

A colossal convergence
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Abstract:

Sperm whales and elephants share similar life histories and social structures, which include social females and roving males. Weilgart et al discuss recent results from long-term studies of sperm whales and African savannah elephants, describing an interesting example of convergent evolution and highlighting the vulnerability to exploitation that results from the mode of life that these animals have evolved.

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Full Text:

Sperm whales and elephants arouse our sense of wonder like few other animals, perhaps because of features they hold in common, especially size and intelligence. These animals are the largest in their categories, toothed whales and terrestrial mammals. In addition, they possess the largest brains in the ocean and on land, which may explain some of the complex behavior that these species perform.

A closer look at the behavior of these animals reveals additional similarities. In a remarkable number of ways, including life history and ranging behavior, sperm whales and elephants resemble each other more than they do other animals--even ones that share similar ancestries, diets, environments and predators. The closest resemblance is found in their complex and unusual, but comparable, social organization. In both species, the females live in highly social family units that rely on well-developed communication, and the much larger males live separate, more solitary lives, roving between female groups during the breeding season and delaying breeding until they are large and dominant.

In the 1970s Peter Best of the University of Pretoria in South Africa first pointed out that elephants and sperm whales resemble one another. In this article we shall build on that observation by exploring recent results from long-term studies of individual sperm whales and African savannah elephants. We have two purposes: describing an interesting example of convergent evolution, especially in social organization, and highlighting the vulnerability to exploitation that results from the mode of life that these animals have evolved.

Ecologically Successful Life-styles

Elephants and sperm whales typify K-selected species--species that live in a rather stable environment that they can fill nearly to its carrying capacity, or K. Such species raise a few well-tended offspring that can survive in competitive environments. Like other K-selected species, elephants and sperm whales live long lives. They mature in their teens and live about 60 years. Females of both species almost always give birth to single calves at approximately five-year intervals. However, once a female reaches her 40s or so, her reproductive rate declines. For instance, aging female sperm whales invest more energy in lactation and calf rearing, thereby reducing their investment in calf bearing to the point where they may stop giving birth. In both species, a female's reproductive rate declines with age. Nevertheless, elderly female elephants, and perhaps sperm whales, maintain a place in their herds as leaders, or matriarchs, in the highly structured female society. The older females also serve as reservoirs of ecological knowledge.

During their long lives, these species eat hundreds of tons of food and cover large distances on land or in water. Elephants eat a wide variety of plant matter, and their home ranges vary enormously, depending on the habitat. About 20 million years ago, during the Miocene epoch, elephants experienced their peak abundance. At that time, this animal and its close relatives inhabited all major land masses, except Australia, New Zealand and Antarctica. Their large size, the handlike maneuverability of their trunks, their wide ranges and their catholic diet made elephants prominent components of their ecosystems. In fact, Richard Laws of the British Antarctic Survey concluded that "after man himself, probably no other animal has had as great an effect on African habitats as the African bush elephant."

It is more difficult to assess the impact of sperm whales on their environment. Although a sperm whale also has a varied diet, its preferred prey--principally squid but including some fish, such as angler fish and deep-water sharks--live far beneath the ocean, where they are so inaccessible to us that much of what is known about some squid species comes from studying the stomach contents of sperm whales. Sperm whales inhabit deep water all over the globe--from the ice edges at the poles, where the large males are found,

to the equator, where females breed. Despite substantial population reductions from whaling, the surviving sperm whales around the world consume very approximately 100 million metric tons (or 100 billion kilograms) of food per year--the annual catch of all human fisheries for all marine species.

Most modern investigations of the social organization of elephants and sperm whales rely on longitudinal studies, in which identified animals are observed over long periods of time. Iain Douglas-Hamilton initiated the first longitudinal study of African elephants in 1965 in Manyara National Park in Tanzania. In 1972 Cynthia Moss of the African Wildlife Foundation started a longitudinal study of elephants in the Amboseli National Park in Kenya. That study--later receiving major contributions from other investigators, including Phyllis Lee of Cambridge University and Joyce Poole of the African Wildlife Foundation--is now in its 24th year. In 1983, Jonathan Gordon, now at Oxford University, and one of us (Whitehead) started long-term studies of living sperm whales off the coast of Sri Lanka. A few studies of living sperm whales are now being carried out in different parts of the world, with the most long-term being the Galapagos Islands research by Whitehead and his colleagues at Dalhousie University. We can piece together the social behavior of these slowly maturing species from the results of these studies.

