entanglement in coastal fishing gear, lines and floats pose threats to individual whales, particularly calves, and can result in injury and death.

Gray whales do not accumulate persistent organochlorine compounds or other environmental contaminants presumably because they feed low on biological food chains, and in areas with low human habitation and industrial development. However, as the ocean environment becomes increasingly contaminated with toxic fat-soluble substances, and as these substances accumulate in a gray whale's body fat and blubber during its life, they may become mobilized during annual periods of winter fasting between periods of summer feeding, and be transferred to calves in mother's milk during the first few months of life when the calves are rapidly growing.

Gray whales received protection from commercial whaling under the 1937 *International Agreement for the Regulation of Whaling*, and more comprehensive protection under the 1946 *International Convention for the Regulation of Whaling*. In the United States, two statutes provide legal protection: the *Marine Mammal Protection Act*, passed in 1972; and the *Endangered Species Act* of 1973. In 1994, the US Department of Interior Fish and Wildlife Service removed the ENP population from the *List of Endangered and Threatened Wildlife and Plants* (under the US Endangered Species Act), and in 1996 it was reclassified by the World Conservation Union [International Union for Conservation of Nature (IUCN)] from e*ndangered* to l*ower risk*: C*onservation dependent* in the *IUCN Red List of Threatened Animals*. However, the WNP gray whale population was reclassified by IUCN from *endangered* to c*ritically endangered* (http://www.iucnredlist.org). The gray whale is listed in Appendix 1 of Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES).

Mexico recognized the importance of the breeding lagoons in Baja California to the recovery of the gray whale, and it is the only nation to provide significant habitat protection. Calving areas lie within the *El Vizcaíno Biosphere Reserve*, created in 1988, in which all whale watching ecotourism is regulated under sustainable management plans established in the 1990s.

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# GROUP BEHAVIOR

**Alejandro Acevedo-Gutiérrez**

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, intelligence, and extent of sexual dimorphism. A group may be viewed as any set of individuals belonging to the same species that 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 nonmutualistic 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.

To describe social structure, it is essential to measure how much time individuals spend together (association patterns) and

**Figure 1** *(A) Fin whales are usually found alone or in small numbers. (B) South American sea lions aggregate in large numbers during the breeding season.*

the rate at which individual associations change 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. Promising advances in the description of social structure are the inclusion of different spatial scales, the evaluation of indirect interactions (friends of friends), and the use of social network analyses.

## I. Theory of Group-Living

There appear to be three conditions under which group-living evolves, the benefits to the individual outweigh the costs, the costs outweigh the benefits but strong ecological constraints prevent dispersal from the natal territory (e.g., 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 a variety of mechanisms such as direct benefits of group-living, direct and indirect reciprocity, and mutualism (Clutton-Brock, 2009). 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. It explains the generalities of cooperative breeding in mammals and birds, and the evolution of cooperation among male chimpanzees (*Pan troglodytes*). Further, mammalian female kin (including several odontocete species) spend more time in close proximity and are more likely to help each other (Möller, 2012). 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). Byproduct 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).

Promiscuity is an important trait affecting group-living. It is predicted that cooperative behavior will evolve with low levels of promiscuity. Yet, in vertebrates, cooperation often occurs between nonrelatives and promiscuity is high. This paradox has been resolved in birds by showing that in cooperative species, helping is more common when promiscuity is low; and that intermediate levels of promiscuity favor kin discrimination (Cornwallis et al., 2010). The relationship between group-living and promiscuity levels has not been examined in marine mammals.

Benefits to increase foraging efficiency and reduce predation, and the number of individuals that can be supported by the available local resources, have typically been viewed as important factors shaping group-living. These benefits apparently apply to all social organisms, e.g., 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 many different mechanisms, such as the ability to exhibit collective intelligence and solve problems due to the interactions between individuals (Morand-Ferron and Quinn, 2011; Berdahl et al., 2013). In addition, increased foraging and reduced predation are sometimes inadequate to explain group-living; the gregariousness of African lions (*Panthera leo*) is best explained as defense of territory against other prides, not as increasing foraging efficiency. Group-living can also impose several costs to individuals, including increased competition over access to resources and mating opportunities, exposure to infection, conspicuousness to predators, and unequal contribution by group members. 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.

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. In this manner, males traveling with their mothers can have large home ranges and thus find potential mates.

