
Group Behavior

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Many animals spend part or all of their lives in groups. Their size and composition have diverse effects on morphology and behavior including relative brain size and extent of sexual dimorphism. A group may be viewed as any set of individuals, belonging to the same species, which remain together for a period of time interacting with one another to a distinctly greater degree than with other conspecifics. Thus, the study of group-living is the study of social behavior, and marine mammal societies can be remarkably diverse (Fig. 1).

Groups can be classified based both on the amount of time individuals interact with each other and on the benefits that individuals receive. Schools last for periods of minutes to hours while groups last for months to decades. Aggregations (or non-mutualistic groups) do not provide a larger benefit to individuals than if they were alone, while groups (or mutualistic groups) do provide such benefit to their members. Aggregations are formed because a nonsocial factor, e.g., food, attracts individuals to the same place; groups are formed because they provide a benefit to their members.

Recent studies have highlighted the challenges of defining marine mammal groups in nature, particularly those of cetaceans. For instance, most scientists determine whether individual dolphins belong to the same group based on the distance separating individuals (usually ≤ 10 m) or the radius comprised by the group (usually ≤ 100 m), and/or by whether individuals are engaging in the same behavior or not. However, a study of bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida, indicates that the communication range of social sounds between females and dependent calves could be at a minimum 487 m and reach up to 2 km or more (Quintana-Rizzo *et al.*, 2006). Hence, the traditional distinctions of a group—practical, replicable, and undoubtedly useful in advancing our understanding of group behavior—are likely not meaningful to a cetacean. Because cetaceans rely on acoustic communication to maintain group cohesion, the study



Figure 1 (A) Blue whales (*Balaenoptera musculus*) are usually found alone or in small numbers. (B) South American sea lions (*Otaria flavescens*) aggregate in large numbers during the breeding season. Photos by A. Acevedo-Gutierrez.

highlights the importance of understanding communication range to define cetacean groups.

To describe the social structure of a population, it is essential to measure how much time individuals spend together (association patterns) and the rate at which individual associations changes over time (lagged association rates). However, the amount of time that animals spend together depends both on genuine social affiliations and on how much individual home ranges overlap. For instance, two individuals may be observed together because they have a similar home range, forming then an aggregation, rather than because they are genuinely affiliated, which would then be a group. Employing network analyses, association analyses, and estimates of lagged association rates at different spatial scales, a study of coastal bottlenose dolphins in eastern Scotland shows that the population is composed of two social units with restricted interactions as a result of social affiliation (Lusseau *et al.*, 2006). The study highlights the importance of network analyses and the use of different temporal (lagged association rates) and spatial scales to understand the organization of social marine mammals.

I. Theory of Group-Living

There appear to be three conditions under which group-living will evolve, the benefits to the individual outweigh the costs, the

costs outweigh the benefits but strong ecological constraints prevent dispersal from the natal territory (for instance, lack of high-quality breeding openings explains within-population dispersal decisions and family groups in birds), and the area where the group lives can accommodate additional individuals at no cost.

A. Benefits and Costs of Group-Living

Group-living is usually explained in terms of benefits to the individual group members via direct or indirect fitness. Increases in direct fitness include mechanisms such as direct benefits of group-living, direct and indirect reciprocity, and mutualism. Increases in indirect fitness are achieved via kin selection. It has been argued that when competition occurs at the level of groups rather than individuals, group-living is best explained in terms of benefits to the groups themselves, group selection. However, many scientists consider that whenever interactions occur at a local spatial scale, and dispersal is limited, then interactions occur among genetic relatives, and thus kin selection rather than group selection is operating (Nowak, 2006).

Kin selection is perhaps the most frequently employed argument to explain benefits of group-living. For instance, kin selection explains the generalities of cooperative breeding in mammals and birds (Brown, 1987; Jennions and Macdonald, 1994), and the evolution of cooperation among male chimpanzees (*Pan troglodytes*) (Morin *et al.*, 1994). Further, mammalian female kin (including several odontocete species) spend more time in close proximity and are more likely to help each other. Females may allosuckle or gain higher reproductive success by forming coalitions with kin. However, explanations based on kin selection are in some cases inadequate and some behaviors are best explained in terms of direct fitness via diverse mechanisms. Direct benefits from early detection of danger explain the sentinel behavior of meerkats (*Suricata suricatta*) (Clutton-Brock *et al.*, 1999) and delayed direct benefits to the subordinate male explain the occurrence of dual-male courtship displays in long-tailed manakins (*Chiroxiphia linearis*) (McDonald and Potts, 1994). By-product mutualism explains territorial coalitions in Australian fiddler crabs (*Uca mjoebergi*), which assist other crabs in defending their neighboring territories; in this manner, the neighbor keeps its territory and the ally pays to retain an established neighbor rather than renegotiate boundaries with a new neighbor (Backwell and Jennions, 2004).