Social Females

Elephants organize socially around a matrilineal family unit, which is composed of about 10 individuals: closely related females and their offspring. A female remains, probably throughout her life, in her original family group. Members of a family move, feed, drink and rest in each other's company, and family members change from one behavior to another at the same time. They often call in synchrony, and an entire family stops all activities to listen synchronously. Members of a family unit often touch, smell and rub one another--comforting, protecting, exploring and playing with their close kin. Calves may even suckle from other females in the family, though the purpose maybe more for comfort than to actually obtain milk.

Every family spends at least one-third of its time in association with one or more other particular families. Within those "bond groups," which typically include from two to four families, foraging behaviors are sometimes coordinated over distances of several kilometers for periods of weeks at a time. After separations, individuals in families and bond groups greet one another with remarkable displays of emotion.

The social bonding that underlies these two levels of elephant society depends strongly on several forms of communication: touch, smell, sight and, especially, sound. In 1984, one of us (Payne) and William Langbauer, also of Cornell University, and Elizabeth Thomas discovered that Asian elephants communicate using infrasound--sound with a frequency below the

range of human hearing. A later study by Poole, Payne, Langbauer and Moss demonstrated that free-ranging African elephants use infrasonic and other low-frequency calls to organize family and bond-group behaviors. Some of the most powerful of these calls (116 decibels, with fundamental frequencies from 12 to 35 hertz) announce the reproductive condition of both males and females. The strongest low-frequency components of these calls elicit responses from elephants 4 kilometers away and are probably responsible for coordinating the behavior of separated individuals and groups.

A similar social structure exists in sperm whales studied off the Galapagos Islands, where more than 1,500 individuals were identified through photographs of their distinctive flukes, or tails. Female sperm whales form permanent units, each composed of about a dozen animals. Mary Dillon, Kenny Richard and Jonathan Wright of Dalhousie University completed genetic studies of pieces of skin that whales slough, and the results show that these units consist of related whales, almost certainly family units. Two or more of these family units may travel together for a few days as a coordinated group.

Members of a sperm-whale group spend much of their time diving to depths of 400 meters or more, where they feed. During this time, they make regularly spaced clicks, which cover a broad range of frequencies, from about 200 to 32,000 hertz. By placing a hydrophone underwater, we can hear these clicks from as far away as 8 kilometers. Most likely, sperm whales use these clicks to locate food--apparently through echolocation, or the decoding of information from echoes that bounce off potential prey. While foraging, a group spreads out over a few hundred meters. Moreover, groups of Galapagos sperm whales often form structured feeding groups--aligning perpendicular to the direction of movement and sweeping the ocean for squid. The calves, which apparently cannot follow their mothers for a complete 40-minute foraging dive, move between the adults that are breathing on the surface. In calf-containing groups off the Galapagos, adults stagger their dives to shorten the periods during which calves are left alone at the surface, seemingly providing communal child care. As a further indication of such care, Gordon has gathered evidence that suggests that calves suckle from a variety of group members. As in elephants, calves may not actually obtain milk from suckling females other than their mother.

For about six hours each day--often in the afternoon--sperm whales stop diving and gather in tight, slow-moving clusters at the surface. During these times, the whales often touch and move about one another, sometimes caressing each another with their flippers and jaws. In addition, such socializing sperm whales usually produce patterned series of clicks (two to 13 clicks in length) called codas, which are reminiscent of our Morse code. Codas serve as a form of communication, perhaps encouraging cohesion in a female group after the periods of dispersion during feeding dives.

Codas may play a role in the coordination of group movements.

Many examples of cooperative care portray the strength of familial bonds in female elephants and sperm whales. All members of an elephants family wait together, allowing new calves to rest during treks between food and water. If a calf makes a distress call, various family members respond immediately by calling and rushing to the calf's aid. In addition, adults other than their mothers often discipline calves, and sometimes nurse or adopt them

Both elephants and sperm whales assume defensive formation to protect their calves in the presence of predators or, in elephants, simply when they are resting. In both species, adults attempt to bear up wounded members. Whalers and elephant hunters have exploited that strong urge by purposely injuring animals, especially calves, to "bait" females that can then be harpooned or shot when they try to help. If a female sperm whale does get harpooned, other males from her group may bite the whaler's line, attempting to break it.

Roving Males

The parallels between the lives of males of these species prove equally remarkable. Once young males leave their family unit--at about age six for sperm whales and 14 for elephants--they become less social. They are often found in Loose-knit "bachelor" groups or alone. When males are attempting to breed, they seem to avoid each other.