What to do with individuals that do not carry their weight in a group? Groups of carrion crows (*Corvus corone*) tolerate lazy members because they pick up the slack and increase their rate of food provisioning to chicks when unfavorable circumstances prevent other group members to provision as usual (Baglione et al., 2010). 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. The tolerance of lazy individuals is an area of research that needs to be examined in marine mammals.

### 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. 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. 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 the 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. The preference and fidelity of female gray seals at North Rona, Scotland 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). Male and female sperm whales (*Physeter macrocephalus*) have different grouping strategies. Adult males are for the most part solitary individuals, leaving their nursing group when they reach puberty and after they have reached their late-20s roam among nursery groups looking for mates. In contrast, females are structured into hierarchically organized tiers: Several adult females, their dependent calves and immature offspring form a unit, each one composed of one or more matrilines; units can temporarily assemble into groups lasting between hours and days. Most females will live out their life as members of their natal unit, forming strong long-term bonds across decades, at least. Units provide care for calves that are too young to follow their mothers during their deep foraging dives (Fig. 2) and also defend themselves against predators. Alloparenting reduces the period in which the calf is unaccompanied and thus provides protection from predators and also perhaps provides communal nursing. Thus key features of the sperm whale society are explained solely by the behavior of females and their interactions with calves (Gero et al., 2013).

## 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 exemplified by the impact of El Niño southern oscillation events on different populations.

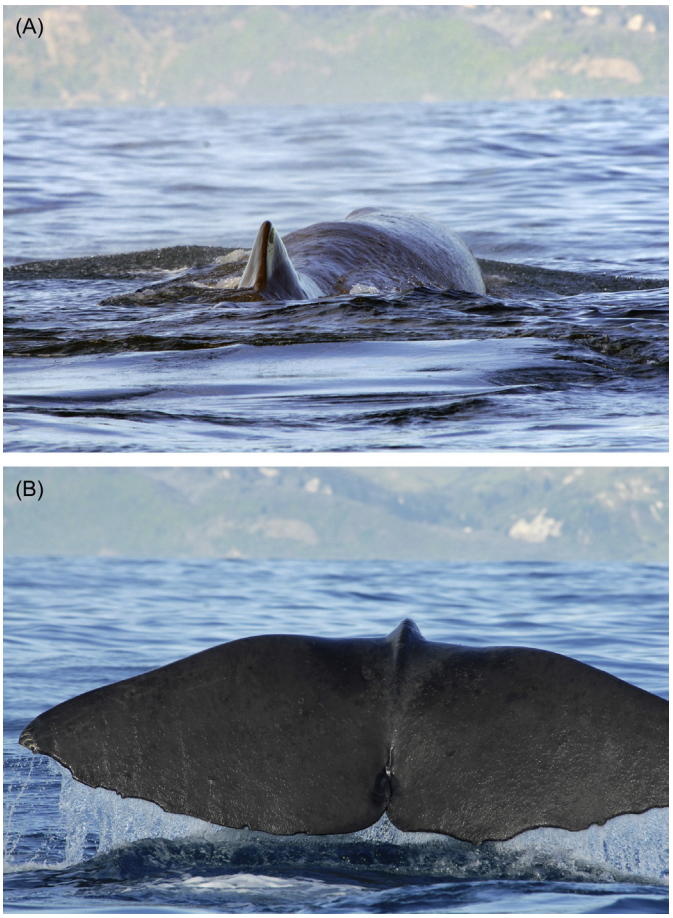


**Figure 2** *(A, B) Alloparenting behavior apparently allows sperm whale mothers to make deep foraging dives.*

### 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 1.0–1.5 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 typically 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. 3). 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

**Figure 3** *(A) In certain species, pinniped females cluster during the breeding season and males are able to monopolize access to them, (B) which results in intraspecific competition with other males.*

**Figure 4** *New Zealand fur seal pups spend irregular periods of time with their mothers for about 10 months before they separate.*

**Figure 5** *Pinnipeds haul-out together outside of the breeding season; there is evidence that such behavior increases vigilance for predators in harbor seals (Photo taken under permit NMFS 18002-00).*

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). The strongest association found in pinnipeds is formed by a mother and her offspring, and lasts from less than 1 week to almost 3 years, depending on the species (Fig. 4). Pinnipeds haul out together outside of the breeding season and although this nonreproductive social behavior is poorly known, there is evidence that it increases vigilance for predators in harbor seals (*Phoca vitulina*, Fig. 5). It is believed that hauling out together also allows pinnipeds to rest, avoid predators, molt or warm themselves. For instance, walruses (*Odobenus rosmarus*) in large numbers may decrease the rate of body heat loss, particularly in calves, when on land or ice.

