins' whistle rates, but it is likely only a small part of an animal's sound environment. Nevertheless, the trainer whistle has a strong social function as a positive reinforcement signal and is directly associated with a food reward. A trainer whistle might therefore potentially be more meaningful than a conspecific's whistle even if these are present at higher rates in the environment. Compared to dolphin whistles, it is especially noticeable that the whistles of human trainers are unmodulated (see Appendix Figure V for spectrogram examples). The duration of the whistles varied between trainers and the fundamental frequency varied both between facility and in some cases also between individuals. Based on the overall contour modulation of the whistle I found no higher similarity to trainer whistles in captive-born calves compared to wild or caught dolphins (Figure 7). When specific whistle parameters rather than the overall modulation of the whistle were compared, only calves exposed to the trainers' whistles during vocal development were significantly more similar to parameters of the trainers' whistles for start and end frequency of the whistle (Figure 18, Appendix Table II)

The overall range of the whistle modulation is very small in the unmodulated trainer whistle and there is a decrease in modulation from wild, to caught, to captive born dolphins (Figure 18e). The group predictor explained 49% of the variation in whistle modulation range. Miksis et al. (2002) described shorter durations in trainer and captive-born calf whistles, while I found longer mean durations of trainer whistles (mean $f_{0\ \mathrm{duration}}$=575ms) compared to wild dolphins (mean $f_{0\ \mathrm{duration}}$=525 ms) and no significant difference in whistle duration between all four groups (Figure 18f). Janik et al. (1994) showed that whistle parameters can vary significantly between different contexts. They recorded one female bottlenose dolphin in isolation and in a discrimination task where the animal was rewarded for a correct choice. The study found significant differences in 9 out of 14 parameters when comparing whistles after rewarded and unrewarded trials.

The dolphins that were caught in the wild were not exposed to trainer whistles during their vocal development but they were exposed to trainer whistles and positive reinforcement training for a minimum of 20 years. Convergence in signature whistles has been described within the natural communication system of bottlenose dolphins when the whistles of associated adult males become acoustically more similar over time (Watwood et al. 2004; Smolker & Pepper 1999) but it was unclear whether this increase in similarity was based on a shared repertoire or on actual convergence. The differences between individuals recorded in captivity and the wild could also be caused by recording context rather than by vocal learning (Janik et al. 1994) but between the two groups recorded within captivity (captive born and caught dolphins) the recording context was the same. Therefore the significant differences in acoustic parameters cannot be explained purely by behavioural context. Vocal learning during whistle crystallisation seems to be the most likely explanation for the parameter similarity to the trainer whistles. Especially with regard to increasing levels of anthropogenic noise in the ocean, further studies on the influences of environmental sounds on the signature whistle development of wild bottlenose dolphins would be valuable.

It is important to stress that a similarity in vocal parameters does not necessarily influence the overall modulation of a whistle and a similar contour modulation (as measured by dynamic time warping) does not allow conclusions about the position of the whistle in frequency-time space. The frequency modulation pattern of the whistle encodes identity information (Janik et al. 2006) while acoustic parameters can vary with behavioural state or social context (Janik et al. 1994). Bottlenose dolphins produce copies of the signature whistles of closely associated individuals to address each other. Copied whistles have similar frequency modulations but vary in acoustic parameters (King et al. 2013). Ralston & Herman (1995) successfully trained a dolphin to discriminate between different whistle modulation patterns even if they were shifted in frequency band. Even though the frequency modulation itself seems to be sufficient for individual recognition, acoustic parameters have been shown to play an additional communicative role (Janik et al. 1994; King et al. 2013). However, further studies are needed to determine which acoustic parameters are important for whistle perception and categorisation in dolphins and which role the environmental acoustic stimuli play in whistle development.

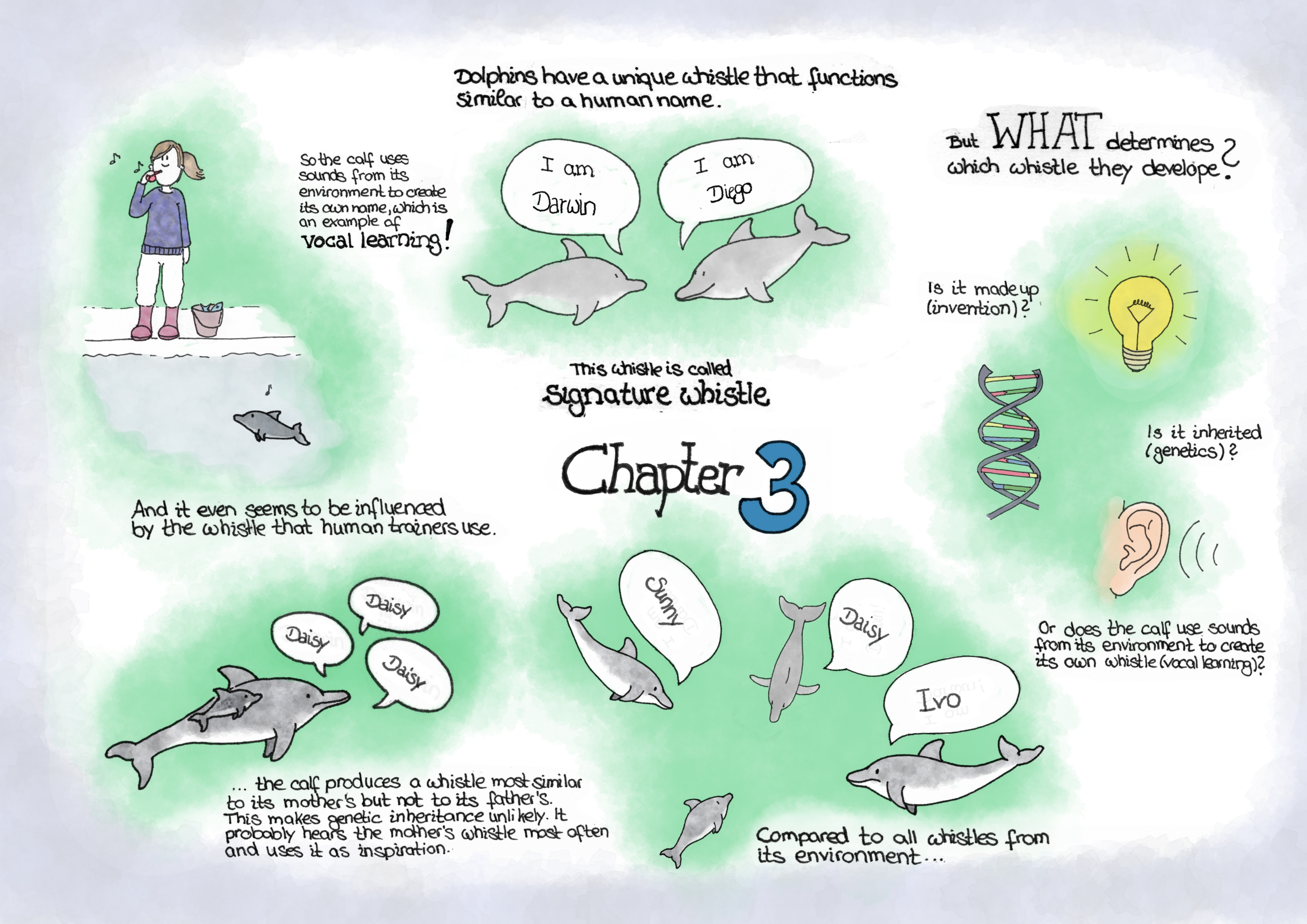
While this study demonstrates the role of vocal production learning in signature whistle development, a potential influence of genetics should be carefully discussed as well. In vocal development, the influences of experience and genetics are often hard to differentiate, which holds particularly true for species with parental care (Tyack 1997). Dolphin calves are strongly associated with their mothers during the first few years of life (Mann and Smuts 1998; Mann and Barnett 1999; Fearnbach et al. 2012) and especially during the first month when whistle crystallisation takes place (see chapter 2.4.4 for details). Dolphin mothers increase their whistle rates by a factor of ten before and after the birth, presumably to familiarise the calf with their vocalisation (Mello and Amundin 2005; Fripp and Tyack 2008; King et al. 2016a; King et al. 2016b). High exposure and close genetic relatedness therefore go hand in hand in the mother-calf relationship and the high similarity between the whistles could be attributed to both vocal learning as well as inheritance. Dolphin males do not invest in parental care and do not closely associate with the mother-calf pair and within the captive settings the fathers were physically separated from the calves during the first months of life. Therefore if genetics, rather than exposure and learning, influences the vocal development of the calf I would expect high levels of similarity to both parents. The absence of similarity between the calves and their fathers' whistles points towards vocal production learning rather than inheritance of the signature whistle frequency modulation. Nevertheless, a matrilineal inheritance via mitochondrial DNA (mtDNA), genomic imprinting, or through maternal sex chromosomes could be a possible genetic explanation for similarities between mothers and calves. In this study, the fact that at least for one mother there was low similarity between her signature whistle and those of her calves suggests this not to be the case. However, in sperm whales (*Physeter microcephalus)* the matrilineal inheritance via mtDNA has been discussed as a potential alternative explanation to cultural transmission of clan-specific click trains (codas)(Rendell and Whitehead 2003). Cultural transmission is defined as social learning on a group level (Rendell and Whitehead 2001). Sperm whales use these click codas in social interactions (Whitehead and Weilgart 1991) and coda dialect was suspected to play a role in group recognition (Rendell and Whitehead 2003). The variation in coda type between groups has been shown to correlate with variation in mtDNA (Whitehead et al. 1998). However, gene flow between groups of sperm whales does exist and they are not strictly matrilineal monophyletic (Whitehead et al. 1998) making genetic inheritance an unlikely explanation for coda variation (Rendell and Whitehead 2001; Tyack 2001).

Within delphinids, Killer whales (*Orcinus orca*) are also organised in matrilineal groups and similar to sperm whales. They also share group specific vocal dialects within their complex calls (Deecke et al. 2000; Yurk et al. 2002). Yurk et al. (2002) showed significant differences in mtDNA between two groups with acoustically distinctive calls. Like bottlenose dolphins, they seem to be capable of vocal imitation (Bowles et al. 1988). In contrast to killer and sperm whales, bottlenose dolphins do not share the same call within a matrilineal group, and there is no evidence for acoustic group recognition or a dialect in bottlenose dolphins even though some whistle parameters appear to be more similar between spatially closer populations (Ding 1995; May-Collado and Wartzok 2008). Bottlenose dolphins also live in so called fission-fusion societies which are much less stable than killer and sperm whale groups (Smolker et al. 1992; Connor et al. 2000). Dolphin calves show a higher similarity between the frequency modulation of their crystallised signature whistle and a sound from their environment (e.g. their mothers' signature whistles). The mother's whistle seems to function as a model sound for the development of the calf's signature whistle and it seems likely that the calf innovates its signature whistle based on this model sound as a form of vocal production learning. If the similarity between mother and calf would be caused solely by genetic inheritance, I would expect that the similarity between closely related individuals would be stable regardless of their presence during the signature whistle crystallisation of a calf. Many terrestrial mammals inherit their call features from their parents and the high similarity is not altered if the offspring is cross-fostered (Owren et al. 1992; Janik and Slater 1997).

Cross-fostering studies in dolphins could help to provide further evidence for the role vocal production learning might play in the development of signature whistles in contrast to genetics. Unfortunately, due to a calf's high dependence on its mother and the resulting rapidly decreasing survival chances of neonates in case of separations from their mothers, cross-fostering experiments are limited to a few anecdotal cases of stranded or abandoned individuals. Due to the intensive social interactions between calves and their mothers, separations are likely to strongly affect the natural development of the calf, and interpretations of these cases have to be made with caution (Janik & Sayigh 2013). After stranding, one calf was adopted by an adult non-related female in captivity and developed a signature whistle that resembled hers (Tyack & Sayigh 1997). A bottlenose dolphin developed a signature whistle similar to a Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) it was housed with (Caldwell and Caldwell 1979). Similar findings were reported from killer whales (*Orcinus orca*) that were exposed to sounds of bottlenose dolphins (*T. truncatus*) and develop similarities with their vocalisations (Musser et al. 2014). After stranding, a Risso's dolphin calf (*Grampus griseus*) was cross-fostered by bottlenose dolphins. The calf developed vocal signals much more similar to bottlenose dolphin vocalisations than to Risso's dolphins, suggesting an influence of vocal production learning on the vocal development of this calf (Favaro et al. 2016). These anecdotal studies combined with evidence from this study, strongly suggest that experience influences the development of an individually distinctive signature whistle modulation rather than explanations based exclusively on genetics.

In conclusion, the results of this study provide clear evidence that bottlenose dolphin calves use vocal production learning during their ontogeny. In particular, bottlenose dolphins use the whistles of conspecifics as model sounds to shape the frequency modulation of their signature whistle. Moreover, I showed that the vocal features of their crystallised whistles are also influenced by other sounds from their environment, such as the trainer whistles, as expected on the basis of previous research. This effect is not only the strongest during vocal development (trainer whistles for captive born individuals) but might also influence individuals that were born in the wild and were brought into captivity as adults.

3.6 Visual abstract chapter 3: Vocal production learning in signature whistle development



Dolphins have a unique whistle that functions similar to a human name.