Although males of both species are physically capable of breeding in their teens, about 10 years elapse before they reach "sociological maturity" and become prime breeders in a population. During the intervening period, when they would have little chance of reproductive success and a high probability of injury in competition with larger males, male sperm whales and elephants concentrate on feeding and growth.

Both species employ a system that excludes younger males from most breeding opportunities. Most of the time, mature and maturing male sperm whales live at higher latitudes (40deg-60deg) than do the females, which principally inhabit the tropics and subtropics, and males younger than the age of sociological maturity apparently skip the long migrations to the breeding grounds. Instead, the younger males concentrate on feeding in the more productive, cool waters, where there is no competition with females for food.

Male elephants also spend most of their time apart from the normal ranges of the family units, but not as far apart as sperm whales. A phenomenon called "musth" excludes younger male elephants from most breeding opportunities. A male in musth dominates--if only temporarily--all nonmusth males. Anthony

Hall-Martin of South Africa and Joyce Poole have described musth as a condition of heightened aggression and sexuality, which is signaled by glandular secretions, urine-marking and vocalizations. Males come into musth asynchronously, and the duration of musth varies from a few days to nearly six months. The oldest males stay in musth the longest and monopolize the prime breeding season. The advantage they gain is increased by female choice, because estrous females select the most dominant males in musth as their mates.

A male elephant in musth or a male sperm whale on the tropical breeding grounds roves between groups of females, checking them for receptivity. If no females are in estrous, the male moves on quickly. When a mature male elephant encounters an estrous female, he attempts to mate with her regardless of his rank, unless a higher-ranking male is present. Estrous females avoid the approaches of low-ranking males, running away from them while making a series of loud, repetitive, low-frequency calls, which attract other males, even those at a distance. As a result, breeding behavior often includes repeated displacements--one male replacing another. We have no information on the behavior of a male sperm whale encountering a receptive female. We know, however, that the male announces his presence through a so-called slow click, which sounds like a clang that repeats every six seconds or so. Likewise, a male elephant makes repeated low, loud, pulsating calls--"musth rumbles"--during, and only during, musth. Both slow clicks and musth rumbles may, thereby, serve as "advertisement" calls. Male sperm whales and elephants probably assess the presence and movements of other males by listening to these calls, and weaker males most likely avoid stronger ones. In elephants, musth rumbles attract females.

Coincidence or Convergence?

Elephants and sperm whales represent extremes for a remarkably diverse set of characteristics. No other large mammals, apart from humans, have been as ecologically successful as elephants and sperm whales (when not decimated by humans) in such a variety of habitats. Moreover, no other male mammals leave their family units, delay competitive breeding for many years and then rove between cooperative groups of related females. These similarities prove particularly striking in view of the radical differences in the habitats of elephants--terrestrial herbivores--and sperm whales--aquatic carnivores.

Are these parallels between elephants and sperm whales significant or coincidental?

A number of the attributes shared by these animals also apply to other species. For instance, many of the more successful species--from cockroaches to human beings--eat a variety of foods and inhabit wide ranges. In addition, the large size of sperm whales and elephants enhances the likelihood that they will share other size-correlated attributes, including large brains. Nevertheless, we argue that the similarities between these species surpass

size-related correlations.

For instance, consider the mammals that most closely share habitats with elephants and sperm whales. Rhinoceros inhabit the same environment as elephants and eat similar food. Compared with elephants, though, rhinos have a less varied diet, a smaller home range, smaller bodies and brains, and a simpler social system, and they are less ecologically successful (as measured by their biomass before they were reduced through human exploitation). Sperm whales can be compared with members of the beaked whale family--including Baird's beaked whale, Cuvier's beaked whale and the bottlenose whale--that also live and feed in the deep ocean. In comparison with sperm whales, however, beaked whales are smaller, have less biomass, cover smaller ranges (according to the limited information that is available), eat more-specialized food and generally form smaller social groups. So elephants and sperm whales resemble each other more than they do mammals that inhabit the same environment. Given that sperm whales and elephants are not closely related through evolutionary history, their shared attributes constitute a convergence, not a coincidence.

How have so many attributes converged--often to extremes--in two species that live in such different habitats? We cannot distinguish a "key" attribute--one that evolved in both species and then favored the evolution of the other common attributes. Instead, the shared characteristics of elephants and sperm whales probably coevolved as a suite of mutually reinforcing characteristics, including social complexity, communal care of offspring, intelligence and longevity.

