

Social evolution in toothed whales

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The toothed whales, or odontocetes, form one of the three independently evolved peaks in brain size among mammals, along with elephants and primates. Like the elephants and most primates, many odontocetes lead rich social lives. A few long-term field studies, in which individual whales and dolphins are identifiable and sometimes genetically typed, allow us to make more detailed comparisons with terrestrial species than was previously possible. Most of the 70 or so odontocete species have not been studied as living individuals (Table 1). However, for some of these species, interesting results have emerged from samples obtained from strandings or by whalers, as well as inferences from anatomic, life history and genetic information. The comparisons with terrestrial mammals reveal both impressive differences and convergence, which researchers are beginning to link with features of the odontocetes' aquatic environment.

Odontocete societies

Dispersal patterns in the fish-eating 'resident' killer whales (*Orcinus orca*) living along the coast of British Columbia, Canada, and Washington State, USA, present a striking contrast with those known in terrestrial mammal societies. Neither males nor females disperse but, as adults, continue to travel with their mothers in stable matrilineal groups (Box 1), averaging 3–4 individuals and including up to four generations¹. Closely related matrilineal groups preferentially associate with one another in 'sub-pods', which in turn often travel together in 'pods' of 10–20 or more individuals.

Dispersal has been observed in the mammal-eating 'transient' killer whales which are sympatric with residents but travel in smaller groups¹. Baird and Dill² link the differences in group size and occurrence of dispersal in transients and residents to the benefits transients receive from foraging in small groups. The average foraging group size of three transients is the optimal group size for hunting their primary prey, the harbor seal, *Phoca vitulina*². Transient groups appear to be comprised of a single matriline with one to two generations, sometimes including an adult male which may be a first born son². Rather than joining another group, dispersing individuals may form their own². Females may disperse when they have their own calves and males disperse alone. Groups composed of single males are not uncommon.

What features of their marine habitat allow killer whales of both sexes to remain in their natal groups? Both resident and transient killer whale groups range over tens of thousands of square kilometers in pursuit of widely distributed

Two contrasting results emerge from comparisons of the social systems of several odontocetes with terrestrial mammals. Researchers have identified remarkable convergence in prominent features of the social systems of odontocetes such as the sperm whale and bottlenose dolphin with a few well-known terrestrial mammals such as the elephant and chimpanzee. In contrast, studies on killer whales and Baird's beaked whale reveal novel social solutions to aquatic living. The combination of convergent and novel features in odontocete social systems promise a more general understanding of the ecological determinants of social systems in both terrestrial and aquatic habitats, as well as the relationship between relative brain size and social evolution.

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resources and territorial behavior is not evident in either type. A male killer whale ranging widely with his mother's pod might expect to encounter enough similar groups with receptive females to render philopatry a viable option. Alternatively, males might leave their natal pod for periods in search of mates (e.g. Ref. 3). Of critical importance in either scenario are the relatively low costs of locomotion enjoyed by the streamlined odontocetes who move efficiently through a medium that, while 800 times denser than air, supports them against gravity⁴.

Killer whales may not be the only odontocetes in which both males and females remain with their natal group. Natal philopatry may explain some unusual behavioral observations such as why, during a three-day period in 1976, a group of 30 male and female false killer whales (*Pseudorca crassidens*) remained in tight formation in shallow water around the largest individual in the group; a male who listed, bleeding from his ear until he died on the third day⁵.

Genetic data provide a strong case for natal philopatry by both sexes in the long-finned pilot whale

(*Globicephala melas*), also a member of the killer whale subfamily, Globicephalinae. Amos *et al.*³ found that females and males were related within each of two schools of 90 and 103 pilot whales captured in a drive-fishery, and that males did not mate with females from the same school.

