A reprint from

American Scientist

the magazine of Sigma Xi, The Scientific Research Society

Monitoring Elusive Mammals

Unattended cameras reveal secrets of some of the world's wildest places

James G. Sanderson and Mogens Trolle

Before the arrival of European settlers, the passenger pigeon *(Ectopistes migratorius)* constituted more than a quarter of the bird population in North America. Ornithologists estimate that there were once billions of them. So it is no wonder that 19th-century hunters went after these birds with abandon. Who could have imagined that such an abundant species would really suffer? But suffer it did—and surprisingly fast. By the 1890s, the species was effectively destroyed, despite some belated attempts to save the few remaining in the wild. The last passenger pigeon, a captive bird named Martha, died at the Cincinnati Zoo on September 1, 1914.

All too many species have met similar fates, prompting biologists to regard modern times as an episode of "mass extinction." Indeed, dramatic losses to our planet's heritage of biological abundance and diversity have become commonplace. Some people are trying to reverse this tide, often with the official blessing of their governments. More than 175 nations, for example,

James G. Sanderson earned a doctorate in mathematics from the University of New Mexico in 1976. He has taught in the Department of Computing and Information Science at the University of New Mexico and in the Department of Wildlife Ecology and Conservation at the University of Florida. He is currently a TEAM research scientist at Conservation International's Center for Applied Biodiversity Science. Mogens Trolle holds an M.Sc. in wildlife biology from the University of Copenhagen. He specializes in the study of large mammals from South America, where he has spent more than five years. Trolle was one of the first to publish camera-trap results from South America in scholarly journals. Among other accomplishments, he discovered a new deer species in Peru. Address for Sanderson: Conservation International, 1919 M Street, NW, Suite 600, Washington, DC 20036. Internet: j.sanderson@conservation.org

have now ratified the Convention on Biological Diversity, an agreement first drawn up in 1992 that obligates countries to combat the loss of biodiversity in several ways. The signatories to the Convention decided, for example, to establish a system of protected areas, giving special consideration to threatened species and ecosystems.

In 1996, participating countries were encouraged to set measurable targets, stepping-stones to achieve their ultimate conservation objectives. As a result, these nations established a core set of biodiversity indicators, which could be followed over time. Monitoring the status of natural populations ranks high among the various efforts undertaken in this regard because it can alert managers when they must do more to protect biodiversity in the regions under their care. It was this need for tracking long-term changes that spurred Conservation International to begin a program called Tropical Ecology, Assessment and Monitoring, or "TEAM."

One of us (Sanderson) began working on the TEAM program three years ago within a wing of Conservation International called the Center for Biodiversity Science, which was set up with a grant from the Gordon and Betty Moore Foundation to help support the role of science in shaping conservation efforts. The particular mission of TEAM: to monitor long-term trends in biodiversity through a network of tropical field stations, thus providing an early warning system that can guide conservation action.

With the help of appropriate experts, we developed protocols to monitor various biodiversity indicators—such as the abundance of leaf-litter ants, birds, fruit-eating butterflies and mammals (including primates), as well as tree growth and

landscape change—at these relatively undisturbed sites. To ease the considerable logistical difficulties involved with such a massive endeavor, we decided that the TEAM efforts should be carried out close to existing research facilities. So far, four TEAM stations are operational: three in Brazil and one in Costa Rica. We plan to set up six more stations in the Americas later this year and, if we obtain adequate support, intend later to establish similar sites in Africa and Asia.

Ideally, one would like to keep track of everything living near a monitoring station, but we have had to limit the scope of our measurements so as to keep the project manageable. In particular, the TEAM program does not involve all mammalian fauna but instead targets those of medium to large size, which are the ones most likely to suffer from alterations to the local landscape, from hunting or even from climate change. The populations of larger mammals thus provide a convenient barometer for the overall heath of the ecosystem.

Regular viewers of nature documentaries might conclude that observing large mammals also has the advantage of being a straightforward exercise. In some

Figure 1. Snapshots of Guatemalan wildlife were captured by the author's "camera trap," a device that can take photos autonomously when it senses the motion of an animal nearby. Such images are useful for determining whether a particular species is present in an area and can even be used to estimate population density. The animals shown here are the white-nosed coati *(Nasua narica, upper left)*, great curassow *(Crax rubra, upper right)*, margay *(Leopardus wiedii, middle left)*, gray fox *(Urocyon cinereoargenteus, middle right)*, tayra *(Eira barbara, lower left)* and ocellated turkey *(Agriocharis ocellata, lower right)*. (Except where noted, all photographs courtesy of James Sanderson.)