This whistle is called signature whistle

Chapter 3

But WHAT determines which whistle they develope?

Is it made up (invention)?

Is it inherited (genetics)?

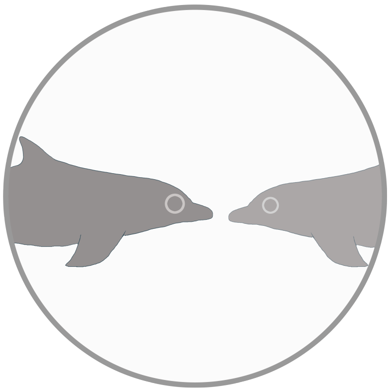
Or does the calf use sounds from its environment to create its own whistle (vocal learning)?

Compared to all whistles from its environment…

… the calf produces a whistle most similar to its mother's but not to its father's. This makes genetic inheritance unlikely. It probably hears the mother's whistle most often and uses it as inspiration.

And it even seems to be influenced by the whistle that human trainers use.

So the calf uses sounds from its environment to create its own name, which is an example of vocal learning!



4

Mirror self-inspection in bottlenose dolphins

4.1 Summary

Self-recognition is a complex cognitive process and represents a significant step in human evolution. It has been demonstrated in all great ape species. However, as of yet only a few other species (elephants and corvids) have been able to pass a standard mark test for mirror self-recognition. Bottlenose dolphins, because of their sociability and complex cognitive abilities, have long been seen as a candidate for mirror self-recognition, but so far no conclusive evidence could be found. To circumvent the primary methodological problem for testing dolphins, namely a lack of suitable limbs to touch a mark on the animal's own body, I suggest an adaptation of the mirror mark test: A dolphin has to orientate itself to one body side in front of the mirror. Both body sides are marked, with visible and transparent dye respectively to control for haptic cues. The animals oriented themselves significantly more often towards their visibly marked side, with one animal even using the water surface reflection as a mirror for inspection of the own body. Through this adapted test, I can provide conclusive evidence for mirror-guided self-inspection in bottlenose dolphins. I also suggest that inspecting oneself in a mirror might be more prevalent in dolphins than in other species that do not encounter reflective surfaces on such a regular basis.

4.2 Introduction

The study of consciousness has fascinated researchers from a variety of different angles and scientific backgrounds (e.g. art, philosophy, psychology, neurobiology, and ethology). Especially the study of consciousness in non-human animals has caused controversial discussions in the past (e.g. Tinbergen 1951; Watson 1994), even leading to a quasi-banishment of the topic from mainstream research in the early 20th century (Bekoff and Allen 1997; Greenspan and Baars 2005; for a review of the history of consciousness science see Herman 2012). A core pitfall for the research field was the initial anthropomorphic approach: definitions were chosen so strictly that consciousness could only be demonstrated in humans and, perhaps not surprisingly, linguistic facets like self-reflection were particularly emphasised. This left hardly any room to study evolutionary precursors to consciousness (Mashour and Alkire 2013). However, from the early 1960s onwards, researchers started to break down the intangible term of consciousness into its components and the field of cognitive ethology started to flourish (Griffin 1976; Griffin 1984).

Subsequently, the two sub-concepts that gained the most traction in the scientific community were the idea of a "Theory of Mind" (ToM) and the potential ability to be aware of one's own self in the animal kingdom. ToM is defined as the "ability to explain and predict the behaviour of ourselves and others by attributing to them independent mental states, such as beliefs, desires, emotions or intentions" (Gallagher and Frith, 2003, p. 77). Premack and Woodruff (1978) were the first to describe ToM in a non-human primate: A female chimpanzee was able, after watching different courses of human action, to then pick a picture that concluded the observed human behaviour. An acknowledged and intensively used test for ToM is the false belief task, where a subject is confronted with information about e.g. a hidden object and has to take into account what an uninformed subject (the guesser) can know about the whereabouts of the object (Wimmer and Perner 1983). The direct selective benefit of a ToM can be the ability to predict the behaviour of conspecifics and manipulate it for the own benefits (Morin 2011).

4.2.1 Self-recognition, mirror-guided self-inspection and the mirror mark test

Self-awareness and the ability to recognise one's own body are other key elements of consciousness. The most common test regarding self-recognition is the mirror mark test, which was first used to test chimpanzees for self-awareness by Gallup (1970). Prior to the mirror mark test itself, several behavioural phases can often be distinguished (Gallup 1970): In a first step individuals are exposed and habituated to a mirror. Initially, many species then display social behaviour. During the mirror habituation process, contingency behaviour (highly repetitive movements in front of the mirror) can sometimes be observed. These behavioural patterns are suspected to be a first testing of the changes in the mirror image caused by the individual's movements. In a second phase, the frequency of social behaviour decreases and the frequency of self-directed behaviour, indicative of self-inspection, increases. At this stage in the experimental design the actual mark test should take place: here, the animals are marked with odourless dye or coloured stickers without being aware of the marking process (while being anesthetised or carefully marked during general handling) at a body part that cannot be visually investigated by the individual without the mirror (i.e. above the eyebrow, ear, neck). After the marking the animal is again exposed to the mirror and the behaviour is observed. A haptically similar but invisible mark usually serves as a control, and sometimes both test trials with and without presence of a mirror are conducted. The mark test is suggested to be passed when the animal starts to touch/manipulate the coloured mark on the own body (rather than in the reflection) while observing one's own mirror image.

Interestingly, even if a species is generally capable of passing the mirror mark test, usually not all individuals do so. Throughout all studies, only a certain amount of the tested individuals were found to pass (Gallup 1970; Povinelli et al. 1993; Plotnik et al. 2006; Prior et al. 2008). The likelihood of passing seems to be especially low in immature or old individuals (de Veer et al. 2003). Povinelli and colleagues (1993) found that the failing proportion, with the exception of humans, increases with the age of individuals. Besides age, the main limiting factor might be the motivational state of the individuals: for the test, they have to be motivated to engage with their mirror reflection and to alter or investigate the body part that has been manipulated with the mark (Bard et al. 2006; Shettleworth 2009). Broesch (2011) also found that human children that grew up in an urban environment pass the mark test earlier in their development which could hint at an additional cultural influence.

4.2.2 Species passing the mirror mark test

Ever since its first use by Gallup (1970), the mirror mark test has been the most intensively used test for visual self-recognition and has been applied to a huge variety of species (for a review see Gallup et al. 2002). Consequently, the test developed additional value from a comparative point of view (Pepperberg et al. 1995). Even though only a small number of species were found to fully pass the mark test, several species show a certain degree of mirror usage or a capability for self-other distinction: For example, male African cichlid fish (*Astatotilapia burtoni*) show aggressive behaviour towards their mirror image that is comparable to fighting a real opponent, but the brain gene expression differs between both situations. Desjardins and Fernald (2010, p. 744) therefore suspected that the individuals might notice a difference between the own reflection and a real opponent that "may reflect a cognitive distinction". De Waal and colleagues (2005) veered towards the same direction when testing Capuchin monkeys (*Cebus apella*): As a control to the mirror exposure, the monkeys were confronted with an unfamiliar individual of the same sex. Even though they did not show any increase in self-directed behaviours, the monkeys showed significantly more positive behaviour towards their own mirror image than towards the stranger.

Additionally, several modifications of the mark test have been established and tested with different species: e.g. marmosets (*Callithrix jacchus*)(Heschl and Burkart 2006), pigs (*Sus scrofa*)(Broom et al. 2009), and New Caledonian Crows (*Corvus moneduloides*)(Medina et al.

2011) can use a mirror to locate hidden food. African Grey Parrots (*Psittacus erithacus*) are able to solve several different object discrimination and spatial-locating tasks with a mirror but do not show any increase in self-directed behaviour in front of a mirror (Pepperberg et al. 1995). All these studies indicate ability for mirror usage in a variety of species, even though the animals might not be capable of recognising the reflection as their own body. Plotnik and colleagues (2010, p. 184) concluded that this variety of middle stages between failure and passing the mirror mark test might hint towards a “cognitive continuum across animal taxa”.

Even though the range and number of applications have been astonishing, interpretations of the mark test have varied widely in the past. Some authors argued that self-exploration in front of the mirror was suggestive of self-awareness or even consciousness (e.g Gallup 1983, 1985, 1998; Marten and Psarakos 1994; Povinelli et al. 1993). In contrast, others have suggested mark-directed behaviours were merely a form of social mirroring, and denied any direct between mirror recognition and awareness of the self (Heyes 1994; Swartz 1997; Morin 2011). The middle ground lies in interpreting a passing of the mirror mark test as having at least a mental concept of one’s own face (Neisser 1997). Certainly, one should treat with extreme caution any extrapolation from passing the mark test towards full consciousness, self-awareness, and advanced social cognition. Today researchers are still divided, with many suggesting that self-exploration in front of a mirror as tested in the mark test serves as evidence for self-recognition (de Veer and van den Bos 1999) while a more conservative view is that it only demonstrates a general ability to collate representations (Suddendorf and Butler 2013). Notwithstanding these debates, it is likely that the ability to differentiate between self and others emerged gradually (Rochat 2003; de Waal et al. 2005; Feinberg and Keenan 2005; Toda and Watanabe 2008), making its study in other species an important step towards understanding the evolution of consciousness.

A full-blown passing of the mirror mark test was initially only found in great apes (Gallup 1970; Amsterdam 1972; Suddendorf and Collier-Baker 2009; Anderson and Gallup 2011). After extensive operant conditioning training, domestic pigeons (*Columba livia domestica*) are able to distinguish between live video of themselves and recorded footage (Toda and Watanabe 2008) and can also reach the passing criteria (Epstein et al. 1981). Rhesus monkeys (*Macaca mulatta*) are able to pass the mirror mark test after visual somatosensory training. However, both species fail to pass without such introduction to the task (Chang et al. 2017). Due to the close relatedness of the species that fully passed the test, it has long been argued that the full ability of mirror self-recognition might result from a homologous evolution and a shared neurological-cognitive background (Gallup Jr 1985; Heyes 1994; Suddendorf and Butler 2013). However, this theory has been challenged by later findings that Asian elephants (Plotnik et al.

2006) and magpies (Prior et al. 2008) also appear to fully pass the test. Evidence for the ability to pass the test in those only distantly related taxa hints at a convergent evolution of this cognitive ability (Prior et al. 2008). To confirm this suggestion, further evidence of mirror self-recognition in species which are not closely related to apes is highly desirable. One promising candidate in this regard is the well-studied bottlenose dolphin.

4.2.3 Dolphins and the mirror mark test

Dolphins in general and the well-studied species of the bottlenose dolphin in particular exhibit several characteristics that could render them an especially promising study species for testing mirror self-recognition: Bottlenose dolphins show a set of remarkable cognitive abilities (Herman 2010; Janik 2013; Güntürkün 2014) similar to great apes, parrots and corvids, all the while not sharing recent evolutionary history with any of them. The phylogenetic distance between dolphins and humans would add a valuable data point for the on-going discussion of whether or not the cognitive ability enabling mirror-guided self-inspection and self-recognition developed in a homologous or convergent way within the animal kingdom. Bottlenose dolphins are a highly social species with a rich repertoire of social communication (see Janik 2006; Janik and Sayigh 2013 for reviews). They use learned signature whistles with their own distinctive frequency modulation pattern to broadcast their identity (Janik et al. 2006) and are not only capable of identifying signature whistles of known individuals (Sayigh et al. 1999; Janik et al 2006) but also of vocally mimicking those whistles to address each other (Tyack 1986; Janik 2000; Tyack 2000; King and Janik 2013). Bruck (2013) showed that individual dolphins can remember known whistles after more than 20 years of separation, showing evidence for long term social memory. Besides the acoustic imitation, bottlenose dolphins also show highly accurate imitations of the behaviour of conspecifics: Motor synchrony (e.g. parallel swimming, synchronic breathing) is commonly observed both in the wild (Sakai et al. 2010)and in captivity (Herman 2002) within social groups and especially among allied males (Connor et al. 2006a; Connor et al. 2006b). To imitate a conspecific and to predict its movements in order to synchronise own behaviour is cognitively challenging. Following Preston and de Waal's (2002) perception-action model on shared representations for perceiving and generating action, it is suspected to involve "mapping of another's actions onto the observer's own motor representations" and adopting the other's point of view (Tsakiris et al. 2007, p.655). This ability could hint at mirror self-recognition as perspective-taking and empathy, which are suggested to co-evolve with the ability to differentiate between self and other, and therefore with self-recognition (Plotnik et al. 2006; de Waal 2008).

Bottlenose dolphins understand referential pointing (Herman et al. 1999) and syntactic rules in sounds and gestures (Herman and Forestell 1985). There is evidence for tool use (Krützen et al. 2005; Mann et al. 2008) and eavesdropping on conspecifics echolocation might hint at the ability of joint attention (Xitco and Roitblat 1996; Janik 2013).

Dolphins live in an aquatic environment that is naturally equipped with an enormous mirror: Jumps out of the water are a frequent part of the animals' behaviour and therefore it is assumed that they might be used to seeing their own reflections on the water surface. Similarly, the water-air interface presents a reflective surface from inside the water (Dibble et al. 2017). Both could have encouraged a development of the ability to recognise their own mirror image.

