Science, they saw evidence that the mantle was moving perpendicular to the plate's motion instead—diverging at about the midpoint of the South American coast and flowing to the north and south.

To explain this odd flow pattern, Silver and Russo invoked South America's westward movement of 3.5 centimeters a year. As the curtain of descending oceanic plate retreats westward before the advancing continent, they and others have noted, it shrinks the space for mantle rock beneath it. The resulting excess mantle, Russo and Silver argued, flows laterally like a bow wave on a very broad ship. Where this ponderous bow wave finally clears the continent far to the north and south, it creates a wake, which can be seen as the swirl of small plates driving eastward off Cape Horn and in the Caribbean.

On South America itself, meanwhile, Russo and Silver suggested that the pressure of the mantle bow wave, transmitted through the descending ocean plate to the adjacent continent, might have pushed up the Andes. The mantle should exert the highest pressure where it backs up at the central coast before flowing north and south. And that's just where the coast has a deep indentation and the highest part of the Andes, called the Altiplano, has risen.

Geologists were doubtful. "I agree with Paul that a lot of the conventional explanations in plate tectonics aren't really sufficient to drive mountain-building," says seismologist Dean Whitman of Florida International University, "but I think he's stretching things too far. It's not entirely clear to me," he says, that you can connect mountain-building in the uppermost 100 kilometers of the South American plate and mantle flow hundreds of kilometers below, on the other side of the subducting ocean plate.

And some geophysicists weren't even convinced that the mantle bow wave exists. Beck, who also works in the area, thinks the mantle flow there "is looking more complicated [than Russo and Silver suggest]. The basic observation of shear-wave splitting is important, but what that means physically is difficult to say." Mantle rock is so viscous, adds Michael Gurnis of the California Institute of Technology, that a subducting plate has to carry it along; north-south flow across the direction of plate motion "seems implausible; it's just a weird model."

Silver has gone back to South America with portable seismographs to take a closer look. He believes that although some mantle may be dragged down with the slab, it still "looks for the most part like trench-parallel flow." And geophysical modeler Larry P. Solheim of DTM, with Silver, has used a simple computer model to test the idea that such flow could raise the Andes. They simulated a triangular continent plowing broadside into mantle with the subducting plate between them. In the model, the relatively rigid subducting plate transmits the pressure in the deep oceanic mantle to the continent's leading edge. That pushes in the central coastline and uplifts the model continent's coast from end to end. The uplift is most dramatic right at the bend—just where the Altiplano is found.

The model's success has led Silver to speculate about what could be driving this process in the first place by pushing South America to the west. One widely accepted driving force of plate motions—the pull of sinking slabs—doesn't work for South America, he notes, because its plate has no subducting edge. Some researchers have invoked a push from the eastern part of the plate, where newborn crust slides off the midocean ridge in the Atlantic, but Silver says that push falls far short of what's needed to raise the Andes. "You need some other force," he says, "and with South America there's not much else to appeal to except westward deep-mantle flow." The mantle beneath the Atlantic must be flowing westward as part of a deep circulation loop, dragging along the continent.

South America is the clearest example of tectonics powered by mantle flow, Silver says, but "what holds for South America probably holds for North America." It too lacks a subducting edge and has high ground along its western edge, which was bordered by a deep-sea trench for much of recent geologic history, and it too is moving westward. To Silver, that implies much the same mountain-building scenario as he and Russo have constructed for South America. "Here you have a mountain range that goes all the way from the Arctic to the Antarctic that people are still arguing about," says Silver. "This explains it."

And he isn't stopping there. He goes on to propose that mantle upwelling beneath the mid-Atlantic spreading ridge could diverge to drag Africa and Eurasia eastward even as it drags the Americas westward. Says Silver, "It looks like the Atlantic half of the world has continents that are being actively driven by deep-mantle flow," while the Pacific half is driven by subduction of oceanic plates.

Having explained the behavior of half the globe starting with a few split waves on a seismogram, Silver and his colleagues will have to do a lot more to convince seismologists, geologists, and geodynamicists that they've got it right. For now, though, "everything just works out," says Silver.

–**Richard A. Kerr**

Additional Reading

R. M. Russo and P. G. Silver, "Trench-parallel flow beneath the Nazca plate from seismic anisotropy," *Science* **263**, 1105 (1994).