Figure 2. Beginning in the late 19th century, George Shiras III, a onetime Pennsylvania congressman, developed techniques for obtaining photographs of wildlife at night. Initially, he mounted his bulky camera and powder flash in the front of a boat *(upper left),* which he used to approach animals foraging the shores of Whitefish Lake, located on Michigan's Upper Peninsula. Shiras's night photo of an adult doe and two fawns *(right)* won him awards in the U.S. and Europe. He also mounted his equipment on land and triggered the shutter remotely, using a long string, a technique that allowed animals to take their own pictures, such as this raccoon tugging on a baited line *(lower left).*

places, it is. In East Africa, for example, casual visitors routinely see elephants, zebras, wildebeest, lions, leopards and cheetahs roaming around in the bush. But in most other locations, even within protected areas, wildlife is just not that easy to view. Indeed, both of us have at times worked for months in the dense tropical forests of Brazil, Suriname, Cambodia or Guatemala without spotting any terrestrial wildlife whatsoever. How then can biologists monitor the famously elusive mammals of tropical forests? How will investigators know whether these species are in imminent danger in places that have been exploited for timber or bush meat?

Without the benefit of firsthand observations, investigators have traditionally had to rely on indirect evidence such as a track or scat to confirm the presence of certain species. Although such methods are still employed, a more helpful technique is now available for the surveillance of wildlife: phototrapping. This approach makes use of ordinary cameras mounted in rugged enclosures to automatically snap photos of animals that wander into the field of view. Phototraps are usually outfitted with a flash, so that even the most skittish noc-

turnal animals can be captured on film. Although conservationists have been taking advantage of phototraps for only a handful of years, the roots of this technique reach back more than a century, springing from the ingenious tinkering of a former American statesman.

Shoot, but Not to Kill
In the summer of 1888 at Whitefish Lake near Marquette, Michigan, George Shiras III, a Yale-educated lawyer and onetime Pennsylvania congressman, perfected a way of photographing wildlife at night with a large-format camera and hand-operated flash. Shiras soon gained considerable acclaim for his stunning night photographs of deer and other animals. At the Paris Exhibition in 1900, he won the gold medal in the forestry division with an exhibit of several wildlife photographs, one of which was of a doe with two spotted fawns. These same photographs helped win him the grand prize for wildlife photography at the St. Louis World's Fair of 1904.

The technique he used for his nature photography was indeed highly unusual: With his large camera mounted on the front of a rowboat, Shiras

would probe the darkness for animals on the shores of Whitefish Lake using a flashlight. He would then position his boat as close as possible before taking a shot, which required him to set off a powder flash.

Later Shiras set up his camera on land, rigging it so that he could take a picture remotely by pulling on a long trip wire. Eventually, it occurred to him that he could arrange the wire so that an animal would itself trigger the picture-taking—an arrangement to which he referred variously as an "automatic," "set" or "trap" camera. In 1913, Shiras wrote: "I have usually found it a waste of effort to try to get pictures in the ordinary way; for, even if occasionally successful, the loss of time can be avoided by the use of the set camera." Accompanied by exquisitely detailed photographs of animals, his articles in *The National Geographic Magazine* from 1906 to 1921 created considerable interest in wildlife photography in preference to the more popular hunting and trapping of his day.

In the late 1920s, Frank M. Chapman (a leading ornithologist from the American Museum of Natural History in New York) used similar cam-

era traps in the tropical rain forest of Central America. Chapman had seen the tracks left by at least two cat species on Barro Colorado Island, Panama, but he had never observed any of these elusive animals. A camera trap, he thought, might satisfy his curiosity. Using the technique Shiras had developed, Chapman stretched trip wires across human-made trails because he suspected that animals used these convenient paths through the jungle. He did not bait his camera traps for the first few nights, but subsequently he left a variety of enticements: meat, fish and fruits, including a banana attached directly to the trip wire. Chapman used a large-format camera containing a single glass plate. He described the sound of the flash charge exploding as being similar to the report of "a small cannon" and remarked that it must have been a terrifying experience for the animal to endure a sudden explosion of blinding light along with a thunderous boom only three meters or so away.

With the help of this noisy device, Chapman quickly demonstrated that white-lipped peccaries, tapirs, ocelots and pumas all lived on Barro Colorado Island. Although mice, rats, agoutis (rabbit-sized rodents), coatis (raccoon-like animals), bats, birds and some of Chapman's colleagues were also routinely photographed, several of the rarer mammals in residence—forest deer, paca (very large rodents) and jaguar—eluded Chapman's camera phototraps for three months.

