

Review



Cite this article: Rendell L, Cantor M, Gero S, Whitehead H, Mann J. 2019 Causes and consequences of female centrality in cetacean societies. *Phil. Trans. R. Soc. B* **374**: 20180066. <http://dx.doi.org/10.1098/rstb.2018.0066>

Accepted: 17 December 2018

One contribution of 17 to a theme issue ‘The evolution of female-biased kinship in humans and other mammals’.

Subject Areas:

behaviour, evolution

Keywords:

cetacean, female, social evolution, kinship

Author for correspondence:

Luke Rendell

e-mail: ler4@st-andrews.ac.uk

Causes and consequences of female centrality in cetacean societies

Luke Rendell¹, Mauricio Cantor^{2,3,4}, Shane Gero⁵, Hal Whitehead⁶ and Janet Mann⁷

¹Sea Mammal Research Unit, School of Biology, University of St Andrews, St Andrews KY16 9TH, UK

²Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis 88040-970, Brazil

³Centro de Estudos do Mar, Universidade Federal do Paraná, Pontal do Paraná 83255-000, Brazil

⁴School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg-Braamfontein, South Africa

⁵Department of Zoophysiology, Institute for Bioscience, Aarhus University, Aarhus 8000, Denmark

⁶Department of Biology, Dalhousie University, Halifax, Canada B3H 4J1

⁷Department of Biology, Georgetown University, Washington, DC 20057, USA

ORCID LR, 0000-0002-1121-9142; MC, 0000-0002-0019-5106; SG, 0000-0001-6854-044X; HW, 0000-0001-5469-3429

Cetaceans are fully aquatic predatory mammals that have successfully colonized virtually all marine habitats. Their adaptation to these habitats, so radically different from those of their terrestrial ancestors, can give us comparative insights into the evolution of female roles and kinship in mammalian societies. We provide a review of the diversity of such roles across the Cetacea, which are unified by some key and apparently invariable life-history features. Mothers are uniparous, while paternal care is completely absent as far as we currently know. Maternal input is extensive, lasting months to many years. Hence, female reproductive rates are low, every cetacean calf is a significant investment, and offspring care is central to female fitness. Here strategies diverge, especially between toothed and baleen whales, in terms of mother–calf association and related social structures, which range from ephemeral grouping patterns to stable, multi-level, societies in which social groups are strongly organized around female kinship. Some species exhibit social and/or spatial philopatry in both sexes, a rare phenomenon in vertebrates. Communal care can be vital, especially among deep-diving species, and can be supported by female kinship. Female-based sociality, in its diverse forms, is therefore a prevailing feature of cetacean societies. Beyond the key role in offspring survival, it provides the substrate for significant vertical and horizontal cultural transmission, as well as the only definitive non-human examples of menopause.

This article is part of the theme issue ‘The evolution of female-biased kinship in humans and other mammals’.

1. Introduction

When cetacean ancestors severed all ties with terrestrial habitats, capable of completing their entire life cycle without recourse to any solid ground, they became subject entirely to the selective forces engendered by the marine habitat. This was the beginning of an evolutionary experiment on how a terrestrial heritage of mammalian sociality would respond to the diverse and sometimes radically different nature of oceanic ecosystems. In this review, we summarize how this natural experiment provides deep comparative insights into social evolution, especially the role of female kinship, and how both flexibility and constraint interact in the evolution of female social roles. While we know a lot about some species, we know almost nothing about the social structure of most of the 80+ cetacean species, which means most of these potential insights remain untapped. Given both the strong parallels and key differences between primate and cetacean social systems—including brain size, life history and diversity in social bonds—comparative analysis of female social roles in

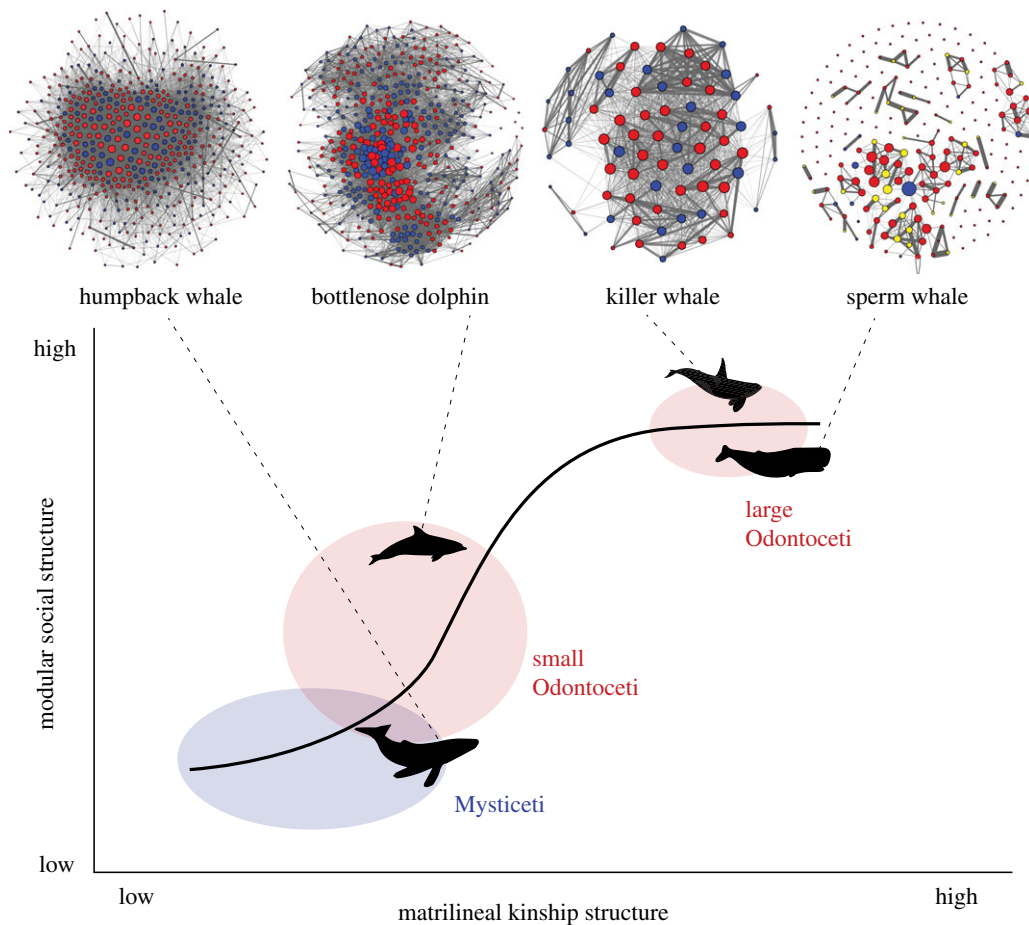


Figure 1. Social and matrilineal kinship structure in cetaceans—a conceptual organization. Cetacean societies across the Mysticeti (baleen whales) and Odontoceti (toothed whales) span a continuum between low and high modularity, increasingly structured into sets of highly connected individuals with the tendency of maternally related individuals to interact among themselves (female kinship organization ranging from matrifocal to more strictly matrilineal). Networks depict empirical data from long-term studies (after [4]) on photo-identified individuals (red nodes = females, blue nodes = males, yellow nodes = calves) connected by association (link thickness is proportional to association index). (Online version in colour.)

cetaceans can inform our understanding of female social roles in primate societies, including our own. This has important implications for understanding socio-cultural changes in modern human societies, where, for example, a comparative understanding of female social roles can guide thinking about sources and solutions to the problem of underrepresentation of women in positions of leadership [1]. Therefore, in this paper, we review the behavioural ecology literature on the cetacean social structure to provide a synthesis of the varied, and sometimes very pronounced, forms of female-based kinship found in this taxon, and try to identify broad principles to organize this diversity. We hope this will help researchers aiming to understand similar variation across both aquatic and terrestrial mammalian societies, including that between human societies.

We shall explain how things are different for a mammal in the ocean, but does this mean that the social evolution predictions formulated over decades of research into terrestrial mammals do not apply to cetacean societies? A recent analysis of mammalian social complexity and kinship by Lukas & Clutton-Brock [2] shows how the distribution of different aspects of social complexity is strongly related to average within-group female relatedness. However, lack of data meant only one cetacean species was included, so here we assess how well our understanding of cetacean sociality matches qualitatively with these predictions. Furthermore, the traditional view of female sociality in primates has centred on

the competition for food, as delineated by the distribution of resources (e.g. [3]), but the nature of such competition can be radically different in a fluid three-dimensional environment where travel costs can be low and resources can be impossible to defend. So can we readily apply such views to cetaceans?

The key message of our treatment is a conceptual relationship, laid out in figure 1, between modularity of social structure (i.e. the extent to which associations are concentrated within rather than between long-term social groups) and the degree to which those social organizations are biased toward females. Where cetacean species have a modular social structure, that modularity is always centred around lineages of close female relatives. Organization into sets of highly connected individuals (i.e. a modular social structure) is associated with a tendency of maternally related individuals to interact among themselves. This ranges from systems described as ‘matrifocal’, a loosely defined term largely reflecting statistical population genetic findings of increased maternal relatedness within social groups compared with between (e.g. [5]), up to true matrilineal kinship structure, in which long-term groups strictly contain individuals related through a recent female ancestor. This relationship differs between baleen and toothed whales. The social systems of baleen whales tend to be generally unstructured (here illustrated by the highly connected, non-modular social network of humpback

whales with a weak matrilineal influence) while the social systems of toothed whales are more variable, with variation across species loosely correlating with body size. The social structures of small species range from low to intermediate levels of both modularity and influence of matrilineal kinship (here, illustrated by the modular social network of bottlenose dolphins, in which females apparently occupy more central positions). Such modularity as exists in the better-known small toothed whales seems to be driven by a variety of other social (e.g. homophily and learning [6]) and non-social mechanisms (e.g. home-range and temporal overlap [7]) and although matrilineal kinship may organize social relationships (e.g. [8]) the organizational bias is not strong enough to create discrete social modules. By contrast, both modularity and the strength of female-biased kinship organization peak among the larger toothed whales, illustrated by the social structures of sperm and killer whales, characterized by lifetime division into social modules of highly related individuals.