BEHAVIORAL ECOLOGY

Cowardly Lions Confound Cooperation Theory

SERENGETI NATIONAL PARK, TANZANIA—A pride of female lions chasing an invading lioness out of its territory may look as single-minded and bent on retribution as a posse hot on the trail of a bank robber. But, on careful observation, the pride's character is as mixed as that of the citizens in the movie *High Noon*: stout-hearted Gary Coopers paired with outright cowards.

The existence of true lionhearts and cowardly lions, however, is not what has scientists excited about these observations of lions in Tanzania's Serengeti National Park and Ngorongoro Crater. What's causing a stir about the Report by Robert Heinsohn from the Australian National University and Craig Packer from the University of Minnesota, on page 1260 of this issue, is the lions' consistency. Lionhearted individuals are always brave, putting their lives on the line to defend their pride's territory, even if they are forced time and again to share defensive duties with a coward. And that throws a big monkey wrench into a classic explanation for the evolution of cooperative behavior in a selfish, dog-eat-dog (or lion-eat-gazelle) world.

"That's the big issue: Why will an animal do something that is a cost to itself and a benefit to others," says Luc-Alain Giraldeau, a behavioral ecologist at Concordia University in Montréal, Québec. "This study shows that the traditional approach to that question is flawed." That approach, based on theoretical models of interactions, suggests that cooperation can arise if animals react to one another's previous behavior: Cooperative actions beget more cooperation, while selfishness only gives rise to selfishness. But in some lions, selflessness comes to the fore regardless. Says Steven Lima, a behavioral ecologist at Indiana State University, "As the lions and empirical studies of other animals show, the models simply don't capture the essence of what's going on in the natural world. It's time there was a reality check."

Since the 1980s, biologists have attempted to understand the costs and benefits underlying animal cooperation by using various models from game theory, a branch of science largely developed by economists attempting to explain market decisions by humans. The two most favored models have been mutualism, in which one animal incidentally benefits from the actions of another, and a model called the Prisoner's Dilemma. The latter has had great appeal because it opens the door for the development of truly altruistic behaviors in animals that are otherwise overwhelmingly selfish. "People would like to see a continuum in nature," explains Stephen T. Emlen, a behavioral ecologist at Cornell University in Ithaca, New York, "from simple cooperation to the altruism we see in ourselves."

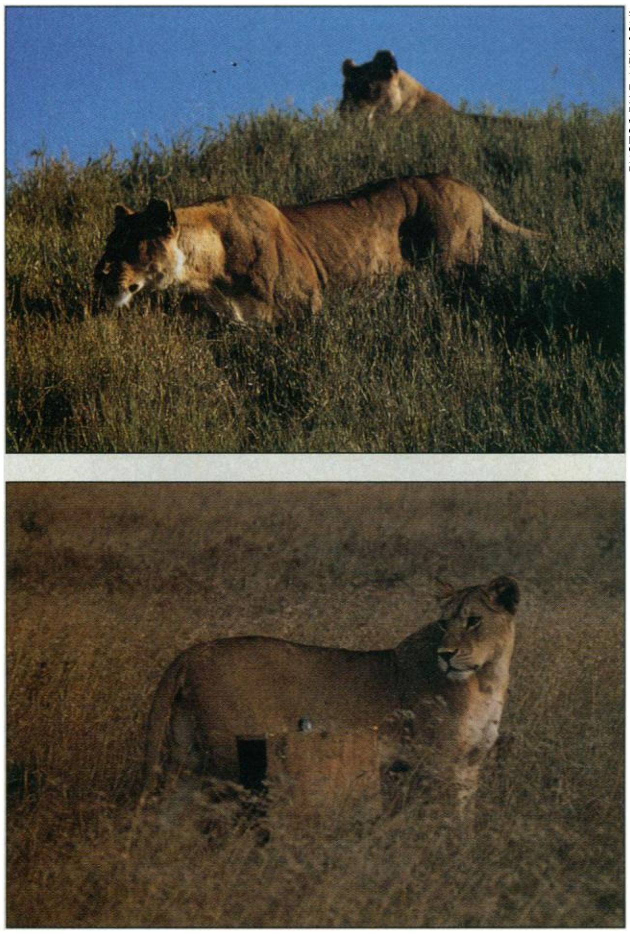
In the Prisoner's Dilemma, two prisoners, held in separate cells, are charged with a crime. The length of their prison sentences depends on whether they cooperate with each other in maintaining their innocence or implicate one another as criminals (defect). And each must choose a strategy blind to the other's choice. If you cooperate while your partner defects, you get a long sentence while he or she goes free. Not knowing what your partner will do, the safest choice is to defect, assuming your partner will do so too, and you'll both get shorter sentences. Translate this principle from the theoretical cell block to animals competing for food or the chance to reproduce, and it's hard to see how altruism could ever emerge.

