The role of touch in marine mammal sociality: a review and future directions

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Abstract

While social living has many advantages, it also has significant challenges associated with differences in individual interests, abilities, and intentions. Individuals in social species rely on diverse behaviours and signals across senses to mediate their relationships. In some species—particularly primates—touch plays a key role in establishing, affirming, and repairing social bonds. However, the degree to which touch is involved in pro-social behaviours in mammalian taxa is poorly understood. Marine mammals have unique adaptations to different levels of aquatic life and environments and display diverse social structures. They, therefore, represent a valuable source of comparison to deepen our understanding of the behavioural mechanisms that enable social living.

Here, we examined current trends in research on social touch in marine mammals and evaluated existing evidence for its affiliative functions. Because of the logistical challenges associated with observing touch in species that spend most of their lives underwater, only a few odontocete species and captive populations dominate the existing literature. The prevalence of tactile interactions outside the mother-infant relationship is influenced by a species' social structure. Still, we found that touch was involved in mediating a range of relations, from ephemeral and presumably anonymous to life-long individualized social bonds. We suggest leveraging emerging technologies, complemented by different behavioural data across modalities, long-term monitoring, and ensuring comparability to expand and deepen our understanding of how animals mediate their social relationships.

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1. Introduction

Group living provides numerous benefits to individuals, but comes with costs arising from competing interests and intentions among group members (De Waal, 2000). Therefore, social species rely on *affiliative signals*—behaviours that promote group cohesion by fostering mutual attraction and tolerance, supporting cooperation, and preventing or resolving conflict—to navigate social interactions. Affiliative signals can be communicated across diverse and often simultaneously occurring modalities, including visual, chemical, acoustic, vibrational, and tactile. Tactile signals (henceforth also referred to as touch), require the highest level of mutual proximity and are therefore often reserved for important interactions (e.g., with kin or social group members) (Weber, 1973).

Traditionally underrepresented in the literature when compared to other modes of communication, the role of touch in mediating social interactions has garnered increasing interest in recent decades (Dunbar, 2010; Hertenstein et al., 2006; Jablonski, 2021; Morrison et al., 2010). This is especially the case for primates, where research on affiliative touch, especially allogrooming and socio-sexual interactions, has been pivotal to our understanding of the nature of species-specific interactions and the evolutionary theories that explain social living (**Figure 1**; De Waal & Aureli, 1997; Dunbar, 2010; Seyfarth & Cheney, 1984; Whitham & Maestripieri, 2003). The importance of affiliative touch in humans has led researchers to refer to skin as a “social organ” attuned to perceiving gentle forms of touch that trigger neurochemical, physiological, and emotional responses that contribute to bonding and social development (Morrison et al., 2010).

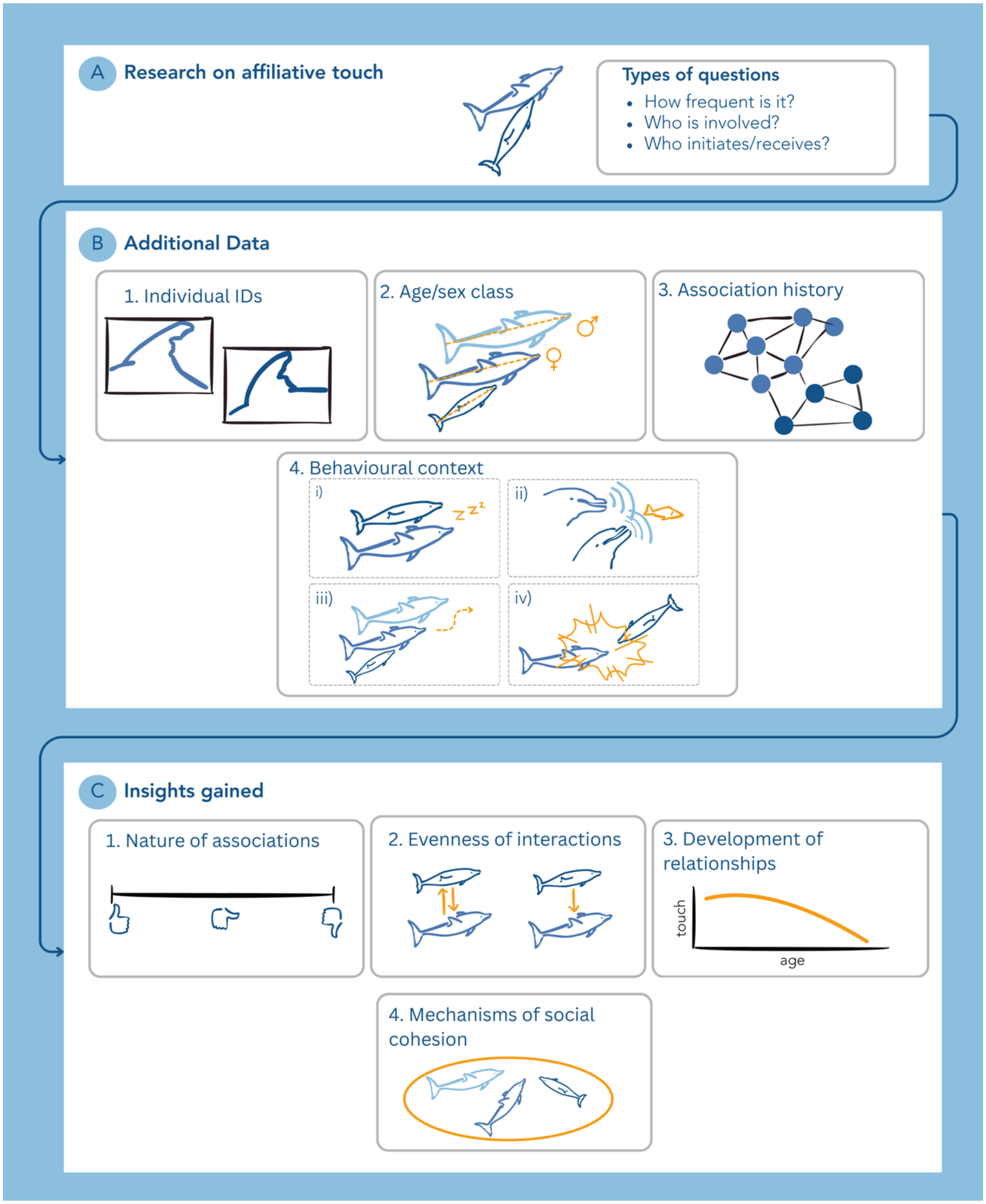

Figure 1. How studies of social touch inform our understanding of the underpinnings of sociality. Research on affiliative touch (A) combined with additional contextual data (B) on individual identity (B-1), age/sex class (B-2), association history (B-3), and the behavioural context (B-4); e.g. resting (i), foraging (ii), travelling (iii) and agonistic interactions (iv)), can provide insights in to various aspects of social living (C). These include the nature of associations beyond proximity-based inferences (C-1), the evenness of interactions (C-2), the development of relationships with age (C-3), and the mechanisms underlying social cohesion (C-4). Image created in Canva.

Most of our knowledge about the social roles of touch comes from research on well-studied terrestrial taxa, including primates, ungulates, rodents and bats. This focus likely reflects an interest in understanding human social behaviours through studying our closest relatives, other primates, and the relative ease in observing these interactions in terrestrial taxa (Carter and Leffer, 2015; Hertenstein et al., 2006; Hodgson et al., 2024; Schino, 1998). Here, we argue that marine mammals (cetaceans—dolphins, porpoises, and dolphins; fissipeds—sea otters and polar bear; pinnipeds—sea lions, seals, and walruses; and sirenians—manatees and dugongs) offer a promising opportunity for expanding our understanding of how individuals navigate social living across diverging phylogenetic histories, social structures, and environmental pressures (Mann et al., 2000; Trillmich and Cantor, 2018).

Marine mammals are a polyphyletic group that displays diverse levels of sociality, from loose and brief interactions to lifelong social bonds, with varying degrees of complexity (Mann et al., 2000; Trillmich and Cantor, 2018). Distinct marine mammal taxa independently evolved for semi- or fully aquatic lives at sea. This process involved dramatically modifying their sensory systems, including their tactile senses (Box 1). Despite experiencing vastly different evolutionary pathways and environmental conditions, some marine mammal species share remarkable similarities in their social structures to those of other terrestrial mammals (Rendell et al., 2019; Whitehead, 2024). Understanding how marine mammal species navigate their social relationships can therefore expand our understanding of sociality. While analyses of association patterns based on spatiotemporal proximity have revealed valuable aspects of the social structure of several species of marine mammals, the nature of their social relationships is not always clear. This gap primarily stems from the difficulty of observing the behaviours of individuals who spend most of their time underwater or in remote locations. Additionally, even when individuals are at the surface, the angle at which they can be seen from a vessel, shoreline, or platform does not usually allow us to discern fine-scale interactions. However, the emergence of newly accessible technologies like uncrewed aerial vehicles (UAVs), animal-borne video recorders (ABVRs), and thermal cameras is pushing the boundaries of what researchers can observe in marine mammals.

In this review, we start by synthesizing the existing theory on the affiliative functions of touch and hypothesized underlying mechanisms. Next, we examine the trends and gaps in research on affiliative touch in marine mammals and critically evaluate the evidence for affiliative functions of touch in this group. We discuss the interplay between observed patterns of affiliative touch and social structure. Finally, we suggest future avenues to deepen our understanding of the role of touch in mediating social interactions across marine mammals and other similarly under-studied taxa.

2. The affiliative role of touch in terrestrial mammals

Touch can be involved in diverse affiliative functions through distinct underlying neurochemical, psychological, and cognitive mechanisms (**Figure 2**). Specifically, touch can contribute towards increasing mutual tolerance and attraction, facilitating cooperation, managing conflict, and as a signal of shared intent (Carter and Leffer, 2015; De Waal and Aureli, 1997; Hertenstein et al., 2006; Hodgson et al., 2024; Moscovice et al., 2019; Seyfarth and Cheney, 1984). While we discuss these affiliative functions separately, they can, and often do, interact and enforce each other.

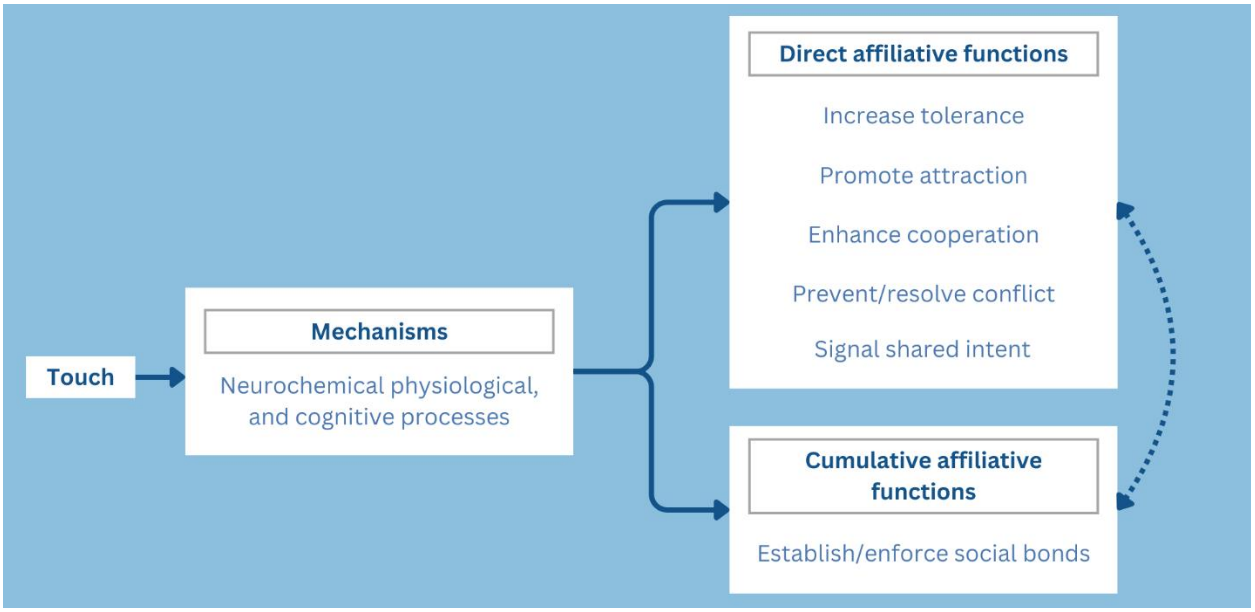

Figure 2. Theoretical framework showing how touch can influence affiliative functions in social species. The hypothesized mechanisms are non-exclusive and may underly diverse affiliative functions simultaneously. **Direct** affiliative functions include those resulting from a single tactile interaction (either immediately or in the near future) while **cumulative** affiliative functions are those which result from a history of repeated interactions. The distinction between direct/cumulative functions exists in a continuum, rather than being truly discrete. As indicated by the dashed arrow, direct affiliative functions may also contribute towards cumulative functions (i.e., the development of a social bond) and vice-versa.

2.1 Establishing and enforcing social bonds

Gentle (i.e., non-painful) forms of touch like petting, grooming, and socio-sexual touch, can promote mutual attraction and tolerance by triggering the release of neuropeptides (e.g., serotonin, oxytocin, dopamine) associated with emotional and physiological well-being, and feelings of pleasure of both givers and receivers (Dunbar, 2010; Hertenstein et al., 2006; Morrison, 2016). Through repeated interactions, touch can contribute towards establishing and affirming *social bonds*, which we define here as a perception shared by two individuals, resulting from cognitive and psychological processes, that gives rise to an affiliative relationship (Dunbar and Shultz, 2010). While assessing internal states may be hard, the strength of social bonds can be inferred from levels of spatial proximity over time and mutual tolerance (Dunbar and Shultz, 2010). The neurophysiological processes set forth by touch are also critical to the establishment of mother-infant bonds in primates and rodents as they contribute to increased maternal behaviour, infant well-being, and social development (Carozza and Leong, 2021; Hertenstein et al., 2006; Okabe et al., 2012).

2.2 Enhancing the likelihood of cooperation

Forms of touch that benefit the receiver (e.g., parasite removal) can also be exchanged for cooperation with varying levels of symmetry (Barelli et al., 2011; Carter et al., 2020; Hodgson et al., 2024; Seyfarth and Cheney, 1984). For example, allogrooming can be reciprocally exchanged for further grooming (Hodgson et al., 2024; Seyfarth, 1977), coalitionary support against threats (Seyfarth and Cheney, 1984), and food sharing (Carter et al., 2020). In hierarchical societies, individuals with higher status—who have access to shareable benefits—are often more likely to receive touch, while subordinates—who could benefit from said social benefits—are more likely to provide touch (Hodgson et al., 2024; Jablonski, 2021; Seyfarth, 1977). These interactions are especially valuable in facilitating cooperation among unrelated individuals and across dominance hierarchies (Seyfarth, 1977; Seyfarth and Cheney, 1984).