For these reasons, numerous authors tried to replicate variations of Gallup's (1970) experiment for mirror self-recognition with dolphins in the last decades. However, they all encountered a variety of obstacles to do with the limitations of the mirror mark test. When applying Gallup's experimental design (Gallup 1970) to dolphins rather than to primates, the most prominent challenge lies in the absence of limbs: Dolphins are physically not capable of touching or manipulating a marked spot on their body while observing their mirror image. Therefore, a simple transfer of established criteria for passing the mirror mark test is not feasible for a dolphin study. To solve this problem, researchers have tried to use mark-oriented behaviours in contrast to social behaviours, latencies, and interaction durations in front of the mirror as indicators for mirror self-recognition (Marino et al. 1994; Marten and Psarakos 1994; Reiss and Marino 2001). While latencies and interaction times can function purely as a criterion for the animal's motivation to interact with the mirror, self-directed behaviours are vague, highly subjective and unsuitable as a criterion for self-recognition. Especially the considerable overlap between social and self-directed behaviours makes this an unreliable variable for mirror self-recognition. This has been demonstrated by the findings of Marten and Psarakos (1994) who described self-directed behaviours (e.g. open mouth, repetitive movements and bubble streams) also in absence of a mirror or in a social context during an encounter with an unfamiliar individual. Therefore, all tests to date remained inconclusive largely because of methodological weaknesses (see for comprehensive reviews: Harley 2013; Manger 2013; Güntürkün 2014).

Marten and Psarakos (1994; 1995b; 1995a) were the first who tested for social vs. self-oriented behaviours of bottlenose dolphins by marking 5 individuals and confronting them with a mirror and a variety of additional control conditions: 1) mirror without mark, 2) no mirror, no mark, 3) an encounter with two unfamiliar false killer whales (*Pseudorca crassidens*) through an underwater gate, and 4) an encounter with an unfamiliar conspecific in the same tank. They observed the individuals' behaviour in front of the mirror and compared it to the control situations. However, inter-rater reliability was not assured and they did not control for an influence of the tactilely noticeable marking colour (e.g. by using a not visually perceivable sham-mark as a control). Additionally, the animals were not separated during the testing. Combined with the huge variation of influences within the different test situations, these factors make the observed behaviour in front of the mirror difficult to interpret.

Marten and Psarakos (1995b) additionally conducted a test with real-time vs. time-delayed video playbacks instead of a mirror in order to distinguish between self-examination and social behaviour. Real-time video has been used as a mirror equivalent by several authors (e.g. Anderson et al. 2009, Law and Lock 1994, Marten and Psarakos 1995b), but has also been criticised as it seems to trigger different brain responses (Suddendorf and Butler 2013). It also lacks the possibility of direct eye-contact and therefore shows no reflection of one's own body in the image's eyes (Senju and Johnson 2009). Human children are capable of passing the mirror mark test reliably from an age of 15 months on (Amsterdam 1972) but tested with real-time video only 35% of one-year-old children are capable of passing the test (Suddendorf et al. 2007).

Marino and colleagues (1994) used a more standardised mirror test in which two dolphins were either confronted with a covered or an uncovered mirror in their tank. They used two differently coloured markings (Neo-Blue, described as hardly visible on the dolphins' skin, and white zinc oxide). The blue marking served as a control sham mark in this setup. More recently, Reiss and Marino (2001) used a slightly modified approach to test two additional dolphins. In this study, they used a pellucid substance rather than a blue one as a sham mark, and a session without any marking served as an additional control. In order to complement the analysis of behaviour and body position in front of the mirror, they presented other less reflecting surfaces to the animals and analysed the time the individuals spent in front of each surface. All video-taped test trials were analysed by two independent raters which were blind to treatment. They found that the animals spent significantly more time in front of the mirror when they were marked, and in 6 out of 8 sessions the animals' initial behaviour was directed towards the mark (e.g. turning towards the marked side). However, the study failed to present conclusive evidence for self-inspection, let alone self-reflection, due to several methodological weaknesses (see Harley 2013 for a review): For one, neither the marking locations nor the observation time were balanced across trials and for most of the sessions no data is presented. Furthermore, the sham-mark control and the test situation triggered the same behavioural responses and therefore "either the control condition does not work or the experimental condition is ineffective" (Harley 2013, p. 573). Additionally, the publication is lacking descriptive statistics and none of the results are conclusive evidence for self-referential behaviour or mirror self-recognition in bottlenose dolphins. This makes further studies highly desirable, but also underlines the necessity for careful research and methodological design. My study below suggests a series of methodological adaptations, including a clearly measurable dependent variable (here: orientation towards the marked side indicative of self-inspection), balanced marking procedures including controls for haptic cues (with coloured and transparent dye invisible against the dolphin's skin), testing in isolation (after careful habituation) and in short intervals (to avoid loss of interest and false negative results), avoidance of any reinforcement through trainers or researchers and use of opaque mirrors (both to avoid false positive results). The latter is in stark contrast to previous studies where researchers and trainers were potentially visible behind a one-way mirror (e.g. Marino et al. 1994), or where the dolphins' attention was actively attracted towards the mirror by tapping against it (e.g. Marten and Psarakos 1994). Based on these adaptations, in my study the dolphin's active body movement towards the marking is suggested to serve as the first suitable proxy for mirror-guided self-inspection in dolphins.

4.3 Methods

4.3.1 Subjects and housing

The dolphins were tested in two German dolphinaria in the Tiergarten Nuremberg and the Zoo Duisburg. Data was collected between August and December 2014 (Nuremberg) and between September and December 2015 (Duisburg). At the time of testing, the three males were 4 years of age and the female was 26 years old. All animals were housed in multi-pool-systems in social groups, but were temporarily separated by mesh gates for the tests described here. Due to a daily training routine, individuals were fully habituated to short-term separation and the marking procedure. Even though reflections are a daily part of a dolphin's environment (e.g. water surface, windows), none of the animals had previous experience with a mirror or was ever reinforced by a trainer to interact with it. To familiarize them to the presence of the mirror and the cameras as novel objects in the pool, the reflective mirror side was covered with an opaque foil and all equipment was slowly introduced to the pool in sessions varying in duration (between 5 and 25 min). After being completely habituated to the objects in the pool, the animals received a varying number of habituation sessions with the uncovered mirror. Each of these sessions was 30 min in duration and had the exact same protocol as the later marking sessions with one exception: the animals never received a marking during the medical training during these habituation sessions. All behaviour patterns were recorded and analysed.

In the original protocol developed by Gallup (1970), contingency checking behaviours (highly repetitive movements in front of the mirror) are used as a criterion to end the habituation and start marking the animal. Since I did not observe contingency checking during habituation sessions, I closely observed each individual's behaviour in front of the mirror and started with marking sessions as soon as the frequency of mirror interactions decreased to avoid over-habituation (mean habituation time ± SE = 180 ± 45 min).

4.3.2 Experimental design and set-up

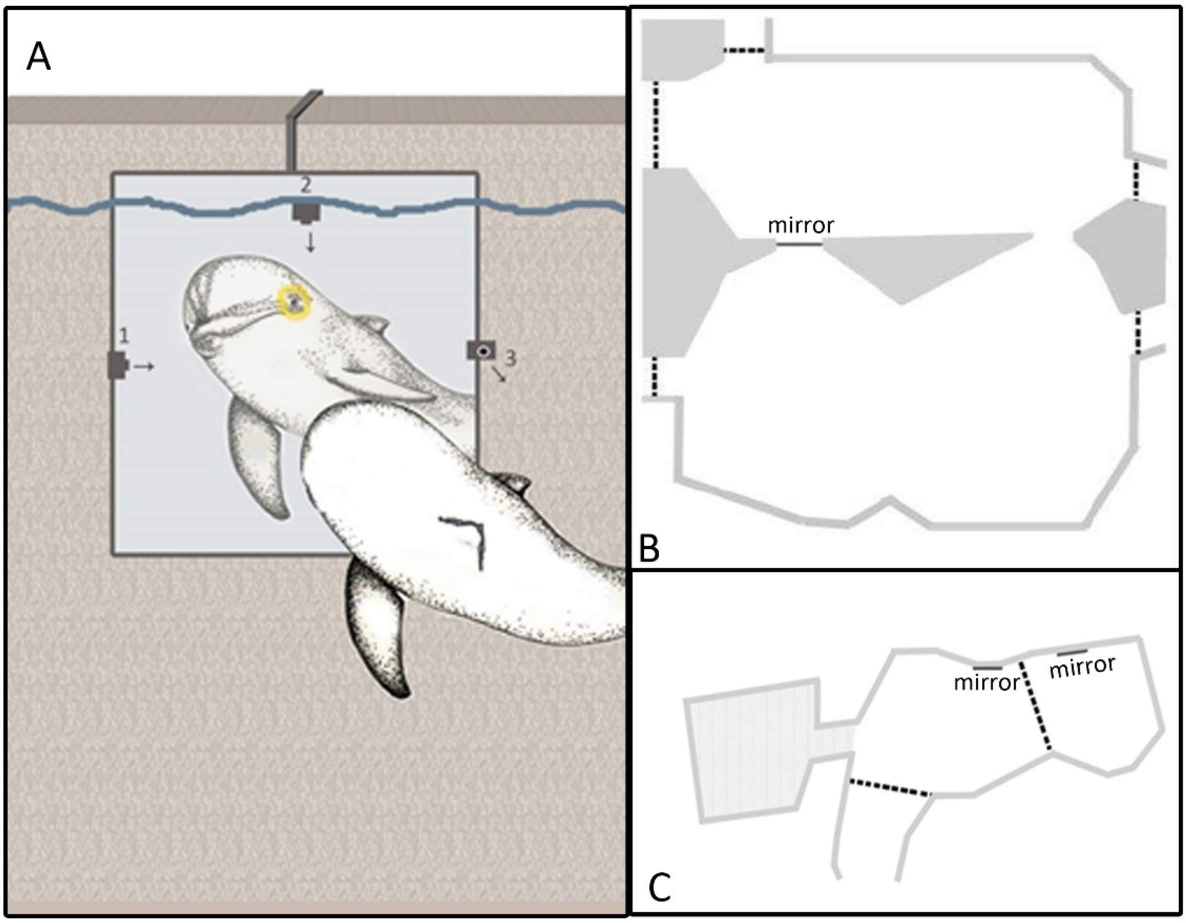


Figure 19: Experimental set-up with the acrylic glass mirror in the pool system. (A) Mirror attached to the pool wall (Duisburg) with underwater cameras filming different angles as indicated by the arrows. Grey pool area with very shallow water was accessible but rarely entered. (B) Test pool in Nuremberg with the mirror integrated into a gate between two pools. (C) Test pools in Duisburg with the mirrors attached to the pool walls.

An acrylic glass mirror (104 cm x 139 cm) was fixed to an opaque PVC board and only presented in the pool during the 30 minutes of each experimental session (Figure 19A). In Nuremberg the two individuals were tested with a mirror integrated into a gate between two pools. They could use both pools and interact with the reflective mirror front as well as with the non-reflective backside (Figure 19B). In Duisburg, the mirror was attached to a pool wall (Figure 19C).

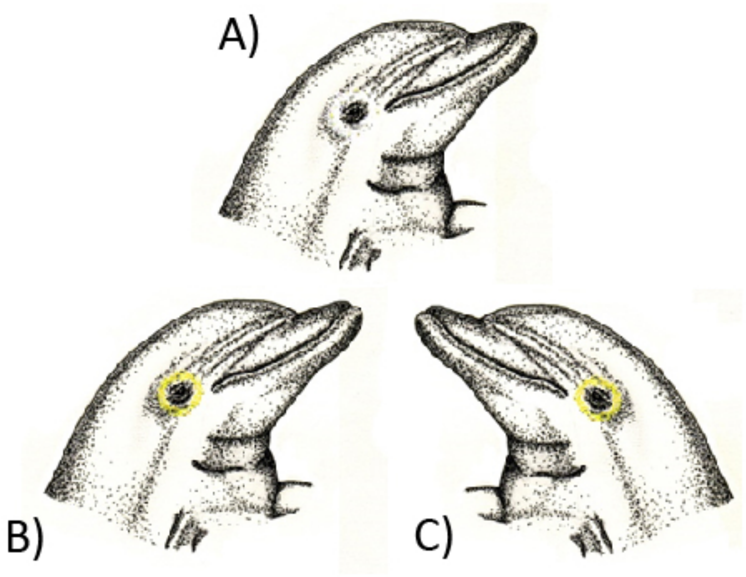


Figure 20: Marking treatments during the test phase. (A) Both eyes marked with transparent dye. (B) Left eye marked transparent, right eye marked yellow. (C) Right eye marked transparent, left eye marked yellow.