We first discuss how and why things are different, ecologically and socially, for mammals in the ocean. We then provide an overview of female kinship organization in cetaceans, structuring our treatment along the most significant taxonomic division in the group, between the baleen and toothed whales. For each, we outline what is known about female kinship and how this relates to foraging ecology and mating systems, but are biased toward the toothed cetaceans, where we see diverse forms of female-biased kinship. In particular, we develop a case study of killer whales, *Orcinus orca*, because it potentially informs us about key aspects of human evolution, such as the evolution of menopause. Finally, we synthesize these findings into an assessment of how well cetaceans fit within the current models of female sociality outlined above.

2. Mammals in the ocean

Cetaceans comprise a diverse collection of animals in terms of length, habitat, life-history strategies and social systems [9]. Body sizes vary from the 1.3 m vaquita, *Phocoena sinus*, to the greater than 30 m adult blue whale, *Balaenoptera musculus*. They are distributed nearly from pole to pole, inhabiting the coldest to the warmest seas, and from shallow riverine and coastal waters to offshore pelagic zones. The most profound differences, both phylogenetically and socioculturally, lie between the generally larger, long-lived 14 species of the suborder Mysticeti and the disparate group of approximately 76 species that compose the suborder Odontoceti (henceforth baleen and toothed whales, respectively). They all occupy intermediate to top trophic levels but have evolved quite different primary feeding adaptations, filter-feeding for baleen and echolocation for toothed whales. These lead to major divergences in anatomy, foraging behaviour and lifestyle. Baleen whales typically migrate to tropical breeding grounds in winter and temperate or polar feeding grounds in summer, where they filter large, dense schools of small planktonic crustaceans and schooling fish from the water. Toothed whales do not follow such strict migration schedules. While their varied lifestyles match the diversity of their body sizes and habitats, all toothed whales use echolocation to hunt prey ranging from a wide diversity of fish and cephalopods, to other marine mammals.

Like all mammals [10], cetacean females play the pivotal role in reproduction and the survival of offspring, including gestation, lactation, weaning, and post-weaning care. Currently, we know of no species in which paternal participation extends beyond copulation. In the thermodynamically challenging aquatic habitat, female reproduction is even more energetically expensive than on land. Cetaceans expend considerable energy to regulate body temperature, and females must help newborns grow quickly and insulate their bodies with blubber layers. Females universally give birth to a single, large precocial calf after long gestation periods, and subsequently produce extremely lipid-rich milk [11]. Young cetaceans take time to achieve behavioural and energetic independence, and so cetaceans are unusual in the ocean where parental care is uncommon. Since their mating systems are, wherever known, polygynous or polygynandrous, such care falls almost entirely on the mothers, who will nourish the young as they learn to feed for themselves, and may go on to protect and accompany them well into their adult lives. Female cetaceans are therefore slow offspring producers with long somatic and reproductive lifespans, and long gestation and maturation periods (figure 2), ramping up the scale of investment represented by each calf and turbocharging the divergent selective pressures on males and females. The mother–calf bond is therefore the cornerstone of cetacean societies.

Outside the mother–calf pair, cetaceans are typically gregarious animals but show a large diversity in observed group size, from pairs to pelagic dolphin shoals that number thousands [12]. They form groups that are tightly clustered spatially. Individuals are usually within a few body lengths of one another, and if not, still within easy communication range [13]. While the groups vary considerably in number of members and stability, cetaceans actively form and maintain these groups by coordinating behaviour with group mates. In several, perhaps most, species, there is substantial sexual segregation, so females primarily accompany other females [14,15]. The drivers of this segregation are not fully understood, but likely reflect the two sexes having divergent ecological and social needs for reproductive success (for example, male sperm whales, *Physeter macrocephalus*, accessing high-latitude food sources to attain competitive size, or male bottlenose dolphins, *Tursiops* spp., increasing mating opportunities by joining alliances [12]). From the perspective of observers, and perhaps for the animals themselves, the most salient attribute of groups is association—the animals are close together and coordinate their movements. This may bring them a number of benefits, including protection against predators and the communal discovery of food, but the association itself may be an important part of maintaining bonds [13]. Repeated observations of associations between individuals leads researchers to think about the relationships underlying the associations, and in female cetaceans, we see a diversity in the strength of such bonds such that there is a parallel diversity in the terminology used to describe collections of individuals who regularly associate—groups, units, pods, herds and so forth. Partly, this reflects a somewhat haphazard historical approach to terminology in the field. For example, stable groups of maternally related mid-sized toothed whales tend to be referred to as ‘pods’, while in sperm whales, the largest toothed whales, they are ‘units’, for reasons that initially appear simply historical (it is also possible to see ‘pod’ used as a default term for assemblages

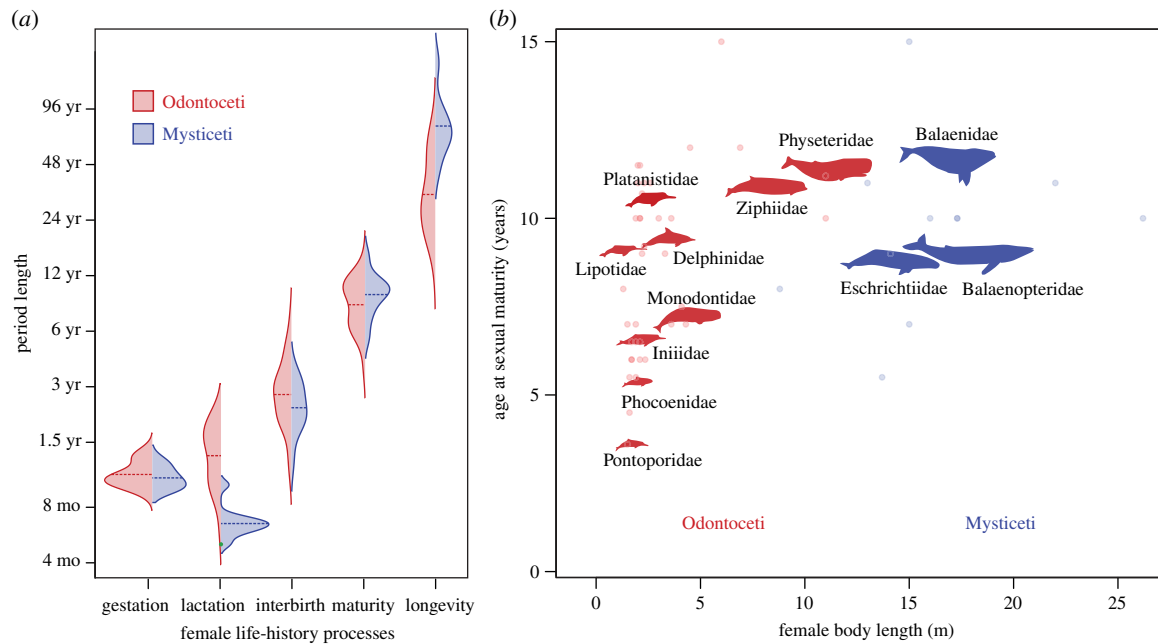


Figure 2. Life-history processes and the central role of females as mothers in cetacean societies. (a) Duration of key life-history processes of female toothed whales (Odontoceti) and baleen whales (Mysticeti). Split violin plots indicate the probability distributions of log-transformed length of gestation and lactation (mean), inter-birth interval (mode), maturity (mean age at first birth) and longevity (maximum lifespan) across 13 Mysticeti species (red) and 43 Odontoceti species (blue). Dashed lines within violins indicate mean values. (b) Speed of female life-history processes relative to body length between toothed and baleen whales. Age at sexual maturity correlates highly with all other life-history traits and thus is used here as a summary measure of the other life-history processes. Shaded circles represent species of Odontoceti (red) and Mysticeti (blue) and solid icons indicate the mean values for each taxonomic family for which data were available. Icon sizes are suggestive of the average body length. Data and estimation methods in [11]. (Online version in colour.)

of cetaceans, regardless of association strength or relatedness). But this also reflects the fact that in many species, we observe relationship patterns that are unique and do not readily extend across multiple species or even populations. For example, killer whale pods can be extremely stable in some populations, but less so in others [16], while there is evidence of membership change in sperm whale units [17]. Here, we use terms that reflect the original literature and try where possible to bring through the original definitions of those terms in order that readers can appreciate the underlying diversity. The diversity is unified, however, by the idea that bonded females can increase mutual fitness through cooperative hunting, alloparental care (care provided by individuals other than the biological parents) and communal defence of each other and their calves, as well as through sharing information. For female cetaceans, we argue, the ramping up of divergent selection pressures has made these benefits even more important and thereby strongly favoured female-biased kinship organization.

Relationships between female cetaceans need not be universally mutualistic of course, but aggression and dominance seem rare—for example, female–female aggression is very rare in the best-studied population of bottlenose dolphins in Shark Bay, Australia [18]. Female dominance hierarchies have been described in captivity, but took years to identify, being based on a handful of ‘flinches’ per year, and these animals were in forced proximity [19]. Interestingly, the hierarchy that emerged among females was based on age, not size. There is little evidence for such hierarchies in the wild, however, as females can readily avoid each other in fission–fusion societies [20]. Furthermore, resource defence is very different in marine habitats. Often it is simply impossible, if not pointless, because of the

abundance of resources—even in a shallow water coastal dolphin population, where resource defence might be more plausible, 32 years of study have yielded just one observation of prey stealing (J. Mann 2017, personal observation) and females are completely tolerant of others closely inspecting their prey catches [21]. Thus, competition between females seems to be largely indirect.

3. Maternal kinship in baleen whales

The baleen whales are among the largest animals that ever lived, with the relatively recent evolution of present gigantism coincident with increases in intense but ephemeral primary productivity resulting from wind-driven upwelling starting in the Pliocene, around 4.5 Ma [22]. Baleen whale lives reflect their reliance on dense aggregations of small, low trophic level prey that are highly abundant only seasonally [23], inducing most species to undertake long, regular feeding/breeding migration cycles [24]. They accumulate energy for reproduction during an intense half-year feeding season during the summer, taking advantage of seasonal resource abundance driven by blooms in primary productivity in temperate and high-latitude waters. For the other half of the year, they largely fast, and migrate to warmer, low-latitude winter breeding grounds. There, males provide their brief reproductive contribution while females engage in the costly tasks of gestation, parturition, lactation and/or offspring protection. Combined, these female life-history processes tend to be fast relative to other cetaceans [11], notable in relatively fast offspring growth during short gestation and lactation periods (figure 2). Most baleen whales are therefore capital breeders. Lactation is

short, six to eight months, with calves typically weaned in their first year after extraordinary energy transfers—blue whales, for example, transfer about 220 kg of milk per day to their calves [25]. Post-weaning maternal care is very limited [26]. Females take about a year to replenish body reserves, breeding every other or every third year, which makes the full reproductive cycle rather short for such large, long-lived mammals [11,23].