Yet stable mutual cooperation could arise, evolutionary theoreticians such as Robert Axelrod of the University of Michigan, Ann Arbor, have argued, if animals repeated these interactions, responding to one another's behavior from the previous game. A strategy called "tit for tat" indicates that if your partner cooperated in the last round, you respond in kind in the current round, and mutual cooperation is born (defection, of course, simply triggers a like response).

Laboratory studies showing tit for tat in guppies and stickleback fish that team up to inspect predators seem to bear this model out, although the research is controversial (*Science* 17 March, p. 1591). But Giraldeau goes on to note that scientists have searched for more than a decade for a nonlaboratory, real-world example of this kind of behavior and have uncovered only one still-debated example of reciprocal feeding in vampire bats. "It's amazing how little data has turned up, even among the primates," notes Emlen.

Lions, the "paragons of cooperation," as Packer puts it, seemed likely candidates to use tit-for-tat stratagems. They band together in order to protect their young from the infanticidal attacks of strange male lions and sometimes pair off—forming duos analogous to the two prisoners—to defend their territory against strange females.

Heinsohn and Packer staged mock invasions of lion territory by playing taped recordings of the roars of strange females to eight resident prides. They knew that a pride of female lions aggressively defends its turf against such invaders. "We know what will happen: Strangers kill strangers," says Packer. "So the costs of being the first into battle are high." Nevertheless, the costs of losing one's home ground are higher: Without a territory, a female lion has little chance of raising her cubs and so loses the chance to pass her genes on to the next generation—the bottom line of evolutionary success.



PHOTOS BY R. HEINSOHN

Dynamic duos. *(Top)* Alerted by a tape-recorded roar that seems to come from an invader, lioness pairs go out to defend their territory. *(Bottom)* But some, like this animal looking around for her cowardly companion, are bolder than others.

But the researchers discovered that when it came to interactions between leaders and laggards, the lionesses did not bear those costs equally. The scientists played their tapes to particular sets of lions, watching to see what would happen when two leaders were paired or when a leader was matched with a laggard. "That's the test of the cooperative strategies expected from the Prisoner's Dilemma," explains Packer.

Paired leaders typically advanced boldly together. The showdown walk was longer and more hesitant, however, when leaders were matched with laggards. "It was a very clear distinction," said Heinsohn: "Some would always advance very strongly and alertly toward the speakers, while others would hang back." "The leaders would constantly glance back at their lagging companions, as if to say, 'Well, where the hell are you?' " adds Packer. "They clearly mistrusted them." But despite that mistrust and despite the number of times a leader might be paired with a laggard, the bold female never altered her behavior. "She never punished her companion by holding back herself, which contradicts the predictions of the model," Packer notes. "So the lions clearly are not following the rules of tit for tat. Their behavior is much more complex." Some nonleaders even employed "conditional" strategies of heroism or cowardice, either rushing forward only at the last minute, or hanging back at that crucial moment.

It is that complexity that has behaviorists increasingly dissatisfied with theory. "We've been trying to shoehorn every example of cooperative behavior into this Prisoner's Dilemma since 1981," fumes David Stephens, a behavioral ecologist at the University of Nebraska, "when it's clear that it's time to step back and look for a model that better covers all the cooperative things animals do." Thus, with the lionesses, Stephens and others wonder how the leaders and laggards behave in other cooperative situations. "Maybe a laggard is an excellent hunter," suggests Alex Kacelnik, a behavioral ecologist at Oxford University, "or maybe she is the top milk-producer, and so you, as the leader, can forgive her for being bad at defense."

Packer and Heinsohn have begun to investigate whether the lions do indeed make allowances for good hunters or baby sitters, or if they simply hold to a pattern of "producers" and "scroungers," with the latter content to let their fellows do most of the work. In a mixed population of this sort, producers continue to be cooperative simply because the advantages of defending their territory outweigh the costs of tolerating the freeloaders. But the researchers' efforts to further understand the lions' cooperative patterns hit a snag last year, when most of the animals in the playback experiments succumbed to an outbreak of canine distemper virus—illustrating once again the many vagaries and complexity of the real world.

–Virginia Morell