Stranger yet are life history data obtained from Baird's beaked whales (*Berardius bairdii*) captured in a Japanese fishery⁶. Found mostly in deep ocean waters, the ziphiids, or 'beaked' whales, are the most enigmatic of all cetaceans. Most of the 20 or more ziphiids – new species are still being described – lack erupted teeth except for a pair of 'battle' teeth in males that, judging from scarring patterns, are employed in male–male combat⁷. Baird's beaked whale is unusual among ziphiids in that both females and males have battle teeth⁸. Males mature an average of four years earlier than females (ages 6–10 versus 11–15), and may live up to 30 years longer (age 84 versus 54) – a difference reflected in a male-biased sex ratio among adults. While sex-biased capture rates could explain these data, Kasuya and Brownell⁶ consider this possibility unlikely to account for the absence of older females. They speculate that the lack of sexual dimorphism in Baird's beaked whales, the higher female mortality and excess of mature males over females all suggest that males may be providing significant parental care. Confidence of paternity would have to be high for selection to favor male investment in their mates' offspring. Kasuya and Brownell⁶ suggest that if Baird's beaked whales exhibit

Table 1. Long-term (multiyear) studies of odontocete social systems in which individuals are identified

Family ^a	No. of species	Size range	Habitat	Mature long-term studies	Long-term studies under way
Iniidae (river dolphins)	3	1.5–3 m	Rivers and coastal waters	–	Boto (<i>Inia geoffrensis</i>)
Platanistidae (river dolphins)	2	2–2.5 m	Rivers	–	–
Phocoenidae (porpoises)	6	1.5–2.5 m	Mostly inshore	–	Dall's porpoise (<i>Phocoenoides dalli</i>)
Delphinidae (dolphins)	c. 33	1–10 m	Rivers to pelagic	Bottlenose dolphin ^b , killer whale ^b , spinner dolphin, Hector's dolphin	Tucuxi (<i>Sotalia fluviatilis</i>), pilot whale (<i>Globicephala macrorhynchus</i>), humpbacked dolphin (<i>Sousa chinensis</i>), spotted dolphin (<i>Stenella frontalis</i>)
Monodontidae (narwhal, <i>Monodon monocerus</i> ; white whale, <i>Delphinapterus leucas</i>)	2	4 m	Arctic waters	–	Beluga (<i>Delphinapterus leucas</i>)
Ziphiidae (beaked whales)	c. 20	4–13 m	Deep waters	–	Northern bottlenose whale (<i>Hyperoodon ampullatus</i>), Blainville's beaked whale (<i>Mesoplodon densirostris</i>)
Physeteridae (sperm whale, <i>Physeter macrocephalus</i> ; dwarf, <i>Kogia breviceps</i> ; and pygmy sperm whales, <i>Kogia simus</i>)	3	2.7–18 m	Deep waters	Sperm whale	–

^aClassification follows Heyning⁴⁵.

^bThree or more studies of this species.

bisexual philopatry like killer whales, males may be investing in the offspring of close female relatives. Left unclear in this scenario is the exact nature of the additional reproductive costs that would produce earlier mortality in females.

While major elements of killer whale, pilot whale and Baird's beaked whale social systems appear alien to researchers familiar with terrestrial mammals, the sperm whale – the largest toothed whale – offers a remarkable case of behavioral convergence with the largest terrestrial mammal, the African elephant (*Loxodonta africana*)^{9,10}. Elephants and sperm whales have unusual, but remarkably similar, life history parameters, wide ranging behavior and ecological success, as well as the largest brains on land and in the ocean¹⁰. Their societies are based on matrilineal groups of about ten related females which often form temporary associations, of a few days or so, with other female groups^{11,12}. After leaving their mother's group around six years of age^{9–11}, male sperm whales become increasingly solitary and range to higher latitudes as they grow to about one-and-a-half times the length and three times the weight of females – the most extreme case of sexual size dimorphism among cetaceans. Another striking parallel with elephants is in the delayed age of effective breeding by males: although male elephants and sperm whales become sexually mature during their late teens, they do not seem to take a significant role in breeding until their late twenties⁹. In the case of elephants, this is because younger males do not enter the behaviorally dominant but physiologically demanding state of musth in the prime breeding season¹³. By analogy, male sperm whales in the same age range usually remain in productive high latitude waters away from the tropical breeding grounds of the females⁹. In these highly sexually dimorphic species it probably pays younger males to concentrate on growth rather than competing with their much larger elders for the few breeding opportunities presented by very slowly reproducing females (one young every 4–5 years)¹⁴. Both large male elephants in musth and large male sperm

Box 1. Groups, pods, schools

Terminology in studies of social structure in odontocetes is not consistent. Depending on the study species and researcher, any of the terms 'group', 'pod' or 'school' (as well as others) may mean anything from an instantaneously observed aggregation of animals at the surface to a temporally stable (perhaps over lifetimes) non-overlapping clustering of members of a population. For consistency within this review, we adopt the following terminology:

School: a set of animals coordinating behavior over periods of minutes to hours.