Benefits to increase foraging efficiency and reduce predation, and the number of individuals that can be supported by the available local resources have been typically viewed as important factors shaping group-living. These benefits apparently apply to all social organisms; for instance, the ability to disperse and exploit new food patches appears to favor the aggregation of solitary slime mold into a multicellular organism known as a slug (Kuzdzal-Fick *et al.*, 2007). However, increased foraging efficiency and reduction of predation can be accomplished through a myriad of different mechanisms (Table I). In addition, increased foraging and reduce predation are sometimes inadequate to explain group-living, in African lions (*Panthera leo*), female-grouping patterns are best explained as facilitating cooperative defense of cubs against infanticidal males and defense of territory against other females, not as increasing foraging efficiency (Packer *et al.*, 1990). Group-living can also impose several costs to individuals, including increased competition over access to resources and mating opportunities, exposure to infection, and conspicuousness to predators (Table II). In general, it is believed that for mammals the main benefit of sociality is protection against predators whereas the main cost is increased competition for resources.

TABLE I
Benefits of Group Living

Reduction of predation[°]

- Enhanced ability to detect predators: sensory integration.
- Enhanced ability to deter predators, even larger than group members.[°]
- Enhanced ability to escape, including predator confusion and coordinated evasion behavior.[°]
- Reduced individual probability of being selected as prey:
 - By associating with conspecifics: dilution effect.[°]
 - By hiding behind conspecifics: selfish herd.[°]

Allocation of time to other activities

- Reduced individual vigilance time
 - Because of group vigilance (many eyes).[°]
 - Because of decreased individual predation risk.[°]
- Increased foraging time for mothers by having babysitters.[°]

Enhanced detection and capture of prey

- Foraging in risky, but profitable, areas.
- Finding prey or reducing variation in food intake through cooperative searching: sensory integration.[°]
- Following more knowledgeable animals in the group to a food source: information transfer.[°]
- Following other species with more specialized senses to a food source.[°]
- Joining resources uncovered by others, also known as conspecific attraction, kleptoparasitism, area copying, scrounging, or tolerated theft.[°]
- Acquisition of innovative feeding behaviors from another group member:
 - Social learning through social facilitation (contagion of motivational states).
 - Directing attention to particular locations or objects: local enhancement.
 - Imitation of knowledgeable tutors.[°]
 - Information sharing and cultural transmission.[°]
- Increased diversity and size of prey that is captured:
 - Due to more individuals foraging.[°]
 - Due to prey flushed by movements of group members.[°]
 - Due to individuals with different skills or abilities foraging together: skill pool effect.
- Increased food intake as a result of communal foraging.[°]
- Lower risks of injury while hunting.[°]

Acquisition or defense of resources

- Large groups defend, occupy, or displace small groups from better territories.
- Large groups acquire or defend localized food sources, including carcasses, from conspecifics or other species.[°]

Improved reproduction

- Caring and protection of offspring.[°]
- Learning to be a parent.[°]
- Finding mates in isolated or vast areas.[°]
- Enhanced reproductive synchrony.[°]
- Enhanced survival when there is prevention of dispersal to neighboring territories.
- Males benefit from cooperative displays, subdominant males receive the payoff later in time.
- Males in large groups gain access to females.[°]

Reduction of parasitism

- When number of hosts in a group increases more rapidly than the number of mobile parasites, reduced individual probability of being parasitized by associating with conspecifics: dilution effect.

Other

- Huddling to survive cold temperatures.[°]

[°]Suggested or documented costs in marine mammals.

The magnitude of the costs of sociality may be important in shaping group-living. It has been suggested that in some species differences in group size may be related to the differences in their costs of locomotion. Under this ecological-constraints model, large group sizes must travel farther each day because they deplete food patches more rapidly or require searching larger areas. Supporting the model, day range, and group size are positively correlated in various primate and carnivore species (Wrangham *et al.*, 1993). Animals that travel further spend more energy and reproduce less efficiently, hence a negative relationship between group size and reproductive performance is predicted within species. However, marine mammals

reduce the costs of locomotion by developing energy-conserving swimming behaviors such as routine transit speeds, wave-riding, porpoising, and gliding. Hence, one would expect that group size in marine mammals is unrelated with distance traveled. Although I am unaware if such correlative study has been conducted, it has been hypothesized that reduced cost of locomotion coupled with a lack of restriction to a particular territory has allowed some populations of killer whales (*Orcinus orca*), and possibly long-finned pilot whales (*Globicephala melas*), to develop societies in which females and males remain with their natal group for life (Fig. 2). In this manner, males traveling with their mothers can have large home ranges and thus find potential mates.

TABLE II
Costs of Group Living

Increased predation

- Large groups more attractive to predators.
- Larger groups more likely to be detected by a predator: encounter effect.

