# The Adaptable Opossum

*The Virginia opossum can adapt quickly to a changing world. Part of its success may be due to a highly efficient reproductive strategy that includes the ability to adjust the sex ratios of its progeny*

by Steven N. Austad

From the time the Spanish explorer Vicente Yáñez Pinzón and his crewmen discovered a mother opossum carrying pouch young in Brazil in February of 1500, Europeans have been moved to rhetorical excess by these New World mammals with their embryonic neonates. As is generally the case with exotic animals, opossums were initially described as if cobbled together from the parts of known species. Richard Eden, for instance, in his 1555 translation of Peter Martyr's *De Orbe Novo,* described the opossum as a "monstrous beaste with a snowte lyke a foxe, a tayle lyke a maramasette, eares lyke a batte, hands lyke a man, and feete lyke an ape, bearing her whelpes abowte with her in an owtwarde bellye much lyke unto a greate bagge or purse." Captain John Smith, leader of the Jamestown colony and the man who transliterated the Algonquian word meaning "white beast" into the English word "opassum," was somewhat more restrained, merely likening them to rats, cats and swine.

Familiarity, however, does breed contempt. Today the opossum—one of the commonest suburban mammals in the U.S.—gets little respect. Wildlife biologist Durward L. Allen, for example, derides the opossum as "a sluggish, smelly, disreputable critter without a semblance of character or self-respect." As a marsupial, moreover, it is regarded as being primitive and therefore inferior to eutherian, or placental, mammals. At a given body size marsupials have a lower body temperature, lower metabolic rate and a smaller brain than eutherians do. They also have fewer chromosomes on the average, a shell membrane around their ova and, except for the bandicoots, only a rudimentary placenta.

Yet the case for marsupial inferiority is hard to sustain, particularly as applied to American opossums. Indeed, the Virginia, or North American, opossum (*Didelphis virginiana*) is one of the ecological success stories of modern times. The species spread throughout most of North America during the late Pleistocene and it has continued its spread in historical times. Since the Colonial era, opossums have expanded their range northward in the eastern U.S. by as much as 500 miles.

In this century alone a few animals were able to establish the species on the West Coast, where it was unknown before the late 19th century. In 1906, near Los Angeles, an anonymous fur trapper captured the first wild opossum to be taken west of the Rocky Mountains. It is not clear whether this animal was descended from opossums brought from Missouri 20 years earlier by one "Uncle Billy" Rubottom or whether some other homesick Southern immigrant had also liberated a few former pets. In any case, the opossums flourished in their new home. By 1927 a wildlife biologist wrote: "The opossum is so prolific and has such a wide distribution in California that it is now too late to exterminate this dangerous species." A decade later they were thriving from Baja California to the Canadian border.

Much of the Virginia opossum's success no doubt stems from its mutualistic relationship with human beings. People provide barns, porches and a variety of other potential den sites as well as a steady supply of edible garbage. Opossums, on the other hand, provide humans with a reliable if not epicurean food source. Archaeological excavations clearly indicate that opossums were a staple of Indian diet throughout the Americas. For instance, opossums now live on a number of Caribbean islands, where there is no paleontological evidence of their presence prior to human colonization. Hence it seems likely they were brought along as a source of meat.

The range expansion of American opossums is not merely an artifact of human range expansion. Recent investigations show that opossums are extraordinarily adaptable. For instance, their small brain and dullness notwithstanding, opossums have a remarkable talent for finding food and remembering where they found it. When tested for ability to remember which of four runways was connected to a food box, opossums scored better than cats, chicks, dogs, goats, pigs, rabbits, rats and turtles, although less well than humans.

Equally surprising is the species' strong resistance to the venom of snakes in the rattlesnake subfamily Crotalinae, which also includes bushmasters, fer-de-lances, copperheads and cottonmouths. This immunity appears to be a specific adaptive response to an environmental threat, rather than an accidental by-product of their physiology, because opossums are not resistant to the bites of most Old World snakes, such as cobras and puff adders. Their immunity to crotalines has, however, enabled them not only to escape from a potential predator but also to eat the reptiles with impunity.