Group: a set of animals which have consistently stronger associations with each other than with other members of the population over periods of months to decades.

In this article, other terms (e.g. 'pod') are used for only one species, have a meaning which is generally consistent for that species, and are explained briefly in the text.

whales on the breeding grounds rove singly between female groups in search of estrus females, usually spending just a short time with each group on any occasion¹⁵.

To understand social convergence between mammals on land and odontocetes at sea, cetologists have invoked familiar themes: predators and resources. The larger odontocetes have extremely low adult mortality but substantial infant mortality, and much infant mortality may result from predation (e.g. Ref. 16). In the open marine habitat, the ability to protect infants from harm may be an important determinant of female reproductive success. This is reflected in the extreme duration of parental care found in some species. Lactose has been detected in the stomachs of sperm whales up to age 7.5 years in females and 13 years in males¹⁷. Short-finned pilot whales (*Globicephala macrorhynchus*) may continue to lactate for up to 15 years after the birth of their last calf, and up to 25% of adult females may be post-reproductive, ceasing to ovulate after age 40 even though the maximum lifespan exceeds 60 years¹⁸. Whether post-reproductive females are nursing their own calf or the calf of another female is presently unclear.

Box 2. Dolphin sponging: tool-use and foraging specialists

Interesting variation in social behavior may occur among individuals within, as well as between populations. Male bottlenose dolphins in Shark Bay are nearly always found with their alliance partners but females may be very sociable or solitary. Given the importance of resource distribution for female reproductive success, it is not surprising to find indications that variation in female social behavior is linked to foraging behavior.

One of the most interesting variations is 'sponge-carrying', a likely foraging specialization exhibited by a small number of females in Shark Bay. Based on many hours of surface observation that yielded rare glimpses of sub-surface behavior, Smolker *et al.*⁴⁶ suggest that females use sponges to ferret prey from the sea floor – perhaps the first case of tool use in cetaceans. The sponge (*Echinodictyum mesenterium*) is worn on the rostrum like a glove, sometimes dropped during active pursuit of fish and sometimes replaced during foraging bouts that may last for hours. The sponge females have been sighted repeatedly over the years, and spend most of their time with a sponge, but otherwise alone. Young females may learn sponge-carrying from their mothers.

Why don't males carry sponges? Smolker *et al.*⁴⁶ suggest that males do not sponge because such a solitary foraging strategy would prohibit them from forming close alliances with other males. Individual strategies such as sponging are likely to reflect tradeoffs between social and developmental factors, resource distribution, and predation.

Cooperative care of vulnerable infants may be the most important factor favoring strong female–female bonds in sperm whales and elephants¹⁰. Apparently, young sperm whales, which are vulnerable to predators such as killer whales and large sharks, cannot match their mother's diving prowess and must remain at the surface while their mother is foraging at depth. Whitehead¹⁹ presented evidence for baby-sitting by female sperm whales. Adults stagger their dives more in groups with calves than when no calf is present, reducing the time calves are unaccompanied by an adult at the surface.

Similar patterns of resource distribution have also been invoked to explain convergent aspects of odontocete and terrestrial mammal societies. Such convergences are of considerable interest given the differing temporal and spatial structure of oceanic and terrestrial ecosystems²⁰. Weiglart *et al.*¹⁰ tentatively identified knowledge of resource distribution over large temporal and spatial scales as a benefit of female–female bonds common to sperm whales and elephants.

The discovery that inshore dolphin species exhibit 'fission–fusion' grouping patterns similar to chimpanzees elicited comparisons based on a generally similar patchy and ephemeral distribution of fruit and fish (e.g. Ref. 21). Like common chimpanzees (*Pan troglodytes*), bottlenose dolphins (*Tursiops* sp.) associate in small schools that often change in composition as individuals join and leave^{21–23}. More recently, these same two species have been found to share features of their social systems. In Shark Bay, Western Australia, male bottlenose dolphins develop tight bonds with 1–2 other males with whom they cooperate to form aggressively maintained consortships with individual females^{24,25}. These consortships may last from a few minutes to over a month and are very similar to herding of females by individual male chimpanzees. Like chimpanzees, bottlenose dolphins have large testes for their body size, suggesting that females mate with many males²². The parallel is made more intriguing by recent observations from Uganda of male chimpanzees cooperating in pairs to guard females²⁶. Might such variation between populations be found in bottlenose dolphins (see Box 2)? Interestingly, in the Moray Firth, Scotland, males do not form stable alliances, but it is unknown if males in temporary coalitions form consortships with females²⁷.