However, interpreting a correlation between likelihood of cooperation and the frequency of tactile interactions requires caution, as different mechanisms can underly this pattern (Brosnan and De Waal, 2002; Schino and Aureli, 2010). On one hand, reciprocity may be achieved by individuals mirroring each other’s disposition, or reflecting a history of mutual affinity resulting from an existing social bond (Brosnan and De Waal, 2002; Schino and Aureli, 2010). Alternatively, calculated reciprocal exchanges can rely on individuals' ability to track past interactions and inform future cooperation (Brosnan and De Waal, 2002). Discerning the processes underlying observed patterns of reciprocity is challenging, as it involves accounting for confounding factors (like general association patterns and kinship) or tracking exchanges within dyads over time (Brosnan and De Waal, 2002).

2.3 Managing conflict

Touch can also play a pivotal role in conflict resolution by alleviating tension and reducing arousal, thereby avoiding conflict, repairing social bonds, and preventing recurrence (De Waal, 2000, 1986; De Waal and Aureli, 1997; Spruijt et al., 1992). Reconciliatory and appeasement behaviours may be initiated by victims, aggressors, and bystanders alike (Baan et al., 2014; De Waal, 1986; Hodgson et al., 2024; Schino, 1998). An ability to mediate conflict is crucial to sustain group living among individuals who may rely on each other for cooperation but have competing interests (De Waal, 2000).

2.3 Signaling shared intent

Some ‘uncomfortable’ forms of touch (e.g., those directed at vulnerable areas such as genitals, eyes, or bellies, as well as play fights) may also be exchanged to test the quality of an association between individuals and establish trust (Zahavi, 1977). According to the “bond-testing hypothesis,” individuals will tolerate stressful or potentially costly contact with others if they have a shared interest, making this type of social touch an honest signal of intent (Zahavi, 1977). The bond-testing hypothesis has been used to explain the non-aggressive, albeit risky, greeting rituals between male bonobos, which involve genital manipulation and mounting (Whitham and Maestripieri, 2003), and the peculiar social rituals of capuchin monkeys, which involve mutual eye-poking and finger intrusions in each other’s nostrils (Perry, 2011).

4. What do we know about touch in marine mammals?

4.1 Trends and gaps

We conducted a scoping review of literature related to *social touch* within marine mammal taxa, which we define here as any form of intraspecific body contact between individuals excluding events classified by authors as aggression, copulation, or suckling/nursing (**Appendix 1 –** Scoping review details). Of 180 initial studies selected for review, those that only referred to social touch as a subset of a broader behavioural category (e.g., socializing or interacting, *n*=43) were omitted from further analyses (**Appendix 2 –** Table S2.1).

Across the remaining 137 studies, we found reports of social touch in all groups of marine mammals, though references were unevenly distributed across 43 species (**Figure 3**). Most studies focused on cetaceans (*n*=93) with fewer on pinnipeds (*n*=28), sirenians (*n*=11), and fissipeds (*n*=5). Only 80 of these studies provided evidence for affiliative functions of touch (**Appendix 2 –** Table S2.2); the rest addressed other aspects of social touch (e.g., its role in disease transmission, thermoregulation, laterality, relation to environmental factors, and individual variation). Twenty-one species were represented in research providing evidence for affiliative functions of touch, with the highest percentage of studies coming from delphinids (54.8%; *n*=46). Moreover, a few odontocete species accounted for a disproportionate number of these studies, with those focused on common bottlenose dolphins (*Tursiops truncatus*), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), and belugas (*Delphinapterus leucas*) representing half of the references (*n*=40).

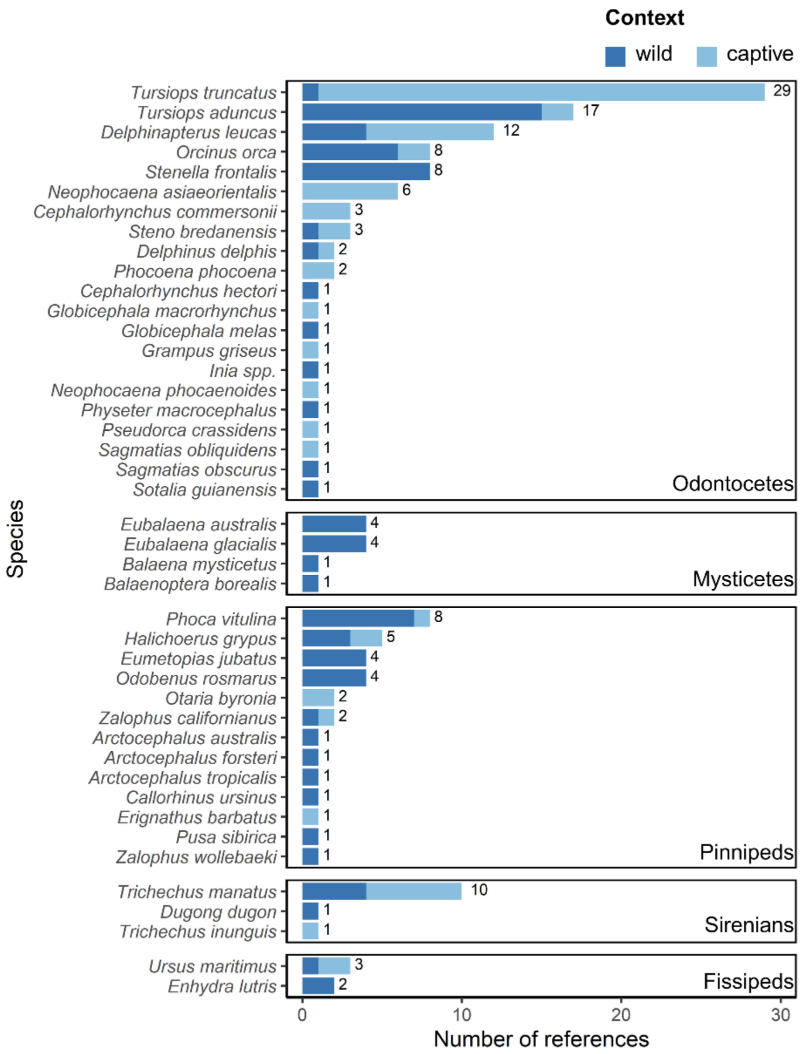

Figure 3. Summary of studies on social touch in marine mammals in our scoping review, by species. Studies are coloured by context. Numbers at the end of each bar show the total number of references for each species.

The uneven taxonomic coverage of research on the affiliative role of touch in marine mammals primarily reflects logistical challenges in observing touch in species that spend most of their lives in aquatic or remote habitats. This results in a substantial knowledge gap regarding behaviours that take place underwater and species that inhabit remote habitats and spend more time at sea. For instance, beaked whales (Ziphiidae), who are typically skittish and spend little time near the surface, and polar bears (*Ursus maritimus*), whose social interactions often occur in dens within harsh Arctic environments, were rarely mentioned (Hooker et al., 2019; Owen, 2021). Researchers may also face challenges or lack the motivation to publish anecdotal observations if these behaviours are observed infrequently. As a result, some observations of tactile behaviours may not be readily accessible in the literature.

Some of the challenges associated with observing tactile behaviours in marine mammals have been overcome by research on captive individuals, where even covert behaviours can more easily be monitored. For example, all research on the social tactile behaviour of common bottlenose dolphins, Commerson's dolphins (*Cephalorhynchus commersonii*), finless porpoises (*Neophocaena asiaeorientalis*), and a high proportion of references on belugas, manatees (*Trichechus manatus),* and polar bears come from studies on captive individuals (**Figure 3**). Captive settings allow for the close observation of a group of known individuals over time, yielding valuable knowledge on the social functions of touch. However, captive research frequently involves small groups of animals (<10) living in more crowded conditions than in the wild. Moreover, captured individuals and those reared in captivity may represent a biased sample of personalities and behaviours (Webster and Rutz, 2020). As such, interactions observed in captivity may not accurately represent natural behaviour in the wild. Moreover, captivity is not viable for a number of cetacean species due to their large size, as in the case of mysticetes, or their physiological sensitivity to captive conditions, as seen in vaquitas (*Phocoena sinus*; Rojas-Bracho et al., 2019), which has also contributed to the existing taxonomic bias in research.

Some of the current gaps in knowledge of tactile interactions among marine mammals result from different naming conventions used to classify behaviours across studies. For instance, it is general knowledge that sea otters frequently rest in rafts in close mutual contact (Barocas and Ben-David, 2021; Dudzinski and Gregg, 2018). However, we found no primary sources describing these behaviours. Instead, most published research on wild sea otter behaviour classifies all directed behaviour between individuals as "interacting." Although these interactions included social touch, these behaviours were grouped with other forms of aggressive and copulatory contact.

In mysticetes, several descriptions of inter-individual contact in baleen whales originated either from observations classified as surface active groups (SAGs) or were observed in conjunction with stereotyped copulatory behaviours (i.e., penis extrusions, ventral-ventral contact, and mounting) in contexts where the sex/age composition of individuals was not discernible (Goodyear, 1996; Würsig et al., 1993). Although more recent definitions of SAGs have veered away from assuming a copulatory function (Kraus and Hatch, 2001), this behaviour remains associated with copulation. It is worth noting that several descriptions of SAGs and sexual contact among baleen whales involve non-conceptive groupings—calves or juveniles, all female, or all male individuals—or have been recorded in months where conception is not expected (Parks et al., 2007; Richardson et al., 1995; Sironi, 2004), which qualifies these interactions as a form of socio-sexual contact. However, some descriptions of socio-sexual interactions are hard to distinguish from aggression/harassment (Lonati et al., 2022).

4.2 Evidence for affiliative functions of touch in marine mammals

Marine mammals engage in a wide diversity of tactile behaviours across social contexts, partly reflecting the anatomical and sensory adaptations of taxa with varying levels of aquatic affinity. We found evidence for touch being involved in mother-calf interactions across all marine mammal taxa (**Appendix 2 –** Table S2.3). Conversely, evidence for an affiliative function of touch in adulthood was limited to pinnipeds, sirenians, and cetaceans. We only found evidence for touch increasing the likelihood of cooperation and being involved in mediating conflict in a few odontocete species. Much of the research we found on tactile interactions classified these behaviours as "play" or socio-sexual," which were sometimes hypothesized to be involved in mediating social relations but more frequently displayed patterns consistent with alternative functions (e.g., development and practice). We next examine the evidence supporting each affiliative function of touch in turn.

4.2.1 Establishing and enforcing social bonds

4.2.1.1 Mother-infant bonds

Several forms of mother-offspring touch reported in marine mammals likely have functions beyond bond establishment, like hygienic maintenance (Osterrieder and Davis, 2011; Sakai et al., 2022, 2013), thermoregulation, predatory defence (Osterrieder and Davis, 2011), locomotory assistance (Hill et al., 2018; Jarman, 1966; Krasnova et al., 2006; Mann and Smuts, 1999; Moore, 1956; Osterrieder and Davis, 2011; Reid et al., 1995; Würsig et al., 1999), and guidance (Guinet, 1991; Orr and Poulter, 1967; Tavolga and Essapian, 1957; Thomas and Taber, 1984). Some of these forms of social contact, along with other tactile interactions with less immediately apparent alternative functions, contribute to cultivating mother-calf bonds.

Many of the tactile interactions among sea otters and pinniped mother-calf dyads involve mutual nose-nose and nose-body contact (Kovacs, 1987; Lang et al., 2011; Osterrieder and Davis, 2011; Perry and Renouf, 1988; Soriano et al., 2009; Wilson, 1974; Wilson et al., 1985; Wilson and Jones, 2020). Although the olfactory sensitivity of sea otters and pinnipeds has not been widely studied, anatomical evidence and behavioural studies on a few species suggest that this sense is well-developed in both groups (Davis, 2019; Pitcher et al., 2011; Riedman and Estes, 1990). Thus, nosing between mothers and pups likely also involves scent cues that facilitate mutual recognition (Kovacs, 1987; Riedman and Estes, 1990; Wilson and Jones, 2020), contributing to developing a mutual bond (Broad et al., 2006). The tactile component of nosing in pinnipeds may be important, as some species adjust the position of their extremely sensitive whiskers during nosing contacts—erecting them against the receiver/giver of touch—likely enhancing mutual tactile perception (Hanlan, 1998; Lawson, 1993; Wilson et al., 1985). Moreover, because nosing and muzzle contact behaviours also occur underwater (Wilson et al., 1985), it is unlikely that these represent entirely chemosensory interactions and that touch also contributes to establishing and developing the mother-pup bonds. Kin recognition is likely particularly valuable for pinnipeds and sea otters, who rarely care for pups other than their own.

In contrast, exclusively aquatic marine mammals have lost or vastly reduced olfactory and gustatory abilities in comparison to their terrestrial counterparts as evidenced by modifications or reductions of associated anatomy, neural structures, and genes (Bauer et al., 2018; Chikina et al., 2016)—but see Bruck et al., 2022 for evidence of gustation-based individual recognition in bottlenose dolphins. Thus, they likely rely on different mechanisms to establish and maintain mother-infant bonds. Manatee calves spend their first 1 – 2 years in very close contact with their mothers, frequently kissing (mouth-mouth contact) and mouthing (mouth-body contact) each other (Hartman, 1979; Hénaut et al., 2010). The high concentration of vibrissae and innervation around sirenian mouths suggests that these interactions likely provide tactile information and may play a role in mutual recognition (Bauer et al., 2018; Hénaut et al., 2022). Manatees display touch-seeking behaviours, which indicates they may enjoy touch (Hartman, 1979), suggesting these tactile exchanges could contribute to reinforcing the mother-calf bond (Broad et al., 2006; Jablonski, 2021). Similarly, cetacean calves and mothers frequently exchange diverse forms of physical contact at rates that decrease as calves become self-sufficient (Dudzinski et al., 2013; Hill et al., 2018; Mann and Smuts, 1999; Sakai et al., 2013; Thomas and Taber, 1984).

In cetaceans, a high proportion of the tactile exchanges between calves and mothers are calf-initiated. Cetacean calves frequently adopt the ‘infant position,’ during which the calf swims below their mother, making frequent contact with the mother’s ventral area (Hill et al., 2018; Mann and Smuts, 1999; Reid et al., 1995; Tavolga and Essapian, 1957). This position may simultaneously give calves easy access to their mothers’ mammary slits (Mann and Smuts, 1999), provide hydrodynamic assistance (Noren and Edwards, 2011), and assure calves of their proximity to their mothers (Sakai et al., 2013). Calves of several odontocete species frequently rub their mothers’ faces and sides and solicit pectoral fin rubs from their mothers (Hill et al., 2018; Mann and Smuts, 1999; Sakai et al., 2013). These behaviours likely mirror the strong touch-seeking tendencies of infant primates, for whom maternal contact provides assurance and comfort, contributing to their social development (Hertenstein et al., 2006). However, unlike primate mothers—who spend considerable time grooming their young (Broad et al., 2006)—cetacean mothers are much less likely to initiate touch towards their calves (Hill et al., 2018; Mann and Smuts, 1999; Sakai et al., 2013). This does not mean dolphin mothers are indolent, as they are primarily responsible for maintaining proximity, although not necessarily contact, with their young (Mann and Smuts, 1999).