Reduced foraging efficiency

- Increased amount of food needed for group.[°]
- Increased energy spent, distance traveled, or area covered to find food for group.[°]
- Increased conspicuousness: prey able to detect predators sooner than if predators are alone.
- Reduction in food intake due to sharing of prey, scramble competition, scrounging, and individual discrepancies in foraging success.
- Reduction in food intake due to interference by the behavior of other individuals.[°]
- Reduce ability to learn innovative foraging skills due to scroungers in the group.

Increased conflicts for resources due to presence of more conspecifics or other species

- Individuals from other groups or species following social parasitism.[°]
- Individuals from other groups or species attracted to feeding parties: local enhancement.[°]

Reduced reproduction, increased competition for mates, or other limited resources

- Individual discrepancies in number or quality of mates obtained.[°]
- Extrapair copulations and loss of fertilizations to other members of group.[°]
- Increased intra-specific competition for limited resources.[°]
- Increased infant mortality.[°]
- Increased risk of exploitation of parental care by conspecifics.
- Theft of nest material.

Increased risk of infection

- Increased contagious parasitism.
- Increased disease transmission.

[°]Suggested or documented costs in marine mammals.



Figure 2 In certain populations male and female killer whales (*Orcinus orca*) remain with their natal groups throughout their lifetime. Photo by Christopher Pearson

Recent studies have documented novel strategies followed by individuals living in groups, including the complexity of intragroup and intergroup interactions. Female African lions cooperate to defend their territory from intruders; however, some individuals consistently lead the approach whereas other individuals lag behind without being punished by the leaders (Heinsohn and Packer, 1995). One potential

explanation for this tolerance is that females need to defend their territories against other groups and their success depends in part on the number of defending females even if some individuals never lead the charge. Pinyon jays (*Gymnorhinus cyanocephalus*) draw sophisticated inferences about their own dominance status relative to that of strangers that they have observed interacting with known individuals (Pazy-Miño *et al.*, 2004). That is, they make judgments about relationships on the basis of indirect evidence rather than by learning through direct interactions with other individuals. The study is the first experimental demonstration of transitive inference in animals and implies that such cognitive capabilities are widespread among social species.

Complex social behaviors have also been reported in marine mammals. In a breeding colony of gray seals (*Halichoerus grypus*) at the island of North Rona, Scotland, a few large males monopolize matings on the breeding beaches, however females over the years give birth to full siblings not sired by the dominant male (Amos *et al.*, 1995). The fathers of the pups are nondominant males that mate with the same females in different seasons. Thus behavioral polygyny and genetic fidelity seem to operate simultaneously in this colony. It has been suggested that this strategy of partner fidelity is maintained in the population because it may diminish aggressive interactions between dominant males and thus reduce the pup mortality originated by these clashes.

Perhaps one of the most complex behaviors described in marine mammals is the formation of alliances among male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia, in which complexity is only matched by humans (Connor *et al.*, 1999; Connor, 2007). Males form strong and stable bonds for over 10 years with one or two other males, males in these first-order alliances cooperate to form aggressively maintained consortships with individual females.

Each first-order alliance forms moderately strong bonds with one or two other alliances, these second-order alliances do not endure for more than a few years and males cooperate to take or defend females from other alliances. Recently, it has been described that some second-order alliances associate regularly and cordially with other groups, suggesting a third level of alliance formation. A different strategy is for males to form a large but loose superalliance that competes with the smaller and more stable first-order or second-order alliances. Members of the superalliance split into smaller alliances of pairs and trios that are constantly changing but are always comprised of males from the superalliance. These pairs and trios join conflicts involving members of the superalliance and are always victorious. It is hypothesized that the large size of the superalliance allows individuals to compete with the smaller alliances and that the fluidity of individual associations within the superalliance allows males to maintain affiliative bonds. Because alliance formation is a strategy to obtain access to females, it has been hypothesized that alliances increase male reproductive success. Supporting this hypothesis, a recent study suggests that the vast majority of paternities are achieved by males involved in some form of alliance. However, within first-order alliances a few males dominate fertilizations, indicating skew in reproductive success among males in stable alliances (Krützen *et al.*, 2004). Given that males in stable first-order alliances formed small second-order alliances are more related to their allies than expected by chance, the reproductive skew among males may be explained in terms of kin selection (Krützen *et al.*, 2003). Interestingly, superalliances, where no reproductive skew has been described, are not formed by closely related males. Finally, the observation that some juvenile males without an alliance may achieve paternities suggests that alternative male tactics other than alliance formation exist in the population. What favors alliance formation among males? A recent model predicts that males will form alliances except when the number of males competing for a receptive female is very few, when there are substantial costs to being in an alliance, or when alliances do not out-compete single males.

