

Divided We Fall: Cooperation among Lions

*Although they are the most social of all cats,
lions cooperate only when it is in their own best interest*

by Craig Packer and Anne E. Pusey

In the popular imagination, lions hunting for food present a marvel of group choreography: in the dying light of sunset, a band of stealthy cats springs forth from the shadows like trained assassins and surrounds its unsuspecting prey. The lions seem to be archetypal social animals, rising above petty dissension to work together toward a common goal—in this case, their next meal. But after spending many years observing these creatures in the wild, we have acquired a less exalted view.

Our investigations began in 1978, when we inherited the study of the lion population in Serengeti National Park in Tanzania, which George B. Schaller of Wildlife Conservation International of the New York Zoological Society

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YOUNG FEMALE LIONS, shown here, band together in groups of six to 10, called prides. Such togetherness does not always make them more successful hunters, as scientists once presumed; loners frequently eat more than individuals in a pride do. Instead communal living makes lions better mothers: pridemates share the responsibilities of nursing and protecting the group's young. As a result, more cubs survive into adulthood.



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SISTERHOOD makes it possible for prides to protect their cubs against invading males (*top*). Angry groups can ward off lone males, which are on average nearly 50 percent larger than females (*middle*). And they will frequently attack and kill less powerful trespassing females (*bottom*).

began in 1966. We hoped to discover why lions teamed up to hunt, rear cubs and, among other things, scare off rivals with chorused roars. All this togetherness did not make much evolutionary sense. If the ultimate success of an animal's behavior is measured by its lifetime production of surviving offspring, then cooperation does not necessarily pay: if an animal is too generous, its companions benefit at its expense. Why, then, did not the evolutionary rules of genetic self-interest seem to apply to lions?

We confidently assumed that we would be able to resolve that issue in two to three years. But lions are supremely adept at doing nothing. To the list of inert noble gases, including krypton, argon and neon, we would add lion. Thus, it has taken a variety of research measures to uncover clues about the cats' behavior. Indeed, we have analyzed their milk, blood and DNA; we have entertained them with tape recorders and stuffed decoys; and we have tagged individuals with radio-tracking collars. Because wild lions can live up to 18 years, the answers to our questions are only now becoming clear. But, as we are finding out, the evolutionary basis of sociality among lions is far more complex than we ever could have guessed.

Claiming Territory

Male lions form lifelong alliances with anywhere from one to eight others—not out of any fraternal goodwill but rather to maximize their own



MALES are quick to challenge lions they do not know—real or not. When the authors played tape recordings of strange males roaring within a coalition's turf, representatives from that coalition immediately homed in on the sound. Moreover, they often took the offensive, pouncing on decoys placed nearby.

chances for reproducing. Most companions are brothers and cousins that have been reared in the same nursery group, or crèche. Others consist of nonrelatives that teamed up after a solitary nomadic phase. Once matured, these coalitions take charge of female lion groups, called prides, and father all offspring born in the pride during the next two to three years. After that, a rival coalition typically moves in and evicts them. Thus, a male lion's reproductive success depends directly on how well his coalition can withstand challenges from outside groups of other males.

Male lions display their greatest capacity for teamwork while ousting invaders—the situation that presents the greatest threat to their common self-interest. At night the males patrol their territory, claiming their turf with a series of loud roars. Whenever we broadcast tape recordings of a strange male roaring within a coalition's territory, the response was immediate. They searched out the speaker and would even attack a stuffed lion that we occasionally set beside it. By conducting dozens of these experiments, our graduate student Jon Grinnell found that unrelated companions were as cooperative as brothers and that partners would approach the speaker even when their companions could not monitor their actions. Indeed, the males' responses sometimes bordered on suicidal, approaching the speaker even when they were outnumbered by three recorded lions to one.