Mothers may rely on other mechanisms, like acoustic signals, to establish contact with their calves and maintain their bonds.

4.2.1.2 Bonds beyond infancy

Cetaceans, pinnipeds, and sirenians also use social contact to affirm and establish social bonds outside the mother-calf pair. For instance, a positive correlation between rates of affiliative contact and the strength of social relationships, indicated by association rates, has been found in killer whales (*Orcinus orca*; Weiss et al., 2021), Atlantic spotted dolphins (*Stenella frontalis;* Danaher-Garcia et al., 2022b), Indo-Pacific bottlenose dolphins (Chereskin et al., 2022; Leu et al., 2020), bottlenose dolphins (Themelin et al., 2020), and South American sea lions (*Otaria byronia*; Llamazares-Martín et al., 2017). While contact-based social networks can be highly correlated with association-based indices, they are not interchangeable (Danaher-Garcia et al., 2022a; Weiss et al., 2021). In killer whales, sex-based association preferences were only detected when contact rates were analyzed (Weiss et al., 2021). This suggests that if frequent contact indicates the value or nature of a relationship, general association rates based only on spatio-temporal proximity may miss key elements of sociality in some species.

In species where social networks are sex-segregated, the hypothesis that touch is involved in enforcing and establishing social bonds predicts that tactile exchanges would be more frequent between members of the same sex (Cooper and Bernstein, 2000). This pattern is observed across odontocetes, including Indo-Pacific bottlenose dolphins and belugas, and often involves socio-sexual touch, described in further detail in subsection ***4.3 A note on socio-sexual*** touch (Acosta, 2015; R. Connor et al., 2006; Glabicky et al., 2010; Lilley et al., 2020; Mann, 2006; Themelin et al., 2020).

Social touch can also help establish and reinforce bonds with less familiar individuals (Hodgson et al., 2024). For instance, Indo-Pacific bottlenose dolphin males engage in frequent affiliative contact with dolphins outside of their core social groups during inter-group reunions (Friedman et al., 2023). As these interactions involve less familiar, but still close individuals, contact likely serves to maintain these more distant social bonds (Friedman et al., 2023). When two previously unfamiliar social groups of Atlantic spotted dolphins merge, individuals frequently engage in affiliative contact with each other (Danaher-Garcia et al., 2022b). Similarly, in a group of captive rough-toothed dolphins (*Steno bredanensis*), introducing new individuals increased the frequency of affiliative contacts, many of which were exchanged between unfamiliar individuals (Yeater et al., 2013).

Although current understanding suggests that most social interactions in pinnipeds and sirenians are transient beyond the mother-calf relationship (Llamazares-Martín et al., 2017; O'Shea et al., 2022), we found evidence for social preferences in the nosing exchanges of harbour seals (*Phoca vitulina*) (Hanlan, 1998), play-fighting of South American sea lions (*Otaria flavescens*) (Llamazares-Martín et al., 2017), and contact between manatees (Hénaut et al., 2010). Captive manatees preferentially interact with maternal kin, but whether this translates to wild populations is unknown (Harper and Schulte, 2005).

4.2.2 Enhancing the likelihood of cooperation

Evidence for touch resulting in increased cooperation was sparse in marine mammals (*n* = 3 studies) and restricted to delphinids. In male Indo-pacific bottlenose dolphins, individuals with lower consortship rates were more likely to initiate flipper rubbing (i.e., flipper – body contact, also described as 'petting') and direct it toward males with higher consortship rates, presumably as a means of ensuring their collaboration for copulation (Friedman, 2017). But whether a history of petting interactions results in an increased likelihood of cooperation within dyads has not been tested.

Indo-Pacific bottlenose dolphins off Mikura Island have been found to reverse roles during flipper rubbing interactions, during which dead skin removal is sometimes observed (Sakai et al., 2022, 2006). However, a direct cooperative exchange is likely not the sole function of flipper rubbing, as it is not always reciprocated, and, in the case of calf-mother dyads, often involves calves initiating flipper-to-body rubs (Sakai et al., 2022, 2006). In captive bottlenose dolphins, individuals preferentially rubbed flippers with individuals who had rubbed them the most in the past (Yamamoto and Ishibashi, 2022). Same-sex socio-sexual behaviours between males were often reciprocated in captive belugas (Glabicky et al., 2010), which may hint towards a mutually beneficial exchange.

4.2.3 Managing conflict

Evidence for tactile exchanges used to mitigate conflict in marine mammals was limited to a few studies of captive dolphins (*n*=4) and manatees (*n*=1). Common bottlenose dolphins have been observed to engage in affiliative physical contact like contact swimming and head rubs following aggressive interactions (Weaver, 2003; Yamamoto and Kashiwagi, 2023). However, these behaviours were not exclusively observed after aggressive interactions (Weaver, 2003). Additionally, the time between aggressive interactions was found to be longer for dyads who engage in pectoral fin rubbing between aggressive bouts, suggesting that tactile exchanges prolonged the lag to re-incidence (Tamaki et al., 2006). Notably, the association between post-conflict flipper-rubbing and increased time between incidents of aggression was only significant among juvenile pairs and not between adult pairs (Tamaki et al., 2006). A slightly higher frequency of affiliative tactile behaviours was also detected in killer whales compared to non-conflict controls (Sánchez–Hernández et al., 2019). Nonetheless, the small number of individuals ($n \leq 6$) observed in the research above warrants caution when generalizing the role of touch in conflict resolution.

In captive Florida manatees, evidence for the use of touch in mitigating conflict is inconclusive. While affiliative tactile interactions are more frequent when individuals were housed at higher densities, possibly to alleviate crowding-induced stress, rates of affiliative contact did not change before, during or feeding sessions, which were also expected to be stress-inducing (Harper and Schulte, 2005).

4.3 A note on socio-sexual touch

Socio-sexual touch is almost ubiquitously distributed across taxa and is thought to serve multiple social functions (Bagemihl, 1999; Bailey and Zuk, 2009; Hohmann and Fruth, 2000). Socio-sexual touch can be immediately pleasurable, contributing to its role in mediating social relationships (Vasey and Duckworth, 2006). Despite being widely documented in sea otters (Packard and Ribic, 1982), pinnipeds (Bagemihl, 1999; Bartholomew, 1959; Renouf and Lawson, 1987; Wilson, 1974), sirenians (Hartman, 1979), and cetaceans (Bagemihl, 1999; Ham et al., 2023), the function(s) remains unclear. In fissipeds, sirenians, and mysticetes, reports of socio-sexual interactions are primarily descriptive, and thus, their function cannot be inferred (Betty et al., 2023; Clark, 1981; Darling, 1977; Hartman, 1979; Packard and Ribic, 1982; Rickard et al., 2022; Sironi, 2004; Würsig et al., 1993).

In pinnipeds, socio-sexual contact, frequently termed “play copulating,” is disproportionately observed among males (Bagemihl, 1999; Bartholomew, 1959; Renouf and Lawson, 1987; Wilson, 1974). The prevalence of socio-sexual playful behaviours in young pinniped males suggests these interactions serve a developmental function. Some patterns of socio-sexual behaviours in pinnipeds remain puzzling. Adult male walruses in shallow waters frequently engage in highly tactile same-sex interactions involving affiliative or exploratory behaviours (like naso-nasal greetings and nasal exploration; Bagemihl, 1999; Edward H. Miller, 1975). This contrasts with the almost exclusively agonistic interactions observed among males on land (Edward H. Miller, 1975). The nature and duration of social relationships in walruses are still not well understood, making it hard to infer if these socio-sexual exchanges have an affiliative or other function (Miller and Kochnev, 2021).

In odontocetes, patterns of socio-sexual interactions suggest that, as in other social mammals, socio-sexual behaviours mediate different relationships. For instance, while there is evidence for preferential socio-sexual partners in captive bottlenose dolphins, these interactions also frequently involve individuals with low-to-medium association rates (Acosta, 2015; Harvey et al., 2017). It is likely that socio-sexual touch can be directed at individuals with different levels of familiarity, which would be particularly valuable in fission-fusion societies. In resident killer whales, males, most often sub-adults, engage in vigorous and highly symmetrical socio-sexual play outside their natal pod (Rose, 1992). These interactions most frequently occur between members of different pods, suggesting they help individuals navigate relationships with unfamiliar whales, even if these affiliations do not persist into adulthood (Rose, 1992).

4.4 Social structure & affiliative touch

Across terrestrial species, differences in the frequency of social touch and patterns of interaction are primarily shaped by social structure (Bagnato et al., 2023; Kerth, 2008; Lehmann et al., 2007). Affiliative touch in mammals is more frequently documented in species that live in groups with stable memberships and cooperative relationships, where it often reflects hierarchical relationships or partner preferences driven by relatedness, opportunities for cooperation, and shared histories of interactions (Kerth, 2008; Kutsukake, 2009; Lehmann et al., 2007).

Some of the research on social touch in marine mammals aligns with these patterns. While social contact among adults is rare in polar bears, sea otters, and pinnipeds—species that are not known to cooperate or form stable social relationships (Miller and Kochnev, 2021; Trillmich and Cantor, 2018)—it is clearly important for some odontocete species, such as bottlenose dolphins and belugas. These species form persistent social bonds in groups characterized by fission-fusion dynamics, in which they may cooperatively feed, mate, and care for their young (Mann et al., 2000; O'Corry-Crowe et al., 2020). Like other terrestrial mammals with highly cooperative fission-fusion societies, some odontocetes use touch to facilitate group-living (Connor et al., 2006; Connor et al., 2006; Friedman et al., 2023; Friedman, 2017; Mann, 2006; Tamaki et al., 2006; Yamamoto and Kashiwagi, 2023). We also found evidence of touch being used to mediate different social relationships among killer whales (Rose, 1992; Sánchez–Hernández et al., 2019; Weiss et al., 2021), who form highly stable matrilineally-based cooperative social groups (Rendell et al., 2019).

Conversely, some aspects of social touch in marine mammal taxa deviate from the patterns mentioned above. Some discrepancies arise from the scarcity of reports of tactile interactions in species known to form long-term social bonds, like sperm whales and long-finned pilot whales (*Globicephala melas*) (Boran and Heimlich, 2019; Whitehead, 2003). However, we have personally observed and are in the process of analyzing social contact events in these species, highlighting that their absence from existing literature on the topic stems from the methodological/publication biases and anecdotal nature of reports discussed above. We also found support for tactile exchanges serving affiliative functions in species not known to form stable social bonds in the wild. Captive manatees, typically solitary outside the mother-calf pair and forming only seasonal aggregations in the wild, have been observed exchanging affiliative contact with long-term, and often related partners in captivity (Harper and Schulte, 2005; Hartman, 1979; Hénaut et al., 2010). This suggests manatees may form social bonds, although the nature and functions of these relationships remain unclear (Hénaut et al., 2022). Touch can also be exchanged during ephemeral interactions in species that don't form preferential associations, like sea lions engaged in play (Llamazares-Martín and Palagi, 2021). In this case, short-lived social bonds may facilitate playful exchanges that are developmentally important during early life stages. In walruses, who have not been confirmed to form stable social bonds, frequent contact involving exploratory and socio-sexual touch (Bagemihl, 1999; E.H. Miller, 1975) may also contribute to mitigating aggression and navigating crowded environments.

5. Recommendations for the future

5.1 Methodological considerations

In non-marine mammal taxa, understanding the drivers and ultimate functions of social touch has benefited from a comparative approach (Kerth, 2008; Morales Picard et al., 2020; Sueur et al., 2011). We expect and hope that reports of fine-scale social interactions, including tactile behaviours, will experience significant growth with the rapid adoption of UAVs. To ensure studies of social touch in marine mammals and other terrestrial taxa can contribute to future comparative research, it is key that they use standardized methods to quantify and report results (see review by Dudzinski et al., 2019).

Comparing the overall frequency with which individuals engage in specific forms of social touch requires the use of standardized field protocols and sampling methods (Altmann, 1974; Mann, 1999). Researchers frequently conduct individual focal follows to systematically collect behavioural data; however, if the protocol is adequately defined, group focal follows can also provide representative behavioural metrics of relative interaction rates (Altmann, 1974; Mann, 1999). Additionally, comparative studies require that the sampling effort be adequately measured, and that biases in the visibility of behaviours are accounted for or recognized (Dudzinski et al., 2019). Therefore, some consideration needs to be given to the types of behaviours that can be compared across species with vastly diverging anatomies – for example, which specific tactile behaviours in marine mammals are comparable to grooming in primates or allopreening in birds? (Dudzinski et al., 2019). A clear description of the restrictions in data collection methods (e.g., the depth range, water surface conditions, and time of day at which behaviours can be reliably observed) is also important.

A fundamental step towards resolving comparability is using descriptive terms referring to specific actions and body parts (like pectoral-fin contact or contact swims) rather than broad interpretive labels (like cavorting, playing, and interacting). Comparing the prevalence of behaviours across studies also assumes that these behaviours can be measured consistently across observers. Incorporating inter-rater reliability measurements into quantitative studies of social touch can contribute to ensuring that this is the case (Martin and Bateson, 2010). Finally, meta-analyses generally rely on both average behavioural metrics, as well as measures of uncertainty. We encourage quantitative assessments of social touch to report overall behavioural metrics (e.g., interaction rates by sex/age class) alongside adequate measures of individual variability (e.g., standard deviation).

5.2 Future directions

Difficulties in observing and quantifying touch in marine species remain a barrier to understanding its functions. Emerging technologies, like UAVs and animal-attached video recorders (or "crittercams"), provide relatively affordable means of overcoming these challenges in the wild across both terrestrial and marine taxa that have been historically hard to observe (Aoki et al. 2013, Torres et al. 2018, King & Jensen 2022, Ramos et al. 2023, Pedrazzi et al. 2025). Through aerial photogrammetry, UAVs can also enable distinguishing the individual identity and sex/age of participants in tactile interactions (O'Callaghan et al., 2024; Vivier et al., 2024). Similarly, automated tracking of social interactions using machine learning has been developed for terrestrial species in lab and wild conditions (Hong et al., 2015; van de Sande et al., 2024). While applying these technologies to other taxa would involve considerable effort and algorithm training, it may be fruitful for long-term studies and projects with large volumes of behavioural recordings (Pedrazzi et al., 2025).