The complexity of cetacean societies appears to be related to amount of time invested in lactating and 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 for less than 1 year. 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. In humpback whales (*Megaptera novaeangliae*), evidence suggests the presence of long-term associations among nonlactating females over many feeding seasons (Ramp et al., 2010). Odontocetes are the most social marine mammals and have different types of societies as suggested by the large variation in school size between species. Short-term associations between adults characterize most phocoenids, or porpoises. Associations between mothers and their offspring last for 8–12 months. Females breed every 1 or 2 years and may give birth to more than or equal to 15 calves during their lifespan.

It is believed that medium-sized delphinids, or dolphin species, live in fission-fusion societies with fluid group membership. Yet, 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. 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. Common bottlenose dolphins live in fission-fusion societies that are believed to reduce feeding competition

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**Figure 6** *Bottlenose dolphin calves remain with their mother for up to 8 years.*



by allowing individuals to disperse. Associations between adults are varied, they last for 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. 6). 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. At least two conceptual frameworks to explain social systems in dolphins have been proposed: One examines the relationship between resource predictability and the ranging patterns and social behavior of dolphins (Gowans et al., 2007), while the other analyzes ecological, life history, and phylogenetic data to predict the formation of kin associations and bonding in dolphins (Möller, 2012). However, many of the predictions of these models remain untested given our lack of information for many dolphin species.

One of the most complex behaviors described in marine mammals (and in animals in general) is the formation of alliances among male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Australia (Connor, 2007). Males form strong and stable bonds for more than 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 bonds with one or two other alliances to form second-order alliances that cooperate to take or defend females from other alliances. These second-order alliances form a continuum that can vary in size from six males to 14 males and maintain bonds for years; as a result, there is no relationship between first-order alliance stability and second-order alliance size, suggesting a third level of alliance formation (Connor et al., 2011). Yet a different strategy is maintained for males to form a large but loose superalliance that competes with smaller first- 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. Alliance formation is a strategy to obtain access to females, and evidence indicates that in Port Stephens, Australia, male reproductive success increases with alliance size in Australia. In Shark Bay, the vast majority of paternities are achieved by males involved in some form of alliance. However, some juvenile males without an alliance may achieve paternities with the existence of alternative male tactics other than alliance formation.

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 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 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 five calves throughout their lifetime, more in the case of long-finned pilot whales. Females may live more than 20 years past their postreproductive years. It has been suggested that this strategy allows old females to transmit and store cultural information, and provides alloparental behavior. In the case of short-finned pilot whales (*Globicephala macrorhynchus*), it is possible that nonreproductive females even provide alloparental nursing (Kasuya, 1995). Male sperm whales and perhaps male short-finned pilot whales leave their nursing group when they reach puberty. However, the former 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 nonreproductive 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. In killer whales in the Salish Sea, western Canada, sharing of food toward close maternal relatives apparently has promoted lifetime natal philopatry in both males and females (Wright et al., 2016). 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.

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. 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 matrilines. Postmenopausal female killer whales help by leading foraging groups in salmon foraging grounds, particularly in years when salmon abundance is low, and are more likely to lead their sons (the sex through which they can gain the greatest inclusive fitness benefits) than they are to lead their daughter (Brent et al., 2015).

This informative role of grandmothers might be the primary motor of eusociality and also supports the growing evidence of culture among cetaceans (Whitehead, 2007). 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 matrilines. For instance, indirect measures of the reproductive success of groups of sperm whales vary according to differences in culture between the groups; even further, the multilevel societies of sperm whales (containing hierarchically nested social levels) appear to be a result of cultural transmission resembling the manner in which complex human culture is generated (Cantor et al., 2015). Cultural transmission of behavior also occurs in baleen whales, specifically humpback whales which maintain independently evolving traditions in their populations, be they songs or feeding behaviors (Allen et al., 2013).

Modification of the course of genetic evolution through culture has been demonstrated in humans; however, it may also exist in killer whales and Indo-Pacific bottlenose dolphins. In the first case, socially transmitted foraging specializations within an ecosystem are proposed to have led to sympatric ecotypes in the absence of physical barriers (Morin et al., 2010). In the second case, the social transmission of sponging, whereby dolphins use marine sponges as hunting tools, has led to fine-scale genetic structure in western Shark Bay (Kopps et al., 2014). These studies may spur further work on the relationship between transmission of social behavior and genetic structure, given the large number of genetic differentiation in relatively small scales among many dolphin populations. 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.