In his writings, one finds confirmation of what we and all other camera trappers learn firsthand: Results may vary. Chapman sometimes went weeks without photographing anything very interesting; then he'd hit the jackpot. He described, for example, returning from one visit to the darkroom with pictures of a puma and two ocelots. His images of these wild cats were sometimes remarkable. One photograph of an ocelot taken in the middle of the night shows the animal unsuccessfully trying to step over the trip wire, which was suspended 25 centimeters or so above the ground, thus recording behavior on film.

On occasion, Chapman was able to recognize individual animals. For instance, he regarded two puma photographs, obtained three months and one mile apart, as being of the same animal, because the figures agreed in size, proportion, markings and the length of a foreleg. Referring to these photographs, Chapman wrote: "Assuming, therefore, that this is but one individual, the two pictures admirably illustrate one of the most distinctive features of camera-hunting, namely, that we may capture the same animal an indefinite number of times and still leave him as free as he was in the beginning."

Different Stripes

Shiras's unique photographs and their widespread dissemination in *National Geographic* engendered an interest in wildlife that went far beyond being about what one could mount on the wall or serve at the dinner table. But because the required equipment was cumbersome and expensive, few but Chapman emulated his example early on. It took three separate developments to spark the widespread use of camera traps decades later.

First, photography became a lot easier. Nowadays one doesn't need to lug around a bulky camera, boxes of glass plates, an ungainly tripod and copious quantities of exploding flash powder. A modern camera phototrap typically consists of nothing more than a tough plastic enclosure containing a 35-millimeter "point-and-shoot" camera and an electronic controller. In place of Chapman's trip wires, these units use a passive infrared detector to trig-ger the shutter when the sensor and its associated circuitry register heat in motion—exactly what goes on in most automatic lights and burglar alarms.

The second thing that helped was that weekend hunters discovered how automatic camera traps could aid them in their search for trophy deer and other game. They have eagerly adopted this tool over the past decade or so, creating a mass market for camera phototraps of all kinds. Prices are thus quite reasonable, and the variety of equipment available is enormous. In addition to finding units containing ordinary film cameras, one can now buy phototraps equipped with digital cameras. Video-camera phototraps are also being marketed.

The third advance came when scientists interested in wildlife populations realized that they could apply analytical methods that they already had on hand to data collected with camera traps. Those statistical tools, known as "mark-recapture "or "capture-recapture" methods, have served for decades to estimate populations of rodents, rabbits and other small animals that can be easily caught, marked in some way and released. But capture-recapture analyses have been applied in conjunction with camera traps only recently. Indeed, widespread use of this combination did not come until after 1998, when K. Ullas Karanth, who works for the Wildlife Conservation Society in India and is one

Figure 3. Modern camera traps, which are mostly sold to weekend hunters in search of prize game, are increasingly being used by conservationists to monitor elusive animals. Here Francisco Braga Ribeiro Filho *(left)* **and Simone Martins deploy a camera trap in Cāxiuana, Brazil.**

Figure 4. Indian tigers, like many other cats, display coat patterns that vary from animal to animal. Paired camera-trap images like these can thus be used to identify individuals. (Photographs courtesy of K. Ullas Karanth, Wildlife Conservation Society.)

of the world's leading experts on tigers, and James D. Nichols, a statistician at the U.S. Geological Survey Patuxent Wildlife Research Center, showed that camera traps and the appropriate analytical software could together be used to estimate the population density of tigers in India.

Karanth and Nichols realized that because every tiger is marked with a unique pattern of stripes, it is usually possible to identify individuals from photographs. Positive identification normally requires images of both sides of the tiger, because these animals are laterally asymmetric. The same is true for many other wild cats, which can thus be monitored effectively using pairs of camera traps set up to take photos from either side of the subject. Species whose individuals are distinguishable in other ways are, of course, also candidates for camera trap–based population studies. For example, it is not uncommon that we identify individual cats by noting unusual scars or cuts to the ears.

The Art of Phototrapping

The main challenge to the phototrapper is to position the subject—an animal of uncertain type and size—in front of, and at a reasonable distance from, the camera so that useful pictures will be taken. The best strategy is not always apparent. Imagine for a moment standing somewhere deep within a dense tropical forest, a place so thick with vegetation that only a smattering of sunlight reaches the ground and the field of view is severely limited in every direction. A rustling alerts you that an animal is moving in the forest nearby. How would you take its picture? With difficulty. It's no wonder that my local field assistants, whose knowledge of these forests always exceeds my

own, invariably ask the same question: Where should we put the cameras? Ought they to be set deep in the forest, among the thickets of lianas and bamboo, or placed on trails, where there is slightly more breathing room? Should camera phototraps be positioned near a burrow or nest?