While we chose to focus this review on affiliative tactile behaviours, individual relationships often encompass a wide variety of interactions, from aggressive to neutral and affective (De Waal, 1989). Although dominant-subordinate interactions were outside the scope of our review, these still play a key role in controlling aggression in many group-living animals. Analyzing social touch across contexts and in relation to agonistic or competitive interactions can tease apart the underlying mechanisms that enable social living in species with different levels of social conflict. Furthermore, communication is multimodal and context-dependent, and studying tactile exchanges in conjunction with visual, acoustic, and chemical cues or signals can clarify how species navigate their relationships. Finally, exploring the dynamics of polyadic tactile interactions can also contribute to our understanding of the nature of social interactions across species.

Hypotheses for the evolution of pro-social behaviours assume some fitness benefits, which can be immediate or delayed (Kutsukake, 2009). While testing of such hypotheses is challenging, there are examples of the individual fitness benefits from engaging in pro-social behaviours across taxa, including recent studies on the reproductive consequences of juvenile social play (Holmes et al., 2024; Palagi, 2018; Seyfarth and Cheney, 1984). We found no empirical tests of the potential fitness gains or costs (e.g., disease transmission) of variation in rates of social touch among marine mammal species, populations, or individuals. Longitudinal studies that follow known individuals over time, alongside direct measurements of individual survival and reproduction offer a valuable means of testing this hypothesis. Moreover, by tracking the social behaviours of individuals throughout their lives, we can characterize the ontogeny of these behaviours and determine whether they contribute to the formation of future social bonds (Mann, 2006).

6. Conclusions

We found that social touch in marine mammals occurs in a diversity of forms across taxa and social contexts. Touch in marine mammals may serve multiple non-exclusive pro-social functions and appears to be involved in navigating a wide range of social relationships, from brief and possibly anonymous interactions to ephemeral individual relationships and life-long social bonds. Still, our understanding of these behaviours is unevenly distributed across species, and the functions of specific behaviours are not always clear. The diversity of social systems between and within species, along with the broad range of ecological niches occupied by marine mammals, makes them promising candidates for comparative research on the behavioural mechanisms that facilitate group living outside of primates, ungulates, bats, and birds. Specifically, applying a comparative approach to the study of pro-social behaviours (both within and between species) would improve our understanding of how ecological drivers and social learning (i.e., culture) enable animals to navigate the politics of communal living.

Boxes

Box 1. Tactile senses of marine mammals

The tactile sensory systems of marine mammals—namely the skin and sensory or sinus hairs called vibrissae—underwent considerable changes that allowed them to navigate the conditions of aquatic environments (Bauer et al., 2018; Dehnhardt and Mauck, 2019).

Sea otters (*Enhydra lutris*), who primarily forage for prey hidden in benthic substrates, rely on their highly sensitive front paw pads and facial vibrissae (i.e., whiskers) to gather information on their environment (Strobel et al., 2022, 2018). Pinnipeds have independently developed similar and extremely complex and diverse whisker morphologies, which enable them to discern subtle water currents and discriminate and manipulate objects in dark, murky environments (Bauer et al., 2018; Dehnhardt et al., 2001). Sirenians (manatees and dugongs) have sensory hairs throughout their bodies that allow them to detect water movements. These are most abundant in the face and around the lips, which they use for object detection and manipulation (Bauer et al., 2018; Dehnhardt and Mauck, 2019). Although no mechanoreceptors have been found in manatee skin, their vibrissal hairs likely provide them with enough tactile sensitivity to assess their environments (Bauer et al., 2018). There is no published knowledge on tactile sensitivity in polar bears. However, as in other Ursids, they seem to rely primarily on smell, hearing, and vision to hunt and navigate the Arctic environment (Davis, 2021).

Conversely, fully aquatic cetaceans lose all or most of their hair at birth (Bauer et al., 2018). Mysticetes preserve some vibrissal hairs, or bristles, in adulthood which are concentrated in the front jaws and near the blowhole (Davis, 2019; Drake et al., 2015). Although the sensory function of these bristles has not been tested, their location and degree of innervation suggest they aid in sensing prey movements (Davis, 2019; Drake et al., 2015; Murphy et al., 2022). Odontocetes primarily rely on highly specialized echolocation abilities to navigate their aquatic environment, and with the exception of the Amazon river dolphin (*Inia geoffrensis*), lose their sensory hairs after birth (Davis, 2019; Hanke and Erdsack, 2015). Dolphin skin near the eyes, rostrum, blowhole, melon, and genitals is populated by a high density of mechanoreceptors and can be as sensitive to touch as human lips or fingertips (Bauer et al., 2018; Brennan et al., 2022; Hanke and Erdsack, 2015; Ridgway and Carder, 1990; Strahan et al., 2020). Cetaceans also have a clear proclivity for touch, demonstrated by the frequent rock and sand rubbing behaviours observed in mysticetes and odontocetes (Dudzinski and Gregg, 2018). While these activities may serve a hygienic function (i.e., parasite removal or skin sloughing) (Fortune et al., 2017; Meynecke et al., 2023), they may also provide sensory pleasure (Nakamura and Sakai, 2014; Whitehead and Rendell, 2014). While our scope is limited to physical contact between individuals, some delphinid species have been observed to direct intense, highly directional acoustic pulses from a distance at each other's genitals, suggesting they may also perceive acoustic stimuli through their skin (Herzing, 2015).

Ethical Note

As this review did not involve original data collection, ethical approval was not required. However, we acknowledge that the resulting studies may have been conducted under varying welfare standards. While we do not condone substandard conditions, we have chosen to include all studies to provide a comprehensive overview of existing literature.

Data Availability

Data is available upon request to the corresponding author

Declaration of Interest

The authors have no conflicts of interest to declare.

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Declaration of generative AI in the Writing Process

During the preparation of this work, the author(s) used ChatGPT and Perplexity to improve conciseness and revise grammar. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

References

Acosta, N.B., 2015. Same-sex socio-sexual interactions among a group of captive bottlenose dolphins (*Tursiops truncatus*) (MA Thesis). The University of Southern Mississippi, United States -- Mississippi.

Altmann, J., 1974. Observational study of behavior: sampling methods. Behaviour 49, 227–266. https://doi.org/10.1163/156853974X00534

Aoki, K., Sakai, M., Miller, P.J.O., Visser, F., Sato, K., 2013. Body contact and synchronous diving in long-finned pilot whales. Behav. Processes 99, 12–20. https://doi.org/10.1016/j.beproc.2013.06.002

Baan, C., Bergmüller, R., Smith, D.W., Molnar, B., 2014. Conflict management in free-ranging wolves, *Canis lupus*. Anim. Behav. 90, 327–334. https://doi.org/10.1016/j.anbehav.2014.01.033

Bagemihl, B., 1999. Biological Exuberance: Animal Homosexuality and Natural Diversity. Stonewall Inn Editions, New York, USA.

Bagnato, S., Pedruzzi, L., Goracci, J., Palagi, E., 2023. The interconnection of hierarchy, affiliative behaviours, and social play shapes social dynamics in Maremmana beef cattle. Appl. Anim. Behav. Sci. 260, 105868. https://doi.org/10.1016/j.applanim.2023.105868

Bailey, N.W., Zuk, M., 2009. Same-sex sexual behavior and evolution. Trends Ecol. Evol. 24, 439–446. https://doi.org/10.1016/j.tree.2009.03.014

Barelli, C., Reichard, U.H., Mundry, R., 2011. Is grooming used as a commodity in wild white-handed gibbons, *Hylobates lar*? Anim. Behav. 82, 801–809. https://doi.org/10.1016/j.anbehav.2011.07.012

Barocas, A., Ben-David, M., 2021. Social structure of marine otters: inter and intraspecific variation, in: Davis, R.W., Pagano, A.M. (Eds.), Ethology and Behavioral Ecology of Sea Otters and Polar

Bears, Ethology and Behavioral Ecology of Marine Mammals. Springer International Publishing, Cham, pp. 83–105. https://doi.org/10.1007/978-3-030-66796-2_5

Bartholomew, G.A., 1959. Mother-young relations and the maturation of pup behaviour in the Alaska fur seal. Anim. Behav. 7, 163–171. https://doi.org/10.1016/0003-3472(59)90005-3

Bauer, G.B., Reep, R.L., Marshall, C.D., 2018. The tactile senses of marine mammals. Int. J. Comp. Psychol. 31. https://doi.org/10.46867/ijcp.2018.31.02.01

Betty, E.L., Zwamborn, E.M.J., Weyn, M., Luck, E., Alves, F., 2023. Life history parameters, sociobiology, and reproductive strategies of pilot whales, in: Würsig, B., Orbach, D.N. (Eds.), Sex in Cetaceans. Springer International Publishing, Cham, pp. 327–351. https://doi.org/10.1007/978-3-031-35651-3_15

Boran, J., Heimlich, S., 2019. Pilot whales: delphinid matriarchies in deep seas, in: Würsig, B. (Ed.), Ethology and Behavioral Ecology of Odontocetes, Ethology and Behavioral Ecology of Marine Mammals. Springer International Publishing, Cham, pp. 281–304. https://doi.org/10.1007/978-3-030-16663-2_13

Brennan, P.L.R., Cowart, J.R., Orbach, D.N., 2022. Evidence of a functional clitoris in dolphins. Curr. Biol. 32, R24–R26. https://doi.org/10.1016/j.cub.2021.11.020

Broad, K.D., Curley, J.P., Keverne, E.B., 2006. Mother–infant bonding and the evolution of mammalian social relationships. Philos. Trans. R. Soc. B Biol. Sci. 361, 2199–2214. https://doi.org/10.1098/rstb.2006.1940

Brosnan, S.F., De Waal, F.B.M., 2002. A proximate perspective on reciprocal altruism. Hum. Nat. 13, 129–152. https://doi.org/10.1007/s12110-002-1017-2

Bruck, J.N., Walmsley, S.F., Janik, V.M., 2022. Cross-modal perception of identity by sound and taste in bottlenose dolphins. Sci. Adv. 8, eabm7684. https://doi.org/10.1126/sciadv.abm7684

Carozza, S., Leong, V., 2021. The role of affectionate caregiver touch in early neurodevelopment and parent–infant interactional synchrony. Front. Neurosci. 14, 613378. https://doi.org/10.3389/fnins.2020.613378

Carter, G., Leffer, L., 2015. Social grooming in bats: Are vampire bats exceptional? PLOS ONE 10, e0138430. https://doi.org/10.1371/journal.pone.0138430

Carter, G.G., Farine, D.R., Crisp, R.J., Vrtilek, J.K., Ripperger, S.P., Page, R.A., 2020. Development of new food-sharing relationships in vampire bats. Curr. Biol. 30, 1275-1279.e3. https://doi.org/10.1016/j.cub.2020.01.055

Chereskin, E., Connor, R.C., Friedman, W.R., Jensen, F.H., Allen, S.J., Sørensen, P.M., Krützen, M., King, S.L., 2022. Allied male dolphins use vocal exchanges to “bond at a distance.” Curr. Biol. 32, 1657-1663.e4. https://doi.org/10.1016/j.cub.2022.02.019

Chikina, M., Robinson, J.D., Clark, N.L., 2016. Hundreds of genes experienced convergent shifts in selective pressure in marine mammals. Mol. Biol. Evol. 33, 2182–2192. https://doi.org/10.1093/molbev/msw112

Clark, C.W., 1981. Acoustic communication and behavior of the Southern right whale (PhD Thesis). State University of New York at Stony Brook, United States -- New York.

Connor, R., Mann, J., Watson-Capps, J., 2006. A sex-specific affiliative contact behavior in Indian ocean bottlenose dolphins, *Tursiops* sp. Ethology 112, 631–638. https://doi.org/10.1111/j.1439-0310.2006.01203.x

Connor, R.C., Smolker, R., Bejder, L., 2006. Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. Anim. Behav. 72, 1371–1378. https://doi.org/10.1016/j.anbehav.2006.03.014

Cooper, M.A., Bernstein, I.S., 2000. Social grooming in Assamese macaques (*Macaca assamensis*). Am. J. Primatol. 50, 77–85. https://doi.org/10.1002/(SICI)1098-2345(200001)50:1<77::AID-AJP7>3.0.CO;2-R

Danaher-Garcia, N., Connor, R., Fay, G., Melillo-Sweeting, K., Dudzinski, K.M., 2022a. Using social network analysis to confirm the 'gambit of the group' hypothesis for a small cetacean. Behav. Processes 200. https://doi.org/10.1016/j.beproc.2022.104694

Danaher-Garcia, N., Connor, R., Fay, G., Melillo-Sweeting, K., Dudzinski, K.M., 2022b. The partial merger of two dolphin societies. R. Soc. Open Sci. 9. https://doi.org/10.1098/rsos.211963

Darling, J.D., 1977. Aspects of the behavior and ecology of Vancouver Island gray whales, *Eschrictus glaucus* Cope (Masters Thesis). University of Victoria, British Columbia, Canada.

Davis, R.W., 2021. Ethology and Behavioral Ecology of Sea Otters and Polar Bears, Ethology and Behavioral Ecology of Marine Mammals Ser. Springer International Publishing AG, Cham.

Davis, R.W., 2019. Sensory systems, in: Marine Mammals. Springer International Publishing, Cham, pp. 177–217. https://doi.org/10.1007/978-3-319-98280-9_7

De Waal, F.B.M., 2000. The first kiss: Foundations of conflict resolution in animals, in: Aureli, F., de Waal, F.B.M. (Eds.), Natural Conflict Resolution. University California Press, pp. 15–33.

De Waal, F.B.M., 1989. Peacemaking among primates. Harvard University Press, Cambridge, Massachusetts, USA.