In general, large groups dominate smaller ones. In larger coalitions, the males are typically younger when they first gain entry into the pride, their subsequent tenure lasts longer and they have more females in their domain. Indeed, the reproductive advantages of cooperation are so great that most solitary males will join forces with other loners. These partnerships of nonrelatives, how-



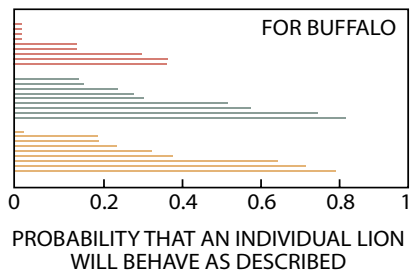
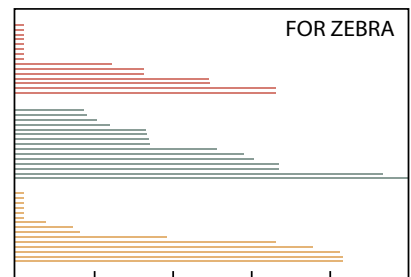
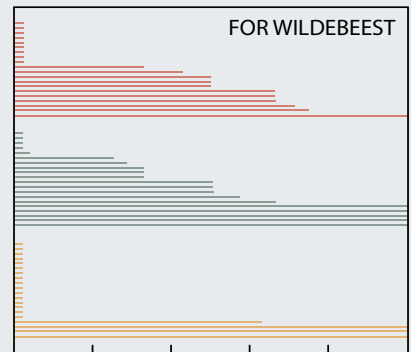
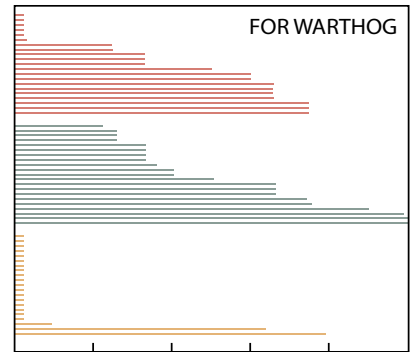
SERENGETI NATIONAL PARK in Tanzania houses a population of lions that has been studied by scientists since 1966.



PREY CAPTURE is usually done by a single lion, when the group is hunting warthog and wildebeest (*photographs*). Because she will very likely succeed in capturing such easy prey, her sisters will probably eat even if they refrain from the chase. Thus, the pride will often stand back at a safe distance, awaiting a free meal. But when a single lion is less likely to make a kill—say, if she is stalking zebra or buffalo—her pridemates will join in to pursue the prey together (*charts*).

HOW INDIVIDUAL LIONS ACT WHEN HUNTING

■ PURSUE ALONE
■ REFRAIN
■ PURSUE WITH OTHERS



PROBABILITY THAT AN INDIVIDUAL LION WILL BEHAVE AS DESCRIBED

KILLS are shared by the entire pride. If kills are made close to home, mothers bring their cubs to the feast. But they deliver nourishment from more distant kills in the form of milk.

ever, never grow larger than three. Coalitions of four to nine males are always composed of close relatives. Why do not solitary males recruit more partners until their groups also reach an insuperable size? The reasons again come down to genetic self-preservation and, in particular, weighing the odds of gaining access to a pride against those of actually fathering offspring.

Although large coalitions produce the most offspring on a per capita basis, this averaging assumes fair division among companions—a form of cooperation that does not happen in the Serengeti. In fact, the first male to find a female in estrus will jealously guard her, mating repeatedly over the next four days and attacking any other male that might venture too close. Dennis A. Gilbert, in Stephen J. O'Brien's laboratory at the National Cancer Institute, performed DNA fingerprinting on hundreds of our lion samples and found that one male usually fathered an entire litter. Moreover, reproduction was shared equally only in coalitions of two males. In the larger coalitions, a few males fathered most of the offspring. Being left childless is not too bad from a genetic standpoint if your more successful partner is your brother or cousin. You can still reproduce by proxy, littering the world with nephews and nieces that carry your genes. But if you are a lone lion, joining forces with more than one or two nonrelatives does not pay off.

Hunting

Traditionally, female lions were thought to live in groups because they benefited from cooperative hunting. (The females hunt more often than the resident males.) But on closer examination, we have found that groups of hunting lions do not feed any better than solitary females. In fact, large groups end up at a disadvantage because the companions often refuse to cooperate in capturing prey.

Once one female has started to hunt, her companions may or may not join her. If the prey is large enough to feed the entire pride, as is the usual case, the companions face a dilemma: although

a joint hunt may be more likely to succeed, the additional hunters must exert themselves and risk injury. But if a lone hunter can succeed on her own, her pridemates might gain a free meal. Thus, the advantages of cooperative hunting depend on the extent to which a second hunter can improve her companion's chances for success, and this in turn depends on the companion's hunting ability. If a lone animal is certain to succeed, the benefits of helping could never exceed the costs. But if she is incompetent, the advantages of a latecomer's assistance may well exceed the costs.