The Australian bottlenose dolphins exhibit a further level of alliance formation as each pair or trio of males forms moderately strong associations with one or two other alliances

whose principle function appears to be to defend against or attack other alliances in competition over females. Relationships between individual alliances vary from affiliative to aggressive, possibly depending on the social context. Such nested or hierarchical male alliances with both aggressive and affiliative interactions between particular alliances are a prominent feature of human society but are unknown in other primates²⁴.

Social interactions and communication

How do dolphins mediate their complex social relationships? Most early studies of captive dolphins described, but did not quantify, social interactions. However, a recent quantitative study of interactions among captive bottlenose dolphins found patterns that are common in sexually dimorphic primates such as chimpanzees and baboons; including higher rates of male agonism, male dominance over females (even when physically smaller), and greater stability of dominance relationships among females²⁸.

Odontocetes, unlike terrestrial mammals, rely predominantly on the acoustic channel for communication. The ocean is highly favorable for acoustic communication over ranges of more than several meters. This is particularly important for highly mobile animals such as cetaceans, where animals that share bonds often separate by kilometers, and where potential mates may be separated by tens of kilometers.

In striking contrast to other mammals, vocal learning, defined as vocalizations that become 'modified in form as a result of experience with those of other individuals', occurs in a diverse assemblage of marine mammals, including some baleen whales and phocid seals as well as odontocetes²⁹. Recent research on vocal learning and the social significance of vocalizations has concentrated on individual- and group-specific characteristics. Stable groups of killer whales and sperm whales have distinctive dialects that are likely to have been acquired culturally and are probably important in mediating coordinated group behavior^{30,31}.

In bottlenose dolphins, which do not live in stable groups, the 'whistle' vocalization has been the primary focus of research on communication and vocal learning. Whistles were originally studied in animals that were isolated or separated, a context that seems to stimulate production of individually distinctive signature whistles³². More recently, studies of dolphins kept together suggest that whistles other than signature whistles can predominate in some contexts^{33–35}. In Shark Bay, mothers often separate from their infants during foraging and whistling occurs just before mother and infant reunite³⁶.

The general phenomenon of vocal learning as well as the specific structure of whistles may be closely related to features of the aquatic environment. Terrestrial mammals can use differences in vocalizations resulting from differences in vocal tract morphology for individual recognition, but this may not be an option in the ocean where the shape of vocal cavities is distorted under pressure³⁷. The narrow-band frequency contours of signature whistles should be relatively impervious to pressure changes and may also be optimal for detection in the noisy underwater environment²⁹.

The bottlenose dolphins' remarkable abilities to mimic³⁸ increases the possible functions of whistles. Since Tyack³³ reported whistle-matching by two captive bottlenose dolphins, whistle-matching has been reported in wild dolphins³⁹. Potentially, whistle-matching could be used deceptively or honestly, but deception seems unlikely in the case where whistles are copied immediately⁴⁰. One possible 'honest' use of whistle-matching is for individuals to learn of the

location of others by producing a copy of an individual's whistle and listening for a response. Testing this hypothesis may hinge on whistle copies being distinguishable from the original³³ and the use of hydrophone arrays to localize sounds using time-of-arrival or phase differences^{41,42}.

The social brain?

The toothed whales and terrestrial mammals that we have described as having convergent social systems (elephants versus sperm whales; bottlenose dolphins versus chimpanzees) share another intriguing characteristic: very large brains. Less widely appreciated is the remarkable degree of variation in relative brain size among toothed whales: 2–3-fold for species of the same body size in some cases^{24,43}. Hypotheses for large brain evolution in terrestrial mammals focus on either the costs of maintaining large brains (energetic constraints) or their benefits (e.g. cognitive mapping of resource distribution or social relationships⁴³). While the apparent parallels in social complexity are intriguing, the possibility of similarly complex patterns of resource distribution, for example, may render these hypotheses as difficult to test in toothed whales as they have been in terrestrial mammals. An approach such as Dunbar's⁴⁴ efforts to quantify the number (if not complexity) of social relationships may allow comparisons not only among large and small brained odontocetes, but with terrestrial mammals as well.