B. Female Social Behavior

One previously neglected area of research is the study of female social behavior. Females and males frequently have different interests, as a result female relationships are important in understanding social evolution independently of the behavior of males. For instance, dominant female chimpanzees have a higher reproductive success than subordinate ones, apparently because they are able to establish and maintain access to good foraging areas, competing in extreme cases as intensely as males (Pusey *et al.*, 1997). Females may also influence behaviors that affect the interests of males, female bird song appears to have evolved in part to compete for males, however this behavior has the potential consequence of preventing polygyny by deterring rival females (Langmore, 1998). In mammals, most females remain within their natal area or group throughout their lives. This female philopatry facilitates the formation of social groups through kin selection. Hence, understanding social behavior in many mammal species requires studying female social behavior. For instance, theoretical and empirical evidence indicates that females live in groups that often exceed the optimal group size (Silk, 2007). This discrepancy is associated with mechanisms regulating group size, such as trying to oust other group members or exclude immigrants, actions that are costly to the individuals performing them.

The study of females is also essential to understand group-living in marine mammals. Captive female bottlenose dolphins

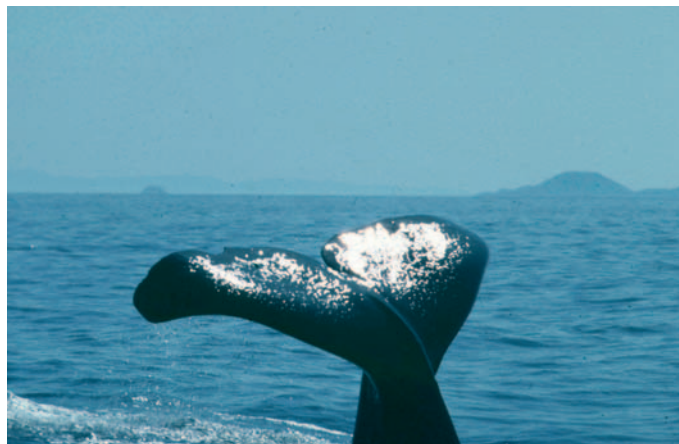


Figure 3 Alloparenting behavior apparently allows sperm whale (*Physeter macrocephalus*) mothers to make deep foraging dives. Photo by A. Acevedo-Gutierrez.

maintain dominance hierarchies and also compete aggressively against each other. However, unlike chimpanzees, it is unknown if female dominance hierarchies in free-ranging dolphins translate into differences in reproductive success. The preference and fidelity of female gray seals at North Rona toward nondominant males undermines the polygynous strategy of dominant males and results in a different mating system from that inferred by behavioral observations (Amos *et al.*, 1995). The large number of females in colonies of certain pinnipeds, such as northern elephant seals (*Mirounga angustirostris*), has permitted the existence of alloparenting and the appearance of a distinct suckling strategy by calves, milk-stealing. Male and female sperm whales (*Physeter macrocephalus*) have different grouping strategies, females appear to spend their entire lives within their natal group, forming strong matrilineal societies. Adult males are less social, leaving their nursing group when they reach puberty and after they have reached their late 20s roam among nursery groups looking for mates. The function of the female groups is to provide care for calves that are too young to follow their mothers during their deep foraging dives (Fig. 3). It has been suggested that this alloparenting reduces the period in which the calf is unaccompanied and thus provides protection from predators and also perhaps provides communal nursing (Whitehead, 1996; Mann *et al.*, 2000a). Thus key features of the sperm whale society are explained solely by the behavior of females.

II. Social Behavior of Marine Mammals

There are several differences between terrestrial and marine environments that have allowed the evolution of distinctive strategies in marine mammals. Drag, heat loss, and density of the water generate differences in scaling and costs of locomotion, allowing many marine mammals to have large body sizes and large home ranges. Sound is the form of energy that best propagates in water, not surprisingly marine mammals employ it for social communication and many species navigate via echolocation. Marine mammals must find food that is for the most part dispersed and patchy, thus they appear to have no territories outside of the breeding season. Due to the global effects of the atmosphere and the ocean in the marine environment, marine mammals are affected by both global and local processes as



Figure 4 In certain species, pinniped females cluster during the breeding season and males are able to monopolize access to them. Photo by A. Acevedo-Gutierrez.

exemplified by the impact of El Niño Southern Oscillation events on different populations.

A. General Strategies

Sirenians, sea otters (*Enhydra lutris*), and polar bears (*Ursus maritimus*) are solitary animals that have few social interactions beyond mating and mother/offspring pairs. The time that these pairs remain together is 1–1.5 years in sirenians, 5–7 months in sea otters, and 2.5 years in polar bears. When a female becomes receptive sirenians form aggregations that have as many as 17 males physically competing for access to the female or defending display territories. During the breeding season male sea otters establish territories that include the areas occupied by several females, whereas male polar bears mate with only one partner because females have a dispersed distribution.