Dolphins were marked circularly around the eye during general medical training prior to each test session. They received one of three marking treatments: “transparent” (both eyes marked with transparent dye), “left” (left eye yellow, right eye transparent) and “right” (right eye yellow, left eye transparent)(Figure 20). The trainer always had both the yellow and the transparent dye on one finger each, regardless of the marking treatment that was applied in the particular session. Additionally, the eye was approached with both fingers in a minimum angle and only the finger with the correct dye touched the dolphin’s skin minimizing the risk that the dolphin could already see the marking treatment before checking its reflection. I always applied dye to both eyes, either all transparent or with colour on one eye or the other. This bilateral marking procedure was used to account for any behavioural reaction that could have been caused by the haptic experience of the marking. The transparent dye contained Vaseline and methylcellulose; for the yellow dye iron oxide and titanium dioxide were added to achieve a high contrast to the dark grey skin without changing the dye’s texture. Both dyes were odourless to avoid potential olfactory cues, and water-resistant for up to 45 minutes. After most sessions the dye faded rapidly and there was no need to remove it. In 5 instances, remaining dye was removed during a training session after the test session. During test sessions no observer or trainer was present around the pool and no signal or food reward was given to the animals. Experimental treatments (transparent, left, right) were randomized and repeated between 2 and 4 times for each individual (mean ± SE = 3.17 ± 0.83). In both facilities, the individuals were potentially able to observe each other’s behaviour in front of the mirror through the mesh underwater gate, but they could not see their own reflection in the mirror other than in a test session. In Nuremberg the individual that was not tested was not observed to be spending time close to the underwater gate. In Duisburg, both individuals were tested simultaneously in bordering tanks and were rarely observed to stop close to the gate and watch the other's behaviour. If dolphins were capable of mirror-guided self-inspection, I would expect to see a longer duration of the yellow-marked head side orientated towards the mirror.

4.3.3 Behavioural coding

Behavioural data was collected with underwater cameras (Gopro Hero3+ and Qumox HD1080P) positioned around the mirror, and additionally on the mirror backside (Nuremberg) or opposite pool wall (Duisburg). All behaviour patterns were coded from the video files using Solomon Coder beta 15.11.19. Head orientation towards the mirror was measured in frequency and duration whenever the animal turned one side of its head towards the mirror. Every behavioural sequence during which the animal had one eye in a 90 degree angle towards the mirror surface and was therefore potentially able to see its reflection was coded as an interaction. For interactions with the water surface, all behaviour patterns were coded when the animal was within 1 m of depth and had one eye towards the surface. In order to calculate the inter-rater reliability, 30% of the videos were randomly picked and re-coded by a second rater who was naïve to the experimental treatment. Calculations showed a high level of agreement between both raters (Spearman's rho correlation: correlation coefficient= 0.943, $P \leq 0.005$).

4.3.4 Statistical analysis

To assess the influence of the marking treatment on the dolphins' side orientation in front of the mirror, generalized linear mixed effects models were performed using R version 3.2.2 and the R package lme4 version 1.1-9 (Bates 2015) with a binomial family, logit link function, and a Poisson error distribution. Within all test sessions, the three males showed a strong preference for a counter-clockwise swimming direction. Therefore they were generally more likely to expose their right eye to the mirror. I used the orientation towards the right eye as a response variable in a mixed model (Table 9) to test for self-exploration in regards to the marking treatment. Cbind was used to create a binary response variable by combining the duration when presenting the right side of the head to the mirror and the total duration of the interaction. Dolphin identity, facility, and marking treatment were incorporated as fixed effects but a model with only marking treatment as a fixed factor showed the best model fit (AICc, Aikaike information criterion) and was significant against the null model (chi-square, $p=0.003$).

Repeated measurements during each test session were accounted for by using session and ID as nested random effects. The diagnostic plots were checked and looked satisfactory. The same mixed model was used to explore the side orientation towards the reflective water surface in relation to the marking treatment. To account for repeated measurements within an individual, session number was incorporated as a random effect. Model selection was performed using the AIC to determine the best model fit. The selected model included treatment as a fixed factor (chi-square, p=0.002). The mean durations of mirror interactions between different marking treatments were compared using Mann-Whitney U tests in IBM SPSS Statistics 23 (version 23).

4.4 Results

All four dolphins interacted with the mirror throughout all test sessions. The two animals with access to the mirror back-side interacted significantly more with the reflective side of the mirror (Wilcoxon signed-rank test: n=31, Z=-3.785, P≤0.000). As summarized in Figure 21, three of the four individuals (Kai, Jenny, and Diego) interacted significantly longer with the mirror when they received a yellow marking compared to test sessions with only transparent markings (Mann-Whitney U test: P≤0.001).The mixed model showed a significant effect of the left and transparent marking treatment on side orientation towards the mirror (Table 9). The animals turned their right eye less often towards the reflection when they received a yellow mark around the left eye (Figure 22).

Table 9: Summary of Generalized linear mixed effects models for side orientation towards (A) the mirror and (B) the reflective water surface. Scale of the response variable was used to present the model coefficients (binomial distribution and logit link function).

		marking treatment	coefficient e^{β}	CI		P
				2.5%	97.5%	
A)	mirror interaction (ALL)	transparent	0.74	0.66	0.82	<0.000
		Left	0.78	0.66	0.90	<0.001
		Right	0.92	0.79	1.06	NS
B)	surface interaction (Darwin)	transparent	0.80	0.37	1.76	NS
		Left	0.55	0.41	0.73	<0.000
		Right	1.71	1.26	2.31	<0.000

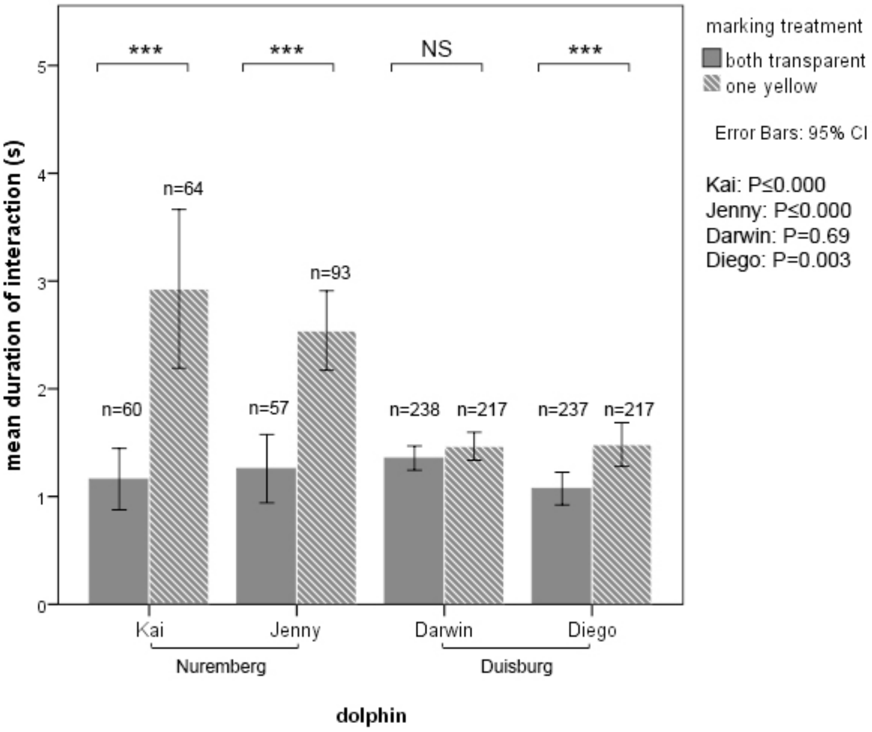


Figure 21: Effects of marking treatment on the duration of interaction with the mirror. Mean duration of interaction with the mirror reflection after receiving two transparent (solid bars) or one transparent and one yellow marking (hashed bars). Mann-Whitney U test: ***P≤0.001, NS =non-significant.

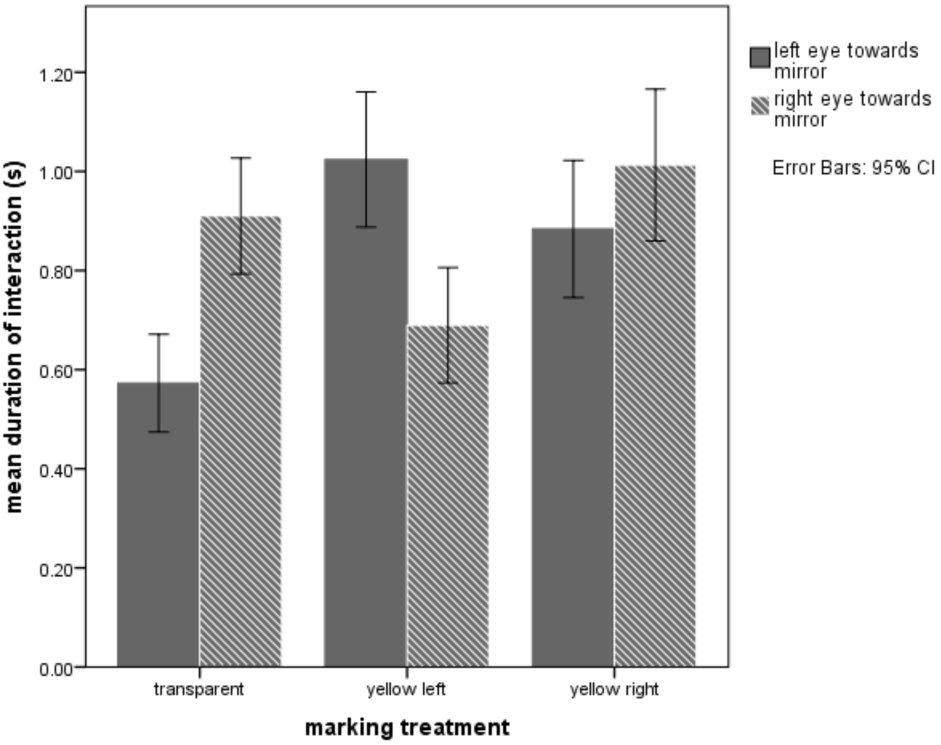


Figure 22: Effects of marking treatment on side orientation towards the mirror. Mean duration of interaction while the left eye (solid bars) or right eye (hashed bars) was orientated towards the mirror.

Since the water surface is a good reflector and likely gave all dolphins extensive experience with mirrors before any tests, I also timed all cases in which an animal turned one or the other eye towards the water surface during the experiment. One individual (Darwin) repeatedly positioned itself within 1 m of depth and turned from side to side during marking trials (Appendix Figure VI). These interactions with the surface occurred more frequently and were significantly longer in duration when the individual had a yellow marking versus only transparent markings (Figure 23). When marked around the left eye, Darwin spent more time looking at his left eye and turned significantly less often to the right side, and when marked right he turned significantly more often towards the right side versus his left (Table 9B). Transparent markings had no significant effect on the side orientation (Figure 24). The other three dolphins were not observed to show this behaviour near the water surface.

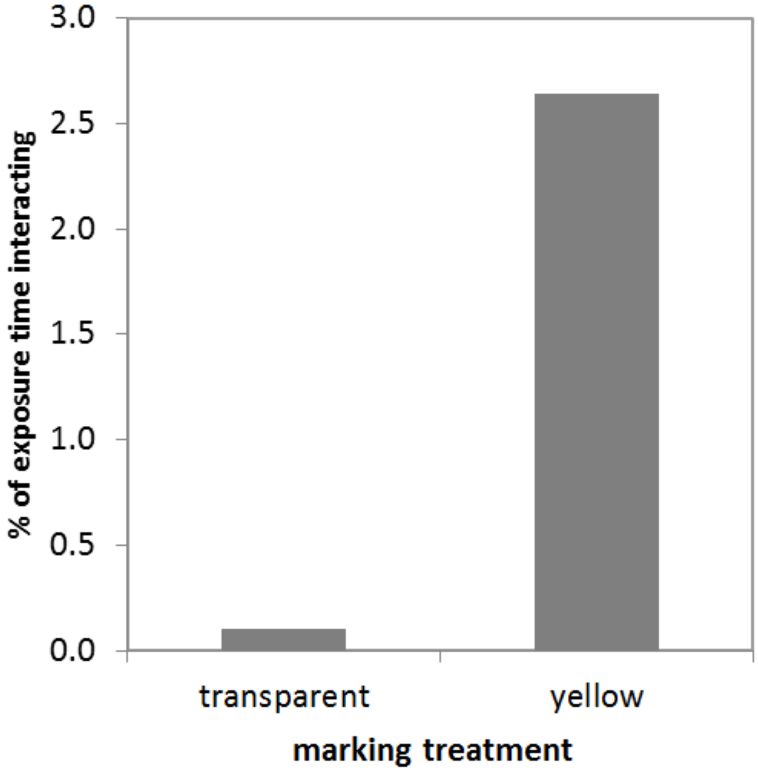


Figure 23: Duration of interaction with the surface reflection. When the animal received a yellow marking, it interacted 26 times more often with the reflection than in sessions with only transparent markings (Habituation: N=0, transparent: N=5, yellow: N=64).