Groups of baleen whales are typically small and temporary, formed by individuals aggregating in feeding and reproductive contexts and then parting ways once the activity is over [11,23]. An individual whale may associate with many others during its lifetime, forming dense, yet weakly connected social networks (figure 1). The exception among the generally short-lived and unstructured social interactions is the mother–calf bond [11]. However, this general picture is based on extremely sparse knowledge, and at least in some cases, there is evidence for subtle longer-term social effects, especially in the relatively well-studied humpback whale, *Megaptera novaeangliae*, on which our discussion primarily focuses. Furthermore, nearly all baleen whale populations were severely impacted by whaling, and only some have recovered to anything like their pre-hunt densities. We expect most mammals to show some degree of flexible responses to ecological conditions, including conspecific density, so we cannot really know the extent to which our current picture of baleen whale sociality is of a markedly shifted baseline as opposed to the conditions under which it primarily evolved (e.g. [27,28]).

While the mother–calf bond is relatively short compared with toothed whales, it is the one form of female kinship organization that most profoundly affects baleen whale populations. During their first year, calves accompany their mothers on a migration cycle to the feeding grounds before returning back to the breeding area. Calves apparently learn the route in so doing, and consequently, both males and females show fidelity to this migration pathway, restricting gene flow between populations that use different seasonal habitats. Multiple studies of the maternally inherited mitochondrial DNA at the global [29–31], ocean basin [32] and single population [33] scale confirm that this basic element of female kinship creates migratory traditions in this species that have profound consequences for the genetic structure of its populations. Similar results have been presented for southern right whales, *Eubalaena australis*, suggesting this may be the case across many migratory baleen whale species [34]. Furthermore, it seems that these traditions conform to more than just general feeding or breeding areas, as returning calves are more likely to return to local habitat features on scales of approximately 50 km [35,36], suggesting that female-based population structure also occurs on a fine scale. A consequence of this second, female-based inheritance system for migratory knowledge is that in the post-whaling era, it is far from certain that all historical breeding populations will be able to recover properly if they lack adequate habitat knowledge [34].

Data on longer-term social bonds that might support female-based kinship are patchy at best, and again largely confined to the relatively well-studied humpback whales. One study of Southern Hemisphere migrating humpback whales showed that once mother–calf pairs were excluded, then there were no obvious relatedness patterns in animals that were sampled either associated during the migration or

on the same day in the same area [37]. This study therefore suggests that there is little obvious social role for female-based kinship among adult females. However, on a Northern Hemisphere feeding ground, more stable associations have been documented, lasting up to 79 days and with pairs of animals re-associating in multiple years [38]. Genetic sampling in this population subsequently showed that when mother–calf pairs were excluded, females were still on average 1.7 times more likely to form social associations with maternally related individuals (i.e. sharing the same mitochondrial DNA haplotype) than by chance, while there was no such evidence for males [39]. This suggests that we are yet to fully understand the fine-scale female kinship organization in these populations. Importantly, these associations appear to have fitness consequences in that there appear to be significant variations in fecundity between matrilineal lines [40]. Similarly, while on a feeding ground in the Gulf of St Lawrence, Canada, pairs of similar-aged non-lactating females were seen associated together for up to six successive summers, and females in the pairs that had the longest history of association also had the highest reproductive output [41]. It therefore seems highly plausible that maternal kinship does affect humpback whale social associations, but in ways that are still too subtle for our current knowledge to detect.

Humpback whales can, however, share more than simply migratory knowledge within their populations. In well-studied populations, evidence for important social learning effects is clear. For example, in the humpback whale population that feeds in the Gulf of Maine a novel foraging technique, lottail feeding, spread through cultural transmission in response to an ecological shift leading to a switch of primary prey species [42]. There was no evidence that females or males were more likely to learn the technique, nor that calves whose mothers used the technique were more likely to acquire it themselves, suggesting a broadly horizontal social transmission pattern. There is circumstantial evidence, however, that, like migration, these foraging preferences and techniques might sometimes pass within maternal lines. It comes from an unusual mortality event in the late 1980s caused by whales eating mackerel (*Scomber scombrus*) contaminated by neurotoxins from an algal bloom [43]. Ten whales that died were sampled, and all had one of two mitochondrial DNA haplotypes sufficiently rare in the broader population to make it statistically implausible to be a chance pattern. Since humpback whales eating mackerel is not common, the authors suggested this shared prey preference could represent foraging preferences transmitted culturally down matrilineal lines just like migratory knowledge [43]. Such preferences could be one mechanism underlying fecundity variation between matrilineal lines. We have also known for some time that in some regions, such as the waters of southeast Alaska, humpback whales cooperate very closely to gather and concentrate shoals of prey (e.g. [44]), but the relationships between members of these cooperating groups are poorly known. Whales in this region are also quick to exploit new resources—in the past decade, they have increasingly targeted juvenile salmon released from hatcheries [45], but again we lack the necessary corollary information to understand any role of female kinship in the spread of the behaviour. We therefore still have much to learn about baleen whale sociality and the role that female kinship organization might play in it, but the hints are there that it might be a significant factor, largely mediated by the transmission of knowledge within the mother–calf bond.

4. Maternal kinship in toothed whales

Toothed whales are a more speciose and more heterogeneous taxon than the baleen whales. Species vary more in size, habitat use and trophic niche, and life-history strategies are not tied to strict migratory schedules. They inhabit riverine, coastal and oceanic ecosystems [9] and exploit a diverse range of niches. Their echolocation apparatus makes them efficient predators on a wide range of sometimes fast-moving prey in all these habitats.

Similarly, social structures among toothed whales tend to be more varied in number, type and stability than in the baleen whales [12]. Most of the smaller species form groups that frequently respond to the risks and resources by adapting their size, membership and cohesion [46]. Smaller pelagic toothed whales typically form loose social networks, whether within the small (*ca* 2–10 members) groups of beaked whales to the large aggregations (10s to 1000s) of pelagic dolphins. But many species also engage in long-lasting social relationships [13,46]. The emergent social structures in toothed whales roughly mirror this contrast between smaller and larger species in the incidence and stability of social modules—sets of individuals that interact more often and more strongly with one another (figure 1). Social stability and influence of females peak among the larger species along with sexual dimorphism—notably in killer and sperm whales [47,48], which are arranged in stable social groups with a marked influence of female kinship.

Female body size also influences the speed of life-history processes (figure 2). Smaller species mature sooner, have slightly shorter gestation, lactation and calf-rearing periods than the larger species, in which pregnancy lasts longer than 1 year and lactation can last anywhere from 8 months to 8 years or more in some species [11,49,50]. The reproductive cycles of toothed whales often take longer than 2 years to complete. In contrast to baleen whales, most toothed whales are income breeders that build nutritional supplies simultaneously with reproduction, thus compensating for slower prenatal growth rates with extended post-weaning care [26]. This care, sometimes provided by group mates, allows the young to rely on their mother's rich milk while they progressively develop independent foraging skills (e.g. [51]). Often these skills, such as location, identification, capture and processing of prey, are learned, typically from the mother (e.g. [52,53]).

Mother and calf are the core unit of every cetacean society, but this is accentuated in toothed whales because the maternal investment is so extensive. Lactation lengths are probably grossly underestimated in the literature, as longitudinal studies find much longer lengths than fisheries (bycatch or harvested animals) or cross-sectional studies report [11,25]. Most studies use inter-birth intervals as a proxy, but these are only useful when restricted to intervals following a surviving offspring. For example, killer whale calving intervals average 4.9 years between viable calves, although there are some 2-year intervals [54], indicating that lactation can almost completely overlap with the next pregnancy. Among the largest toothed whales with stable matrilineal units, offspring of at least one sex remain with their mothers for a lifetime. Among the smaller toothed whales with highly dynamic fission–fusion societies, maternal kin maintain strong bonds in the social network (e.g. *Tursiops* spp.: [55–59]). Post-weaning maternal

investment and influence are also extensive in a number of species. These effects are likely born from the longer-term nature of the mother–calf bond, with toothed whale mothers hunting through the extensive lactation period. This sets up dramatic trade-offs between direct maternal care and foraging, but it also helps explain the vertical transmission of social and foraging tactics among toothed whales.

Immediately after birth, neonates tag alongside their mothers in echelon position—which is a hybrid of the ‘follower’ and ‘carrying’ strategies of terrestrial mammals in that it imposes energetic costs (hydrodynamic drag) on the mother while boosting the calf's swimming [60,61]. Within months, the calf transitions from mostly echelon to mostly infant position, under the mother's abdomen and tail, which provides protection, hydrodynamic benefits and nursing access, again at an energetic cost to the mother [60,61]. In Shark Bay, bottlenose dolphin calves average 39% (range 10–80%) of their time in infant position from the fourth month of life until weaning [62].

Early calf care is intense. Unlike terrestrial mammals, cetaceans have unihemispheric sleep. Newborn calves hardly sleep at all and newly parturient mothers also forgo rest [63,64] and hunt minimally in the early days [65]. But lactating females must increase their food intake by more than 40% [66,67], so diving and separating from the calf for brief periods becomes necessary. Mothers shorten their dive times or spend more time at the surface to accommodate limited calf diving ability (e.g. bottlenose dolphins [68]; beluga whales [69]). Mother–calf separations are prolonged in some deep-diving species, although allomaternal support can compensate for the mother's absence in some species (e.g. sperm whales [70,71]) but not others (such as northern bottlenose whales [72] and other beaked whales [73]).

While low levels of relatedness among associated individuals are a common occurrence among baleen whales, the extent of association among parent, offspring and other female kin varies over a broad spectrum in toothed whales. The range encompasses the relatively loose fission–fusion networks of bottlenose dolphins, species like narwhal (*Monodon monoceros*) that have been described as ‘matrifocal’ [74], through to various forms of matrilineal social structure from social ‘units’ containing multiple matrilines in sperm whales (e.g. [75]) to the extreme case of bisexual social philopatry seen in the fish-eating ‘resident’ ecotype of killer whales found in the waters of the NE Pacific (e.g. [76]).