Most pinnipeds aggregate in colonies during the breeding season, a major factor influencing the size of these colonies is the distribution of habitat available for parturition. Pinnipeds give birth out of the water and thus the areas favored for parturition are oceanic islands, ice, or isolated mainland regions not easily accessible to terrestrial predators. When available space is limited, females become densely aggregated in large colonies that favor mating systems in which males defend either aggregations of females or areas occupied by females, or aggregate and display before aggregations of females (Fig. 4). However, when parturition space is dispersed, females are isolated, males usually have access to only one female, and no colonies are formed. At small spatial scales (within colonies), lack of suitable habitat might also explain high density of females in many cases; however, in various populations there is plenty of unoccupied space and females are still clustered. Hence, other factors need to be invoked to explain this clustering. For instance, females reduce the individual probability of being harassed by less competitive males by clustering (Trillmich and Trillmich, 1984). Female Galápagos sea lions (*Zalophus wollebaeki*) avoid overheating by clustering along the wet shoreline, which in turns determines the distribution of dominant and subdominant males (Wolf *et al.*, 2005). The strongest association found in pinnipeds is formed by a mother and her offspring, and lasts for less than 1 week to almost 3 years, depending on the species. Pinnipeds haul out together outside of the breeding season.

Although this non-reproductive social behavior is poorly known, there is evidence that it increases vigilance for predators in harbor seals (*Phoca vitulina*). It is believed that hauling out together also allows pinnipeds to rest, avoid predators, molt or warm themselves. For instance, walrus (*Odobenus rosmarus*) in large numbers may decrease the rate of body heat loss, particularly in calves, when on land or on ice.

The complexity of cetacean societies appears to be related to amount of time invested in lactating and in rearing their calf after weaning. Baleen whales are found in schools of varying size, from single individuals to more than 20 whales. Pairs of mothers and their offspring form stable associations that last less than 1 year. It is currently unclear if long-term associations exist among adult whales. Most females give birth every 2–3 years, and have the potential to produce more than 20 calves throughout their lifetime. Schools of baleen whales have been observed in both feeding and breeding grounds. For instance, feeding humpback whales (*Megaptera novaeangliae*) forage alone, in aggregations, or as a group, depending on prey type, while aggregations of breeding males display acoustically or compete directly for access to females. Odontocetes are the most social marine mammals and have different types of societies as suggested by the large variation in school size between species (Table III). Short-term associations between adults characterize porpoises. Associations between mothers and their offspring last for 8–12 months. Females breed every 1 or 2 years and may give birth to 15 calves or more during their life span.

It is believed that medium-sized dolphin species live in fission–fusion societies with fluid group membership. Yet, a recent study indicates that spinner dolphins (*Stenella longirostris*) around Midway Atoll live in stable bisexually bonded societies of long-term associates with strong geographic fidelity, no obvious fission–fusion, and limited contacts with other populations (Karczmarski *et al.*, 2005). It is hypothesized that the geographic isolation and small size of the remote atoll favor long-term group fidelity and social stability over the fluidity of the fission–fusion society is replaced. Bottlenose dolphins live in fission–fusion societies that are believed to reduce feeding competition by allowing individuals to disperse. Associations between adults are varied, they last a short amount of time in some individuals and several years in others. In certain populations males form relatively stable groups and rove among female groups. Females give birth at least every 3 years and may produce close to 10 calves throughout their lifetime. Calves remain with their mothers 2–11 years (Fig. 5). Adult females form strong bonds with their calves as well as stable, moderate-level associations with other females within social clusters named bands. Bands tend to be composed of female relatives, but they can also include unrelated females. It has been hypothesized that reproductive condition (e.g., females with same-aged calves) determines associations within bands while kinship determines band membership. Why do female bottlenose dolphins form groups? Two leading hypothesis are protection from predators and defense against sexual coercion by males.

Little is known about the social structure of beaked whales (Ziphiidae) given their pelagic and deep-diving behavior. However, the northern bottlenose whale (*Hyperoodon ampullatus*) society in the northwestern Atlantic appears to comprise roving strong male–male bonds and weaker female–female bonds (Gowans *et al.*, 2001). Female and immature whales form a loose network of associations, showing neither preferential associations with particular individuals nor long-term bonds. Although males form many short-term associations, associations between some males last for several years. This social organization is reminiscent of that observed in some bottlenose