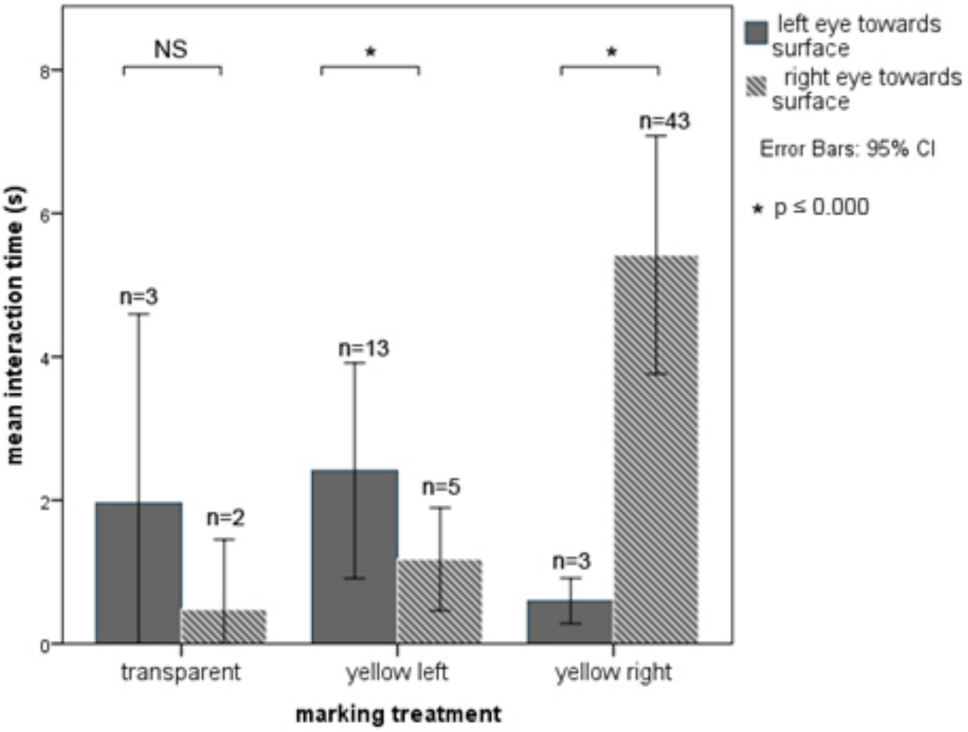


Figure 24: Effects of marking treatment on Darwin's side orientation towards the water surface. Mean duration of interaction while the left eye (solid bars) or right eye (hashed bars) was orientated towards the surface.

4.5 Discussion

Here I present conclusive evidence for mirror-guided self-inspection in bottlenose dolphins by use of an adapted mirror mark test procedure that is more suitable to test marine mammals. I propose that the active orientation of the dolphin's body towards the marked side can serve as a suitable test for mirror-guided self-inspection.

Previous studies on mirror self-recognition in dolphins were riddled with methodological problems that rendered their results inconclusive (Harley 2013; Güntürkün 2014). In all cases the main problem was the lack of a convincing control. Marten & Psarakos (1994) described the behaviour of marked and unmarked dolphins in front of a mirror anecdotally. While they claimed that they found mirror self-recognition, they reported that all of the behaviour patterns seen as suggestive of self-recognition were also observed in their control when the mirror was absent. Furthermore, no quantitative data for the control condition were presented making a comparison not possible. Similar problems compromised other studies. Marino et al. (1994) also thought behaviours such as jaw opening, producing bubble streams and head dipping were "suggestive" of mirror self-recognition in their study on two dolphins, but could not find a statistically significant difference in the comparison of the marked and the unmarked condition. All of the "suggestive" behaviour patterns listed by Marino et al. (1994) and later reanalysed by Sarko et al. (2002) can be observed in social interactions between dolphins (Overstrom 1983; Marten and Psarakos 1994) and are therefore clearly not suggestive of self-recognition. Furthermore, they defined suggestive behaviour patterns as those only observed in front of the mirror in their study, which introduced a circularity into their argument. In a much discussed study by Reiss and Marino (2001), the animals also showed no difference in their behaviour between the marked and the sham-marked condition. While the sham-mark was initially introduced as a control condition, it was re-labelled as a treatment and pooled with the mark trials when the animals failed to show a different response in later controls. Reiss and Marino (2001) then claimed that the behaviour in front of the mirror demonstrated self-recognition. This re-labelling of a control condition is highly questionable and left the study without a control for the effect that was reported. Furthermore, the results were presented in a way that was equivocal. In the first animal, the total time that the animal showed self-orienting behaviour in front of a mirror was compared between conditions, but the total duration of observations was different between treatments (see also Harley 2013). The labelling of a behaviour as self-orienting was not clearly explained and, as in previous studies, could include normal social behaviour found between dolphins. In a comparison of time spent in front of a mirror for the second animal, the dolphin seemed to spend time at mirror locations during mark and sham-mark tests even when mirrors were covered. The main result here was that the dolphin spent more time at the mirror location (this time reported to be a mean but not reporting the values) and went there more quickly when marked or sham-marked than when it had been required to just station in front of the trainers. It is unclear whether the animals simply had a higher motivation to interact at the mirror locations when touched (which only happened during marking and sham marking, but not during no-mark conditions). In our experience, dolphins increase time at the location of novel objects when they perceive themselves to be in a conditioning task. In this condition, they also increase time near trainers who would be visible behind these mirrors if the animals approached closely. Reiss and Marino (2001) did not provide information on the location of trainers during their study. These examples show that, all previous mirror studies with dolphins had substantial problems. They have been widely criticized for their shortcomings in the literature (Gregg 2013; Harley 2013; Manger 2013; Güntürkün 2014), and left us with no reliable information on mirror self-recognition in dolphins.

My study aims to overcome these challenges and provide a more convincing demonstration of mirror-guided self-inspection in bottlenose dolphins by suggesting methodological adaptations to the mirror mark test. I marked dolphins with yellow dye on either their left or their right side while marking the other side with transparent dye in the same trial. Therefore, the animal had to make a decision to turn its marked side to the mirror to inspect the marking should it be able to recognise that the mirror reflection is in fact an image of its own body. Therefore, I measured the duration of the dolphin's side orientation in relation to the marking in front of the mirror as a dependent variable. I showed that the animals clearly orientated themselves to look at their marked side when yellow dye was applied.

Apart from the side preferences for the marked side when looking at the mirror image, I found very few of the behaviour patterns previously reported as suggestive of mirror self-recognition. In the tests reported here, I only used fully opaque rather than one-way mirrors and presented them away from any underwater windows in the pool. However, in a pilot phase, I did present one-way mirrors at underwater windows. In these pilot tests, the occurrence of "suggestive" behaviour appeared to be associated with using one-way mirrors. Even slight differences in brightness between the water body and the room behind the mirror allow a clear view through the reflective side. This effect is especially strong when the eye is close to the mirror surface. Reiss and Marino (2001) described the "close viewing of the eye" as a self-directed behaviour in front of the mirror and took it as evidence for mirror self-recognition rather than as an indicator that the animal potentially tried to peer behind the glass. In some studies, the mirror only covered part of the underwater window (Marten and

Psarakos 1994), making this an even bigger problem. The uncontrolled influences from the backside of a one-way mirror (e.g. visible movements by the experimenter, technical equipment) make them unsuitable for testing dolphins for mirror self-recognition.

Unlike most other animals in zoos and aquaria, dolphins are usually exposed to regular training for husbandry, enrichment and visitor presentation. This gives them experience and expectations in the interaction with their trainers and their environment. Repetitive or unusual behaviour in front of a one-way mirror may be connected to training effects caused by operant conditioning or triggered by movements behind a one-way mirror. Reinforcement effects may lead to dolphins showing unusual behaviour patterns because they seek attention and when showing them are reinforced by social attention or reactions by trainers or visitors. Furthermore, many dolphin facilities work with the so-called capturing method, a training paradigm based on positive reinforcement in which the animal offers a variety of different behaviours and the trainer will reinforce and shape what is desirable for the specific training goal. Animals used to this technique are more likely to offer a variety of behaviours in front of a new object such as a mirror when unsure about what is being expected from them. Additionally, the introduction of an unfamiliar object into the tank can also cause various behaviours driven by curiosity, play behaviours, or even fear (Herman 1980; Delfour and Beyer 2012), again rendering the coding of what seem to be suggestive behaviour patterns in front of a mirror unsuitable for testing self-recognition in dolphins. Instead, I used a differential test with a clear control treatment to investigate mirror guided self-inspection in dolphins.

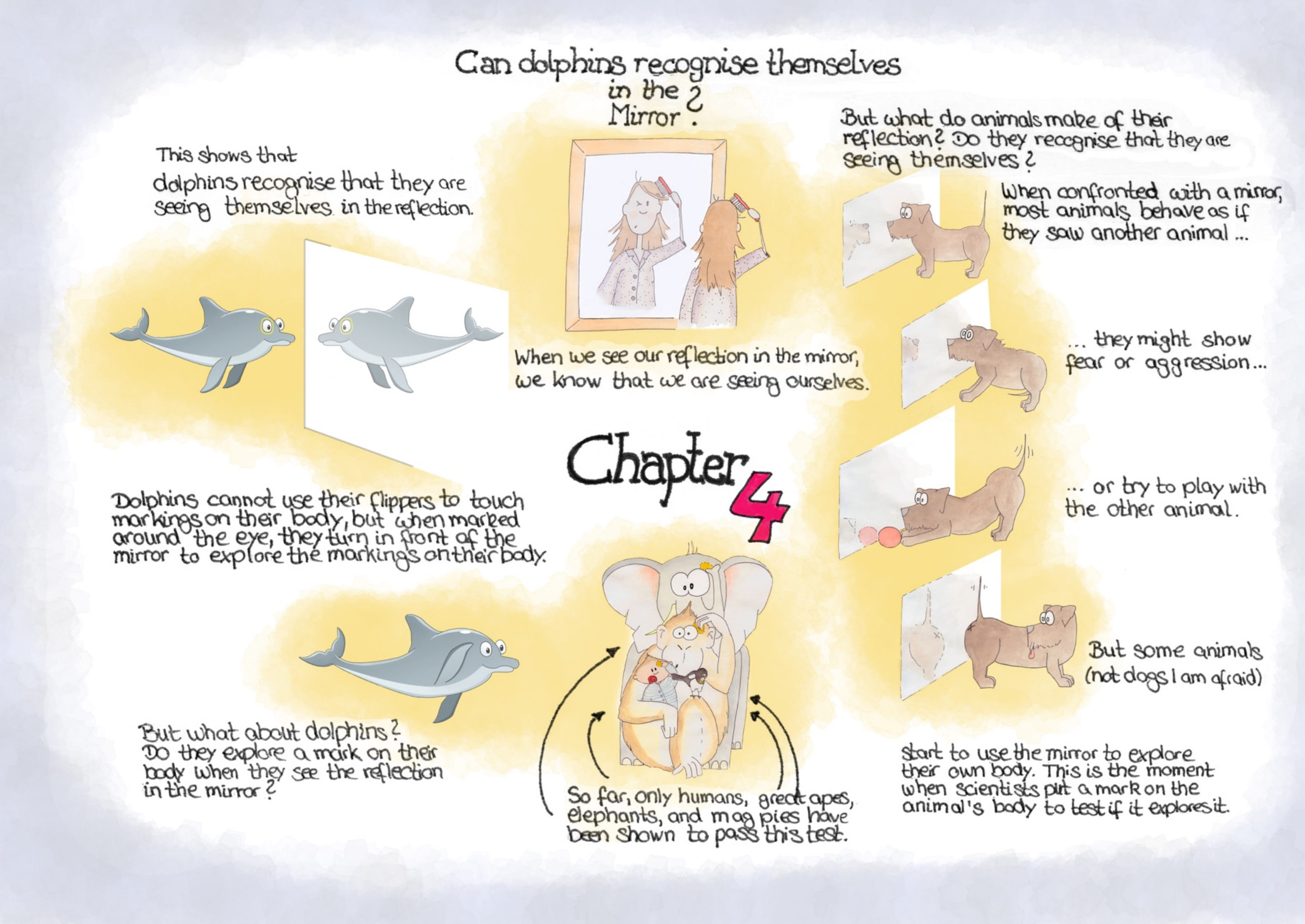
A caveat for testing which eye a dolphin uses to inspect a mirror lies in the potential for a general side bias in the animals. I found that the dolphins showed a preferred counter-clockwise swimming direction within test sessions resulting in the right eye seeing the mirror first. A preference for using the right eye in visual tasks has been described in a range of species (see Rogers et al. 2013 for a review) and specifically for bottlenose dolphins (von Fersen et al. 2000; Yaman et al. 2003), suggesting a dominance of the left brain hemisphere in visual processing. However, by using the orientation towards the preferred right eye as a dependent variable, I could show that the animals turned less often towards the right side when they had a yellow marking applied around the left eye. They also turned less often to the right when they had transparent markings around both eyes, suggesting that they visually examine both sides when incentivized to do so. All previous studies failed to control for such haptic cues caused by the marking procedure. This was addressed for the first time in our study by the use of bilateral markings so that the dolphins were always marked on both sides with markings of identical haptic properties (either both sides transparent or one transparent and the opposite side yellow).