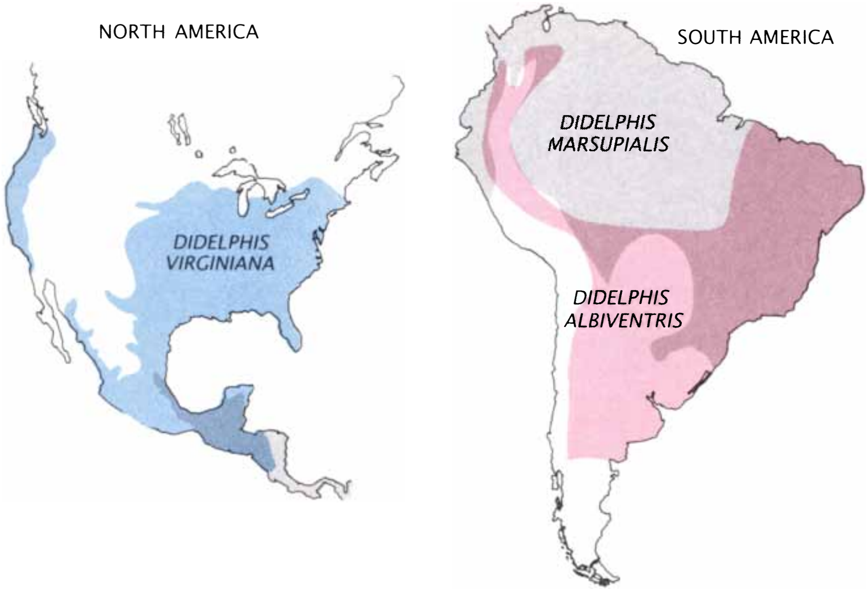
In our own studies we have found that opossums adjust the sex ratios of their offspring in a manner consistent with gaining optimal reproductive success under varying amounts of parental investment. This evidence that opossums are capable of high reproductive efficiency under changing ecological conditions could help to explain how the species was able to evolve an entire array of other sophisticated adaptations that may have allowed them to compete successfully with their more "advanced" mammalian relatives.

Marsupials and eutherians diverged some 100 million years ago, and within about 35 million years North America had a rich marsupial fauna, consisting of at least three families, five genera and 13 species. Indeed, the oldest clearly recognizable marsupial fossils are from Canada, and the prevailing (although not unanimous) opinion is that marsupials originated in the Americas, possibly in North America. For reasons not known all North American marsupials became extinct by 15 million years ago, whereas marsupials continued to radiate successfully in South America, Australia and New Guinea. Today Central and South America together have nearly 80 marsupial species, or more than 30 percent of the world's total. The American opossum family, the Didelphidae, alone accounts for about 70 species. (It is not closely related to the several Australian families of "possums.")

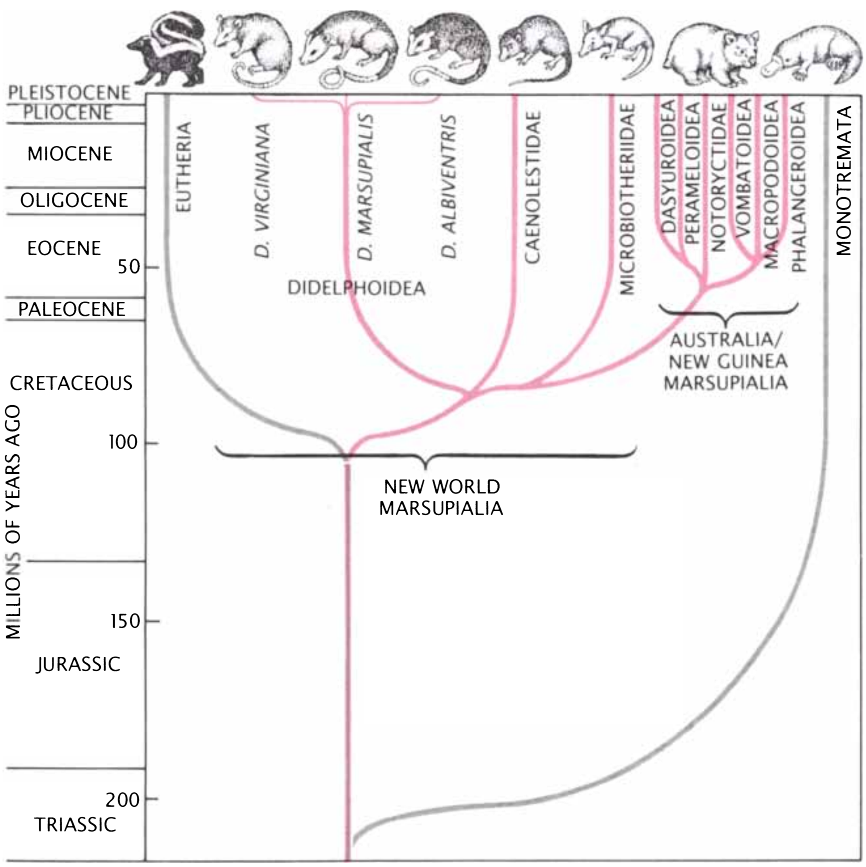
The only marsupial in the U.S. today is the Virginia opossum. It is one of three species in the genus *Didelphis,* which ranges from southern Canada to southern Argentina, making it one of the more widely distributed mammalian genera in the hemisphere and by far the most widely distributed marsupial genus in the world. Because *Didelphis* opossums bear a morphological resemblance to some of the earliest fossil marsupials, they have been erroneously called living fossils. Indeed, because of their conservative morphology, Virginia opossums are often used as research paradigms for the functional anatomy of primitive mammals.