Towards one end of this spectrum (figure 1), we find the bottlenose dolphins, and likely other small toothed cetaceans (e.g. [77]). Bottlenose dolphins exhibit both sexual segregation and a highly dynamic fission–fusion social structure [15,78–80]. While there is some variation among populations around the globe, females have strong bonds with their offspring, but particularly their daughters [55,81], and form female-dominated social networks within their community [6,65,78]. By contrast, males often form small, long-term alliances that compete with other alliances to sequester females [82–85].

We have recently begun to understand more about the key role of female kinship organization in bottlenose dolphin societies. For example, a recent study shows a clear sex-bias in maternal accommodation of limited calf diving ability [68]. Specifically, Shark Bay bottlenose dolphin mothers shortened their dives only when young daughters, but not young sons, were close-by. There was no sex difference when the calves

were tens of metres away and unable to observe maternal behaviour directly. This pattern suggests that mothers were affording their daughters more learning opportunities with respect to foraging than sons, a pattern consistent with the sex biases in foraging tactics in Shark Bay [53,86]. Although offspring of both sexes engage in maternal foraging tactics pre-weaning [52], daughters are more likely to retain these tactics well into adulthood [87,88]. While more than 20 distinct foraging tactics have been observed in Shark Bay, females specialize in the rare tactics (those exhibited by a small subset of the population), ranging from sponge tool use to strand-foraging/beaching to trevally hunting [86,87]. Non-genetic processes of social inheritance, specifically strong vertical cultural transmission and maternal effects [6,8], are heavily implicated in these ecological patterns. This inheritance also includes vertical transmission of social tactics, with high mother–calf similarity, although again more so for daughters than sons [6,89,90]. Female dolphins, more than males, inherit their mother's social network [8]. Such matrilineal bonds prove critical, as female calving success is linked to having a network of successful mothers [56], and male juvenile survival also depends on the maternal network [91].

Narwhal are an arctic species that appears to occupy an intermediate position both in terms of modularity of their social structures and the degree of matrilineal social structure. They occur in 'herds', aggregations of hundreds of individuals [92]. Herds are composed of several small clusters (between 3 and 20 individuals) that tend to be segregated based on age and sex [92,93]. Genetic evidence shows that animals sampled on different summer feeding grounds vary in mitochondrial DNA haplotype frequencies [74]. This suggests a role for female-based kinship in structuring the population during summer, presumably through passing habitat knowledge down the female line, while on winter breeding grounds it seems the different lineages mix much more readily. Thus, apparently while not strictly matrilineal, this social structure is described as 'matrifocal' [74], which we understand to mean reflecting a general tendency for shared maternal ancestry while noting that there is still much detail to be discovered about the social structure of the species. While narwhal social dynamics and kinship are difficult to study, their vocal diversity is consistent with the individual-and/or group-specific calls [94], suggesting more social complexity than is currently understood.

The beluga whale, *Delphinapterus leucas*, is another circumpolar species for which more is known. There are at least 16 recognized stocks of beluga whale around the world, distinguished primarily by their summer habitat, but also differing in morphology, behaviour and genetics [95]. Among the most studied are the three stocks in Hudson Bay, Canada, which show clear differentiation among both sexes in their mitochondrial, but not nuclear, DNA [96,97]. This pattern could stem from both sexes showing matrilineal site fidelity to summer grounds [96,98,99], or a stable matrilineal group structure with bisexual social philopatry [100]. Such structure would facilitate allonursing, which has been observed in captive belugas [101]. Furthermore, during migration, female belugas in particular travel with close kin, and within migrating herds, close kin are, on average, more likely to be proximate in space and time [5,99]. While males do not appear to disperse geographically, sexual segregation occurs in which males typically remain

with their kin as juveniles but then leave to associate mostly with other mature males, often farther north and in deeper waters [5,102,103], resulting in modest male dispersal [99]. Beluga populations are therefore strongly structured by fidelity to maternally inherited migratory culture and female kin relationships, resulting in populations that retain demographic and evolutionary independence despite partial sympatry [99].

In the open ocean pelagic habitat, both long- and short-finned pilot whales (*Globicephala melas* and *G. macrorhynchus*) exhibit bisexual natal philopatry according to genetic evidence [104,105]. Social analyses across multiple study sites suggest that long-finned pilot whales live in stable 'units' containing up to 30 animals of both sexes, which regularly interact to form larger, but temporary, 'groups' [106–109]. Recent genetic evidence based on mass strandings suggests that these larger groups contain multiple matrilineal units as well as distant relatives, consistent with the presence of multiple matrilineal units [110]. Within groups calves regularly associate with non-maternal females, and this does not appear to be limited to unit members [111], although more data are needed to confirm alloparental care. These patterns of social structure and kinship appear to be mirrored in the congeneric, but typically more tropically distributed, short-finned pilot whale [105,112,113].

Nearing the other end of the spectrum, sperm whales are the most sexually dimorphic cetacean in terms of body size and allometry and live in a society that is strongly sexually segregated post-maturity. Females live in a multi-levelled society which has at its base social 'units'—technically defined as animals identified together on multiple occasions at least 30 days apart or in multiple years [17,114], but in practice remaining stable over decades [115], units are groups of females and immatures that travel together. They are largely, but not rigidly, defined by kinship, they often contain multiple matrilineal units, and their members communally raise and defend their offspring [17,70,71,115,116]. Males leave their natal units in their early teens. Units form temporary 'groups' with other units that share the same vocal dialect. All units that share a dialect are members of the same 'clan' [117,118]. Clans exhibit variation in behavioural repertoire that appears to affect fitness [119–122]. Kinship among female sperm whales seems to drive associations, but not fully explain them, particularly those between units within clans [123,124]. It also is closely related to allonursing in the form of babysitting and allonursing [125]. There also appears to be significant variation in social structure between ocean basins. In the Pacific, units are larger and composed of multiple matrilineal units, while units in the eastern Caribbean are smaller and based on closer kin, typically single matrilineal units [126]. One hypothesis for these differing patterns of kinship relates to differences in prey species affecting optimal group size, as appears to be the case among killer whales [127], while another is varying levels of predation threat from killer whales in the two places [126].

Finally, killer whales are the most extreme example among the cetaceans of how matrilineal kinship can structure societies. In some populations, both sexes exhibit natal philopatry to the matrilineal 'pods' into which they are born (pods here are defined as groups containing related matrilineal units that are associated during more than 50% of sightings [76]). Their global population is divided into 'ecotypes' which differ not only genetically, but also morphologically and behaviourally

[128]. The current hypothesis is that ecotypes result from culturally driven ecological specialization through vertical social learning within matrilineally based social groups, followed by reproductive isolation through behavioural and possibly genetic mechanisms [128–130]. The strong fidelity to particular ecological specializations likely results from the high investment in learning needed to acquire the complex, often cooperative, and sometimes highly risky nature of the foraging tactics involved (e.g. [131]).

While killer whales are among the most globally distributed species, the various ecotypes show considerable variation in social organization and behaviour, particularly in relation to foraging specialization. While many ecotypes have highly specialized diet preferences, others are more generalized [128]. There are at least 10 recognized ecotypes of killer whales—five each in the Northern and Southern Hemispheres, and there is still debate about their status as species or subspecies [132]. The two best-studied forms are the Bigg's (formerly 'transient') mammal-eating ecotype and the resident or fish-eating ecotype found in sympatry in the northeastern Pacific Ocean.

Fish-eating, resident type killer whales have larger social units, and unlike Bigg's killer whales, exhibit bisexual natal philopatry. Post-reproductive resident females are known to physically lead their matriline around, particularly when prey abundance is low, suggesting that the ecological knowledge of the elder females can boost the fitness and survival of her matriline or pod [133,134]. Mammal-eating, Bigg's type killer whales form small social units of fewer than six members that are generally composed of a reproductive female and her offspring. In this ecotype, there is evidence that offspring of both sexes sometimes disperse either permanently or temporarily [135], which leads to significantly different kinship structure among and within pods compared with the resident type. While it remains unclear if post-reproductive lifespans have evolved among Bigg's killer whales [136], there is a documented case of infanticide among this ecotype [137], where a post-reproductive female and her mature male offspring cooperatively killed the calf of an unrelated female in the same population. This may represent an extreme case of late-life helping, driven by inclusive fitness and likely sexual selection [137], illustrating how highly modular social structure organized around female kinship structure can draw boundaries across which rather direct competition can be selected for. In killer whales then, we have the opportunity to explore the consequences of some of the most extreme forms of female-based kinship structure in mammals.

5. Consequences and perspectives

The nature of the interactions and relationships between female cetaceans, most notably the strong transitive bonds within the social units of the large matrilineal odontocetes, are the consequence of ecological pressures and evolutionary histories. But there is feedback, and these female–female relationships have, in turn, consequences for ecology and evolution.

Cetaceans are big players in the ecology of the ocean [138,139]. The female-centred societies of the whales and dolphins have an important role in this. Most obviously, cetaceans can use complex cooperative foraging techniques to

efficiently exploit, and sometimes expand, their prey base [140–142]. However, in none of these remarkable cases are the sexes of the animals recorded, so we do not know whether the cooperation is just among females, driven by females, or not sexually biased. There is some suggestion that one such technique, cooperative mud-ring feeding, in which animals take specific roles in stirring up sediment to create barriers against which to herd fish, but the small sample sizes preclude certainty [143]. We do know that some individually based foraging techniques are passed through the female line, as recorded in detail for the bottlenose dolphins in Shark Bay [52,86], and can be inferred from the differential isotope-ratio profiles of sympatric clans of sperm whales [120] as well as the distinctive foraging specializations of different killer whale types [47,128].

In the case of the killer whales, the ecological implications of their female-based socio-cultural structure are likely profound. Social learning within matrilineal groups likely drove the deep division of killer whales into sometimes-sympatric, but highly ecologically distinctive and specialized, ecotypes [128]. Models suggest that this culturally driven ecological specialization, while adaptive in the short term, leaves ecotypes vulnerable to extirpation, while reducing overall population size and resource abundance [130].

The female-based socio-cultural structure of cetacean societies also influences who is available to eat what. Beluga whales have not recolonized habitats from which they were extirpated by whaling despite migration routes of extant populations passing nearby, and this is likely a result of the stability of matrilineally transmitted knowledge about habitat and migration [96]. This will have affected the distribution and abundance of their prey, as will the dynamics of space-use by different clans of sperm whales [144].