Conclusions

Research on the behavioral ecology of toothed whales, and on cetaceans in general, has lagged behind the study of terrestrial mammals for a number of reasons of which the most obvious is the difficulty facing a terrestrial mammal attempting to observe an aquatic one. Now that the early returns are in, it is apparent that the effort is worthwhile; not only do we find remarkable convergence in a vastly different physical environment and ecosystem, we are also finding social phenomena which have no precedent on *terra firma*. As established studies of identified individuals acquire more long-term and detailed data, and as a growing number of new initiatives on a much wider range of species begins to bear fruit (Table 1), the social systems of odontocetes will probably become both less mysterious and more interesting. Further inquiry into this combination of convergence and novelty in odontocete social systems may ultimately broaden our understanding of social evolution in both terrestrial and marine environments.

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Hydraulic lift: a potentially important ecosystem process

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It is well known that water availability influences plant geographic distribution¹. Globally, water availability in terrestrial ecosystems is the most important factor limiting CO₂ fixation and growth of individual plants, as well as ecosystem net primary productivity^{1–3}. This is true in arid and semi-arid regions, as well as in mesic regions that are prone to short-term seasonal water deficits^{3–5}.

When plant demand exceeds water supply, plants must find other sources of water or make more conservative use of available water to minimize water stress and meet metabolic requirements⁵. Mooney and co-workers⁶ suggested that *Prosopis tamarugo*, a shrub growing in the Atacama Desert in Chile (an area with an average annual rainfall of 0.3 to 0.7 mm), reduced water stress by transporting ground water into its deep roots and then releasing it, from its roots, into the upper soil layers where it can be utilized later. This process of taking water from deeper, moister soil layers and transporting it through plant roots to upper, drier soil layers has been termed hydraulic lift⁷. Hydraulic lift has been proposed as a mechanism that can buffer plants against water stress during seasonal water deficits⁸.

Hydraulically lifted water (HLW) can benefit the plant that lifts it but might also benefit neighboring plants^{5,8}. The volume of HLW can be such that it might influence seasonal water balances of individuals, communities, or even ecosystems^{5,7,9} (Table 1). If this phenomenon is widespread, it should be

Hydraulic lift is the process by which some deep-rooted plants take in water from lower soil layers and exude that water into upper, drier soil layers.

Hydraulic lift is beneficial to the plant transporting the water, and may be an important water source for neighboring plants. Recent evidence shows that hydraulically lifted water can promote greater plant growth, and could have important implications for net primary productivity, as well as ecosystem nutrient cycling and water balance.

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incorporated into models of competitive interactions⁵, as well as ecosystem process models and water budgets¹⁰.

Evidence for hydraulic lift

Mooney and co-workers⁶ found that *P. tamarugo* possessed a dense root mat about 1 m under the surface. This mat was located in a moist soil layer that could exceed field capacity (Box 1), even though the soil above and below was much drier. The authors attributed this to hydraulic lift. The mechanism used to explain this phenomenon is based on passive movement of water down a water potential (Ψ) gradient. During the day, if a plant is transpiring, the Ψ gradient is from the ground water into the plant's roots and out through stomata to the atmosphere. At night,

when the stomata close, water moves into the shoots until shoot Ψ is equal to the Ψ in the deep soil. The Ψ gradient is now from both the deeper soil and the plant shoot into the drier surface soil around the root mat. Water moves from the roots into this soil layer where it can be used for transpiration the next day⁷.

In the semi-arid Great Basin of Utah, USA, Richards and Caldwell⁷ observed significant diel fluctuations in soil water potential (Ψ_s) in areas around the sagebrush (*Artemisia tridentata*). Soil water potential decreased during the day, as plants were actively transpiring, but increased in the upper soil layers at night, when plants were no longer transpiring (Fig. 1). The nocturnal increase in Ψ_s was several orders