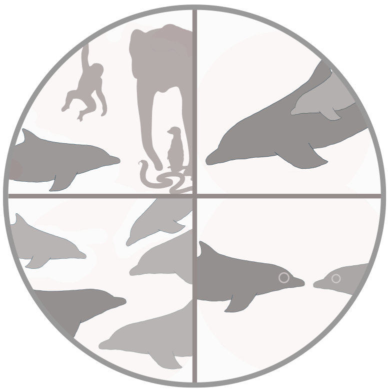
The one question that remains is what this version of the mirror mark test can show. The animals were clearly looking at the side on which they saw a mark. The classic mirror mark test required the animal to touch the mark on its own body once it sees it in the mirror. This is different to an animal just looking at a mark, but given the lack of arms and hands in delphinids cannot be tested in this taxon. My paradigm in which the animal had to make a clear decision which way to turn comes closer to the classic mirror mark test than any other previous attempt with dolphins. Indeed, mirror-guided self-inspection may be seen as suggestive of capacities for (mirror) self-recognition akin to the original mark test. However, per the evidentiary bars established for self-recognition, the observed behaviour (i.e. side orientation towards the mark) cannot count as evidence of self-recognition. Had the dolphins been observed, for example, to attempt to rub off the mark on the own body after inspecting it in the mirror (which was not the case), a case for self-recognition could have been made. Future studies could attempt to test for such follow-up behaviours more methodically. Until then, as per the definitions suggested in chapter 1, the observed behaviours must be considered conclusive evidence for self-inspection rather than self-recognition.

The mirror mark test is a powerful comparative tool to test a diverse range of species for self-recognition, but the method has to be carefully adjusted to species-specific characteristics and limitations to avoid both negative as well as false positive results. Independent repetitions and further studies of self-recognition in dolphins are highly desirable to gain a better understanding of the extent to which dolphins are gaining information from their mirror reflections, how self-recognition develops, and whether surface reflections play a role in their natural environment.

In this study, I also found evidence that mirrors may be used by dolphins in their natural environment. One of the animals spontaneously started to use the water surface as a mirror and showed a significant orientation towards the marked side while stationed very close to the water surface. The dolphin showed this behaviour exclusively within marking sessions and never during habituation sessions when no mark was applied. Just as above the water surface, light is reflected at the boundary between water and air, creating a mirror image below the water surface (Wolf and Krotzsch 1995). The degree to which the surface can function as a mirror for an animal is influenced by underwater visibility (range in which the reflection can be seen), the stillness of the surface, and light conditions inside and out of the water. This is true both for the captive as well as the natural environment of dolphins, ensuring that all dolphins have access to reflecting surfaces and potential experience with their own mirrored image. This could explain why I did not observe contingency behaviour when animals were presented with additional mirrors. They already have extensive experience with mirrors. It is uncertain whether dolphins in the wild use the water surface to inspect themselves (e.g. when remoras attach themselves to a dolphin). Future studies should look at the potential use of the water surface in this way. If this is a common behaviour, dolphins may have a unique pre-disposition to use mirrors that could influence their perception of themselves.

4.6 **Visual abstract chapter 4:** Mirror self-inspection in bottlenose dolphins





5

General Discussion

5.1 Introduction

This thesis has contributed to research on animal recognition by focusing on specific aspects of acoustic individual recognition as well as visual self-inspection in bottlenose dolphins. As outlined in chapter 1, the field of animal recognition studies is growing, with contributions spanning most taxa of the animal kingdom, and, variously, focusing on acoustic, visual, tactile, or chemosensory cues, and recognition processes interrogated from species-level down to the individual animal. In a first step, this thesis suggested ordering this vast field of research by introducing the categories of recognition level and modality. Level refers to the different types of recognition which take place between animals, ranging from recognition between different species, to recognition between parents and their offspring, to individuals within a social group. Modality refers to the mechanistic process by which recognition cues are transferred between sender and receiver. This thesis demonstrated the added benefit such a categorisation could bring to the field of animal recognition studies by surveying a broad spectrum of scientific contributions and discussing them according to its two ordering categories. In doing so, this thesis provided a comprehensive review of scientific contributions to the field of animal recognition studies in general, and it also highlighted several shortcomings and gaps in the field which future research should aim to address: Firstly, studies should aim to explore the range of modalities within the recognition processes of a specific species. Especially crossmodal recognition studies and experiments could be highly beneficial to explore the role of different cue modalities and their relative contribution to the recognition process. This would also serve to appropriately contextualise studies on specific modalities within the larger communication and recognition process. Secondly, recognition studies should not only identify the signal modality involved in a recognition process, but also the level of recognition at which the signal is hypothesised to be processed by the receiver. On occasion, animal recognition research suffers from imprecision with regards specifically to clearly differentiated recognition levels. Such under-specification of levels may have contributed to a gap in research on individual recognition processes. Clearly, both shortcomings may stem both from the fact that animals frequently communicate cross-modally, as well as from signals functioning at different levels of recognition simultaneously. For example, the identification of own offspring may operate both at kin level as well as at individual level. A precise use and discussion of existing terms and concepts could help to remedy some of the definitional confusion still present in the field, and allow for easier comparison. In order to contribute to a better understanding of animal recognition, then, it appears to be crucial to both facilitate comparative approaches to describe the underlying mechanisms involved and their evolution across the recognition field. Additionally, it would help to identify knowledge gaps within a species to add to a more comprehensive description and analysis of recognition patterns specific to that species. A focus on individual recognition processes in particular would contribute to closing existing gaps in the field of animal recognition studies.

This thesis added to the field of animal recognition studies by focusing on bottlenose dolphins. Previous research on bottlenose dolphins has shown that their advanced vocal communication and cognitive abilities make them promising subjects for recognition research in general. Previous efforts have often focused on signature whistles, an acoustic signal with a distinctive frequency modulation that allows for individual recognition in this species. Indeed, the acoustic modality appears to be the most sophisticated in bottlenose dolphin recognition, likely because it is most reliable given the dolphins' aquatic lifestyle and corresponding slow transmission of chemosensory signals and often very limited visibility underwater. The high dependence of dolphin calves on their mothers makes reliable recognition signals especially crucial for mother-calf pairs to maintain contact. However, past work has not investigated how dolphin calves develop their signature whistles, and at which point during ontogeny the whistles become stable enough to allow for reliable recognition. I researched this question in chapter 2 by performing a fine-scale analysis of the acoustic changes in the development and the process of signature whistle crystallisation which allow for individual recognition of the calves.

An important source of evidence for vocal production learning involves studies showing that dolphin calves use model sounds from their environment during the development of their signature whistles. I explored this aspect in chapter 3 by analysing the influence of sounds from the environment on the crystallised frequency modulation pattern of signature whistles.

The focus on individual acoustic recognition has left other recognition levels and modalities underexplored. Specifically, the suggestion of highly developed cognitive abilities in bottlenose dolphins has raised questions as to the extent of their recognition of one's own self. Previous studies on these fascinating questions unfortunately suffered from several theoretical and methodological shortcomings, and researchers failed to adjust the mirror mark test methodology to marine mammals. This in turn complicated both insights into bottlenose dolphin capacities for self-recognition as well as comparison across species valuable to assess evolutionary mechanisms towards this specific cognitive ability. I filled this gap within the study field by establishing an adjusted mirror mark methodology that is suitable for testing marine mammals. In chapter 4 I applied this method to test four bottlenose dolphins for their ability for mirror-guided self-inspection.

In the following paragraphs, I discuss the findings of my three chapters in greater detail and with a view to contributing to the recognition field specific insights relevant both to the study of bottlenose dolphins, as well as to future research into mechanisms and processes involved in individual recognition and self-recognition more broadly.

5.2 Acoustic development of an individual recognition signal in bottlenose dolphins

Likely favoured by the limited visibility and the slow transmission of chemosensory signals within the aquatic environment, bottlenose dolphins appear to use mainly the acoustic modality for individual recognition, which is crucial for the maintenance of social relationships in fission-fusion societies. Individual acoustic recognition in terrestrial mammals is often based on voice cues, which are individual differences in sound parameters caused by variation in the morphology of the vocal tract. Voice cues affect every sound that an individual produces. Meerkats (*Suricata suricatta*) for example use voice cues to recognise conspecifics from their social group on an individual basis (Townsend et al. 2012). However, in marine mammals, pressure changes during dives have been shown to affect the vocal tract and its air cavities to an extent that makes voice cues unreliable for diving animals. Bottlenose dolphins encode their identity in whistles with individually distinctive frequency modulations to broadcast their identity, to maintain contact, or when reuniting at sea (Janik and Slater 1998; Janik et al. 2006; Quick and Janik 2012). These so-called signature whistles are true identity signals because, in contrast to voice cues, information necessary for individual recognition is encoded in the modulation of one specific acoustic signal.

Within the fission-fusion societies of dolphins, reliable recognition appears to be most crucial between mothers and their dependent offspring. Dolphin calves are born fully mobile but their survival depends on contact to the mother (e.g. for nursing and protection). Quickly after birth, mothers must start hunting for fish again to be able to provide themselves as well as the calf with nutrients, and it might well happen that the calf stays behind while the mother speeds up to follow prey. In such and other possible scenarios, mother and calf might be separated and have to rely on an acoustic recognition mechanism to be reunited.

Past research has shown that dolphin mothers produce their signature whistles ten times more often before and after giving birth (Mello and Amundin 2005; Fripp and Tyack 2008; King et al. 2016a; King et al. 2016b). This could potentially facilitate imprinting of the calf on its mother’s identity signal, thus allowing the calf to recognise its mother. Calves in turn have been reported to develop a signature whistle within the first year (Caldwell and Caldwell 1979; Sayigh et al. 1990). However, a systematic and comprehensive analysis of the development of the calves’ signature whistles during ontogeny and a calculation of a more accurate crystallisation day have previously been lacking. In chapter 2, I demonstrated how the acoustic structure of dolphin calf vocalisations changes during the first months of life as the whistles become stable and reliable as a recognition signal, and introduced a measurement of stability for signature whistles.

By using the crystallised signature whistles of 48 adult bottlenose dolphins, I calculated a within-individual similarity score to establish a measurement of stability for signature whistles. Even though a calf might produce its final signature whistle (or close variations of it) already early on during ontogeny, it takes between 19 and 23 days until the whistle modulation crystallises and becomes repeatable enough to serve as a reliable recognition signal. In the past, researchers often only reported when a specific modulation pattern started to emerge during ontogeny without taking into account that, crucially, an identity signal must have a high level of repeatability to serve as a reliable recognition signal. Here, I provided the first calculation of the signature whistle crystallisation process in bottlenose dolphin calves. In addition, I described the acoustic changes in the calves’ vocalisations that might facilitate recognition before the calf’s signature whistle even crystallises, and discussed these acoustic findings in light of mother-calf recognition.

Bottlenose dolphin calves start vocalising almost immediately after birth, producing both tonal sounds (whistles) as well as broadband clicks. The occurrence of nonlinear phenomena and biphonations within the early vocalisations of calves is especially noticeable compared to adult dolphins: Young calves often produce whistles with sidebands and chaos, both of which decrease during ontogeny. These nonlinear phenomena are often described in infant cries or scream sounds and it was argued that the high signal variation caused by these phenomena makes them hard to ignore or habituate to. Nonlinear phenomena in infant vocalisations could therefore trigger an additional caregiver response and draw attention to the vocalising calf. Another striking acoustical difference between adult and infant whistles is the occurrence of two independent or overlapping fundamental frequencies (biphonations). In terrestrial mammals biphonations are also a nonlinear phenomenon caused by irregular vibrations of coupled oscillators (Fitch et al. 2002). Dolphins, however, have two independent sets of phonic lips, which means that biphonations can be either a nonlinear phenomenon caused by one pair of phonic lips or two independent vocalisations produced in each nasal passage. This simultaneous vocalisation with both sets of phonic lips regularly takes place when, for example, dolphins whistle and click at the same time (e.g. for echolocation). The percentage of whistles with two fundamental frequencies decreases during ontogeny, while the percentage of whistles with overlapping broadband clicks simultaneously increases. The lack of vocalisations recorded with both two fundamental frequencies as well as broadband clicks could hint at a production of the two sounds in both nasal passages rather than a nonlinear phenomenon. It is likely that the calves' control of their vocal production apparatus improves over time, and that nonlinear phenomena and biphonations are effects of both maturation and production control.

As nonlinear phenomena as well as biphonations appear to be quite rare within adult whistles, they could also have an adaptive value as a recognition cue to separate calves from adults within a social group. The whistles of calves undergo a number of drastic acoustic changes during the first weeks of life until a stereotyped frequency modulation pattern gradually crystallises within the third week of life. But even before the calves start to produce signature whistles, their whistle parameters are already acoustically distinctive enough to allow for recognition based on voice cues. As discussed before, voice cues are unreliable for marine mammals as they are strongly affected by pressure changes during dives, and maturation and physical growth of the body and the vocal tract during ontogeny cause rapid changes in these cues. However, it might well be possible that voice cues (as well as nonlinear phenomena) help the mother bridge the crucial first weeks before the calf develops a signature whistle that allows for recognition independently of voice cues.

The development of true identity signals, such as dolphin signature whistles, has often been suspected to require the ability of vocal production learning, which means that an individual uses the experience with sounds from its environment to shape the modulation of its own identity signal. Greater horseshoe bats (*Rhinolphus ferrumequinum*), for example, develop signature calls that are partly influenced by vocal learning and show high similarities to acoustic aspects of the mother's call (Jones & Ransome 1993). Previous research into bottlenose dolphins has shown that dolphin calves develop signature whistles most similar to not closely associated individuals from the same population (Fripp et al. 2005). Alternatively, one study reported that especially male calves appear to develop signature whistles most similar to their mothers' (Sayigh et al. 1990), but this sex bias could have been mainly driven by the small sample size in this study. In captive facilities it has been reported that calf whistles show acoustic similarities to the whistle that human trainers produce during positive reinforcement training (Miksis et al. 2002). It remained unclear, however, whether vocal production learning actually plays a role in signature whistle development.