A number of benefits derive from this suite of characteristics. For instance, intelligent animals that live in groups have the benefit of the knowledge of the group's older members. A group of female elephants--especially one that includes old, experienced individuals--possesses a pool of knowledge about resources, such as the location of ephemeral watering areas or regions with seasonally available food. John Eisenberg of the University of Florida has argued that such knowledge may be invaluable during harsh times in most elephant populations: It is surely the lifeline of the Namibian-desert elephants. We speculate that the same is true for sperm whales. During warm "El Nino" years, when food runs scarce off the Galapagos, groups of sperm whales do not linger; they move fast and straight, perhaps to areas a thousand kilometers away where an older female remembers fair feeding during previous Ninis.

In elephants and whales, living in a cohesive group may lessen the effects of environmental variation and reduce mortality. This results in longevity, and as females give prolonged care to calves that are likely to survive, the birth rate will probably fall. Finally, longevity and low fecundity should encourage strong bonds between individuals in a group, leading to increased sociality, which produces groups that include older and more

experienced females.

In elephants and sperm whales, such a feedback loop may have been further enhanced by large body size, which makes predator defense more effective, long migrations more efficient and temporary food shortages less hazardous. In addition, larger animals tend to have larger brains. However, brain size is generally also correlated with more complex social systems, which in turn are supported by advanced communicative capabilities. Finally, intelligence--including the ability to retrieve and respond to memories from long ago--helps an animal exploit a sizable and diverse home range. When all these factors combine to reduce mortality from predation and from environmental variation, a population can remain near its carrying capacity--as populations of both elephants and sperm whales seem to have done through most of their recent evolution.

Perilous Parallels

Unfortunately, there is a downside to this story. Within the suite of characteristics that gave elephants and sperm whales their success are some that have left them vulnerable to sudden changes in population size and structure, because slowly maturing populations are slow to recover. For example, a depleted sperm-whale population recovers its numbers at less than one percent per year. In modern times, humans have suddenly endangered these once robust species by slaughtering them in huge numbers. To make matters worse, 20th-century hunting practices have unbalanced the social structure in many populations of both species by concentrating on large males.

Ironically, the International Whaling Commission encouraged the preferential harvesting of males for a number of years until the mid-1980s, assuming that sperm whales relied on a harem mating system that included "surplus males." On the contrary, Robert Clarke and his colleagues found that as the proportion of males declined in sperm-whale catches off the coast of Pen so did the pregnancy rate of the females. Even a decade after the end of whaling in that area, calves and mature males remain scarce. It seems that the reduced numbers of roving males encounter females too rarely to ensure pregnancy. Mathematical models developed by members of the Scientific Committee of the International Whaling Commission suggest that--even after a complete ban on whaling--preferential slaughter of male sperm whales could cause a population to continue declining for at least 20 years, largely because of the time required for young males to mature sociologically.

A similar story exists for elephants, because poachers kill the largest males for their valuable tusks. Several heavily poached populations of elephants in East Africa have lost all their largest musth-age males. Andrew Dobson of Princeton University and Poole used the results from studies of four East African populations to construct a model of elephant populations

faced with poaching; this model suggests that the current levels of reduction in males in some populations may have triggered long-term declines, which may be irreversible. The social behavior of elephants generates a threshold population size below which females do not mate frequently enough, and the population falls to extinction.

Beyond direct slaughter, humans generate other problems for elephants and sperm whales. Almost everywhere that elephants live, they are hemmed in by growing human populations. Restricting these wide-ranging animals to smaller areas increases the likelihood that they will damage the local vegetation. In fact, such restrictions plus a drought in the early 1970s caused elephants to destroy their own resources in Tsavo National Park in Kenya.

Even though sperm whales live deep in the ocean, usually far from shore, they must live with human-generated pollution. During 1988 and 1989, 32 dead male sperm whales were discovered off the shores of northern Europe; that figure roughly matches the total deaths reported in that area during the previous century. In late 1994, another 20 sperm whales were found dead in and around the North Sea. Claude Joiris of the Free University of Brussels believes that high levels of polychlorinated biphenyls (PCBs) in these animals may be contributing to their deaths. Noise pollution also poses a serious threat, with loud ship traffic, oil exploration and naval and oceanographic experiments potentially interfering with sperm-whale foraging and communication.

A combination of mutually reinforcing characteristics has twice led to ecological success during the convergent evolution of elephants and sperm whales. The same characteristics plus human intervention could produce another convergence between these species--a convergence toward extinction. It will be a terrible indictment of our "progress" if it sweeps away the largest brains and two of the most cooperative societies on our planet.

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