Evolution—be it the evolution of phenotypes, genotypes or cultures—needs heritability. For cetaceans, indeed for most mammals, a disproportionate amount of heritability runs through the female line. While males provide half the nuclear genes, females do that as well as transmitting all the mitochondrial DNA, maternal effects and many epigenetic effects [145], and, perhaps especially in cetaceans, being the primary conduit for culture [146].

Interactions between female-to-offspring or female-to-female transmissions of genes and culture have set up population structures in cetaceans at scales ranging from a few kilometres (e.g. bottlenose dolphins in Shark Bay, Australia [147]) to a few thousand kilometres (e.g. southern right whales [34]). These patterns result primarily because females give their offspring not only genes but also socially learned information, including foraging strategies (in the case of the bottlenose dolphins) and migration routes (in the case of the right whales).

The parallel transmission of genes and culture has effects beyond the population structure. Gene-culture hitchhiking is a process by which diversity at a neutral genetic locus is reduced owing to selection on culturally inherited traits that are being transmitted in parallel with the genes. This is a plausible mechanism for the very low mitochondrial DNA diversities of the large matrilineal toothed whales [148]. The basic scenario is of matrilineally structured social groups possessing characteristic cultures as well as characteristic distributions of mitochondrial haplotypes. The haplotypes residing in groups with selectively advantageous cultural

elements will prosper at the expense of those haplotypes that are primarily restricted to groups with less well-tuned behaviour. This process reduces overall mitochondrial DNA diversity.

When important transmission processes run through a female-centred social network, selection may work to improve their efficiency. An unusual case of this is the evolution of menopause, the typical cessation of reproduction in females long before the end of life. Found only in several species of matrilineal whale and in humans [136], the evolution of menopause is an evolutionary puzzle, but comparisons of female social organization partly stimulated by findings in cetaceans have borne fruit in recent years. Theory [149], as well as some empirical evidence [133], suggests that in species where females are increasingly related to their group mates as they age and have increasing levels of ecological knowledge with experience, the inclusive fitness benefits of assisting and leading group members may outweigh the direct fitness of reproduction. This is apparently augmented in killer whales by the competitive consequences of lifelong associations between female kin when mothers and daughters breed at the same time in the same group [150,151]. Selection is expected to favour increased investment in competition in younger females, and indeed calves of older females co-breeding with their daughters suffer much higher mortality than those of their daughters in the same groups [150]. The importance of studying female sociality in cetaceans is underlined by these elegant—and unique outside humans—descriptions of how cooperation and conflict between female kin can explain the evolution of a striking feature of human life history.

6. Closing remarks

Kinship may drive complexity in cetacean societies differently among species. Lukas & Clutton-Brock [2] distinguish two concepts of social complexity: organizational social complexity is a reproductive division of labour between breeders and non-breeders, while relational complexity constitutes ‘conflicts of interest between group members and the social traits associated with them, including well-defined dominance hierarchies, competitive alliances and other behavioural tactics used to maintain social status’. Organizational complexity might be higher among the larger toothed whales in which killer whale and sperm

whales exhibit high levels of alloparental care and defence and in which multilevelled societies might impose upon individual preferences. By contrast, within the looser female networks of dolphins, relational complexity is likely higher such that conflicts of interest might arise and be dealt with through fission–fusion dynamics and individually specific long-term bonds confer a range of social and reproductive benefits. However, to understand this properly, it is clear that we need more quantitative data from cetacean studies so that they can be included in these types of large-scale analyses.

Explaining the diversity of female-biased kinship structures in cetaceans remains a significant challenge. It seems clear that there is no simple phylogenetic explanation for these differences: the family Delphinidae includes exemplars from both ends of the toothed whale social spectrum, from fission–fusion to stable kin-based groups (bottlenose dolphins and killer whales, respectively). However, there is perhaps a tipping point, as kin structures become increasingly modular, where female relatedness becomes sufficiently high within groups (compared with between them) that inclusive fitness benefits from increased cooperation and reduced conflicts among group members become an important driver of life-history and cultural evolution in some species. Cooperative care of calves emerges from our treatment as a major factor driving some of this diversity, associated with stronger female bias in kinship organization, but movement ecology, foraging specializations and perhaps size-based refugia from predation may also interact to produce a complex selective landscape. This spectrum among cetaceans, from weak social bonds outside the mother–calf pair, through various forms of matrifocal and partially matrilineal societies, through to strictly matrilineal structures, provides a potentially powerful opportunity to test these hypotheses going forward. We therefore anticipate many insights into the evolution of sociality driven by female kinship from future studies of cetaceans.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

Funding. S.G. is supported by a Research Grant from the Villum Foundation. M.C. was supported by PMP/BS (PGSISCO-UFRP 46/2016) and CNPq (153797/2016-9) postdoctoral fellowships.

Acknowledgements. We thank Monique Borgerhoff Mulder, Stephanie King and an anonymous reviewer for comments that improved our manuscript.

References

1. Smith JE, Ortiz CA, Buhbe MT, van Vugt M. In press. Obstacles and opportunities for female leadership in mammalian societies: a comparative perspective. *Leadership Q.* (doi:10.1016/j.leaqua.2018.09.005)
2. Lukas D, Clutton-Brock T. 2018 Social complexity and kinship in animal societies. *Ecol. Lett.* **21**, 1129–1134. (doi:10.1111/ele.13079)
3. Kappeler PM, van Schaik CP. 2002 Evolution of primate social systems. *Int. J. Primatol.* **23**, 707–740. (doi:10.1023/A:1015520830318)
4. Gero S, Rendell LE. 2015 Oceanic societies: studying cetaceans with a social network approach. In *Animal social networks* (eds J Krause, R James, DW Franks, DP Croft), pp. 139–149. Oxford, UK: Oxford University Press.
5. Colbeck GJ, Duchesne P, Postma LD, Lesage V, Hammill MO, Turgeon J. 2013 Groups of related belugas (*Delphinapterus leucas*) travel together during their seasonal migrations in and around Hudson Bay. *Proc. R. Soc. B* **280**, 20122552. (doi:10.1098/rspb.2012.2552)
6. Mann J, Stanton MA, Patterson EM, Bienenstock EJ, Singh LO. 2012 Social networks reveal cultural behaviour in tool-using dolphins. *Nat. Commun.* **3**, 980. (doi:10.1038/ncomms1983)
7. Cantor M, Wedekin LL, Guimarães PR, Daura-Jorge FG, Rossi-Santos MR, Simões-Lopes PC. 2012 Disentangling social networks from spatiotemporal dynamics: the temporal structure of a dolphin society. *Anim. Behav.* **84**, 641–651. (doi:10.1016/j.anbehav.2012.06.019)
8. Frère CH, Krutzen M, Mann J, Connor RC, Bejder L, Sherwin WB. 2010 Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proc. Natl Acad. Sci. USA* **107**, 19 949–19 954. (doi:10.1073/pnas.1007997107)