De Waal, F.B.M., 1986. The integration of dominance and social bonding in primates. Q. Rev. Biol. 61, 459–479. https://doi.org/10.1086/415144

De Waal, F.B.M., Aureli, F., 1997. Conflict resolution and distress alleviation in monkeys and apes. Ann. N. Y. Acad. Sci. 807, 317–328. https://doi.org/10.1111/j.1749-6632.1997.tb51929.x

Dehnhardt, G., Mauck, B., 2019. Mechanoreception in secondarily aquatic vertebrates, in: Thewissen, J.G.M.H., Nummela, S. (Eds.), Sensory Evolution on the Threshold. University of California Press, pp. 295–314. https://doi.org/10.1525/9780520934122-019

Dehnhardt, G., Mauck, B., Hanke, W., Bleckmann, H., 2001. Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). Science 293, 102–104. https://doi.org/10.1126/science.1060514

Drake, S.E., Crish, S.D., George, J.C., Stimmelmayr, R., Thewissen, J.G.M., 2015. Sensory hairs in the bowhead whale, *Balaena mysticetus* (Cetacea, Mammalia). Anat. Rec. 298, 1327–1335. https://doi.org/10.1002/ar.23163

Dudzinski, K.M., Danaher-García, N., Gregg, J.D., 2013. Pectoral fin contact between dolphin dyads at Zoo Duisburg, with comparison to other dolphin study populations. Aquat. Mamm. 39, 335–343. https://doi.org/10.1578/AM.39.4.2013.335

Dudzinski, K.M., Gregg, J.D., 2018. Communication, in: Encyclopedia of Marine Mammals. Elsevier, pp. 210–215. https://doi.org/10.1016/B978-0-12-804327-1.00096-0

Dudzinski, K.M., Hill, H.M., Botero, M., 2019. Methodological considerations for comparison of cross-species use of tactile contact. Int. J. Comp. Psychol. 32. https://doi.org/10.46867/ijcp.2019.32.01.01

Dunbar, R.I.M., 2010. The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. Neurosci. Biobehav. Rev. 34, 260–268. https://doi.org/10.1016/j.neubiorev.2008.07.001

Dunbar, R.I.M., Shultz, S., 2010. Bondedness and sociality. Behaviour 147, 775–803. https://doi.org/10.1163/000579510X501151

Fortune, S.M.E., Koski, W.R., Higdon, J.W., Trites, A.W., Baumgartner, M.F., Ferguson, S.H., 2017. Evidence of molting and the function of “rock-nosing” behavior in bowhead whales in the eastern Canadian Arctic. PLOS ONE 12, e0186156. https://doi.org/10.1371/journal.pone.0186156

Friedman, W.R., Krützen, M., King, S.L., Allen, S.J., Gerber, L., Wittwer, S., Connor, R.C., 2023. Inter-group alliance dynamics in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). Anim. Cogn. 26, 1601–1612. https://doi.org/10.1007/s10071-023-01804-y

Friedman, W.R.G., 2017. Social and cognitive complexity in wild bottlenose dolphins (*Tursiops* sp.) (Doctoral Thesis). University of California, San Diego, United States -- California.

Glabicky, N., DuBrava, A., Noonan, M., 2010. Social–sexual behavior seasonality in captive beluga whales (*Delphinapterus leucas*). Polar Biol. 33, 1145–1147. https://doi.org/10.1007/s00300-010-0790-3

Goodyear, J.D., 1996. Significance of feeding habitats of North Atlantic right whales based on studies of diel behaviour, diving, food ingestion rates, and prey (Doctoral Thesis). University of Guelph (Canada), Canada -- Ontario, CA.

Guinet, C., 1991. Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). Can. J. Zool. 69, 2712–2716. https://doi.org/10.1139/z91-383

Ham, J.R., Lilley, M.K., Manitzas Hill, H.M., 2023. Non-conceptive sexual behavior in cetaceans: Comparison of form and function, in: Würsig, B., Orbach, D.N. (Eds.), Sex in Cetaceans. Springer International Publishing, Cham, pp. 129–151. https://doi.org/10.1007/978-3-031-35651-3_7

Hanke, W., Erdsack, N., 2015. Ecology and evolution of dolphin sensory systems, in: Herzing, D.L., Johnson, C.M. (Eds.), Dolphin Communication and Cognition. The MIT Press, pp. 49–74. https://doi.org/10.7551/mitpress/9939.003.0005

Hanlan, S.K., 1998. Nosing behaviour in captive harbour seals (*Phoca vitulina concolor*): Implications for olfaction and affiliation (MSc Thesis). Memorial University of Newfoundland, Canada.

Harper, J.Y., Schulte, B.A., 2005. Social interactions in captive female Florida manatees. Zoo Biol. 24, 135–144. https://doi.org/10.1002/zoo.20044

Hartman, D., 1979. Ecology and Behavior of the Manatee (*Trichechus manatus*) in Florida. American Society f Mammalogists, Pittsburgh ,USA.

Harvey, B.S., Dudzinski, K.M., Kuczaj, S.A., 2017. Associations and the role of affiliative, agonistic, and socio-sexual behaviors among common bottlenose dolphins (*Tursiops truncatus*). Behav. Processes 135, 145–156. https://doi.org/10.1016/j.beproc.2016.12.013

Hénaut, Y., Becerra Lopez, S.P., MacHkour-M’Rabet, S., Morales-Vela, B., Winterton, P., Elfour, F., 2010. Activities and social interactions in captive Antillean manatees in Mexico. Mammalia 74, 141–146. https://doi.org/10.1515/MAMM.2010.016

Hénaut, Y., Charles, A., Delfour, F., 2022. Cognition of the manatee: past research and future developments. Anim. Cogn. 25, 1049–1058. https://doi.org/10.1007/s10071-022-01676-8

Hertenstein, M.J., Verkamp, J.M., Kerestes, A.M., Holmes, R.M., 2006. The communicative functions of touch in humans, nonhuman primates, and rats: a review and synthesis of the empirical research. Genet. Soc. Gen. Psychol. Monogr. 132, 5–94. https://doi.org/10.3200/MONO.132.1.5-94

Herzing, D., 2015. Synchronous and rhythmic vocalizations and correlated underwater behavior of free-ranging Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in the Bahamas. Anim. Behav. Cogn. 2, 14–29. https://doi.org/10.12966/abc.02.02.2015

Hill, H., Dietrich, S., Jantea, R.F., Garza, S., Lacy, K., 2018. The frequency of contact in beluga (*Delphinapterus leucas*) calf social interactions. Aquat. Mamm. 44, 62–75. https://doi.org/10.1578/AM.44.1.2018.62

Hodgson, G.M.W., Flay, K.J., Perroux, T.A., McElligott, A.G., 2024. You lick me, I like you: Understanding the function of allogrooming in ungulates. Mammal Rev. 54. https://doi.org/10.1111/mam.12351

Hohmann, G., Fruth, B., 2000. Use and function of genital contacts among female bonobos. Anim. Behav. 60, 107–120. https://doi.org/10.1006/anbe.2000.1451

Holmes, K.G., Krützen, M., Ridley, A.R., Allen, S.J., Connor, R.C., Gerber, L., Flaherty Stamm, C., King, S.L., 2024. Juvenile social play predicts adult reproductive success in male bottlenose dolphins. Proc. Natl. Acad. Sci. 121, e2305948121. https://doi.org/10.1073/pnas.2305948121

Hong, W., Kennedy, A., Burgos-Artizzu, X.P., Zelikowsky, M., Navonne, S.G., Perona, P., Anderson, D.J., 2015. Automated measurement of mouse social behaviors using depth sensing, video tracking, and machine learning. Proc. Natl. Acad. Sci. 112. https://doi.org/10.1073/pnas.1515982112

Hooker, S.K., De Soto, N.A., Baird, R.W., Carroll, E.L., Claridge, D., Feyrer, L., Miller, P.J.O., Onoufriou, A., Schorr, G., Siegal, E., Whitehead, H., 2019. Future directions in research on beaked whales. Front. Mar. Sci. 5, 514. https://doi.org/10.3389/fmars.2018.00514

Jablonski, N.G., 2021. Social and affective touch in primates and its role in the evolution of social cohesion. Neuroscience 464, 117–125. https://doi.org/10.1016/j.neuroscience.2020.11.024

Jarman, P.J., 1966. The status of the dugong (*Dugong dugon moller*); Kenya, 1961. Afr. J. Ecol. 4, 82–88. https://doi.org/10.1111/j.1365-2028.1966.tb00885.x

Kerth, G., 2008. Causes and consequences of sociality in bats. BioScience 58, 737–746. https://doi.org/10.1641/B580810

King, S.L., Jensen, F.H., 2022. Rise of the machines: Integrating technology with playback experiments to study cetacean social cognition in the wild. Methods Ecol. Evol. 2041–210X.13935. https://doi.org/10.1111/2041-210X.13935

Kovacs, K.M., 1987. Maternal behaviour and early behavioural ontogeny of harp seals, Phoca groenlandica. Anim. Behav. 35, 844–855. https://doi.org/10.1016/S0003-3472(87)80120-3

Krasnova, V.V., Bel'kovich, V.M., Chernetsky, A.D., 2006. Mother-infant spatial relations in wild Beluga (*Delphinapterus leucas*) during postnatal development under natural conditions. Biol. Bull. 33, 53–58. https://doi.org/10.1134/S1062359006010079

Kraus, S.D., Hatch, J.J., 2001. Mating strategies in the North Atlantic right whale (*Eubalaena glacialis*). J. Cetacean Res. Manag. 237–244.

Kutsukake, N., 2009. Complexity, dynamics and diversity of sociality in group-living mammals. Ecol. Res. 24, 521–531. https://doi.org/10.1007/s11284-008-0563-4

Lang, S.L.C., Boness, D.J., Bowen, W.D., Iverson, S.J., 2011. Primiparous females do not exhibit reduced maternal care in gray seals (*Halichoerus grypus*). Mar. Mammal Sci. 27, E153–E164. https://doi.org/10.1111/j.1748-7692.2010.00443.x

Lawson, J.W., 1993. A descriptive and quantitative comparison of the communication of grey seals, *Halichoerus grypus*, at three sites in the North Atlantic Ocean (Doctoral Thesis). Memorial University of Newfoundland, Canada.

Lehmann, J., Korstjens, A.H., Dunbar, R.I.M., 2007. Group size, grooming and social cohesion in primates. Anim. Behav. 74, 1617–1629. https://doi.org/10.1016/j.anbehav.2006.10.025

Leu, S.T., Sah, P., Krzyszczyk, E., Jacoby, A.-M., Mann, J., Bansal, S., 2020. Sex, synchrony, and skin contact: Integrating multiple behaviors to assess pathogen transmission risk. Behav. Ecol. 31, 651–660. https://doi.org/10.1093/beheco/araa002

Lilley, M.K., Ham, J.R., Hill, H.M., 2020. The development of socio-sexual behavior in belugas (*Delphinapterus leucas*) under human care. Behav. Processes 171. https://doi.org/10.1016/j.beproc.2019.104025

Llamazares-Martín, C., Palagi, E., 2021. Playing at the edge of the sea: a comparative analysis in otariids and odobenids, in: Campagna, C., Harcourt, R. (Eds.), Ethology and Behavioral Ecology of Otariids and the Odobenid, Ethology and Behavioral Ecology of Marine Mammals. Springer International Publishing, Cham, pp. 391–412. https://doi.org/10.1007/978-3-030-59184-7_20

Llamazares-Martín, C., Scopa, C., Guillén-Salazar, F., Palagi, E., 2017. Strong competition does not always predict play asymmetry: The case of South American sea lions (*Otaria flavescens*). Ethology 123, 270–282. https://doi.org/10.1111/eth.12594

Lonati, G.L., Hynes, N.J., Howe, K.R., Durette-Morin, D., Brown, M.W., Davies, K.T.A., 2022. Observations of adult–calf nonreproductive copulatory behavior in North Atlantic right whales (*Eubalaena glacialis*). Aquat. Mamm. 48, 639–645. https://doi.org/10.1578/AM.48.6.2022.639

Mann, J., 2006. Establishing trust: socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins, in: Sommer, V. (Ed.), Homosexual Behaviour in Animals: An Evolutionary Perspective. Cambridge Univ. Press, Cambridge, pp. 107–130.

Mann, J., 1999. Behavioral sampling methods for cetaceans: a review and critique. Mar. Mammal Sci. 15, 102–122. https://doi.org/10.1111/j.1748-7692.1999.tb00784.x

Mann, J., Connor, R., Tyack, P., Whitehead, H. (Eds.), 2000. Cetacean Societies: Field Studies of Dolphins and Whales. The University of Chicago Press, Chicago, USA.

Mann, J., Smuts, B., 1999. Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). Behaviour 136, 529–566. https://doi.org/10.1163/156853999501469

Martin, P., Bateson, P., 2010. Measuring behaviour: an introductory guide, 3rd Edition. ed. Cambridge University Press, New York, USA.

Meynecke, J.-O., Gustafon, J., Cade, D.E., 2023. Exfoliating whales–sandy bottom contact behaviour of humpback whales. J. Mar. Sci. Eng. 11, 600. https://doi.org/10.3390/jmse11030600

Miller, Edward H., 1975. Walrus ethology. I. The social role of tusks and applications of multidimensional scaling. Can. J. Zool. 53, 590–613. https://doi.org/10.1139/z75-073

Miller, E.H., 1975. A comparative study of facial expressions of two species of pinnipeds. Behaviour 53, 268–284. https://doi.org/10.1163/156853975X00227

Miller, E.H., Kochnev, A.A., 2021. Ethology and behavioral ecology of the walrus (*Odobenus rosmarus*), with emphasis on communication and social behavior, in: Campagna, C., Harcourt, R. (Eds.), Ethology and Behavioral Ecology of Otariids and the Odobenid, Ethology and Behavioral Ecology of Marine Mammals. Springer International Publishing, Cham, pp. 437–488. https://doi.org/10.1007/978-3-030-59184-7_22

Moore, J.C., 1956. Observations of manatees in aggregations. Amer Mus Novit. 1811, 1–24.

Morales Picard, A., Mundry, R., Auersperg, A.M., Boeving, E.R., Boucherie, P.H., Bugnyar, T., Dufour, V., Emery, N.J., Federspiel, I.G., Gajdon, G.K., Guéry, J., Hegedič, M., Horn, L., Kavanagh, E., Lambert, M.L., Massen, J.J.M., Rodrigues, M.A., Schiestl, M., Schwing, R., Szabo, B., Taylor, A.H., Van Horik, J.O., Von Bayern, A.M.P., Seed, A., Slocombe, K.E., 2020. Why preen others? Predictors of allopreening in parrots and corvids and comparisons to grooming in great apes. Ethology 126, 207–228. https://doi.org/10.1111/eth.12999

Morrison, I., 2016. Keep calm and cuddle on: Social touch as a stress buffer. Adapt. Hum. Behav. Physiol. 2, 344–362. https://doi.org/10.1007/s40750-016-0052-x

Morrison, I., Löken, L.S., Olausson, H., 2010. The skin as a social organ. Exp. Brain Res. 204, 305–314. https://doi.org/10.1007/s00221-009-2007-y

Moscovice, L.R., Surbeck, M., Fruth, B., Hohmann, G., Jaeggi, A.V., Deschner, T., 2019. The cooperative sex: Sexual interactions among female bonobos are linked to increases in oxytocin, proximity and coalitions. Horm. Behav. 116, 104581. https://doi.org/10.1016/j.yhbeh.2019.104581

Murphy, C.T., Marx, M., Martin, W.N., Jiang, H., Lapseritis, J.M., French, A.N., Simmons, N.B., Moore, M.J., 2022. Feeling for food: Can rostro-mental hair arrays sense hydrodynamic cues for foraging North Atlantic right whales? Anat. Rec. 305, 577–591. https://doi.org/10.1002/ar.24858

Nakamura, M., Sakai, M., 2014. Social touch in apes and dolphins, in: Yamagiwa, J., Karczmarski, L. (Eds.), Primates and Cetaceans, Primatology Monographs. Springer Japan, Tokyo, pp. 355–383. https://doi.org/10.1007/978-4-431-54523-1_19

Noren, S., Edwards, E., 2011. Infant position in mother-calf dolphin pairs: formation locomotion with hydrodynamic benefits. Mar. Ecol. Prog. Ser. 424, 229–236. https://doi.org/10.3354/meps08986

O'Callaghan, S.A., Al Abbar, F., Costa, H., Prieto, R., Gammell, M., O'Brien, J., 2024. Aerial photo-identification of sperm whales (*Physeter macrocephalus*). Aquat. Mamm. 50, 479–494. https://doi.org/10.1578/AM.50.6.2024.479

O'Corry-Crowe, G., Suydam, R., Quakenbush, L., Smith, T.G., Lydersen, C., Kovacs, K.M., Orr, J., Harwood, L., Litovka, D., Ferrer, T., 2020. Group structure and kinship in beluga whale societies. Sci. Rep. 10, 11462. https://doi.org/10.1038/s41598-020-67314-w

Okabe, S., Nagasawa, M., Mogi, K., Kikusui, T., 2012. The importance of mother–infant communication for social bond formation in mammals. Anim. Sci. J. 83, 446–452. https://doi.org/10.1111/j.1740-0929.2012.01014.x

Orr, R.T., Poulter, T.C., 1967. Some observations on reproduction, growth, and social behavior in the Steller sea lion *Eumetopias jubata*. Proc. Calif. Acad. Sci. 35, 103–226.