TABLE III
School Sizes of Odontocetes

Species ^a	Average school size	Maximum school size
<i>Phocoenoides dalli</i> (7)	2.3–7.4	5–500
<i>Neophoca phocaenoides</i> (1)	2.0	13
<i>Phocoena phocoena</i> (6)	1.2–5.7	15–100
<i>P. sinus</i> (1)	1.9	7
<i>P. spinipinnis</i> (1)	4.5	10
<i>Cephalorhynchus commersonii</i> (1)	6.9	110
<i>Lissodelphis borealis</i> (2)	9.9–110.2	60–2000
<i>Delphinus</i> sp. (4)	46.8–385.9	650–4000
<i>Grampus griseus</i> (9)	6.3–63	20–500
<i>Lagenodelphis hosei</i> (1)	394.9	1500
<i>Lagenorhynchus acutus</i> (1)	53.2	?
<i>L. obliquidens</i> (3)	10.8–88	50–6000
<i>L. obscurus</i> (3)	9.5–86	24–1000
<i>Sotalia fluviatilis</i> (1)	2.5	10
<i>Sousa plumbea</i> (1)	6.6	25
<i>Stenella attenuata</i> (5)	26.0–360.0	148–2400
<i>S. clymene</i> (1)	41.6	100
<i>S. coeruleoalba</i> (3)	60.9–302	500–2136
<i>S. frontalis</i> (2)	6.0–10.0	50–65
<i>S. longirostris</i> (4)	37.6–134.1	95–1700
<i>Steno bredanensis</i> (2)	14.7–40.0	53
<i>Tursiops aduncus</i> (2)	10.2–140.3	80–1000
<i>T. truncatus</i> (29)	3.1–92.0	18–5000
<i>Feresa attenuata</i> (1)	27.9	70
<i>Globicephala macrorhynchus</i> (2)	12.2–41.1	33–230
<i>G. melas</i> (3)	9.3–84.5	220
<i>Orcinus orca</i> (10)	2.6–12.0	5–100
<i>Pseudorca crassidens</i> (1)	18	89
<i>Peponocephala electra</i> (2)	135.3–199.1	400
<i>Delphinapterus leucas</i> (3)	3.8–32.9	100–500
<i>Monodon monoceros</i> (1)	3	50
<i>Inia geoffrensis</i> (2)	1.6–2.0	8–10
<i>Lipotes vexillifer</i> (1)	3.4	10
<i>Platinista gangetica</i> (1)	1.4	3
<i>Kogia sima</i> (1)	1.7	?
<i>Physeter macrocephalus</i> (6)	3.7–22.1	17
<i>Berardius bairdii</i> (1)	7.2	25
<i>Ziphius cavirostris</i> (1)	2.3	7

^aValues in parentheses indicate number of studies.

dolphin populations foraging in shallow, enclosed bays rather than that of sperm whale populations, which forage in deep water canyons as northern bottlenose whales do. Baird's beaked whales (*Berardius bairdii*) apparently employ a novel social strategy. Males live longer than females and thus there is an excess of mature males over



Figure 5 Bottlenose dolphin (*Tursiops truncatus*) calves remain with their mother for up to 8 years.

females (Kasuya, 1995). It has been hypothesized that these traits indicate a society in which males provide significant parental care by rearing weaned calves, protecting them from predators and teaching them foraging skills.

In the case of the sperm whale and large-sized delphinids (pilot whales and some populations of killer whales), females appear to spend their entire lives within their natal group, forming strong matrilineal societies. Females usually breed every 3–6 years and may give birth to about 5 calves throughout their lifetime, more in the case of long-finned pilot whales. Females may live over 20 years past their post-reproductive years. It has been suggested that this strategy allows old females to transmit and store cultural information, and provide alloparental behavior. In the case of short-finned pilot whales (*Globicephala macrorhynchus*), it is possible that non-reproductive females even provide alloparental nursing (Kasuya, 1985). Male sperm whales and perhaps male short-finned pilot whales leave their nursing group when they reach puberty. However the former, after they have reached their late 20s, roam among nursery groups looking for mates; the latter appear to join a different nursery group and remain in it, engaging in few clashes with other males, apparently because they are able to engage in non-reproductive mating with old females, as it apparently occurs in bonobos (*Pan paniscus*). Male killer whales in some populations, and perhaps male long-finned pilot whales, remain in their natal group for life but mate with females from other groups when they meet, hence avoiding inbreeding. It is important to explain the absence of male dispersal because in the majority of social mammals males disperse from their natal group and do not interact with relatives (in a few species it is the females who disperse). The accepted explanation is that this sexually dimorphic dispersal and lack of interaction with relatives avoids inbreeding in mammals. The lack of male dispersal in killer whales has been explained in terms of the benefits that male apparently provide to the offspring of related females, such as assistance in hunting and teaching (Mann *et al.*, 2000a).

Among vertebrates, female killer whales, short-finned pilot whales, humans (*Homo sapiens*), and probably sperm whales, spend a substantial part of their adult life reproductively sterile and helping their close relatives. As such, the females undergo menopause and the species can be viewed as eusocial (McAuliffe and Whitehead, 2005). Cetacean menopause is believed to be adaptive, where the benefits of assisting kin outweigh the costs of reproductive cessation. Similar to human grandmothers, cetacean grandmothers appear to help by

storing and providing information to the other members of their matriline. This informative role of grandmothers might be the primary motor of eusociality and also supports the growing evidence of culture among cetaceans (Whitehead, 1998, 2007; Whitehead *et al.*, 2004). An important impact of culture can be found in social learning among matrilineal odontocetes, whereby learned behaviors passed on to family members are being conserved within matriline and affecting the course of genetic evolution. For instance, it has been suggested that the division of sympatric resident and transient killer whales off the west coast of Washington State and Canada was originally cultural; however, they show enough differences in feeding behavior, vocalizations, social systems, morphology, and genetics that they may be incipient species. In another example, indirect measures of the reproductive success of groups of sperm whales vary according to differences in culture between the groups. Although modification of the course of genetic evolution through culture has only been demonstrated in humans, further studies in more species and longer datasets on well-studied species will shed more light into the impact of culture on cetacean evolution. Why do some cetacean species engage in social learning? Apparently the prevalence of social learning and culture in cetaceans is related to patterns of environmental variation (Whitehead, 2007). Under this scenario, social learning is advantageous in environments where variation in biotic and abiotic factors is large over long time scales, such as marine ecosystems.