9. Würsig B, Thewissen JGM, Kovacs KM (eds). 2017 *Encyclopedia of marine mammals*. London, UK: Academic Press.
10. Clutton-Brock TH. 2016 *Mammal societies*. Oxford, UK: Wiley-Blackwell.
11. Whitehead H, Mann J. 2000 Female reproductive strategies of cetaceans. In *Cetacean societies: field studies of dolphins and whales* (eds J Mann, RC Connor, PL Tyack, H Whitehead), pp. 219–246. Chicago, IL: University of Chicago Press.
12. Connor RC, Mann J, Tyack PL, Whitehead H. 1998 Social evolution in toothed whales. *Trends Ecol. Evol.* **13**, 228–233. (doi:10.1016/S0169-5347(98)01326-3)
13. Connor RC. 2000 Group living in whales and dolphins. In *Cetacean societies: field studies of dolphins and whales* (eds J Mann, RC Connor, PL Tyack, H Whitehead), pp. 199–218. Chicago, IL: University of Chicago Press.
14. Wearmouth VJ, Sims DW. 2008 Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Adv. Mar. Biol.* **54**, 107–170. (doi:10.1016/S0065-2881(08)00002-3)
15. Galezo AA, Krzyszczyk E, Mann J. 2018 Sexual segregation in Indo-Pacific bottlenose dolphins is driven by female avoidance of males. *Behav. Ecol.* **29**, 377–386. (doi:10.1093/beheco/axx177)
16. Baird RW. 2000 The killer whale – foraging specializations and group hunting. In *Cetacean societies: field studies of dolphins and whales* (eds J Mann, RC Connor, PL Tyack, H Whitehead), pp. 127–153. Chicago, IL: University of Chicago Press.
17. Christal J, Whitehead H, Lettevall E. 1998 Sperm whale social units: variation and change. *Can. J. Zool.* **76**, 1431–1440. (doi:10.1139/z98-087)
18. Scott E, Mann J, Watson-Capps J, Sargeant B, Connor R. 2005 Aggression in bottlenose dolphins: evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour* **142**, 21–44. (doi:10.1163/1568539053627712)
19. Samuels A, Gifford T. 1997 A quantitative assessment of dominance relations among bottlenose dolphins. *Mar. Mammal Sci.* **13**, 70–99. (doi:10.1111/j.1748-7692.1997.tb00613.x)
20. Strickland K, Levengood A, Foroughirad V, Mann J, Krzyszczyk E, Frère CH. 2017 A framework for the identification of long-term social avoidance in longitudinal datasets. *R. Soc. open sci.* **4**, 170641. (doi:10.1098/rsos.170641)
21. Mann J, Sargeant BL, Minor M. 2007 Calf inspections of fish catches in bottlenose dolphins (*Tursiops* sp.): opportunities for oblique social learning? *Mar. Mammal Sci.* **23**, 197–202. (doi:10.1111/j.1748-7692.2006.00087.x)
22. Slater GJ, Goldbogen JA, Pyenson ND. 2017 Independent evolution of baleen whale gigantism linked to Plio-Pleistocene ocean dynamics. *Proc. R. Soc. B* **284**, 20170546. (doi:10.1098/rspb.2017.0546)
23. Trillmich F, Cantor M. 2017 Socioecology. In *Encyclopedia of marine mammals* (eds B Würsig, JGM Thewissen, KM Kovacs), pp. 882–887. London, UK: Academic Press.
24. Corkeron PJ, Connor RC. 1999 Why do baleen whales migrate? *Mar. Mammal Sci.* **15**, 1228–1245. (doi:10.1111/j.1748-7692.1999.tb00887.x)
25. Oftedal OT. 1997 Lactation in whales and dolphins: evidence of divergence between baleen- and toothed-species. *J. Mammary Gland Biol. Neoplasia* **2**, 205–230. (doi:10.1023/A:1026328203526)
26. Huang S-L, Chou L-S, Shih N-T, Ni I-H. 2011 Implication of life history strategies for prenatal investment in cetaceans. *Mar. Mammal Sci.* **27**, 182–194. (doi:10.1111/j.1748-7692.2010.00392.x)
27. Jackson JA, Carroll EL, Smith TD, Zerbini AN, Patenaude NJ, Baker CS. 2016 An integrated approach to historical population assessment of the great whales: case of the New Zealand southern right whale. *R. Soc. open sci.* **3**, 150669. (doi:10.1098/rsos.150669)
28. Noad MJ, Dunlop RA, Mack AK. 2017 Changes in humpback whale singing behavior with abundance: implications for the development of acoustic surveys of cetaceans. *J. Acoust. Soc. Am.* **142**, 1611–1618. (doi:10.1121/1.5001502)
29. Baker CS, Palumbi SR, Lambertsen RH, Weinrich MT, Calambokidis J, O'Brien SJ. 1990 Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* **344**, 238–240. (doi:10.1038/344238a0)
30. Baker CS *et al.* 1994 Hierarchical structure of mitochondrial DNA gene flow among humpback whales *Megaptera novaeangliae* world-wide. *Mol. Ecol.* **3**, 313–327. (doi:10.1111/j.1365-294X.1994.tb00071.x)
31. Jackson JA, Steel DJ, Beerli P, Congdon BC, Olavarria C, Leslie MS, Pomilla C, Rosenbaum H, Baker CS. 2014 Global diversity and oceanic divergence of humpback whales (*Megaptera novaeangliae*). *Proc. R. Soc. B* **281**, 20133222. (doi:10.1098/rspb.2013.3222)
32. Baker C *et al.* 2013 Strong maternal fidelity and natal philopatry shape genetic structure in North Pacific humpback whales. *Mar. Ecol. Prog. Ser.* **494**, 291–306. (doi:10.3354/meps10508)
33. Garrigue C, Dodemont R, Steel D, Baker C. 2004 Organismal and 'gametic' capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Mar. Ecol. Prog. Ser.* **274**, 251–262. (doi:10.3354/meps274251)
34. Carroll EL, Baker CS, Watson M, Alderman R, Bannister J, Gaggiotti OE, Gröcke DR, Patenaude N, Harcourt R. 2015 Cultural traditions across a migratory network shape the genetic structure of southern right whales around Australia and New Zealand. *Sci. Rep.* **5**, 16182. (doi:10.1038/srep16182)
35. Weinrich M. 1998 Early experience in habitat choice by humpback whales (*Megaptera novaeangliae*). *J. Mammal.* **79**, 163–170. (doi:10.2307/1382851)
36. Barendse J, Best PB, Carvalho I, Pomilla C. 2013 Mother knows best: occurrence and associations of resighted humpback whales suggest maternally derived fidelity to a Southern Hemisphere coastal feeding ground. *PLoS ONE* **8**, e81238. (doi:10.1371/journal.pone.0081238)
37. Valsecchi E, Hale P, Corkeron P, Amos W. 2002 Social structure in migrating humpback whales (*Megaptera novaeangliae*). *Mol. Ecol.* **11**, 507–518. (doi:10.1046/j.0962-1083.2001.01459.x)
38. Weinrich MT. 1991 Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Can. J. Zool.* **69**, 3012–3018. (doi:10.1139/z91-425)
39. Weinrich MT, Rosenbaum H, Scott Baker C, Blackmer AL, Whitehead H. 2006 The influence of maternal lineages on social affiliations among humpback whales (*Megaptera novaeangliae*) on their feeding grounds in the southern Gulf of Maine. *J. Hered.* **97**, 226–234. (doi:10.1093/jhered/esj018)
40. Rosenbaum HC, Weinrich MT, Stoleson SA, Gibbs JP, Baker CS, DeSalle R. 2002 The effect of differential reproductive success on population genetic structure: correlations of life history with matrilineal structure in humpback whales of the Gulf of Maine. *J. Hered.* **93**, 389–399. (doi:10.1093/jhered/93.6.389)
41. Ramp C, Hagen W, Palsbøll P, Bérubé M, Sears R, Palsbøll P, Berube M. 2010 Age-related multi-year associations in female humpback whales (*Megaptera novaeangliae*). *Behav. Ecol. Sociobiol.* **64**, 1563–1576. (doi:10.1007/s00265-010-0970-8)
42. Allen J, Weinrich M, Hoppitt W, Rendell L. 2013 Network-based diffusion analysis reveals cultural transmission of lobe-tail feeding in humpback whales. *Science* **340**, 485–488. (doi:10.1126/science.1231976)
43. Baker CS, Weinrich MT, Early G, Palumbi SR. 1994 Genetic impact of an unusual group mortality among humpback whales. *J. Hered.* **85**, 52–54. (doi:10.1093/oxfordjournals.jhered.a111394)
44. D'Vincent CG, Nilson RM, Hanna RE. 1985 Vocalization and coordinated feeding behavior of the humpback whale in southeastern Alaska. *Sci. Rep. Whales Res. Inst.* **36**, 41–47.
45. Chenoweth EM, Straley JM, McPhee MV, Atkinson S, Reifensstuhl S. 2017 Humpback whales feed on hatchery-released juvenile salmon. *R. Soc. open sci.* **4**, 170180. (doi:10.1098/rsos.170180)
46. Gowans S, Würsig B, Karczmarski L. 2007 The social structure and strategies of delphinids: predictions based on an ecological framework. *Adv. Mar. Biol.* **53**, 195–294. (doi:10.1016/S0065-2881(07)53003-8)
47. Baird RW. 2000 The killer whale: foraging specializations and group hunting. In *Cetacean societies: field studies of dolphins and whales* (eds J Mann, RC Connor, PL Tyack, H Whitehead), pp. 127–153. Chicago, IL: University of Chicago Press.
48. Whitehead H, Weilgart L. 2000 The sperm whale: social females and roving males. In *Cetacean societies: field studies of dolphins and whales* (eds J Mann, RC Connor, PL Tyack, H Whitehead), pp. 154–172. Chicago, IL: University of Chicago Press.