Conservative though it may be morphologically, *Didelphis* is a recently evolved and in some ways highly specialized genus. The first positively identified *Didelphis* fossils appear about four million years ago

**OPOSSUM confronts a canebrake rattlesnake with impunity. The marsupial is impervious to the venom of snakes in the rattlesnake subfamily and views the reptiles not as lethal enemies but as a food source. In parts of Texas, copperhead snakes constitute up to 6 percent of the opossum's diet. Resistance to venom may have evolved as a specific adaptive response to an environmental threat, because the species is immune to the venom of New World snakes but succumbs to that of Old World snakes.**




**RANGE of *Didelphis* opossums extends from southern Canada to southern Argentina, making them the most widely distributed marsupial genus in the world. The white-eared opossum (*D. albiventris*) is found chiefly in cooler climates in South America. The common opossum (*D. marsupialis*) inhabits warm, tropical woodlands. The Virginia opossum (*D. virginiana*) migrated into nontropical North America during the Pleistocene. It thrives in most habitats, excluding desert and mountains exceeding 10,000 feet. Since Colonial times its range has expanded 500 miles northward to Canada. Human settlers introduced the species to the West Coast around the turn of the century.**

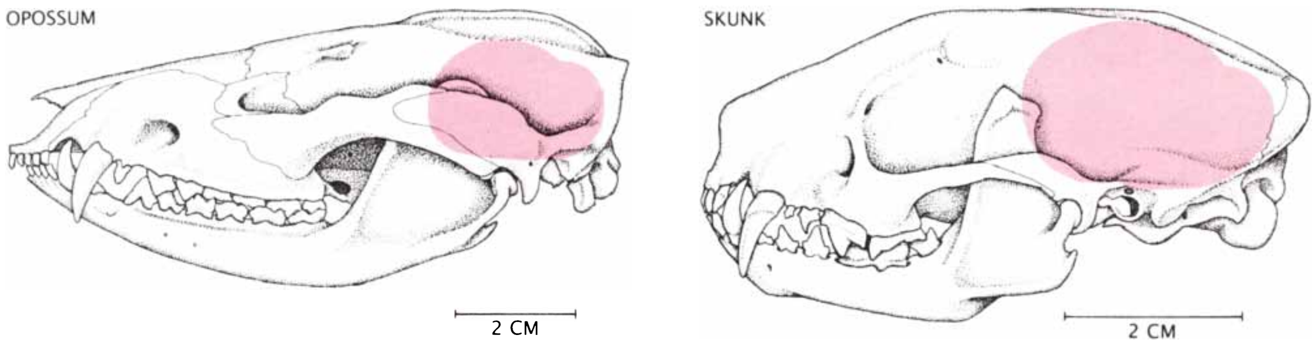



**MARSUPIALS may have originated about 100 million years ago in the New World. Didelphoidea, to which the Virginia opossum belongs, is considered the oldest superfamily to survive to the present day. Morphologically *Didelphis* is remarkably similar to the earliest marsupial fossils. *D. virginiana*, which appeared only 75,000 years ago, is the sole marsupial species that has been able to range into nontropical North America.**

in South America. Alfred L. Gardner of the National Museum of Natural History has convincingly argued, from chromosomal analysis, the fossil record and paleoclimatological evidence, that the Virginia opossum is the most recent of the three species in the genus, having diverged from its ancestral species, the common opossum (*Didelphis marsupialis*), in the past 75,000 years.