Evidence from a wide variety of bird, insect and mammalian species suggests that, as expected, cooperation is most wholehearted when lone hunters do need help. The flip side of this trend is that species are least cooperative when hunters can most easily succeed on their own. Consistent with this observation, our graduate student David Scheel found that the Serengeti lions most often work

together when tackling such difficult prey as buffalo or zebra. But in taking down easy prey—say, a wildebeest or warthog—a lioness often hunts alone; her companions watch from the sidelines.

Conditions are not the same throughout the world. In the Etosha Pan of Namibia, lions specialize in catching one of the fastest of all antelopes, the springbok, in flat, open terrain. A single lion could never capture a springbok, and so the Etosha lions are persistently cooperative. Philip Stander of the Ministry of Environment and Tourism in Namibia has drawn an analogy between their hunting tactics and a rugby team's strategy, in which wings and centers move in at once to circle the ball, or prey. This highly developed teamwork stands in sharp contrast to the disorganized hunting style of the Serengeti lions.

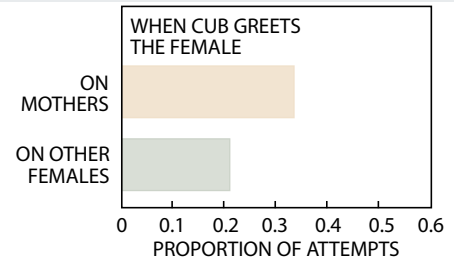
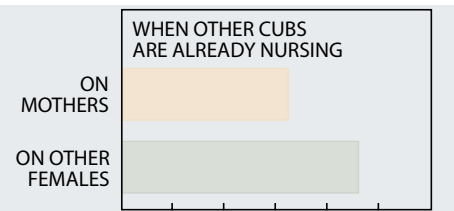
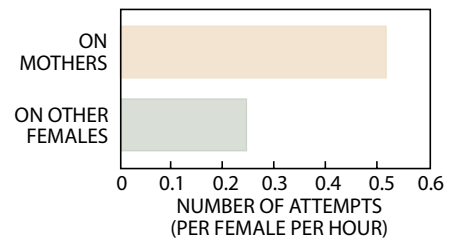
All female lions, whether living in the Serengeti or elsewhere, are highly cooperative when it comes to rearing young. The females give birth in secrecy and





NURSING is a job shared by all mothers in a pride, not out of generosity but, rather, fatigue. Cubs feed when their mothers return from hunting (*top*). If the mothers stay awake, they will not let cubs other than their own, such as the large adolescent shown, take milk from them (*bottom*). Although cubs try to nurse most often from their own mothers, they can be quite cunning in their attempts to nurse from other females (*charts*).

NURSING ATTEMPTS BY CUBS



keep their litters hidden in a dry riverbed or rocky outcrop for at least a month, during which time the cubs are immobile and most vulnerable to predators. Once the cubs can move, though, the mothers bring them out into the open to join the rest of the pride. If any of the other females have cubs, they form a crèche and remain in near-constant association for the next year and a half before breeding again. The mothers lead their cubs to kills nearby but deliver nourishment from more distant meals in the form of milk. When they return from faraway sites, the mothers collapse, leaving their youngsters to nurse while they sleep. We have studied over a dozen crèches, and in virtually every case, each cub is allowed to nurse from each mother in the group. Communal nursing is a major component of the lion's cooperative mystique.

And yet, as with most other forms of cooperation among lions, this behavior

is not as noble as it seems. The members of a crèche feed from the same kills and return to their cubs in a group. Some are sisters; others are mother and daughter; still others are only cousins. Some have only a single cub, whereas a few have litters of four. Most mothers have two or three cubs. We milked nearly a dozen females and were surprised to discover that the amount of milk from each teat depended on the female's food intake and not on the actual size of her brood.

Because some females in a pride have more mouths to feed, yet all produce roughly the same amount of milk, mothers of small litters can afford to be more generous. And in fact, mothers of single cubs do allow a greater proportion of their milk to go to offspring that are not their own. These females are most generous when their crèchemates are their closest relatives. Thus, milk distribution depends in large part on a pattern of surplus production and on kinship. These

factors also influence female behavior across species: communal nursing is most common in those mammals—including rodents, pigs and carnivores—that typically give birth to a wide range of litter sizes and live in small kin groups.