49. Karniski C, Krzyszczyk E, Mann J. 2018 Senescence impacts reproduction and maternal investment in bottlenose dolphins. *Proc. R. Soc. B* **285**, 20181123. (doi:10.1098/rspb.2018.1123)
50. Kasuya T, Marsh H. 1984 Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. *Rep. Int. Whal. Comm.* **6**, 259–310.
51. Tønnesen P, Gero S, Ladegaard M, Johnson M, Madsen PT. 2018 First-year sperm whale calves echolocate and perform long, deep dives. *Behav. Ecol. Sociobiol.* **72**, 165. (doi:10.1007/s00265-018-2570-y)
52. Sargeant BL, Mann J. 2009 Developmental evidence for foraging traditions in wild bottlenose dolphins. *Anim. Behav.* **78**, 715–721. (doi:10.1016/J.ANBEHAV.2009.05.037)
53. Sargeant BL, Mann J. 2009 From social learning to culture: intrapopulation variation in bottlenose dolphins. In *The question of animal culture* (eds KN Laland, BG Galef), pp. 152–173. Cambridge, MA: Harvard University Press.
54. Olesiuk PF, Ellis GM, Ford JKB. 2005 *Life history and population dynamics of resident killer whales *Orcinus orca* in the coastal waters of British Columbia. Research document 2005/045*. Nanaimo, BC, Canada: Fisheries and Oceans Canada.
55. Tsai Y-JJ, Mann J. 2013 Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. *Mar. Mammal Sci.* **29**, 261–279. (doi:10.1111/j.1748-7692.2011.00559.x)
56. Frère CH, Krützen M, Mann J, Watson-Capps JJ, Tsai YJ, Patterson EM, Connor R, Bejder L, Sherwin WB. 2010 Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. *Anim. Behav.* **80**, 481–486. (doi:10.1016/J.ANBEHAV.2010.06.007)
57. McHugh KA, Allen JB, Barleycorn AA, Wells RS. 2011 Natal philopatry, ranging behavior, and habitat selection of juvenile bottlenose dolphins in Sarasota Bay, Florida. *J. Mammal.* **92**, 1298–1313. (doi:10.1644/11-MAMM-A-026.1)
58. Möller LM, Beheregaray LB, Allen SJ, Harcourt RG. 2006 Association patterns and kinship in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. *Behav. Ecol. Sociobiol.* **61**, 109–117. (doi:10.1007/s00265-006-0241-x)
59. Wiszniewski J, Lusseau D, Möller LM. 2010 Female bisexual kinship ties maintain social cohesion in a dolphin network. *Anim. Behav.* **80**, 895–904. (doi:10.1016/J.ANBEHAV.2010.08.013)
60. Noren SR, Biedenbach G, Redfern JV, Edwards EF. 2008 Hitching a ride: the formation locomotion strategy of dolphin calves. *Funct. Ecol.* **22**, 278–283. (doi:10.1111/j.1365-2435.2007.01353.x)
61. Noren S, Edwards E. 2011 Infant position in mother-calf dolphin pairs: formation locomotion with hydrodynamic benefits. *Mar. Ecol. Prog. Ser.* **424**, 229–236. (doi:10.3354/meps08986)
62. Foroughirad V, Mann J. 2013 Long-term impacts of fish provisioning on the behavior and survival of wild bottlenose dolphins. *Biol. Conserv.* **160**, 242–249. (doi:10.1016/J.BIOCON.2013.01.001)
63. Lyamin O, Pryaslova J, Lance V, Siegel J. 2005 Continuous activity in cetaceans after birth. *Nature* **435**, 1177. (doi:10.1038/4351177a)
64. Lyamin O, Pryaslova J, Kosenko P, Siegel J. 2007 Behavioral aspects of sleep in bottlenose dolphin mothers and their calves. *Physiol. Behav.* **92**, 725–733. (doi:10.1016/J.PHYSBEH.2007.05.064)
65. Mann J, Smuts BB. 1998 Natal attraction; allomaternal care and mother–infant separations in wild bottlenose dolphins. *Anim. Behav.* **55**, 1097–1113. (doi:10.1006/anbe.1997.0637)
66. Cheal AJ, Gales NJ. 1991 Body mass and food intake in captive, breeding bottlenose dolphins, *Tursiops truncatus*. *Zoo Biol.* **10**, 451–456. (doi:10.1002/zoo.1430100603)
67. Williams R *et al.* 2011 Competing conservation objectives for predators and prey: estimating killer whale prey requirements for Chinook salmon. *PLoS One* **6**, e26738. (doi:10.1371/journal.pone.0026738)
68. Miketa ML, Patterson EM, Krzyszczyk E, Foroughirad V, Mann J. 2018 Calf age and sex affect maternal diving behaviour in Shark Bay bottlenose dolphins. *Anim. Behav.* **137**, 107–117. (doi:10.1016/J.ANBEHAV.2017.12.023)
69. Heide-Jørgensen MP, Hammeken N, Dietz R, Orr J, Richard PR. 2001 Surfacing times and dive rates for narwhals (*Monodon monoceros*) and belugas (*Delphinapterus leucas*). *Arctic* **54**, 284–298. (doi:10.14430/arctic788)
70. Whitehead H. 1996 Babysitting, dive synchrony, and indications of alloparental care in sperm whales. *Behav. Ecol. Sociobiol.* **38**, 237–244. (doi:10.1007/s002650050238)
71. Gero S, Engelhaupt D, Rendell L, Whitehead H. 2009 Who cares? Between-group variation in alloparental caregiving in sperm whales. *Behav. Ecol.* **20**, 838–843. (doi:10.1093/beheco/arp068)
72. Gowans S, Whitehead H, Hooker SK. 2001 Social organization in northern bottlenose whales, *Hyperoodon ampullatus*: not driven by deep-water foraging? *Anim. Behav.* **62**, 369–377. (doi:10.1006/anbe.2001.1756)
73. Macleod CD, D'Amico A. 2006 A review of beaked whale behaviour and ecology in relation to assessing and mitigating impacts of anthropogenic noise. *J. Cetacean Res. Manag.* **7**, 211–221.
74. Palsbøll PJ, Heide-Jørgensen MP, Dietz R. 1997 Population structure and seasonal movements of narwhals, *Monodon monoceros*, determined from mtDNA analysis. *Heredity* **78**, 284–292. (doi:10.1038/hdy.1997.43)
75. Mesnick SL. 2001 Genetic relatedness in sperm whales: evidence and cultural implications. *Behav. Brain Sci.* **24**, 346–347. (doi:10.1017/S0140525X01463965)
76. Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb III KC. 1990 Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. *Rep. Int. Whal. Comm.* **12**, 383–405.
77. Gaspari S, Azzellino A, Airoldi S, Hoelzel AR. 2007 Social kin associations and genetic structuring of striped dolphin populations (*Stenella coeruleoalba*) in the Mediterranean Sea. *Mol. Ecol.* **16**, 2922–2933. (doi:10.1111/j.1365-294X.2007.03295.x)
78. Smolker RA, Richards AF, Connor RC, Pepper JW. 1992 Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour* **123**, 38–69. (doi:10.1163/156853992X00101)
79. Wallen MM, Patterson EM, Krzyszczyk E, Mann J. 2016 The ecological costs to females in a system with allied sexual coercion. *Anim. Behav.* **115**, 227–236. (doi:10.1016/J.ANBEHAV.2016.02.018)
80. Connor RC, Wells RS, Mann J, Read AJ. 2000 The bottlenose dolphin: social relationships in a fission-fusion society. In *Cetacean societies: field studies of dolphins and whales* (eds J Mann, RC Connor, PL Tyack, H Whitehead), pp. 91–126. Chicago, IL: Chicago University Press.
81. Mann J, Connor RC, Barre LM, Heithaus MR. 2000 Female reproductive success in bottlenose dolphins (*Tursiops* sp.): life history, habitat, provisioning, and group-size effects. *Behav. Ecol.* **11**, 210–219. (doi:10.1093/beheco/11.2.210)
82. Connor RC, Smolker RA, Richards AF. 1992 Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proc. Natl Acad. Sci. USA* **89**, 987–990. (doi:10.1073/pnas.89.3.987)
83. Krützen M, Sherwin WB, Connor RC, Barre LM, Van De Castele T, Mann J, Brooks R, Barré LM. 2002 Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* sp.) with different alliance strategies. *Proc. R. Soc. Lond. B* **270**, 497–502. (doi:10.1098/rspb.2002.2229)
84. Connor RC, Krützen M. 2015 Male dolphin alliances in Shark Bay? Changing perspectives in a 30-year study. *Anim. Behav.* **103**, 223–235. (doi:10.1016/j.anbehav.2015.02.019)
85. Owen EC, Wells RS, Hofmann S. 2002 Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Can. J. Zool.* **80**, 2072–2089. (doi:10.1139/z02-195)
86. Mann J, Sargeant B. 2003 Like mother, like calf: the ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). In *The biology of traditions: models and evidence* (eds DM Fragaszy, S Perry), pp. 236–266. Cambridge, UK: Cambridge University Press.
87. Sargeant BL, Mann J, Berggren P, Krützen M, Krützen M. 2005 Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). *Can. J. Zool.* **83**, 1400–1410. (doi:10.1139/z05-136)
88. Mann J, Sargeant BL, Watson-Capps JJ, Gibson QA, Heithaus MR, Connor RC, Patterson E. 2008 Why do dolphins carry sponges? *PLoS ONE* **3**, e3868. (doi:10.1371/journal.pone.0003868)
89. Gibson QA, Mann J. 2008 Early social development in wild bottlenose dolphins: sex differences, individual variation and maternal influence. *Anim.*

- Behav.* **76**, 375–387. (doi:10.1016/J.ANBEHAV.2008.01.021)
90. Stanton MA, Gibson QA, Mann J. 2011 When mum's away: a study of mother and calf ego networks during separations in wild bottlenose dolphins (*Tursiops* sp.). *Anim. Behav.* **82**, 405–412. (doi:10.1016/J.ANBEHAV.2011.05.026)
 91. Stanton MA, Mann J. 2012 Early social networks predict survival in wild bottlenose dolphins. *PLoS ONE* **7**, e47508. (doi:10.1371/journal.pone.0047508)
 92. Marcoux M, Auger-Méthé M, Humphries MM. 2009 Encounter frequencies and grouping patterns of narwhals in Koluktoo Bay, Baffin Island. *Polar Biol.* **32**, 1705–1716. (doi:10.1007/s00300-009-0670-x)
 93. Marcoux M, Larocque G, Auger-Méthé M, Dutilleul P, Humphries MM. 2010 Statistical analysis of animal observations and associated marks distributed in time using Ripley's functions. *Anim. Behav.* **80**, 329–337. (doi:10.1016/J.ANBEHAV.2010.04.027)
 94. Marcoux M, Auger-Méthé M, Humphries MM. 2012 Variability and context specificity of narwhal (*Monodon monoceros*) whistles and pulsed calls. *Mar. Mammal Sci.* **28**, 649–665. (doi:10.1111/j.1748-7692.2011.00514.x)
 95. COSEWIC. 2004 *COSEWIC assessment and update status report on the beluga whale *Delphinapterus leucas* in Canada*. Ottawa, Canada: Committee on the Status of Endangered Wildlife in Canada. See www.sararegistry.gc.ca/status/status_e.cfm.
 96. Turgeon J, Duchesne P, Colbeck GJ, Postma LD, Hammill MO. 2012 Spatiotemporal segregation among summer stocks of beluga (*Delphinapterus leucas*) despite nuclear gene flow: implication for the endangered belugas in eastern Hudson Bay (Canada). *Conserv. Genet.* **13**, 419–433. (doi:10.1007/s10592-011-0294-x)
 97. De March BGE, Postma LD. 2003 Molecular genetic stock discrimination of belugas (*Delphinapterus leucas*) hunted in eastern Hudson Bay, northern Quebec, Hudson Strait, and Sanikiluaq (Belcher Islands), Canada, and comparisons to adjacent populations. *Arctic* **56**, 111–124. (doi:10.14430/arctic607)
 98. Brown GJG, Ferguson MM, Friesen MK, Clayton JW. 1999 Population structure of North American beluga whales (*Delphinapterus leucas*) based on nuclear DNA microsatellite variation and contrasted with the population structure revealed by mitochondrial DNA variation. *Mol. Ecol.* **8**, 347–363. (doi:10.1046/j.1365-294X.1998.00559.x)
 99. O'Corry-Crowe G *et al.* 2018 Migratory culture, population structure and stock identity in North Pacific beluga whales (*Delphinapterus leucas*). *PLoS ONE* **13**, e0194201. (doi:10.1371/journal.pone.0194201)
 100. Palsbøll PJ, Heide-Jørgensen MP, Bérubé M. 2002 Analysis of mitochondrial control region nucleotide sequences from Baffin Bay beluga, (*Delphinapterus leucas*): detecting pods or sub-populations? *NAMMCO Sci. Publ.* **4**, 39–50. (doi:10.7557/3.2836)
 101. Leung ES, Vergara V, Barrett-Lennard LG. 2010 Allonursing in captive belugas (*Delphinapterus leucas*). *Zoo Biol.* **29**, 633–637. (doi:10.1002/zoo.20295)
 102. Hauser DDW, Laidre KL, Suydam RS, Richard PR. 2014 Population-specific home ranges and migration timing of Pacific Arctic beluga whales (*Delphinapterus leucas*). *Polar Biol.* **37**, 1171–1183. (doi:10.1007/s00300-014-1510-1)
 103. Loseto LL, Richard P, Stern GA, Orr J, Ferguson SH. 2006 Segregation of Beaufort Sea beluga whales during the open-water season. *Can. J. Zool.* **84**, 1743–1751. (doi:10.1139/z06-160)
 104. Amos B, Schlotterer C, Tautz D. 1993 Social structure of pilot whales revealed by analytical DNA profiling. *Science* **260**, 670–672. (doi:10.1126/science.8480176)
 105. Alves F, Quérouil S, Dinis A, Nicolau C, Ribeiro C, Freitas L, Kaufmann M, Fortuna C. 2013 Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **23**, 758–776. (doi:10.1002/aqc.2332)
 106. Bloch D, Heide-Jørgensen MP, Stefansson E, Mikkelsen B, Ofstad LH, Dietz R, Andersen LW. 2003 Short-term movements of long-finned pilot whales *Globicephala melas* around the Faroe Islands. *Wildl. Biol.* **9**, 47–58. (doi:10.2981/wlb.2003.007)
 107. Ottensmeyer CA, Whitehead H. 2003 Behavioural evidence for social units in long-finned pilot whales. *Can. J. Zool.* **81**, 1327–1338. (doi:10.1139/Z03-127)
 108. de Stephanis R, Verborgh P, Pérez S, Esteban R, Minvielle-Sebastia L, Guinet C. 2008 Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the Strait of Gibraltar. *Acta Ethol.* **11**, 81–94. (doi:10.1007/s10211-008-0045-2)
 109. Augusto JF, Frasier TR, Whitehead H. 2017 Social structure of long-finned pilot whales (*Globicephala melas*) off northern Cape Breton Island, Nova Scotia. *Behaviour* **154**, 509–540. (doi:10.1163/1568539X-00003432)
 110. Oremus M, Gales R, Kettles H, Baker CS. 2013 Genetic evidence of multiple matrilineal and spatial disruption of kinship bonds in mass strandings of long-finned pilot whales, *Globicephala melas*. *J. Hered.* **104**, 301–311. (doi:10.1093/jhered/est007)
 111. Augusto JF, Frasier TR, Whitehead H. 2017 Characterizing alloparental care in the pilot whale (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada. *Mar. Mammal Sci.* **33**, 440–456. (doi:10.1111/mms.12377)
 112. Heimlich-Boran JR. 1993 Social organization of the short-finned pilot whale, *Globicephala macrorhynchus*, with special reference to the comparative social ecology of delphinids. PhD Thesis, University of Cambridge.
 113. Mahaffy SD, Baird RW, McSweeney DJ, Webster DL, Schorr GS. 2015 High site fidelity, strong associations, and long-term bonds: short-finned pilot whales off the island of Hawai'i. *Mar. Mammal Sci.* **31**, 1427–1451. (doi:10.1111/mms.12234)
 114. Gero S *et al.* 2014 Behavior and social structure of the sperm whales of Dominica, West Indies. *Mar. Mammal Sci.* **30**, 905–922. (doi:10.1111/mms.12086)
 115. Gero S, Gordon J, Whitehead H. 2015 Individualized social preferences and long-term social fidelity between social units of sperm whales. *Anim. Behav.* **102**, 15–23. (doi:10.1016/j.anbehav.2015.01.008)
 116. Mesnick SL *et al.* 2011 Sperm whale population structure in the eastern and central north Pacific inferred by the use of single nucleotide polymorphisms (SNPs), microsatellites and mitochondrial DNA. *Mol. Ecol. Resour.* **11**, 278–298. (doi:10.1111/j.1755-0998.2010.02973.x)
 117. Rendell LE, Whitehead H. 2003 Vocal clans in sperm whales (*Physeter macrocephalus*). *Proc. R. Soc. Lond. B* **270**, 225–231. (doi:10.1098/rspb.2002.2239)
 118. Gero S, Bottcher A, Whitehead H, Madsen PT. 2016 Socially segregated, sympatric sperm whale clans in the Atlantic Ocean. *R. Soc. open sci.* **3**, 160061. (doi:10.1098/rsos.160061)
 119. Whitehead H, Rendell L, Osborne RW, Würsig B. 2004 Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. *Biol. Conserv.* **120**, 431–441. (doi:10.1016/j.biocon.2004.03.017)
 120. Marcoux M, Whitehead H, Rendell L. 2007 Sperm whale feeding variation by location, year, social group and clan: evidence from stable isotopes. *Mar. Ecol. Prog. Ser.* **333**, 309–314. (doi:10.3354/meps333309)
 121. Marcoux M, Rendell L, Whitehead H. 2007 Indications of fitness differences among vocal clans of sperm whales. *Behav. Ecol. Sociobiol.* **61**, 1093–1098. (doi:10.1007/s00265-006-0342-6)
 122. Cantor M, Whitehead H. 2015 How does social behavior differ among sperm whale clans? *Mar. Mammal Sci.* **31**, 1275–1290. (doi:10.1111/mms.12218)
 123. Konrad CM, Gero S, Frasier T, Whitehead H. 2018 Kinship influences sperm whale social organization within, but generally not among, social units. *R. Soc. open sci.* **5**, 180914. (doi:10.1098/rsos.180914)
 124. Rendell L, Mesnick SL, Dalebout ML, Burtenshaw J, Whitehead H. 2012 Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? *Behav. Genet.* **42**, 332–343. (doi:10.1007/s10519-011-9513-y)
 125. Konrad CM, Frasier TR, Whitehead H, Gero S. 2019 Kin selection and allocare in sperm whales. *Behav. Ecol.* **20**, 194–201. (doi:10.1093/beheco/ary143)
 126. Whitehead H, Antunes R, Gero S, Wong SNP, Engelhaupt D, Rendell L. 2012 Multilevel societies of female sperm whales (*Physeter macrocephalus*) in the Atlantic and Pacific: why are they so different? *Int. J. Primatol.* **33**, 1142–1164. (doi:10.1007/s10764-012-9598-z)
 127. Baird RW, Dill LM. 1996 Ecological and social determinants of group size in transient killer whales. *Behav. Ecol.* **7**, 408–416. (doi:10.1093/beheco/7.4.408)