Gardner suggests that *D. marsupialis* colonized Mexico when land bridges reconnected South America and North America during the Pliocene, from five to two million years ago. Because they are not tolerant of arid or cold weather, however, they were not able to venture into what is now the U.S. During the Pleistocene, roughly between one million and 10,000 years ago, when repeated glaciation in North America led to major climatic fluctuation in Mexico, *D. marsupialis* spread throughout the mountains of western Mexico in warm periods but had to retreat to isolated lowland valleys in cool periods. Within one of these small isolated populations major chromosomal rearrangements occurred, which cut the group off genetically and collaterally probably helped to adapt the incipient species to cooler climates, allowing it to move northward. By 4,000 years ago the Virginia opossum had spread throughout most of the eastern U.S. Gardner also finds evidence of extreme inbreeding, which might predispose the species to be good colonizers because tolerance for inbreeding would enable a few animals to found new populations.

A further characteristic that may contribute to the opossum's ecological resilience is high reproductive efficiency. This begins even before conception with unusually efficient use of sperm. The male inseminates females with only about three million sperm, some 5 percent of which reach the site of fertilization; in comparison, a rabbit inseminates a female with about 150 million sperm, of which .01 percent reach the site of fertilization. The opossum's efficiency may be linked to sperm pairing, a feature of American marsupials that may be unique among vertebrates. In *Didelphis* two sperm conjugate side by side while they are still in the testes and then swim together through the female reproductive tract before separating in the oviduct. Some investigators think the pairing allows exceptionally good sperm transport and high




**OPOSSUM'S BRAIN is small compared with a skunk's. Another primitive feature is the large number of teeth: no eutherian has more than three incisors or molars, but opossums have five incisors in the top jaw, four incisors in the bottom and four molars.**

sperm survival within the reproductive tract.

After conception, female marsupials spend much less time gestating their young than eutherian females. Marsupial neonates are virtually mobile embryos, and most of their development occurs externally, often in a pouch. *Didelphis* opossums, for example, gestate their young for approximately 13 days, and each pup at birth weighs less than .2 gram, or one ten-thousandth of the body weight of the mother. In comparison, the striped skunk, a North American eutherian mammal of about the same size, gestates its young for 65 days and the kits weigh about 33 grams at birth, or more than 150 times as much as opossum neonates.

Newborn opossums are deaf and blind, and their hind limbs and tail are vestigial. Yet their forelimbs are precocially developed and equipped with deciduous claws, which assist the neonates on their trip to the pouch, a distance of four or five centimeters that each must traverse on its own without maternal help. They make their way there with a kind of swimming motion—sometimes referred to as the Australian crawl. More young are born than can be successfully raised: Virginia opossums have about 13 teats and bear some 22 young, yet their surviving litter size is usually from six to eight.

For the first 60 days the pouch young are sealed to their mother's nipples, which have swollen inside their inflexible mouths. By the age of 70 days they can grasp and release the nipples and move short distances independently. They are weaned at about 100 days, after which there is little contact between mother and offspring. All in all, then, female opossums invest about 112 days in rearing a single litter from conception to weaning. The striped skunk spends 121 days, about the same time, from conception to weaning, but whereas opossum young are completely independent after weaning, skunk young remain closely allied with their mother for another month or more. Early independence allows opossums to produce two and occasionally three litters per year compared with the single litter of skunks. Thus opossums expend a greater effort in reproduction each year.

Because development takes place externally where it can be monitored, Melvin E. Sunquist of the University of Florida and I thought opossums might be excellent animals in which to study the way animals allocate their reproductive energies. In particular, we were interested in an existing theory predicting that animals adjust the sex ratio of their offspring depending on the absolute amount of reproductive investment of which they are capable. This intuitively satisfying theory, developed by Robert L. Trivers and Dan E. Willard at Harvard University in the early 1970's, states that in mammals females capable of very large investment in each offspring should produce mainly males, and females capable of only a small investment should produce mainly females.

The underlying assumption is that the fitness of male offspring would be affected more than that of female offspring by the amount of parental investment. Because in mammals males generally have more than one mate and do not contribute to parental care, females do not usually lack mates. Consequently nearly all females are likely to reproduce, but none will produce as many offspring as the most successful males. Weak males, on the other hand, may end up with no mates or offspring. Assuming, then, that the amount of parental investment affects an animal's future reproductive fitness, males should be helped more by high investment and hurt more by low investment than females are. Hence mothers capable of high investment should produce primarily males and those capable of low investment should produce primarily females.