Social structure is a flexible trait that varies within species in relation to resource availability and perhaps other environmental traits. For example, the connectivity of the killer whale social network in the Salish Sea is related to the abundance of Chinook salmon (*Oncorhynchus tshawytscha*), with a more interconnected social network in years of high salmon abundance (Foster et al., 2012). Social structure can also affect other traits such as genetic structure. For instance, spinner dolphins exhibit different social behaviors in the Hawaiian Archipelago: A fission-fusion society off the high volcanic islands in the SE archipelago and long-term stable groups in the atolls of the NW archipelago. These social traits along with differences in habitat and resource availability have resulted in the highest gene flow between the populations with the stable social structure and the lowest gene flow in a population with dynamic fluid social structure (Andrews et al., 2010).

## B. Foraging

Increased foraging efficiency is considered to be one of the principal roles of group-living in cetaceans (Fig. 7). 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. 8). Communal foraging 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.

**Figure 7** *One benefit of living in groups is increased individual foraging efficiency.*

**Figure 8** *Many dolphin species coordinate their movements while swimming fast in pursuit of prey.*

### 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. Walruses 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. Specifically, differences in the social structure of sperm whales between two oceans appear to be driven by risk of predation by killer whales. In the Pacific, female sperm whales live in nearly permanent units that contain individuals of multiple unrelated matrilines and form temporary groups with other units for periods of days, apparently exclusively with other units from the same cultural clan. In the North Atlantic social units rarely group with other units, and there is no evidence for sympatric cultural clans.

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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. However, comparative research of group sizes in *Delphinoidea* (*Delphinidae*, *Phocoenidae*, and *Monodontidae*)—including phylogeny, physical environment, diet, predation pressure, and life history—indicated that phylogeny explained most of the observed variation in group size.

### 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). At 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 (~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. As such, dolphins appear to increase group size when sharks are present but not when they are absent by leaping and/or producing sounds to attract other dolphins. Dolphins leap out of the water and slap the water with their flukes and body more often while feeding than while engaged in any other type of behavior (Fig. 9). 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 contests over food are relatively common and are more important than currently viewed in influencing group-living in marine mammals.

**Figure 9** *Leaps and slaps at the water may attract other dolphins to feeding events.*

## 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, ensuring 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, 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 we have vastly increased our knowledge on the group behavior of marine mammals but many questions remain unanswered and much work remains to be done. Promising avenues of research include describing the relationship between group-living and reproductive success, incorporating indirect effects (friends of friends) in the description of social structure, studying tolerance and/or punishment of lazy group members, analyzing the role promiscuity may play in the evolution of social behavior, determining the influence of the social transmission of behavior on genetic structure, and describing cultural tradition in nonodontocete species. Other topics not covered here or barely touched upon, but deserve further study as well, are the impact of group behavior on the evolution of brain structure and function, and intelligence (Connor, 2007; Sallet et al., 2012), and how social information alters gene expression in the brain to influence behavior, and how genetic variation influences brain function and social behavior (Robinson et al., 2008).

Long-term studies of free-ranging populations have provided critical information to understand the evolution of group-living in marine mammals. Given that more such studies are being started in many taxa, our understanding of marine mammal group-living in the next 10 years will be more thorough, inclusive and exciting.

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# GUADALUPE, JUAN FERNÁNDEZ, AND GALAPAGOS FUR SEALS

## *Arctocephalus townsendi, A. philippii, A. galapagoensis*

**David Aurioles-Gamboa and Fritz Trillmich**

The Guadalupe (*A. townsendi*), Juan Fernández (*A. philippii*), and Galapagos fur seals (*A. galapagoensis*) belong to the Family Otariidae. These three species are among the seven currently recognized fur seals in the genus *Arctocephalus*. Their common names reflect their geographic distributions within the mid-latitudes of the Pacific Ocean.

### I. Characteristics and Taxonomy

These three closely related species are all sexually dimorphic, with males being larger than females. Guadalupe fur seals are characterized by a collie-like snout and have varying color from chestnut-brown through to dusky-black. Adult males are slightly darker than females (Figs 1 and 2). Adult female Juan Fernández fur seals