In chapter 3, I found that sounds from the calves' environment indeed influence the modulation pattern of the crystallised signature whistle. This in turn strengthens the evidence for vocal production learning in the development of signature whistles. The signature whistles of six out of seven dolphin mothers appear to serve as a model sound for the signature whistles of their calves. Regardless of sex, seven (out of nine) calves produced crystallised whistles with the highest similarity to their mother's whistle, but no significant higher similarity to their father's (compared to other dolphins within the facility), which renders genetic reasons an unlikely explanation for the similarity to the mothers. To investigate whether the whistles of human trainers can function as model sounds for vocal production learning, I compared trainer whistles to the signature whistles of three different groups of dolphins: wild dolphins, individuals that were born in the wild but then transferred into human care, and dolphins born and raised in captivity. Even though there was no higher similarity between the overall frequency modulation pattern of the whistle contours in the signature whistles of dolphins born and raised in captivity and the trainer whistles, these dolphins' whistles showed significantly higher acoustic similarities to the trainers in specific sound parameters (compared to the two other dolphin groups). In particular, they showed higher similarities in the start and end frequency, and had a lower frequency modulation range that was most similar to the unmodulated trainer whistle (compared to the two other dolphin groups).

5.3 The mirror mark test in marine mammals and the evolution of self-recognition

The mirror mark test has been developed as a method to test non-human primates for self-recognition. For the first time, it allowed testing for self-recognition in animals without language abilities (Gallup 1970). While initially developed for primates, the procedure has been applied to a huge variety of species, which adds high comparative value to the test. Early research efforts could only find evidence for self-recognition in humans and apes, hinting at the possibility that these cognitive abilities might have evolved in our primate ancestors. This was challenged when first an Asian elephant (Plotnik et al. 2006), and then magpies (Prior et al. 2008) also passed the mirror mark test. These findings indicated a convergent rather than homologous evolution of self-recognition. Bottlenose dolphins may be seen as especially promising candidates to test for self-recognition because they show many advanced cognitive abilities despite not sharing any significant evolutionary history with primates. Evidence for self-recognition in dolphins would therefore allow for better insights into the evolution of self-recognition. However, their different physiology and ecology makes a direct application of the standard mirror mark test difficult if not impossible. And indeed, several previous approaches to applying the mirror mark test to dolphins in the past exhibited crucial methodological flaws, and thus results remained inconclusive (Gregg 2013; Harley 2013; Manger 2013; Güntürkün 2014). In chapter 4, I aimed to fill this gap by introducing an adjusted mirror mark test procedure suitable for marine mammals. In the original test, individuals were first marked on a body part they could not see without a mirror. The test was then passed if the animal checked its reflection and in response showed a self-directed behaviour by touching the marked spot on its own body. As an adaptation to the aquatic environment, dolphins have very streamlined bodies and are physically not able to touch a marked spot on their body with their limbs. While previous research provided initial descriptions of potentially explorative behaviours in front of the mirror, I used the orientation of the body towards a marking as a possibly passing criterion. By testing four bottlenose dolphins with this adjusted methodology, I could show that the animals orientate themselves towards the visibly marked side, providing evidence for mirror-guided self-inspection in this species. Note that evidence for mirror-guided self-inspection need not be interpreted as directly causally linked to self-recognition abilities. This distinction mirrors debates around the interpretation of the original mark test: some authors claim that passing the test suggests self-awareness or even consciousness (e.g. Gallup 1983, 1985, 1998; Marten and Psarakos 1994; Povinelli et al. 1993), or may at least serve as evidence for self-recognition (de Veer and van den Bos 1999). Others argue that mark-directed behaviours are merely a form of social mirroring (Heyes 1994; Swartz 1997; Morin 2011) and demonstrate a general ability to collate representations (Suddendorf and Butler 2013). Similarly, the extrapolation from mirror-guided self-inspection to self-recognition in bottlenose dolphins should be treated with caution. It is possible, however, that the former may function as a preliminary step towards the latter in terms of neural capacity. While independent replication and additional evidence from other species would be highly desirable, my findings thus support an independent evolution of the neural capacities necessary for mirror-guided self-inspection.

During the marking trials of the mirror mark tests, one of the dolphins started to position itself within one meter of depth, all the while turning the marked eye to the water surface and repeatedly turning over to the other side. The dolphin showed this stationary turning behaviour exclusively when it received a visible marking, and turned significantly more often towards the marked side. The water-air boundary presents a reflective surface from inside the water due to the reflection of light (Wolf and Krotzsch 1995; Dibble et al. 2017). Dolphins thus have extensive access to reflecting surfaces, both in captivity as well as in the wild. It remains unclear, however, to which extend wild dolphins have experience with their own reflection and whether they use the water surface for self-inspection.

5.4 Conclusion and further research

This thesis analysed the field of animal recognition studies in general, established criteria to sort the field (focusing on recognition level and modality), and addressed gaps within the field on two different levels. First, I focused on acoustic individual recognition in bottlenose dolphins and explored the acoustic development of signature whistles in neonates to gain a better understanding of when and how these signals allow for individual recognition. I then focused on the potential learning mechanisms involved during ontogeny and provided evidence for vocal production learning. Future work should focus both on more specific questions within dolphin signature whistle development as well as on using the methods and stability thresholds established in this thesis in research on other species to gain a more comprehensive understanding of the development of individually distinctive recognition signals. Some particularly interesting study questions to follow up on include:

- Are dolphin mothers capable of acoustically recognising their calves before signature whistle crystallisation? Which role do nonlinear phenomena and voice cues play in this process, and do nonlinear phenomena trigger an additional caregiver response?

- Are the two independent fundamental frequencies in calf vocalisations produced in one or both nasal passages? Are these biphonations an indicator that the calf has to learn how to control its vocal apparatus?

- Is the similarity between the signature whistles of calves and sounds from their environment (as a result of vocal production learning) influenced by association indices between the individuals or by whistle exposure rates? Does the frequency modulation of the mother's signature whistle influence the likelihood of the whistle serving as a model sound? Does the level of contingent vocal feedback influence the development of signature whistles?

Secondly, I focused on adapting the mirror mark test for bottlenose dolphins, and established a method that is suitable to testing marine mammals for mirror-guided self-inspection. This allows for a more comprehensive understanding of the evolution of underlying cognitive abilities necessary for self-recognition. In future work on self-inspection and self-recognition, it would be highly desirable to address the following research goals:

- To check for a potential reinforcement effect caused by the yellow markings. This could be achieved by testing the dolphins' reaction towards markings on other individuals.

- To collect behavioural data from wild populations to explore the usage of the water surface for self-inspection in the natural environment.

- To check for behaviour towards markings on other individuals compared to marking on the own body as an indicator for self/other discrimination

- To develop additional controls with self-directed behaviours as a proxy for self-recognition (e.g. the potential removal of a mark by rubbing it off after checking the mirror reflection)

- To use the adjusted mirror mark test presented in this thesis to test other marine mammal species to gain a better understanding about the evolution of self-recognition.

- To adjust the mirror mark test to other taxa that might have been tested with false negative results due to an unsuitable test method.

- To further improve our understanding about the self-recognition process by using crossmodal testing. This could not only help improve comprehension of the modalities involved in bottlenose dolphin self-recognition, but also greatly increase our understanding about self-recognition in other taxa.

Finally, studies in the field of animal recognition should aim to follow the recognition framework suggested in chapter 1 by addressing the following questions:

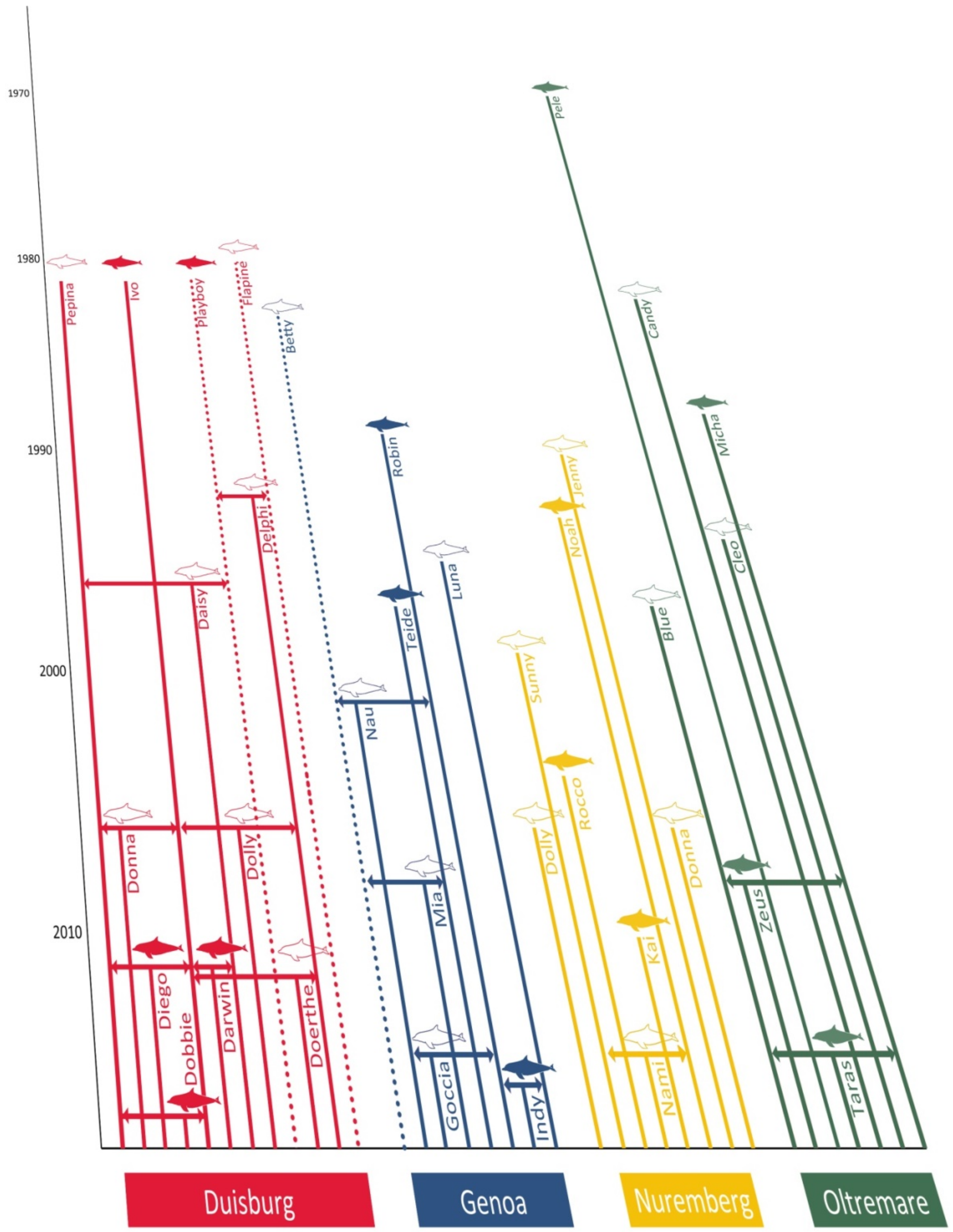
- Is the appropriate term for the studied recognition level used, and are the criteria for this recognition level fulfilled?

- Can a different type of recognition (e.g. individual recognition) be excluded? If not, can and/or should it be investigated?

- Which signal modality or which crossmodal combination was investigated in the study? Which modalities might play an additional role in the recognition process of the respective species and should be investigated in future research?

- Should the respective recognition process be discussed and investigated in a broader and possibly comparative approach to add to a better understanding of evolutionary mechanisms behind recognition?