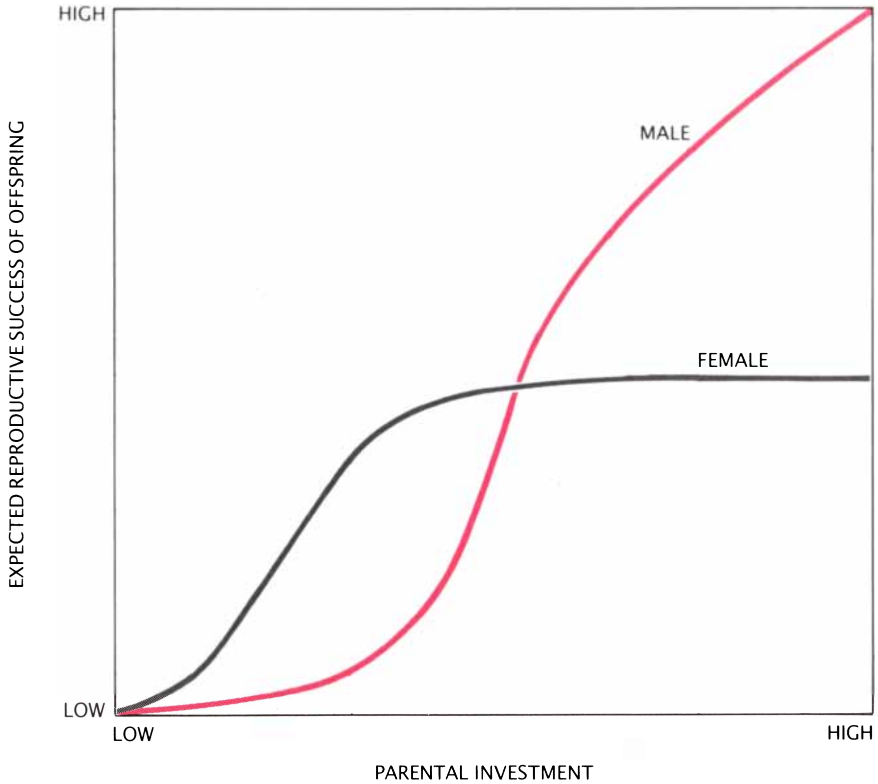
Plausible as it seems, there are reasons to be skeptical about mammals' ability to adjust offspring sex ratios. First of all, a believable mechanism is hard to imagine. The sex of the offspring is determined by whether the egg is fertilized by a sperm bearing an *X* chromosome or a *Y* chromosome, and there is no evidence that males can control the relative proportions of these sperm depending on the female they happen to be mating with. Second, domestic livestock, well-fed and cosseted, are presumably capable of much greater reproductive investment than their free-living relatives, and yet most livestock produce a balanced sex ratio. On the other hand, valid scientific theories have been developed (plate tectonics, for example) before the underlying mechanisms were discovered, and because domesticated animals have been artificially selected for such a long time, any meaning of current trends in their offspring sex ratio is not clear.

We tested the hypothesis by supplementing the food of wild female opossums, hoping we could develop specific females capable of extraordinarily high investment. Because our females wore radio collars, we could find them in their den during the day and place food near the entrance at dusk, so that they could eat soon after emerging for their nightly foraging treks. For controls we had a second group of females, which were also radio-collared and lived in the same habitat but were not fed. There were 20 animals in the test group and 18 in the control group.

Our results were clear-cut. Control

females produced a balanced sex ratio and food-supplemented females produced more males. Females in both groups bore equivalent numbers of pouch offspring. Individual pouch young from the food-supplemented group, however, were consistently larger than those from the controls, showing that the females that were fed were indeed investing more. An indication that males benefited more than females from the additional investment is the fact that our recapture rate for juveniles improved more for males than for females when we compared offspring from food-supplemented mothers with the control group.