O'Shea, T.J., Beck, C.A., Hodgson, A.J., Keith-Diagne, L., Marmontel, M., 2022. Social and reproductive behaviors, in: Marsh, H. (Ed.), Ethology and Behavioral Ecology of Sirenia, Ethology and Behavioral Ecology of Marine Mammals. Springer International Publishing, Cham, pp. 101–154. https://doi.org/10.1007/978-3-030-90742-6_4

Osterrieder, S.K., Davis, R.W., 2011. Sea otter female and pup activity budgets, Prince William Sound, Alaska. J. Mar. Biol. Assoc. U. K. 91, 883–892. https://doi.org/10.1017/S0025315410001426

Owen, M.A., 2021. Polar bear maternal care, neonatal development, and social behavior, in: Davis, R.W., Pagano, A.M. (Eds.), Ethology and Behavioral Ecology of Sea Otters and Polar Bears, Ethology and Behavioral Ecology of Marine Mammals. Springer International Publishing, Cham, pp. 293–310. https://doi.org/10.1007/978-3-030-66796-2_15

Packard, J.M., Ribic, C.A., 1982. Classification of the behavior of sea otters (*Enhydra lutris*). Can. J. Zool. 60, 1362–1373. https://doi.org/10.1139/z82-184

Palagi, E., 2018. Not just for fun! Social play as a springboard for adult social competence in human and non-human primates. Behav. Ecol. Sociobiol. 72, 90. https://doi.org/10.1007/s00265-018-2506-6

Parks, S.E., Brown, M.W., Conger, L.A., Hamilton, P.K., Knowlton, A.R., Kraus, S.D., Slay, C.K., Tyack, P.L., 2007. Occurrence, composition, and potential functions of North Atlantic right whale (*Eubalaena glacialis*) surface active groups. Mar. Mammal Sci. 23, 868–887. https://doi.org/10.1111/j.1748-7692.2007.00154.x

Pedrazzi, L., Naik, H., Sandbrook, C., Lurgi, M., Fürtbauer, I., King, A.J., 2025. Advancing animal behaviour research using drone technology. Anim. Behav. 222, 123147. https://doi.org/10.1016/j.anbehav.2025.123147

Perry, E., Renouf, E., 1988. Further studies of the role of harbour seal *Phoca vitulina* pup vocalizations in preventing separation of mother-pup pairs. Can. J. Zool. 66, 934–938. https://doi.org/10.1139/z88-138

Perry, S., 2011. Social traditions and social learning in capuchin monkeys (*Cebus*). Philos. Trans. R. Soc. B Biol. Sci. 366, 988–996. https://doi.org/10.1098/rstb.2010.0317

Pitcher, B.J., Harcourt, R.G., Schaal, B., Charrier, I., 2011. Social olfaction in marine mammals: Wild female Australian sea lions can identify their pup's scent. Biol. Lett. 7, 60–62. https://doi.org/10.1098/rsbl.2010.0569

Ramos, E.A., Hartman, K.L., Baird, R.W., Lerma, J.K., Missael Rodríguez-González, F., Orbach, D.N., 2023. Drone perspectives on cetacean mating and sex, in: Würsig, B., Orbach, D.N. (Eds.), Sex in Cetaceans. Springer International Publishing, Cham, pp. 225–249. https://doi.org/10.1007/978-3-031-35651-3_11

Reid, K., Mann, J., Weiner, J.R., Hecker, N., 1995. Infant development in two aquarium bottlenose dolphins. Zoo Biol. 14, 135–147. https://doi.org/10.1002/zoo.1430140207

Rendell, L., Cantor, M., Gero, S., Whitehead, H., Mann, J., 2019. Causes and consequences of female centrality in cetacean societies. Philos. Trans. R. Soc. B Biol. Sci. 374, 20180066. https://doi.org/10.1098/rstb.2018.0066

Renouf, D., Lawson, J.W., 1987. Quantitative aspects of harbour seal (*Phoca vitulina*) play. J. Zool. 212, 267–273. https://doi.org/10.1111/j.1469-7998.1987.tb05989.x

Richardson, W.J., Finley, K.J., Miller, G.W., Davis, R.A., Koski, W.R., 1995. Feeding, social and migration behavior of bowhead whales, *Balaena mysticetus*, in Baffin Bay vs. the Beaufort Sea - Regions with different amounts of human activity. Mar. Mammal Sci. 11, 1–45. https://doi.org/10.1111/j.1748-7692.1995.tb00272.x

Rickard, M.E., Lomac-MacNair, K.S., Ireland, D.S., Leiter, S.M., Poster, M.D., Zoidis, A.M., 2022. Evidence of large whale socio-sexual behavior in the New York Bight. Aquat. Mamm. 48, 401–417. https://doi.org/10.1578/AM.48.5.2022.401

Ridgway, S.H., Carder, D.A., 1990. Tactile sensitivity, somatosensory responses, skin vibrations, and the skin surface ridges of the bottle-nose dolphin, *Tursiops truncatus*, in: Thomas, J.A., Kastelein, R.A. (Eds.), Sensory Abilities of Cetaceans. Springer US, Boston, MA, pp. 163–179. https://doi.org/10.1007/978-1-4899-0858-2_9

Riedman, M.L., Estes, J.E., 1990. The sea otter (*Enhydra lutris*): Behavior, ecology, and natural history (Biological Report No. 90 (14)). U.S. Department of the Interior Fish and Wildlife Service, Washington D.C.

Rojas-Bracho, L., Gulland, F., Smith, C., Taylor, B., Wells, R., Thomas, P., Bauer, B., Heide-Jørgensen, M., Teilmann, J., Dietz, R., Balle, J., Jensen, M., Sinding, M., Jaramillo-Legorreta, A., Abel, G., Read, A., Westgate, A., Colegrove, K., Gomez, F., Martz, K., Rebolledo, R., Ridgway, S., Rowles, T., Van Elk, C., Boehm, J., Cardenas-Hinojosa, G., Constandse, R., Nieto-Garcia, E., Phillips, W., Sabio, D., Sanchez, R., Sweeney, J., Townsend, F., Vivanco, J, Vivanco, Jc, Walker, S., 2019. A field effort to capture critically endangered vaquitas *Phocoena sinus* for protection from entanglement in illegal gillnets. Endanger. Species Res. 38, 11–27. https://doi.org/10.3354/esr00931

Rose, N.A., 1992. The social dynamics of male killer whales, *Orcinus orca*, in Johnstone Strait, British Columbia. University of California, Santa Cruz, United States.

Sakai, M., Hishii, T., Takeda, S., Kohshima, S., 2006. Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). Mar. Mammal Sci. 22, 966–978. https://doi.org/10.1111/j.1748-7692.2006.00082.x

Sakai, M., Katsumata, H., Kohshima, S., 2022. Observations of flipper rubbing in mother–calf pairs of captive bottlenose dolphins (*Tursiops truncatus*) suggest a body-surface care function. J. Ethol. 40, 257–264. https://doi.org/10.1007/s10164-022-00754-1

Sakai, M., Morisaka, T., Iwasaki, M., Yoshida, Y., Wakabayashi, I., Seko, A., Kasamatsu, M., Kohshima, S., 2013. Mother–calf interactions and social behavior development in Commerson's dolphins (Cephalorhynchus commersonii). J. Ethol. 31, 305–313. https://doi.org/10.1007/s10164-013-0380-2

Sánchez–Hernández, P., Krasheninnikova, A., Almunia, J., Molina–Borja, M., 2019. Social interaction analysis in captive orcas (*Orcinus orca*). Zoo Biol. 38, 323–333. https://doi.org/10.1002/zoo.21502

Schino, G., 1998. Reconciliation in domestic goats. Behaviour 135, 343–356. https://doi.org/10.1163/156853998793066302

Schino, G., Aureli, F., 2010. Primate reciprocity and its cognitive requirements. Evol. Anthropol. Issues News Rev. 19, 130–135. https://doi.org/10.1002/evan.20270

Seyfarth, R.M., 1977. A model of social grooming among adult female monkeys. J. Theor. Biol. 65, 671–698. https://doi.org/10.1016/0022-5193(77)90015-7

Seyfarth, R.M., Cheney, D.L., 1984. Grooming, alliances and reciprocal altruism in vervet monkeys. Nature 308, 541–543. https://doi.org/10.1038/308541a0

Sironi, M., 2004. Behavior and social development of juvenile southern right whales (*Eubalaena australis*) and interspecific interactions at Península Valdés, Argentina (Doctoral Thesis). The University of Wisconsin, United States.

Soriano, A.I., González, R., Maté, C., 2009. A study into the mother-pup relationship in three California sea lion *Zalophus californianus* mothers and pups at Barcelona Zoo. Int. Zoo Yearb. 43, 176–188. https://doi.org/10.1111/j.1748-1090.2008.00080.x

Spruijt, B.M., Van Hooff, J.A., Gispen, W.H., 1992. Ethology and neurobiology of grooming behavior. Physiol. Rev. 72, 825–852. https://doi.org/10.1152/physrev.1992.72.3.825

Strahan, M.G., Houser, D.S., Finneran, J.J., Mulsow, J., Crocker, D.E., 2020. Behaviorally measured tactile sensitivity in the common bottlenose dolphin, *Tursiops truncatus*. Mar. Mammal Sci. 36, 802–812. https://doi.org/10.1111/mms.12676

Strobel, S.M., Miller, M.A., Murray, M.J., Reichmuth, C., 2022. Anatomy of the sense of touch in sea otters: Cutaneous mechanoreceptors and structural features of glabrous skin. Anat. Rec. 305, 535–555. https://doi.org/10.1002/ar.24739

Strobel, S.M., Sills, J.M., Tinker, M.T., Reichmuth, C.J., 2018. Active touch in sea otters: In-air and underwater texture discrimination thresholds and behavioral strategies for paws and vibrissae. J. Exp. Biol. 221, jeb181347. https://doi.org/10.1242/jeb.181347

Sueur, C., Deneubourg, J.-L., Petit, O., Couzin, I.D., 2011. Group size, grooming and fission in primates: A modeling approach based on group structure. J. Theor. Biol. 273, 156–166. https://doi.org/10.1016/j.jtbi.2010.12.035

Tamaki, N., Morisaka, T., Taki, M., 2006. Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. Behav. Processes 73, 209–215. https://doi.org/10.1016/j.beproc.2006.05.010

Tavolga, M.C., Essapian, F.S., 1957. The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. Zool. Sci. Contrib. N. Y. Zool. Soc. 42, 11–31. https://doi.org/10.5962/p.203386

Themelin, M., Ribic, C.A., Melillo-Sweeting, K., Dudzinski, K.M., 2020. A new approach to the study of relationship quality in dolphins: Framework and preliminary results. Behav. Processes 181, 104260. https://doi.org/10.1016/j.beproc.2020.104260

Thomas, P.O., Taber, S.M., 1984. Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. Behaviour 88, 42–60. https://doi.org/10.1163/156853984x00470

Torres, L.G., Nieukirk, S.L., Lemos, L., Chandler, T.E., 2018. Drone up! Quantifying whale behavior from a new perspective improves observational capacity. Front. Mar. Sci. 5, 319. https://doi.org/10.3389/fmars.2018.00319

Trillmich, F., Cantor, M., 2018. Sociobiology, in: Perrin, W.F., Würsig, B., Thewissen, J.G.M. (Eds.), Encyclopedia of Marine Mammals. Academic Press, USA, pp. 882–886.

van de Sande, Y., Pouw, W., Southern, L.M., 2024. Automated recognition of grooming behavior in wild chimpanzees. Proc. Annu. Meet. Cogn. Soc. 46, 691–697.

Vasey, P.L., Duckworth, N., 2006. Sexual reward via vulvar, perineal, and anal stimulation: A proximate mechanism for female homosexual mounting in Japanese macaques. Arch. Sex. Behav. 35, 523–532. https://doi.org/10.1007/s10508-006-9111-x

Vivier, F., Andrés, C., Gonzalvo, J., Fertitta, K., Van Aswegen, M., Foroughirad, V., Mann, J., McEntee, M., Wells, R.S., Bejder, L., 2024. Inferring dolphin population status: using unoccupied aerial systems to quantify age-structure. Anim. Conserv. acv.12978. https://doi.org/10.1111/acv.12978

Weaver, A., 2003. Conflict and reconciliation in captive bottlenose dolphins, *Tursiops truncatus*. Mar. Mammal Sci. 19, 836–846. https://doi.org/10.1111/j.1748-7692.2003.tb01134.x

Weber, I., 1973. Tactile communication among free-ranging langurs. Am. J. Phys. Anthropol. 38, 481–486. https://doi.org/10.1002/ajpa.1330380251

Webster, M.M., Rutz, C., 2020. How STRANGE are your study animals? Nature 582, 337–340. https://doi.org/10.1038/d41586-020-01751-5

Weiss, M.N., Franks, D.W., Giles, D.A., Youngstrom, S., Wasser, S.K., Balcomb, K.C., Ellifrit, D.K., Domenici, P., Cant, M.A., Ellis, S., Nielsen, M.L.K., Grimes, C., Croft, D.P., 2021. Age and sex influence social interactions, but not associations, within a killer whale pod. Proc. R. Soc. B Biol. Sci. 288, 20210617. https://doi.org/10.1098/rspb.2021.0617

Whitehead, H., 2024. Sperm whale clans and human societies. R. Soc. Open Sci. 11, 231353. https://doi.org/10.1098/rsos.231353

Whitehead, H., 2003. Sperm whales: Social evolution in the ocean. The University of Chicago Press, Chicago, USA.