B. Foraging

Increased foraging efficiency is considered to be one of the principal roles of group-living in cetaceans. However thus far transient killer whales provide the only clear example supporting the argument that marine mammals live in groups because of foraging benefits (Baird and Dill, 1996). Transient killer whales live in the Pacific Northwest and prey on harbor seals and other small marine mammals. Individuals maximize their caloric intake if they feed in groups of three, which is the size of the group in which they live. The small size of these groups is apparently maintained by the departure of all female offspring and all but one male offspring from their natal group.

Two benefits of group-living through foraging efficiency are the ability to search for prey as a group and to forage communally (Fig. 6). Searching for prey as a group allows individuals to combine their sensory efforts, which should be an advantage when prey has a dispersed and a patchy distribution. Communal foraging allows individuals to combine efforts to pursue and capture prey. This behavior has been reported in dolphins, baleen whales, including blue whales (*Balaenoptera musculus*) and bowhead whales (*Balaena mysticetus*), and pinnipeds, such as fur seals and sea lions. However, in some instances it is unclear whether individuals combine efforts to pursue and capture prey, or merely aggregate in an area where food is concentrated. A particular type of communal foraging behavior, termed prey herding, has been observed when feeding on shoaling fish. Individuals encircle shoals of fish and thus create a tight, motionless ball of prey from which they can grab individual fish with their mouths, in some cases individuals release bubbles to further tighten the ball of prey. This herding of prey has been well described in humpback whales, dusky dolphins (*Lagenorhynchus obscurus*), and killer whales. However, it has also been reported in other species, such as bottlenose dolphins, common dolphins (*Delphinus* spp.), clymene dolphins (*Stenella clymene*), and Atlantic spotted dolphins (*S. frontalis*). It is difficult to document this behavior, and no study has yet quantified the success of cetaceans in herding prey.



Figure 6 Communal foraging allows dolphins to combine pursuing efforts.

C. Predation

Reduction of predation is considered to be another principal function of group-living in cetaceans, certain shark species and some large delphinids attack cetaceans, and calves suffer higher mortality than adults do. However, pinnipeds apparently also form groups in response to predation. Walrus sometimes form groups lasting throughout the year in the water and on haul-out sites. It has been suggested that this may be a female strategy for pup defense against predation by polar bears.

Thus far no conclusive evidence shows that group-living in cetaceans is driven because of benefits in reduction of predation, although it has been suggested that this could be the case in sperm whales. Nonetheless group-living may provide several benefits to reduce predation. Groups are able to mob and chase away predators, as has been observed in hump-backed dolphins (*Sousa* spp.) when attacked by a shark. It is believed that other dolphins also employ this antipredatory strategy. Sperm whales, and perhaps humpback whales, employ the marguerite formation, in which adults surround young individuals by having their heads toward the center (horizontal formation) or toward the surface (vertical formation). Adults have their flukes toward the periphery and employ them to slap at the predators, which in the majority of observations have been killer whales.

Group-living appears to be mostly related to food and predation in terrestrial and marine mammals. Thus it has been argued that the variation of group sizes among dolphin species is related to food availability, related to prey habitat, or to the need to defend from predators. For instance, the reproductive success of female Indo-Pacific bottlenose dolphins is highest in shallow waters, either because calves and their mothers are able to detect and avoid predators or because prey density is highest (Mann *et al.*, 2000b).

I compiled data on the average school size from 24 species of the family Delphinidae (Table III). Because definitions of school vary among researchers, I attempted to make values comparable by selecting only studies with at least 30 observations throughout a season and that defined schools as the number of individuals engaged in similar activities regardless of distance between them. I averaged the values from species belonging to the same genus and related them to crude measures of predation pressure and prey habitat, measures that were obtained from the literature. Results indicate that regardless of the body weight of the genus, average school sizes are larger when predation pressure is high rather than low, and when prey