Appendix

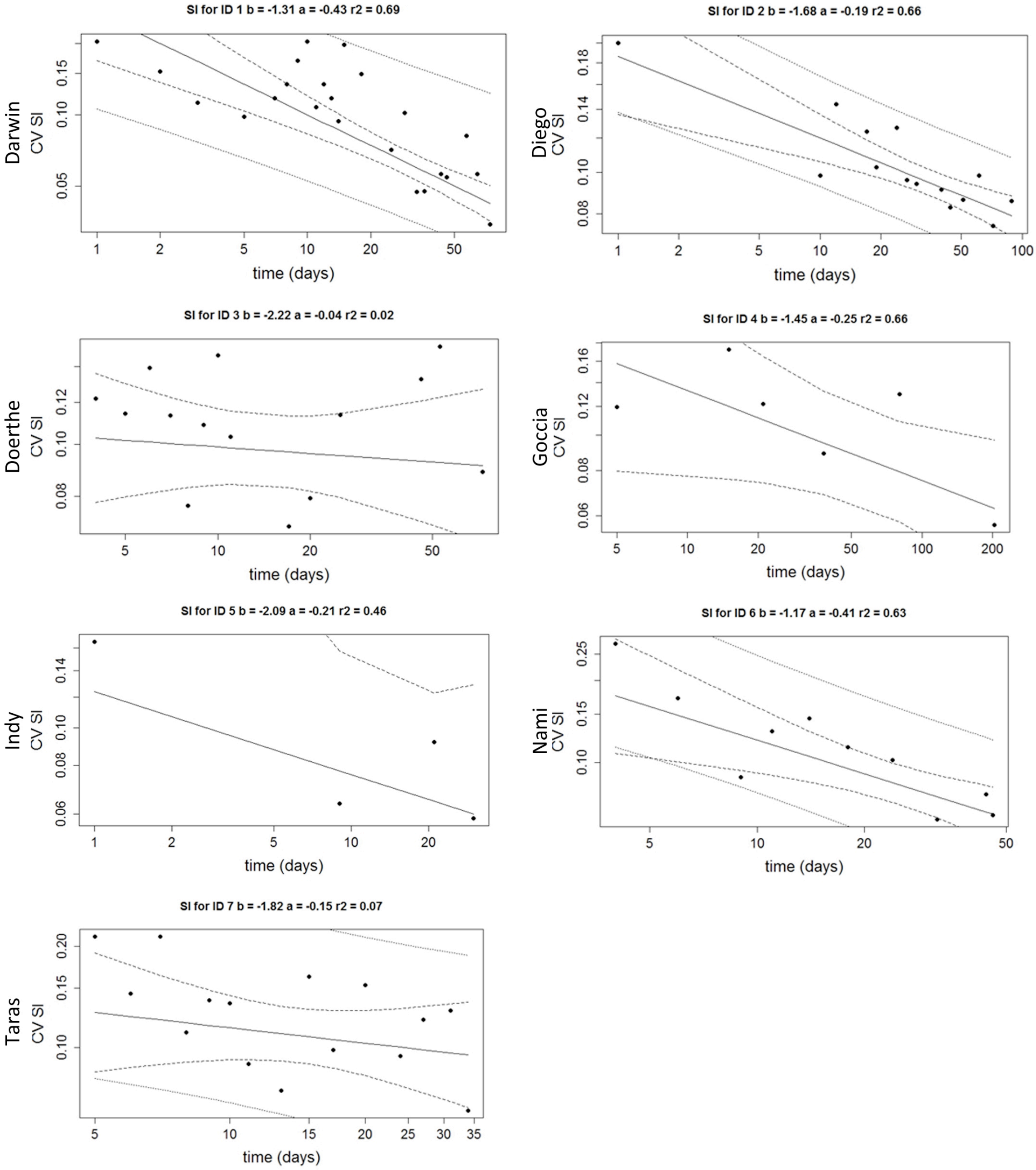


Appendix Figure I: Genealogical tree of the four zoological facilities. Males are indicated by solid symbols, females by no-fill symbols, horizontal lines indicate the birth year as well as parentage, and dotted lines indicate individuals that were not present in the facility during data recording.

Appendix

Appendix Table I: Life history data and recording days during ontogeny of the seven calves.

facility	calf ID	calf sex	date of birth	mother ID	father ID	Day of life recorded																						
Zoo Duisburg	**Darwin**	male	05.09.2011	Daisy	Ivo	1	2	3	5	7	8	9	10	11	12	13	14	15	18	25	29	33	36	43	46	57	64	74
	Diego	male	21.08.2011	Pepina	Ivo	1	10	12	17	19	24	27	30	40	44	51	61	72	89									
	Doerthe	female	27.08.2011	Delphi	Ivo	4	5	6	7	8	9	10	11	17	20	25	46	53	73									
Tiergarten Nuremberg	**Nami**	female	31.10.2014	Sunny	Noah	4	6	9	11	14	18	24	32	44	46													
Aquarium Genoa	**Goccia**	female	01.09.2014	Nau	Teide	5	15	21	38	80	204																	
	Indy	male	20.08.2015	Luna	Robin	1	9	21	30																			
Parco Tematico Oltremare	**Taras**	male	09.08.2014	Blue	Micha	5	6	7	8	9	10	11	13	14	15	17	20	24	27	31	34							



Appendix Figure II: Coefficient of variation of the similarity score (CV_{SI}) over time plotted for each calf (least-square regression model).

Appendix Table II: Comparison of whistle parameters between different groups of dolphins and human trainer whistles. Results of two-way ANOVA and post-hoc test.

Whistle parameter	p	r^2	pairwise comparisons					N
$\log(F_{min})$	<0.001	0.23	group	1	2	3	4	
			1		**p=0.001** SE=0.012 Δμ=0.04	**p=0.005** SE=0.007 Δμ=-0.021	p<0.001 SE=0.011 Δμ=-0.195	728
			2	**p=0.001** SE=0.012 Δμ=-0.04		p<0.001 SE=0.012 Δμ=-0.061	p<0.001 SE=0.015 Δμ=-0.236	141
			3	**p=0.005** SE=0.007 Δμ=0.021	p<0.001 SE=0.012 Δμ=0.061		p<0.001 SE=0.011 Δμ=-0.175	604
			4	p<0.001 SE=0.011 Δμ=0.195	p<0.001 SE=0.015 Δμ=0.236	p<0.001 SE=0.011 Δμ=0.175		199
$\log(F_{max})$	<0.001	0.38	1		**p=0.001** SE=0.010 Δμ=0.039	**p=0.001** SE=0.006 Δμ=0.141	p<0.001 SE=0.008 Δμ=0.237	728
			2	**p=0.001** SE=0.010 Δμ=-0.039		p<0.001 SE=0.010 Δμ=0.102	p<0.001 SE=0.012 Δμ=0.197	141
			3	**p=0.001** SE=0.006 Δμ=-0.141	p<0.001 SE=0.010 Δμ=-0.102		p<0.001 SE=0.009 Δμ=0.096	604
			4	p<0.001 SE=0.008 Δμ=-0.237	p<0.001 SE=0.012 Δμ=-0.197	p<0.001 SE=0.009 Δμ=-0.096		199
$\log(F_{start})$	<0.001	0.05	1		**p=0.257** SE=0.016 Δμ=0.018	p<0.001 SE=0.009 Δμ=-0.084	p<0.001 SE=0.014 Δμ=-0.122	728
			2	**p=0.257** SE=0.016 Δμ=-0.018		p<0.001 SE=0.016 Δμ=-0.102	p<0.001 SE=0.019 Δμ=-0.140	141
			3	p<0.001 SE=0.009 Δμ=0.084	p<0.001 SE=0.016 Δμ=0.102		**p=0.007** SE=0.014 Δμ=-0.038	604
			4	p<0.001 SE=0.014 Δμ=0.122	p<0.001 SE=0.019 Δμ=0.140	**p=0.007** SE=0.014 Δμ=0.038		199
$\log(F_{end})$	<0.001	0.22	1		**p=0.4** SE=0.016 Δμ=0.014	p<0.001 SE=0.01 Δμ=0.18	p<0.001 SE=0.014 Δμ=0.158	728
			2	**p=0.4** SE=0.016 Δμ=-0.014		p<0.001 SE=0.017 Δμ=0.167	p<0.001 SE=0.02 Δμ=0.144	141
			3	p<0.001 SE=0.01 Δμ=-0.18	p<0.001 SE=0.017 Δμ=-0.167		**p=0.125** SE=0.015 Δμ=0.022	604
			4	p<0.001 SE=0.014 Δμ=-0.158	p<0.001 SE=0.02 Δμ=-0.144	**p=0.125** SE=0.015 Δμ=-0.022		199
$\log(F_{range})$	<0.001	0.49	1		**p=0.223** SE=0.024 Δμ=0.029	p<0.001 SE=0.014 Δμ=0.296	p<0.001 SE=0.021 Δμ=1.053	728
			2	**p=0.223** SE=0.024 Δμ=-0.029		p<0.001 SE=0.024 Δμ=0.267	p<0.001 SE=0.028 Δμ=1.024	141
			3	p<0.001 SE=0.014 Δμ=-0.296	p<0.001 SE=0.024 Δμ=-0.267		p<0.001 SE=0.021 Δμ=0.757	604
			4	p<0.001 SE=0.021 Δμ=-1.053	p<0.001 SE=0.028 Δμ=-1.024	p<0.001 SE=0.021 Δμ=-0.757		199
$\log(F_{duration})$	0.3	0.002						

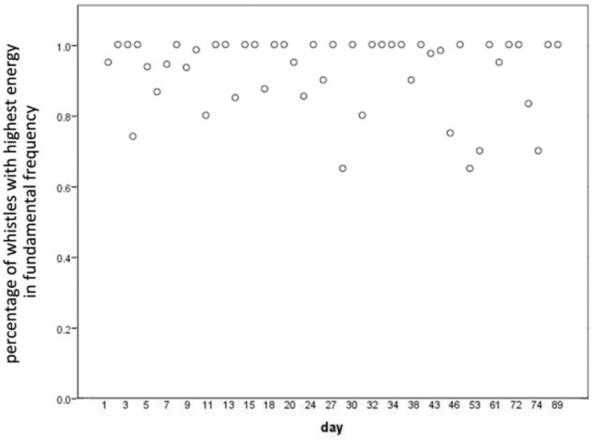
Groups: 1) wild population; 2) born in the wild, lives in captivity; 3) born in captivity; 4) trainer
P-values of pairwise comparisons that showed no significant difference (p≥0.001) are marked in **bold**.

Appendix Table III: Life-history data of all dolphins from the Nuremberg and Duisburg facilities.

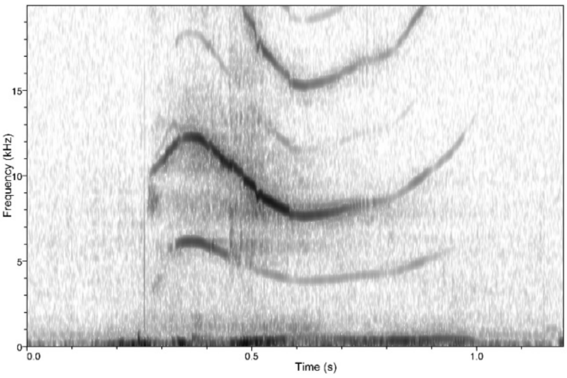
Facility	Name	Sex	Year born	facility born	born in captivity
Nuremberg	Anke	female	~1983	Wild	No
	Arnie	male	2000	Soltau	Yes
	Dolly	female	2007	Duisburg	Yes
	Donna	female	2007	Duisburg	Yes
	Jenny	female	~1987	Wild	No
	Kai	male	2010	Haderwijk	Yes
	Moby	male	~1960	Wild	No
	Noah	male	1993	Nuremberg	Yes
	Rocco	male	2005	Haderwijk	Yes
	Sunny	female	1999	Soltau	Yes
Duisburg	Daisy	female	1996	Duisburg	Yes
	Darwin	male	2011	Duisburg	Yes
	Delphi	female	1992	Duisburg	Yes
	Djego	male	2011	Duisburg	Yes
	Dörthe	female	2011	Duisburg	Yes
	Ivo	male	~1979	wild	No
	Pepina	female	~1981	wild	No
	Debbie	female	2015	Duisburg	Yes
	Dobbie	male	2016	Duisburg	Yes

Appendix Table IV: ID, sex, and year of birth of dolphins recorded in Sarasota.

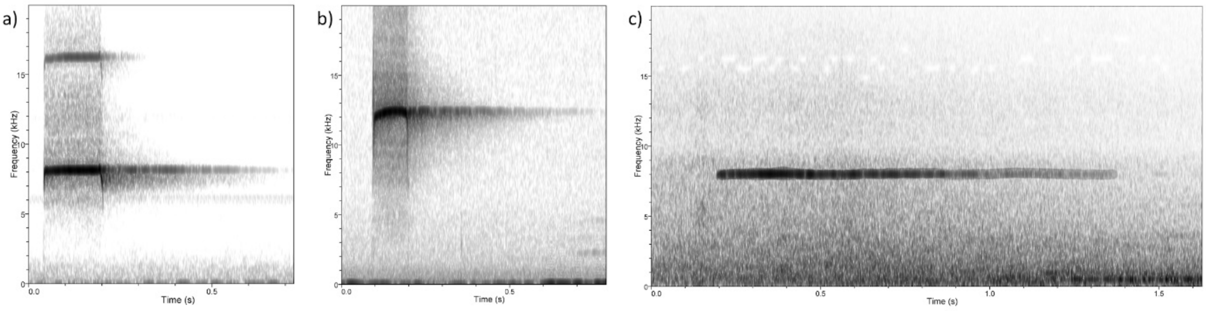
ID	sex	born
F20	male	1989
F33	female	1982
F128	male	1992
F137	female	2000
F187	female	2003
F221	female	2009
F229	female	2008
F235	female	2010
F280	male	2010
F282	male	2008



Appendix Figure III: Percentage of whistles with energy in the fundamental frequency (f_0) over time during the developmental phase of seven calves.



Appendix Figure IV: Spectrogram of a whistle with the highest energy in the first harmonic.



Appendix Figure V: Spectrogram examples of trainer whistles from different facilities: a) Nuremberg (ID2), b) Oltremare (ID1), c) Duisburg (ID3).

Appendix Figure VI: Darwin positioning himself right underneath the reflective water surface during a marking trial and turning from side to side.

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An understanding of the natural world and what's in it
is a source of not only a great curiosity but great fulfillment.

(David Attenborough)