Whitehead, H., Rendell, L., 2014. The Cultural Lives of Whales and Dolphins. University of Chicago Press.

Whitham, J.C., Maestripieri, D., 2003. Primate rituals: the function of greetings between male Guinea baboons. Ethology 109, 847–859. https://doi.org/10.1046/j.0179-1613.2003.00922.x

Wilson, S., 1974. Juvenile play of the common seal *Phoca vitulina vitulina* with comparative notes on the grey seal *Halichoerus grypus*. Behaviour 48, 37–60. https://doi.org/10.1163/156853974X00246

Wilson, S., Miller, L., Hursey, M., Frantz, M., Gorte, J., 1985. The social development of a captive gray seal (*Halichoerus grypus*) pup for the first six months. Aquat. Mamm. 11, 89–100.

Wilson, S.C., Jones, K.A., 2020. Behaviour of harbour seal (*Phoca vitulina vitulina*) pups in Dundrum Bay, North-East Ireland, during transition from filial dependency to weaning. Biol. Environ. 120B, 187–202. https://doi.org/10.3318/bioe.2020.17

Würsig, B., Guerrero, J., Silber, G.K., 1993. Social and sexual behavior of bowhead whales in fall in the Western Arctic: A re-examination of seasonal trends. Mar. Mammal Sci. 9, 103–115. https://doi.org/10.1111/j.1748-7692.1993.tb00434.x

Würsig, B., Koski, W.R., Richardson, W.J., 1999. Whale riding behavior: Assisted transport for bowhead whale calves during spring migration in the Alaskan Beaufort Sea. Mar. Mammal Sci. 15, 204–210. https://doi.org/10.1111/j.1748-7692.1999.tb00791.x

Yamamoto, C., Ishibashi, T., 2022. Flipper rubbing reciprocity and partner choice in common bottlenose dolphins. J. Ethol. 40, 49–59. https://doi.org/10.1007/s10164-021-00729-8

Yamamoto, C., Kashiwagi, N., 2023. Affiliative behavior after aggressions in common bottlenose dolphins (*Tursiops truncatus*). Aquat. Mamm. 49, 288–293. https://doi.org/10.1578/AM.49.3.2023.288

Yeater, D.B., Miller, L.E., Caffery, K.A., Kuczaj, S.A., 2013. Effects of an increase in group size on the social behavior of a group of rough-toothed dolphins (*Steno bredanensis*). Aquat. Mamm. 39, 344–355. https://doi.org/10.1578/AM.39.4.2013.344

Zahavi, A., 1977. The testing of a bond. Anim. Behav. 25, 246–247. https://doi.org/10.1016/0003-3472(77)90089-6

Appendix 1– Scoping Review Methods

We conducted a scoping review using the electronic databases Scopus, Biological Abstracts, and ProQuest Dissertations and Theses Global (Table S1.1 & Table S1.2). We included research that mentioned body contact within marine mammal taxa (i.e., contact, touch, tactile socio-sexual behaviour, play, grooming) and excluded research in which contact between individuals was absent (e.g., directed at objects or humans) or categorized by authors as aggression, copulation, or suckling/nursing. We merged studies that reported common data (e.g., thesis chapters later published as articles). We considered publications available in English until April 2024. We compiled sources, removed duplicates, and screened texts using a web-based review manager software (Figure S4.1)(Covidence Systematic Review Software, 2024).

We supplemented our findings with additional references left out through our initial approach. For this, we inspected relevant references in the articles from our scoping review and conducted targeted searches in Google Scholar and Scopus. Our analyses of the trends and gaps in the study of social touch are limited to the references obtained through our initial review protocol to ensure future repeatability. However, our overview of the tactile abilities of marine mammals and discussion on the evidence for affiliative functions of touch incorporated additional sources.

Table S1.1. Search terms used for scoping review. Taxon-related words are coloured blue, and touch-related words are coloured orange. Exclusion terms are shown in grey.

Taxon	**Search terms**
Cetaceans	(cetacea* OR dolphin* OR whale* OR porpois* OR mysticet* OR odontocet* OR "marine mamm*" OR narwhal*) AND (contact* OR sociosex* OR "socio-sex*" OR touch* OR "affiliat*" OR tactil* OR epimelet*) AND NOT (molecul* OR cell* OR algor* OR robot* OR dentist* OR carie* OR clinic*)
Pinnipeds	(pinniped* OR seal OR seals OR "sea lion*" OR walrus OR phocid* OR odoben* OR otariid*) AND ("body contact*" OR sociosex* OR "socio-sex*" OR "social touch" OR "affiliat*" OR tactil*) AND NOT (molecul* OR cell* OR algor*)
Sirenians	(sirenia* OR manatee* OR dugong* OR "sea cow*") AND ("body contact*" OR sociosex* OR "socio-sex*" OR "social touch" OR "affiliat*" OR tactil*) AND NOT (molecul* OR cell* OR algor*)
Fissipeds	("sea otter*" OR "polar bear*") AND ("body contact*" OR sociosex* OR "socio-sex*" OR "social touch" OR "affiliat*" OR tactil*) AND NOT (molecul* OR cell* OR algor*)

Table S1.2. Search strategies and outcomes from the electronic databases used in this review

Database	Search Specifications	Results
Biological Abstracts (Web of Sciences)	Search in Topic	706
Scopus*	Search in Title, Abstract, Keywords Excluded results within the Energy, Engineering, Earth & Planetary Sciences, Materials Science, Medicine, and Physics & Astronomy subject areas.	964

ProQuest Dissertations & Theses Global	Search in Title, Abstract, Keywords	350
Snowball	We extracted the relevant research referenced in reviews resulting from our original search and added it to our screening process. Only sources which did not emerge through are original search were included.	37

*In Scopus, we excluded results within the Energy, Engineering, Earth & Planetary Sciences, Materials Science, Medicine, and Physics & Astronomy subject areas. Most of these results dealt with some form of seal (noun).

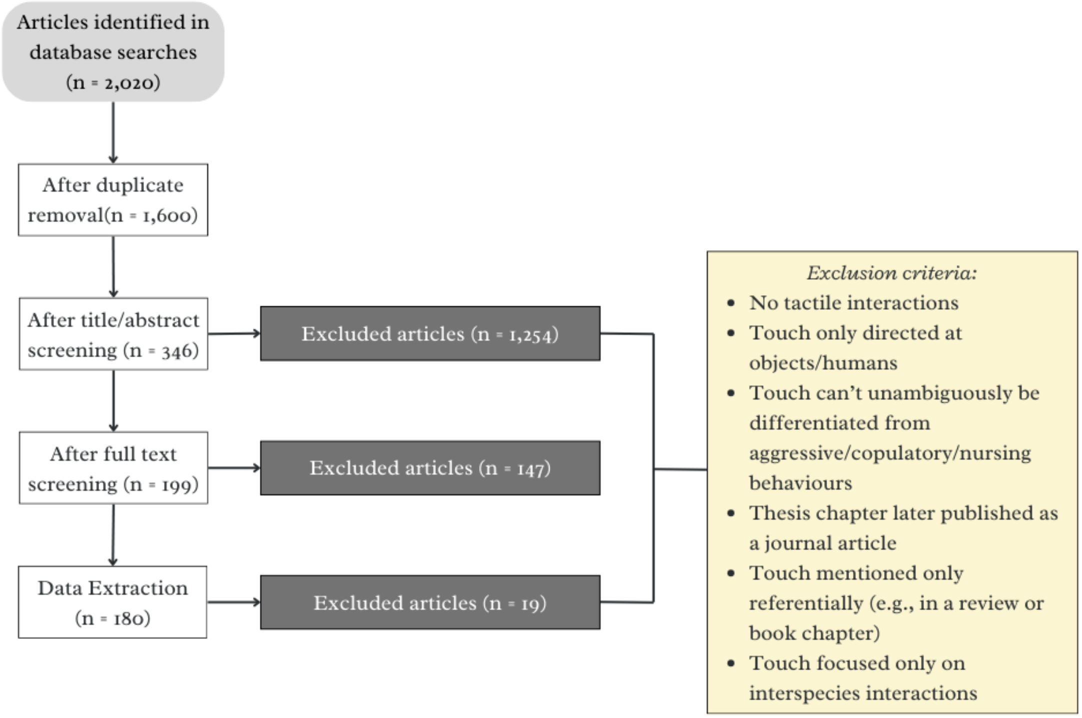

Figure S4.1. Flowchart for scoping review of social touch in marine mammals.

Appendix 2 – Summarized results of scoping review

Table S2. 1 Output references from scoping review by study level and taxon

Study Level	Carnivore	Cetacean	Pinniped	Sirenian	Total
Mention	4	39	0	0	43
Descriptive	2	32	14	6	54
Quantitative	3	62	14	5	83
Total	9	132	28	11	180

Table S2. 2 Output references from scoping review providing evidence for affiliative functions of social touch (either qualitative or quantitative). Results in which touch was merely mentioned as a subset of a broader behavioural category were omitted.

Provides evidence for social function?	Type of evidence	Carnivore	Cetacean	Pinniped	Sirenian	Total
No		3	37	10	7	57
Yes	-	2	56	18	4	80
	Quantitative	1	44	8	3	59
	Qualitative	1	12	10	1	22
Total		5	93	28	11	137

Table S2. 3 Species in which published works provide evidence for affiliative touch. References include results from our scoping review and complimentary searches. Legend: ● Wild – quantitative, ○ Wild – descriptive, ■ Captive – quantitative, ☐ Captive – descriptive.

Social function	Taxon	Species	References
Establishing & enforcing social bonds			
- Mother – infant	Cetaceans		
	Odontocetes		(Cockroft & Ross, 1990; Dudzinski, 1998; Dudzinski et al., 2013;

Social function	Taxon	Species	References
bonds and care		■ Cephalorhynchus commersoni ● Delphinapterus leucas ○ Orcinus orca ● Stenella frontalis ● Tursiops aduncus ■ Tursiops truncatus	Eskelinen et al., 2017; Fellner et al., 2013; Gibson & Mann, 2008; Guinet, 1991; Hill et al., 2018; Hill et al., 2016; Krasnova et al., 2006, 2009; Leu et al., 2020; Mann & Smuts, 1999; McBride & Kritzler, 1951; Reid et al., 1995; Sakai et al., 2006, 2013, 2022; Tavolga, 1966; Tavolga & Essapian, 1957; von Streit et al., 2011)
	Mysticetes	○ Balaena mysticetus ○ Eubalaena australis	(Thomas & Taber, 1984; Würsig et al., 1999)
	Carnivores Mustelids	● Enhydra lutris	(Osterrieder & Davis, 2011)
	Pinnipeds Phocidae	● Haliochoerus grypus ● Phoca groenlandica ● Phoca vitulina	(Cairns, 2013; Kovacs, 1987; Wilson, 1974)
	Otariidae	○ Eumetopias jubata	(Farentinos, 1971; Orr & Poulter, 1967)
	Sirenians Dugongs	○ Dugong dugong	(Jarman, 1966)
- Bonds beyond infancy Affirm social bonds with preferred associates	Cetaceans Odontocetes	■ Orcinus orca ● Stenella frontalis ■ Steno bredanensis ● Tursiops aduncus	(Acosta, 2015; Chereskin et al., 2022; R. Connor et al., 2000, 2006; Danaher-Garcia et al., 2022a, 2022b; Dudzinski et al., 2010, 2013; Dudzinski & Ribic, 2017; Friedman, 2017; Harvey et al., 2017; Herzing, 1993; Mann, 2006; Moreno, 2017;

Social function	Taxon	Species	References
		■ Tursiops truncatus	Richards, 1996; Sakai et al., 2006; Themelin et al., 2020; Weiss et al., 2021; Yamamoto & Ishibashi, 2022; Yeater et al., 2013)
	Pinnipeds		
	Phocids	■ Phoca vitulina	(Hanlan, 1998)
	Otarids	■ Otaria flavescens	(Llamazares-Martín et al., 2017)
	Sirenians		
	Manatees	■ Trichechus manatus	(Harper & Schulte, 2005; Hénaut et al., 2010)
Affirm social bonds with out-group members	Cetaceans		
	Odontocetes	● Orcinus orca ● Stenella frontalis ■ Steno bredanensis ● Tursiops aduncus	(Connor et al., 2006; Danaher-Garcia et al., 2022a; Dudzinski, 1998; Friedman et al., 2023; Rose, 1992; Yeater et al., 2013)
Facilitating cooperation			
	Cetaceans		
	Odontocetes	■ Delphinapterus leucas ● Tursiops aduncus ■ Tursiops truncatus	(Friedman, 2017; Glabicky et al., 2010; Sakai et al., 2006; Yamamoto & Ishibashi, 2022)
Managing conflict			
	Cetaceans		
	Odontocetes	■ Orcinus orca ■ Tursiops truncatus	(Sánchez–Hernández et al., 2019; Tamaki et al., 2006; Weaver, 2003; Yamamoto & Kashiwagi, 2023)

Supplementary References

Acosta, N. B. (2015). Same-sex socio-sexual interactions among a group of captive bottlenose dolphins (*Tursiops truncatus*) (1729468182; Issue 1603203) [MA Thesis]. The University of Southern Mississippi.

Cairns, C. L. (2013). The early ethology of wild grey seal (*Halichoerus grypus*) neonates over the period of maternal dependency: An assessment of the nature and function of behaviour [Masters Thesis] University of Durham.

Chereskin, E., Connor, R. C., Friedman, W. R., Jensen, F. H., Allen, S. J., Sørensen, P. M., Krützen, M., & King, S. L. (2022). Allied male dolphins use vocal exchanges to "bond at a distance." *Current Biology*, *32*(7), 1657-1663.e4. https://doi.org/10.1016/j.cub.2022.02.019

Cockroft, V. G., & Ross, G. (1990). Observations on the early development of a captive bottlenose dolphin calf. In S. Leatherwood & R. R. Reeves (Eds.), *The Bottlenose Dolphin* (pp. 461–478). Academic Press.

Connor, R. C., Smolker, R., & Bejder, L. (2006). Synchrony, social behaviour and alliance affiliation in Indian Ocean bottlenose dolphins, *Tursiops aduncus*. *Animal Behaviour*, *72*(6), 1371–1378. https://doi.org/10.1016/j.anbehav.2006.03.014

Connor, R., Mann, J., & Watson-Capps, J. (2006). A sex-specific affiliative contact behavior in indian ocean bottlenose dolphins, *Tursiops* sp. *Ethology*, *112*(7), 631–638. https://doi.org/10.1111/j.1439-0310.2006.01203.x

Connor, R., Wells, R., Mann, J., & Read, A. J. (2000). The bottlenose dolphin, social relationships in a fission-fussion society. In *Cetacean Societies* (pp. 91–126). The University of Chicago Press.