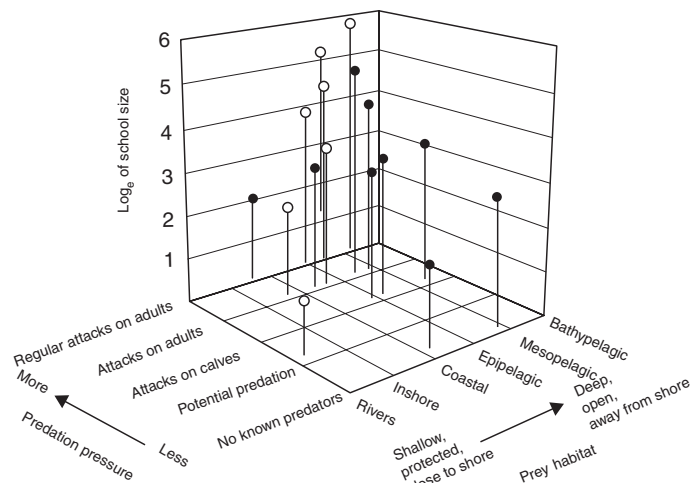


Figure 7 Relationship between predation pressure, prey habitat, and average school size of 16 genera of the family Delphinidae. Open circles indicate small genera (females weigh less than 150 kg), solid circles indicate large species (females weigh more than 150 kg).

is found in open rather than enclosed waters (Fig. 7). School sizes are largest when both predation pressure is high and prey lives at depth in oceanic waters. Thus it appears that the average school size of dolphin genera is related both to the predation they experience and the habitat where their prey lives. However, comparative research of group size in Delphinoidea (Delphinidae, Phocoenidae, Monodontidae)—including phylogeny, physical environment, diet, predation pressure, and life history—indicated that phylogeny explained most of the observed variation in group size (Gygax, 2002a, b). Although group size also increased with openness of the habitat and showed a U-shaped relationship with temperature, the simplest interpretation of the study is that group size resulted from a random process and has been marginally shaped by direct selection.

D. Resource Defense

Interspecific contests over food are thought to also influence the group size and the group composition of predators. In the case of marine mammals, one study has documented the influence of competitive interactions with sharks on dolphin food intake and apparently on group size (Acevedo-Gutiérrez, 2002). As Isla del Coco, an oceanic island off Costa Rica, underwater observations indicate that bottlenose dolphins eat less food if there are many silky sharks (*Carcharhinus falciformis*) converging on the same fish school. The observations also indicate that the interactions between sharks and dolphins represent contests over food between these two similarly sized species, and not predation on the dolphins by the sharks. Dolphin groups of moderate size (around 10 individuals) are able to chase sharks away from the shoal and monopolize it. However, dolphins are not always found in such numbers when feeding because individual dolphins eat less as the number of dolphins increases. (There are fewer cookies available per person the more people are at the party.) As such, dolphins appear to increase group size when sharks are present but not when they are absent by leaping and/or by producing sounds to attract other dolphins. Dolphins leap out of the water and slap the water



Figure 8 Leaps and slaps at the water may attract other dolphins to feeding events.

with their flukes and body more often while feeding than while engaged in any other type of behavior (Fig. 8). They also increase whistle production in the presence of sharks but not when sharks are absent. Given the patchy and ephemeral nature of food resources in the open ocean, it is expected that further observations from species living in pelagic zones will indicate that interspecific contest over food are relatively common and are more important than currently viewed in influencing group-living in marine mammals.

III. Conclusion

Group-living involves benefits and costs, and the resultant society represents a balance between the different interests of all group members. The aquatic environment has allowed marine mammals to pursue complex and sometimes unique social strategies. At the same time, the basic needs of finding food, insuring reproduction and evading predators are also found in terrestrial environments. This convergence provides interesting parallels between the social strategies of marine mammals and those of terrestrial mammals, chimpanzees and bottlenose dolphins, elephants and sperm whales. Not surprisingly, much insight on group-living in marine mammals is gained by examining the societies of other taxa, most notably birds and terrestrial mammals. Of particular usefulness are comparative studies examining traits that are both consistent across taxa and common in some groups but not in others. These comparisons will allow us to examine specific hypotheses and test predictions regarding sociality as well as assist us in identifying data gaps and research needs.

It is clear that many questions about the group behavior of marine mammals remain unanswered and that much work remains to be done. For instance, the relationship between group-living and fitness remains to be described. However, studies on previously neglected topics such as female social behavior have increased in the last years and have improved our understanding of marine mammal societies.

As is the case of studies on terrestrial mammals, long-term studies of free-ranging populations have provided the most critical information to understand the evolution of group-living of marine mammals. Examples include bottlenose dolphins in Florida, Australia and, recently, Scotland; killer whales in the Pacific Northwest; sperm whales in the Galapagos Islands; humpback whales in their breeding and foraging grounds; northern elephant seals in California;

Antarctic fur seals (*Arctocephalus gazella*) and, recently, southern elephant seals (*Mirounga leonina*), and gray seals in the United Kingdom and Canada. A cursory review of the literature indicates that many more such studies are being started in other populations and, most importantly, on other taxa. It seems certain that our understanding of marine mammal group-living in the next 10 years will be not only more thorough but more inclusive.

See Also the Following Articles

Behavior, Overview ■ Communication ■ Sociobiology

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