We did no experiment to determine whether females capable of particularly little investment produced mostly female offspring, but we have some observations suggesting that is so. Most opossums in the wild live for only one reproductive season. Moreover, the few that do live into a second year show signs of advanced aging, such as cataracts, weight loss and lack of motor coordination. In captive colonies of Virginia opossums, second-year females also show atrophy of reproductive organs, decreased litter size and a higher incidence of litter failure. Those facts suggest that second-year females may not be capable of investing as much as first-year females. Our sample of second-year females is small, because they are rare, yet over the years we have managed to trap 19 such animals. Their pouch young have been female-biased to an even greater degree than the food-supplemented litters were male-biased.




**SEX-RATIO HYPOTHESIS assumes that reproductive success varies more widely for males than for females in polygynous mammals: strong males will have many mates but weak males may have none, whereas nearly all females will be able to mate. Hence if the amount of parental investment affects the future reproductive fitness of offspring, mothers capable of high investment should produce more male offspring than female, and mothers capable of low investment should produce more females than males.**

Our study of second-year females brings up yet another unusual feature: opossums are among the shortest-lived mammals in the world for their size. Among common opossums in Venezuela we found that of 78 radio-collared mature females, 18 percent lived to breed in a second season, 1.2 percent lived to breed in a third season and none survived to a fourth. In his study of the Virginia opossum in Florida, Sunquist found that 8.3 percent lived to a second season, 3 percent lived to a third and none lived to a fourth. Even in breeding colonies where adequate records are kept, two years is about an average life span, with from three to four years the maximum. Opossums are also unusual in that older individuals show obvious physiological signs of advanced aging in nature, something the conventional wisdom has declared rare. And yet the received wisdom may be wrong, because almost no studies of aging in wild mammal populations have been done.

Traditionally there have been two approaches to the study of aging. The physiological approach seeks to determine what immediate cellular and biochemical mechanisms underlie the aging process itself. The evolutionary approach analyzes how natural selection may account for aging and seeks evidence from the comparative aging rates of different species, or of the same species in different environments, and from the genetic correlations between aging rate and other life-history traits such as reproductive rate.

A general evolutionary theory of aging was first elaborated by the late Sir Peter Medawar in the 1940's and extended in the 1950's by George C. Williams of the State University of New York at Stony Brook. Medawar noted that even if animals did not become gradually enfeebled by age, the influence of natural selection would wane as individuals grow older because of the increasing probability of accidental death—death resulting from causes external to the animal itself, such as predators or infectious diseases. As a result deleterious mutations that act late in life will be only weakly selected against. Medawar also noted that mutations that boost early reproduction may be favored evolutionarily, even if they increase the probability of premature death.

An intuitive grasp of both aspects of this hypothesis may be had if one examines a simple example. Imagine a population of individuals that do not age. In demographic terms this means the probabilities of death and of successful reproduction are constant in the course of time. If the probability of accidental death is 10 percent per year, then after 20 years only about 12 percent of the original population will be alive; after 40 years little more than 1 percent will be alive. Any deleterious mutation that is not expressed until late in life will affect only a small fraction of the population, and any mutation that causes instant death at age 60 would have almost no selection against it. Hence there is nothing to prevent an accumulation of late-acting lethal or enfeebling mutations. If the accidental death rate is higher, mutations can accumulate that have lethal effects much earlier in life.