Covidence Systematic Review Software. (2024). [Computer software]. Veritas Health Innovation. http://www.covidence.org

Danaher-Garcia, N., Connor, R., Fay, G., Melillo-Sweeting, K., & Dudzinski, K. M. (2022a). The partial merger of two dolphin societies. *Royal Society Open Science*, *9*(8). https://doi.org/10.1098/rsos.211963

Danaher-Garcia, N., Connor, R., Fay, G., Melillo-Sweeting, K., & Dudzinski, K. M. (2022b). Using social network analysis to confirm the 'gambit of the group' hypothesis for a small cetacean. *Behavioural Processes*, *200*. https://doi.org/10.1016/j.beproc.2022.104694

Dudzinski, K. M. (1998). Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals*, *24*(3), 129–142.

Dudzinski, K. M., Danaher-García, N., & Gregg, J. D. (2013). Pectoral fin contact between dolphin dyads at Zoo Duisburg, with comparison to other dolphin study populations. *Aquatic Mammals*, *39*(4), 335–343. https://doi.org/10.1578/AM.39.4.2013.335

Dudzinski, K. M., Gregg, J. D., Paulos, R. D., & Kuczaj, S. A. (2010). A comparison of pectoral fin contact behaviour for three distinct dolphin populations. *Behavioural Processes*, *84*(2), 559–567. https://doi.org/10.1016/j.beproc.2010.02.013

Dudzinski, K., & Ribic, C. (2017). Pectoral fin contact as a mechanism for social bonding among dolphins. *Animal Behavior and Cognition*, *4*(1), 30–48. https://doi.org/10.12966/abc.03.02.2017

Eskelinen, H. C., Borger-Turner, J. L., & Kuczaj, S. A. (2017). Observations of a paternal male with bottlenose dolphin calf (Tursiops truncatus): A case study. *International Journal of Comparative Psychology*, *30*. https://www.scopus.com/inward/record.uri?eid=2-s2.0-85053237869&partnerID=40&md5=8b3979ef29180b7ddf73f6a52e4cb403

Farentinos, R. C. (1971). Some observations on the play behavior of the Steller sea lion (*Eumetopias jubata*). *Zeitschrift Für Tierpsychologie*, *28*(4), 428–438. https://doi.org/10.1111/j.1439-0310.1971.tb00826.x

Fellner, W., Bauer, G. B., Stamper, S. A., Losch, B. A., & Dahood, A. (2013). The development of synchronous movement by bottlenose dolphins (*Tursiops truncatus*). *Marine Mammal Science*, *29*(3), E203–E225. https://doi.org/10.1111/j.1748-7692.2012.00609.x

Friedman, W. R. G. (2017). Social and cognitive complexity in wild bottlenose dolphins (*Tursiops sp.*) [Doctoral Thesis]. University of California, San Diego.

Friedman, W. R., Krützen, M., King, S. L., Allen, S. J., Gerber, L., Wittwer, S., & Connor, R. C. (2023). Inter-group alliance dynamics in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). *Animal Cognition*, *26*(5), 1601–1612. https://doi.org/10.1007/s10071-023-01804-y

Gibson, Q. A., & Mann, J. (2008). Early social development in wild bottlenose dolphins: Sex differences, individual variation and maternal influence. *Animal Behaviour*, *76*(2), 375–387. https://doi.org/10.1016/j.anbehav.2008.01.021

Glabicky, N., DuBrava, A., & Noonan, M. (2010). Social–sexual behavior seasonality in captive beluga whales (*Delphinapterus leucas*). *Polar Biology*, *33*(8), 1145–1147. https://doi.org/10.1007/s00300-010-0790-3

Guinet, C. (1991). Intentional stranding apprenticeship and social play in killer whales (*Orcinus orca*). *Canadian Journal of Zoology*, *69*(11), 2712–2716. https://doi.org/10.1139/z91-383

Hanlan, S. K. (1998). *Nosing behaviour in captive harbour seals (*Phoca vitulina concolor*): Implications for olfaction and affiliation* [MSc Thesis]. Memorial University of Newfoundland.

Harper, J. Y., & Schulte, B. A. (2005). Social interactions in captive female Florida manatees. *Zoo Biology*, *24*(2), 135–144. https://doi.org/10.1002/zoo.20044

Harvey, B. S., Dudzinski, K. M., & Kuczaj, S. A. (2017). Associations and the role of affiliative, agonistic, and socio-sexual behaviors among common bottlenose dolphins (*Tursiops truncatus*). *Behavioural Processes*, *135*, 145–156. https://doi.org/10.1016/j.beproc.2016.12.013

Hénaut, Y., Becerra Lopez, S. P., MacHkour-M’Rabet, S., Morales-Vela, B., Winterton, P., & Elfour, F. (2010). Activities and social interactions in captive Antillean manatees in Mexico. *Mammalia*, *74*(2), 141–146. https://doi.org/10.1515/MAMM.2010.016

Herzing, D. L. (1993). *Dolphins in the wild: An eight year field study on dolphin communication and interspecies interaction* (304097781; Issue 9410246) [The Union Institute]. https://ezproxy.library.dal.ca/login?url=https://www.proquest.com/dissertations-theses/dolphins-wild-eight-year-field-study-on-dolphin/docview/304097781/se-2?accountid=10406

Hill, H., Dietrich, S., Jantea, R. F., Garza, S., & Lacy, K. (2018). The frequency of contact in beluga (*Delphinapterus leucas*) calf social interactions. *Aquatic Mammals*, *44*(1), 62–75. https://doi.org/10.1578/AM.44.1.2018.62

Hill, H. M., Alvarez, C. J., Dietrich, S., & Lacy, K. (2016). Preliminary Findings in Beluga (Delphinapterus leucas) Tactile Interactions. *Aquatic Mammals*, *42*(3), 277–291. https://doi.org/10.1578/AM.42.3.2016.277

Jarman, P. J. (1966). The status of the dugong (*Dugong dugon moller*); Kenya, 1961. *African Journal of Ecology*, *4*(1), 82–88. https://doi.org/10.1111/j.1365-2028.1966.tb00885.x

Kovacs, K. M. (1987). Maternal behaviour and early behavioural ontogeny of harp seals, *Phoca groenlandica*. *Animal Behaviour*, *35*(3), 844–855. https://doi.org/10.1016/S0003-3472(87)80120-3

Krasnova, V. V., Bel’kovich, V. M., & Chernetsky, A. D. (2006). Mother-infant spatial relations in wild Beluga (*Delphinapterus leucas*) during postnatal development under natural conditions. *Biology Bulletin*, *33*(1), 53–58. https://doi.org/10.1134/S1062359006010079

Krasnova, V. V., Belkovich, V. M., & Chernetsky, A. D. (2009). Formation of behavior of White Sea beluga Dilphinapterus leucas infants in early postnatal ontogenesis. *Biologiya Morya (Vladivostok)*, *35*(1), 41–47.

Leu, S. T., Sah, P., Krzyszczyk, E., Jacoby, A.-M., Mann, J., & Bansal, S. (2020). Sex, synchrony, and skin contact: Integrating multiple behaviors to assess pathogen transmission risk. *Behavioral Ecology*, *31*(3), 651–660. https://doi.org/10.1093/beheco/araa002

Llamazares-Martín, C., Scopa, C., Guillén-Salazar, F., & Palagi, E. (2017). Strong competition does not always predict play asymmetry: The case of South American sea lions (*Otaria flavescens*). *Ethology*, *123*(4), 270–282. https://doi.org/10.1111/eth.12594

Mann, J. (2006). Establishing trust: Socio-sexual behaviour and the development of male-male bonds among Indian Ocean bottlenose dolphins. In V. Sommer (Ed.), *Homosexual Behaviour in Animals: An Evolutionary Perspective* (pp. 107–130). Cambridge Univ. Press.

Mann, J., & Smuts, B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Behaviour*, *136*(5), 529–566. https://doi.org/10.1163/156853999501469

McBride, A. F., & Kritzler, H. (1951). Observations on Pregnancy, Parturition, and Postnatal Behavior in the Bottlenose Dolphin. *Journal of Mammalogy*, *32*(3), 251. https://doi.org/10.2307/1375657

Moreno, K. (2017). *Cetacean Exhalation: An Examination of Bottlenose Dolphin (Tursiops truncatus) Use of Three Bubble Production Types through Associated Behaviors* (1976958493; Issue 10641390) [The University of Southern Mississippi]. https://ezproxy.library.dal.ca/login?url=https://www.proquest.com/dissertations-theses/cetacean-exhalation-examination-bottlenose/docview/1976958493/se-2?accountid=10406

Orr, R. T., & Poulter, T. C. (1967). Some observations on reproduction, growth, and social behavior in the Steller sea lion *Eumetopias jubata*. *Proceedings of the California Academy of Sciences*, *35*((10)), 103–226.

Osterrieder, S. K., & Davis, R. W. (2011). Sea otter female and pup activity budgets, Prince William Sound, Alaska. *Journal of the Marine Biological Association of the United Kingdom*, *91*(4), 883–892. https://doi.org/10.1017/S0025315410001426

Reid, K., Mann, J., Weiner, J. R., & Hecker, N. (1995). Infant development in two aquarium bottlenose dolphins. *Zoo Biology*, *14*(2), 135–147. https://doi.org/10.1002/zoo.1430140207

Richards, A. F. (1996). *Life history and behavior of female dolphins (Tursiops sp.) in Shark Bay, Western Australia* (304244807; Issue 9712068) [University of Michigan]. https://ezproxy.library.dal.ca/login?url=https://www.proquest.com/dissertations-theses/life-history-behavior-female-dolphins-tursiops-sp/docview/304244807/se-2?accountid=10406

Rose, N. A. (1992). *The social dynamics of male killer whales,* Orcinus orca*, in Johnstone Strait, British Columbia* (304032111; Issue 9312443). University of California, Santa Cruz.

Sakai, M., Hishii, T., Takeda, S., & Kohshima, S. (2006). Flipper rubbing behaviors in wild bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science*, *22*(4), 966–978. https://doi.org/10.1111/j.1748-7692.2006.00082.x

Sakai, M., Katsumata, H., & Kohshima, S. (2022). Observations of flipper rubbing in mother–calf pairs of captive bottlenose dolphins (*Tursiops truncatus*) suggest a body-surface care function. *Journal of Ethology*, *40*(3), 257–264. https://doi.org/10.1007/s10164-022-00754-1

Sakai, M., Morisaka, T., Iwasaki, M., Yoshida, Y., Wakabayashi, I., Seko, A., Kasamatsu, M., & Kohshima, S. (2013). Mother-calf interactions and social behavior development in Commerson's dolphins (*Cephalorhhynchus commersonii*). *Journal of Ethology*, *31*(3), 305–313. https://doi.org/10.1007/s10164-013-0380-2

Sánchez–Hernández, P., Krasheninnikova, A., Almunia, J., & Molina–Borja, M. (2019). Social interaction analysis in captive orcas (*Orcinus orca*). *Zoo Biology*, *38*(4), 323–333. https://doi.org/10.1002/zoo.21502

Tamaki, N., Morisaka, T., & Taki, M. (2006). Does body contact contribute towards repairing relationships? The association between flipper-rubbing and aggressive behavior in captive bottlenose dolphins. *Behavioural Processes*, *73*(2), 209–215. https://doi.org/10.1016/j.beproc.2006.05.010

Tavolga, M. C. (1966). Behaviour of the bottlenose dolphin (*Tursiops truncatus*): Social interactions in a captive colony. In *First International Symposium on Cetacean Research: Whales, dolphins, and porpoises, Washington, Dist. Columbia, August, 1963* (BIOABS:BACD19674800016051; p. 730).

Tavolga, M. C., & Essapian, F. S. (1957). The behavior of the bottle-nosed dolphin (*Tursiops truncatus*): Mating, pregnancy, parturition and mother-infant behavior. *Zoologica: Scientific Contributions of the New York Zoological Society.*, *42*(2), 11–31. https://doi.org/10.5962/p.203386

Themelin, M., Ribic, C. A., Melillo-Sweeting, K., & Dudzinski, K. M. (2020). A new approach to the study of relationship quality in dolphins: Framework and preliminary results. *Behavioural Processes*, *181*, 104260. https://doi.org/10.1016/j.beproc.2020.104260

Thomas, P. O., & Taber, S. M. (1984). Mother-infant interaction and behavioral development in southern right whales, *Eubalaena australis*. *Behaviour*, *88*, 42–60. https://doi.org/10.1163/156853984x00470

von Streit, C., Ganslosser, U., & von Fersen, L. (2011). Ethogram of Two Captive Mother-Calf Dyads of Bottlenose Dolphins (Tursiops truncatus): Comparison with Field Ethograms. *Aquatic Mammals*, *37*(2), 193–197. https://doi.org/10.1578/AM.37.2.2011.193

Weaver, A. (2003). Conflict and reconciliation in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science*, *19*(4), 836–846. https://doi.org/10.1111/j.1748-7692.2003.tb01134.x

Weiss, M. N., Franks, D. W., Giles, D. A., Youngstrom, S., Wasser, S. K., Balcomb, K. C., Ellifrit, D. K., Domenici, P., Cant, M. A., Ellis, S., Nielsen, M. L. K., Grimes, C., & Croft, D. P. (2021). Age and sex influence social interactions, but not associations, within a killer whale pod. *Proceedings of the Royal Society B: Biological Sciences*, *288*(1953), 20210617. https://doi.org/10.1098/rspb.2021.0617

Wilson, S. (1974). Mother-Young Interactions in the Common Seal, Phoca Vitulina Vitulina. *Behaviour*, *48*(1–4), 23–35. https://doi.org/10.1163/156853974X00237

Würsig, B., Koski, W. R., & Richardson, W. J. (1999). Whale riding behavior: Assisted transport for bowhead whale calves during spring migration in the Alaskan Beaufort Sea. *Marine Mammal Science*, *15*(1), 204–210. https://doi.org/10.1111/j.1748-7692.1999.tb00791.x

Yamamoto, C., & Ishibashi, T. (2022). Flipper rubbing reciprocity and partner choice in common bottlenose dolphins. *Journal of Ethology*, *40*(1), 49–59. https://doi.org/10.1007/s10164-021-00729-8

Yamamoto, C., & Kashiwagi, N. (2023). Affiliative behavior after aggressions in common bottlenose dolphins (*Tursiops truncatus*). *Aquatic Mammals*, *49*(3), 288–293. https://doi.org/10.1578/AM.49.3.2023.288

Yeater, D. B., Miller, L. E., Caffery, K. A., & Kuczaj, S. A. (2013). Effects of an increase in group size on the social behavior of a group of rough-toothed dolphins (*Steno bredanensis*). *Aquatic Mammals*, *39*(4), 344–355. https://doi.org/10.1578/AM.39.4.2013.344