Although female lions do nurse the offspring of other females, they try to give milk primarily to their own cubs and reject the advances of other hungry cubs. But they also need sleep. When they doze for hours at a time, they present the cubs with an enormous temptation. A cub attempting to nurse from a lioness who is not its mother will generally wait until the female is asleep or otherwise distracted. The females must therefore balance the effort needed to resist the attentions of these pests against their own exhaustion.

Generosity among female lions, then, is largely a matter of indifference. Females that have the least to lose sleep best—owing either to the small size of

AFFECTION is common among prides, which rely on one another to help protect their young. Male lions present one of the greatest threats: if one coalition takes over a new pride, the newcomers—eager to produce their own offspring—will murder all the pride's small cubs and drive the older cubs away.



their own litter or to the company of close relatives. Female spotted hyenas have resolved this conflict by keeping their cubs in a well-protected den. Mothers return to their cubs for short periods, feed their brood and then sleep somewhere else in peace. By watching hyenas at the den, we found that mother hyenas received as many nursing attempts from the cubs of other females as did mother lions, but the hyenas were more alert and so prevented any other than their own offspring from nursing.

Surviving in the Serengeti

As we have seen, female lions are most gregarious when they have dependent young; the crèche is the social core of the pride. Childless females occasionally visit their maternal companions but generally keep to themselves, feeding well and avoiding the social complexities of the dining room or nursery. Mothers do not form a crèche to improve their cubs' nutrition. And gregarious mothers may actually eat less than solitary mothers; they have no system of baby-sitting to ensure a more continuous food supply. Instead mother lions form a crèche only to defend themselves and their cubs.

A female needs two years to rear her cubs to independence, but should her cubs die at any point, she starts mating within a few days, and her interval between births is shortened by as much as a year. Male lions are rarely affectionate to their offspring, but their territorial excursions provide effective protection. Should the father's coalition be

ousted, however, the successors will be in a hurry to raise a new set of offspring. Any cubs left over from the previous regime are an impediment to the new coalition's immediate desire to mate and so must be eliminated. More than a quarter of all cubs are killed by invading males. The mothers are the ultimate victims of this never-ending conflict, and they vigorously defend their cubs against incoming males. But the males are almost 50 percent larger than the females, and so mothers usually lose in one-on-one combat. Sisterhood, on the other hand, affords them a fighting chance; in many instances, crèchemates succeed in protecting their offspring.

Male lions are not their only problem. Females, too, are territorial. They defend their favorite hunting grounds, denning sites and water holes against other females. Large prides dominate smaller ones, and females will attack and kill their neighbors. Whereas most males compress their breeding into a few short years, females may enjoy a reproductive life span as long as 11 years. For this reason, boundary disputes between prides last longer than do challenges between male coalitions, and so the females follow a more cautious strategy when confronted by strangers. Karen E. Mc-

Comb, now at the University of Sussex, found that females would attempt to repel groups of tape-recorded females only when the real group outnumbered the taped invaders by at least two. Females can count, and they prefer a margin of safety. Numbers are a matter of life and death, and a pride of only one or two females is doomed to a futile existence, avoiding other prides and never rearing any cubs.

The lions' pride is a refuge in which individuals united by common reproductive interests can prepare for the enemy's next move. The enemy is other lions—other males, other females—and they will never be defeated. Over the years, we have seen hundreds of males come and go, each coalition tracing the same broad pattern of invasion, murder and fatherhood, followed by an inevitable decline and fall. Dozens of prides have set out to rule their own patch of the Serengeti, but for every new pride that has successfully established itself, another has disappeared. Lions can seem grand in their common cause, battling their neighbors for land and deflecting the unwanted advances of males. But the king of beasts above all exemplifies the evolutionary crucible in which a cooperative society is forged. ■

The Authors

CRAIG PACKER and ANNE E. PUSEY are professors in the department of ecology, evolution and behavior at the University of Minnesota. They conducted their studies at the Serengeti Wildlife Research Institute, the University of Chicago and the University of Sussex. Packer completed his Ph.D. in 1977 at Sussex. That same year, Pusey received her Ph.D. from Stanford University.

Further Reading

A MOLECULAR GENETIC ANALYSIS OF KINSHIP AND COOPERATION IN AFRICAN LIONS. C. Packer, D. A. Gilbert, A. E. Pusey and S. J. O'Brien in *Nature*, Vol. 351, No. 6327, pages 562–565; June 13, 1991.
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