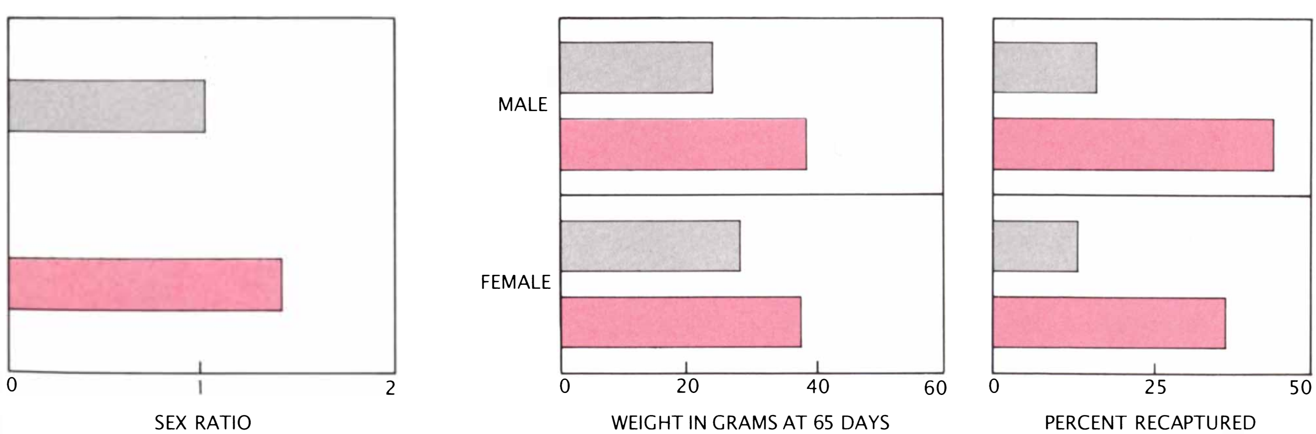
Depending on the rate of accidental mortality, there might also be an evolutionary advantage in increased early reproduction, even if there were an unavoidable survival cost associated with the increase. For instance, if the accidental mortality rate is 40 percent per year and individuals produce one offspring per year beginning at age one, then individuals will on the average produce 1.5 offspring in their lifetime. Now imagine that there is a mutation resulting in the production of two offspring per year beginning at age one, but that the cost of this excess early reproduction is a doubling of the postreproductive probability of death. These individuals would produce on the average slightly more than 1.7 offspring and so would eventually replace the original population. Again, the higher the accidental death rate, the greater the advantage of intense and early reproduction. In general, then, one would expect populations that are subject to high accidental mortality to show high reproductive effort at early ages and accelerated aging, and the converse in populations subject to low accidental mortality.

The major practical difficulty with testing the hypothesis in natural populations is to find an appropriate yardstick for aging. Longevity is not a good measure, because one cannot distinguish accidental death from senescent death. Ideally one needs a physiological measure of aging that can be applied at any age and on the same individual at different ages. One such measure may be the changing physical properties of mammalian tail-tendon fibers. Tendon is a simple tissue consisting almost entirely of bundles of parallel collagen fibers. Collagen increases in strength and decreases in solubility and flexibility in a regular manner as animals age. Moreover, the rate at which tail collagen ages responds to factors such as underfeeding and hormonal treatments that are known to affect aging in animals.

A convenient method of measuring the aging of tail collagen, developed by Harry Elden and Robert Boucek of the Howard Hughes Medical Institute in the early 1960's, is to record the breaking time of single fibers suspended by a standardized weight in a concentrated solution of urea at a standardized temperature. In laboratory rodents, breaking time has been shown to increase geometrically with the age of the animal. In the field, fiber bundles can be taken from captured animals in a quick and simple surgical procedure done under local anesthetic. The animal is then released to continue its normal existence. By sampling the same animal repeatedly one can compute the rate of change of collagen aging, which can be compared across individuals.

The two hypotheses being examined in my laboratory at Harvard are that opossums age rapidly because they expend a great effort in early reproduction and because they are subject to exceptionally high levels of accidental mortality. Our current study involves artificially reducing the reproductive effort of opossums by manipulating the size of their litters in order to see what effect this will have on collagen aging. Because prenatal reproductive investment is trivial, we can drastically influence overall reproductive effort simply by creating a range of litter sizes by transplanting young among females. We are studying the accidental death rate by comparing collagen aging, reproduction and longevity in our main study area at the Savannah River Plant in South Carolina with that of opossums living on Sapelo Island, Ga., where most of their major predators are absent and hence accidental mortality should be lower. The work is in a preliminary phase. So far we have established that the collagen technique distinguishes differences in age of as little as two months in opossums, that litter transplantation can be accomplished successfully and that the island population has been genetically isolated for at least several thousand years.

It seems ironic that the ecological success of *Didelphis* opossums has led indirectly to the low esteem in which they are generally held. That opinion might be changing, at least among scientists, as the genus helps to illuminate diverse aspects of mammalian biology. Research done to date suggests that opossums make particularly fine study animals because individuals can easily be monitored and manipulated both in the field and in the laboratory. They enable one to address broad ecological and evolutionary questions as well as to explore mechanistic details. In the future, opossums may reveal the mechanisms by which ecological forces determine sex ratios and aging rates, and physiologists may find the animals valuable for understanding such questions as the process of aging itself and the mechanisms of venom resistance.




**FOOD-SUPPLEMENT EXPERIMENT showed that offspring of mothers that were given extra food (*color*) were larger and had a higher male-to-female ratio than offspring from the control group (*gray*). The recapture rate for the test group compared with the controls improved more for males than for females, implying that males derived greater benefit from high investment.**