128. Riesch R, Barrett-Lennard LG, Ellis GM, Ford JKB, Deecke VB. 2012 Cultural traditions and the evolution of reproductive isolation: ecological speciation in killer whales? *Biol. J. Linn. Soc.* **106**, 1–17. (doi:10.1111/j.1095-8312.2012.01872.x)
129. Foote AD *et al.* 2016 Genome-culture coevolution promotes rapid divergence of killer whale ecotypes. *Nat. Commun.* **7**, 11693. (doi:10.1038/ncomms11693)
130. Whitehead H, Ford JKB. 2018 Consequences of culturally-driven ecological specialization: killer whales and beyond. *J. Theor. Biol.* **456**, 279–294. (doi:10.1016/J.JTBI.2018.08.015)
131. Guinet C, Bouvier J. 1995 Development of intentional stranding hunting techniques in killer whale (*Orcinus orca*) calves at Crozet Archipelago. *Can. J. Zool.* **73**, 27–33. (doi:10.1139/z95-004)
132. Morin PA *et al.* 2010 Complete mitochondrial genome phylogeographic analysis of killer whales (*Orcinus orca*) indicates multiple species. *Genome Res.* **20**, 908–916. (doi:10.1101/gr.102954.109)
133. Brent LJJ, Franks DW, Foster EA, Balcomb KC, Cant MA, Croft DP. 2015 Ecological knowledge, leadership, and the evolution of menopause in killer whales. *Curr. Biol.* **25**, 746–750. (doi:10.1016/j.cub.2015.01.037)
134. Foster EA, Franks DW, Mazzi S, Darden SK, Balcomb KC, Ford JKB, Croft DP. 2012 Adaptive prolonged postreproductive life span in killer whales. *Science* **337**, 1313. (doi:10.1126/science.1224198)
135. Baird RW, Whitehead H. 2000 Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Can. J. Zool.* **78**, 2096–2105. (doi:10.1139/z00-155)
136. Ellis S, Franks DW, Natrass S, Currie TE, Cant MA, Giles D, Balcomb KC, Croft DP. 2018 Analyses of ovarian activity reveal repeated evolution of post-reproductive lifespans in toothed whales. *Sci. Rep.* **8**, 12833. (doi:10.1038/s41598-018-31047-8)
137. Towers JR, Hallé MJ, Symonds HK, Sutton GJ, Morton AB, Spong P, Borrowman JP, Ford JKB. 2018 Infanticide in a mammal-eating killer whale population. *Sci. Rep.* **8**, 4366. (doi:10.1038/s41598-018-22714-x)
138. Bowen W. 1997 Role of marine mammals in aquatic ecosystems. *Mar. Ecol. Prog. Ser.* **158**, 267–274. (doi:10.3354/meps158267)
139. Roman J *et al.* 2014 Whales as marine ecosystem engineers. *Front. Ecol. Environ.* **12**, 377–385. (doi:10.1890/130220)
140. Torres LG, Read AJ. 2009 Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. *Mar. Mammal Sci.* **25**, 797–815. (doi:10.1111/j.1748-7692.2009.00297.x)
141. Gazda SK, Connor RC, Edgar RK, Cox F. 2005 A division of labour with role specialization in group-hunting bottlenose dolphins (*Tursiops truncatus*) off Cedar Key, Florida. *Proc. R. Soc. B* **272**, 135–140. (doi:10.1098/rspb.2004.2937)
142. Similä T, Ugarte F. 1993 Surface and underwater observations of cooperatively feeding killer whales in northern Norway. *Can. J. Zool.* **71**, 1494–1499. (doi:10.1139/z93-210)
143. Weiss J. 2006 Foraging habitats and associated preferential foraging specializations of bottlenose dolphin (*Tursiops truncatus*) mother–calf pairs. *Aquat. Mamm.* **32**, 10–19. (doi:10.1578/AM.32.1.2006.10)
144. Cantor M, Whitehead H, Gero S, Rendell L. 2016 Cultural turnover among Galápagos sperm whales. *R. Soc. open sci.* **3**, 160615. (doi:10.1098/rsos.160615)
145. Kim JK, Samaranyake M, Pradhan S. 2009 Epigenetic mechanisms in mammals. *Cell. Mol. Life Sci.* **66**, 596–612. (doi:10.1007/s00018-008-8432-4)
146. Whitehead H, Rendell L. 2014 *The cultural lives of whales and dolphins*. Chicago, IL: University of Chicago Press.
147. Koppes AM, Ackermann CY, Sherwin WB, Allen SJ, Bejder L, Krützen M. 2014 Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. *Proc. R. Soc. B* **281**, 20133245. (doi:10.1098/rspb.2013.3245)
148. Whitehead H, Vachon F, Frasier TR. 2017 Cultural hitchhiking in the matrilineal whales. *Behav. Genet.* **47**, 324–334. (doi:10.1007/s10519-017-9840-8)
149. Johnstone RA, Cant MA. 2010 The evolution of menopause in cetaceans and humans: the role of demography. *Proc. R. Soc. B* **277**, 3765–3771. (doi:10.1098/rspb.2010.0988)
150. Croft DP *et al.* 2017 Reproductive conflict and the evolution of menopause in killer whales. *Curr. Biol.* **27**, 298–304. (doi:10.1016/j.cub.2016.12.015)
151. Cant MA, Johnstone RA. 2008 Reproductive conflict and the separation of reproductive generations in humans. *Proc. Natl Acad. Sci. USA* **105**, 5332–5336. (doi:10.1073/PNAS.0711911105)