Putting cameras near burrows seems logical: When the resident emerges to forage, a picture will be snapped. The problem is that when this creature returns, another picture will also be taken. Indeed, the comings and goings of one animal might be all the camera records for the next 30 days, which is not particularly helpful if one's aim is to survey the general population.

With experience, one can locate traps in less problematic places frequented by animals. We both have now developed the knack, having worked with camera traps for a variety of projects. One of us (Sanderson) has, in addition to his recent work on the TEAM program, been using camera traps to search for small cats in the wild at various places around the world. At Barito Ulu research station in the heart of Kalimantan (the Indonesian part of the island of Borneo), Rupert Ridgeway, a consultant to the University of Cambridge, and Sanderson mounted a camera trap facing a log that had fallen across a small stream, figuring that wild cats might well take advantage of this natural bridge to cross over the water. The result, ironically, was a fine photograph of a pangolin (a "scaly anteater").

Deciding where to place cameras when there is nothing so obvious as a log bridge is difficult; even the general strategy to follow isn't obvious. At La Selva, a world-famous ecological research station in Costa Rica, David B. Clark, a bi-

ologist at the University of Missouri-St. Louis (the former director of the La Selva facility and now an adviser for TEAM), argued against placing camera traps on trails. He knew that the biologists working there often walked these jungle paths, perhaps more frequently than did animals, and he feared that these people would inadvertently trip the cameras, using up the film. Random placement in the forest, Clark reasoned, would serve better. Sanderson disagreed. So TEAM members tried both strategies. After two months they compared results from cameras placed on trails against those obtained from traps positioned at random spots in the forest. The large number of photos of people walking the trails and the complete absence of human images from the randomly placed sites showed that Clark's hunch was correct. There was just one problem: The randomly placed camera traps returned only a handful of pictures of animals. Fortunately, the traps mounted by trails recorded many such images, despite Clark's initial concerns.

What exactly do conservation biologists do with trap photos? Most commonly, we use the images just to document the presence of a particular species. An example comes from the Udzungwa Mountains in Tanzania, where one of us (Sanderson) and Francesco Rovero of the Museum of Natural Sciences in Trento, Italy, obtained the first photograph ever of a live Abbott's duiker, a medium-sized forest antelope. (Remarkably, the duiker is eating a frog.) Another instance comes from the efforts of Sutrisno Mitro of the STINASU Foundation for Nature Conservation in Suriname, who used camera phototraps in the Brownsberg Nature Reserve, a protected area in that country. There he obtained photos of a small

spotted cat called the margay *(Leopardus wiedii)* and of the elusive tayra *(Eira barbara*, a kind of weasel), adding to the list of mammals known to live there. In similar fashion, Anthony Simms, working for Conservation International in the Cardamom Mountains of Cambodia, documented the presence of the Siamese crocodile *(Crocodylus siamensis)*, which has been extirpated throughout much of its former range.

The failure to photograph a particular species cannot be used to establish absence—just because you don't see an animal doesn't mean it is not present—but the lack of evidence might suggest relative rarity. Relative abundance, too, can be gauged from the number of times a species is photographed compared with the total number of frames taken. And for certain animals, a full-blown capture-recapture analysis provides an estimate of population density.

One assumption required of any density study is that all individuals of the target species have a nonzero probability of being detected. For camera trapping this means that no individual can live between phototrap sites without there being at least a possibility that it will be captured on film. With enough phototraps and enough time, all individuals in a fixed area can thus be photographed—in principle. In practice, the number of cameras we can afford to deploy is far too small to saturate an area with coverage. For this reason, and because human scent sometimes discourages shy animals from visiting a site, some individuals escape detection. Hence statistical methods are essential for estimating the size of the population.

Measuring the Invisible

It might seem far-fetched that field biologists can determine the size of a population even when they (or their cameras) have captured only a fraction of the animals living in the area under study. In fact, the task is relatively straightforward using a capture-recapture analysis. The procedure is perhaps best illustrated with a hypothetical example, say, for the mice living in your cellar. Want to know how many there are? Simply put out some traps that can capture them live.

Suppose that on the first night of an informal two-night study you catch n_1 of these rodents. Mark each with a dab of paint and then release it. Then, on the second night, say that you catch n_2 mice. Of this set, sup-
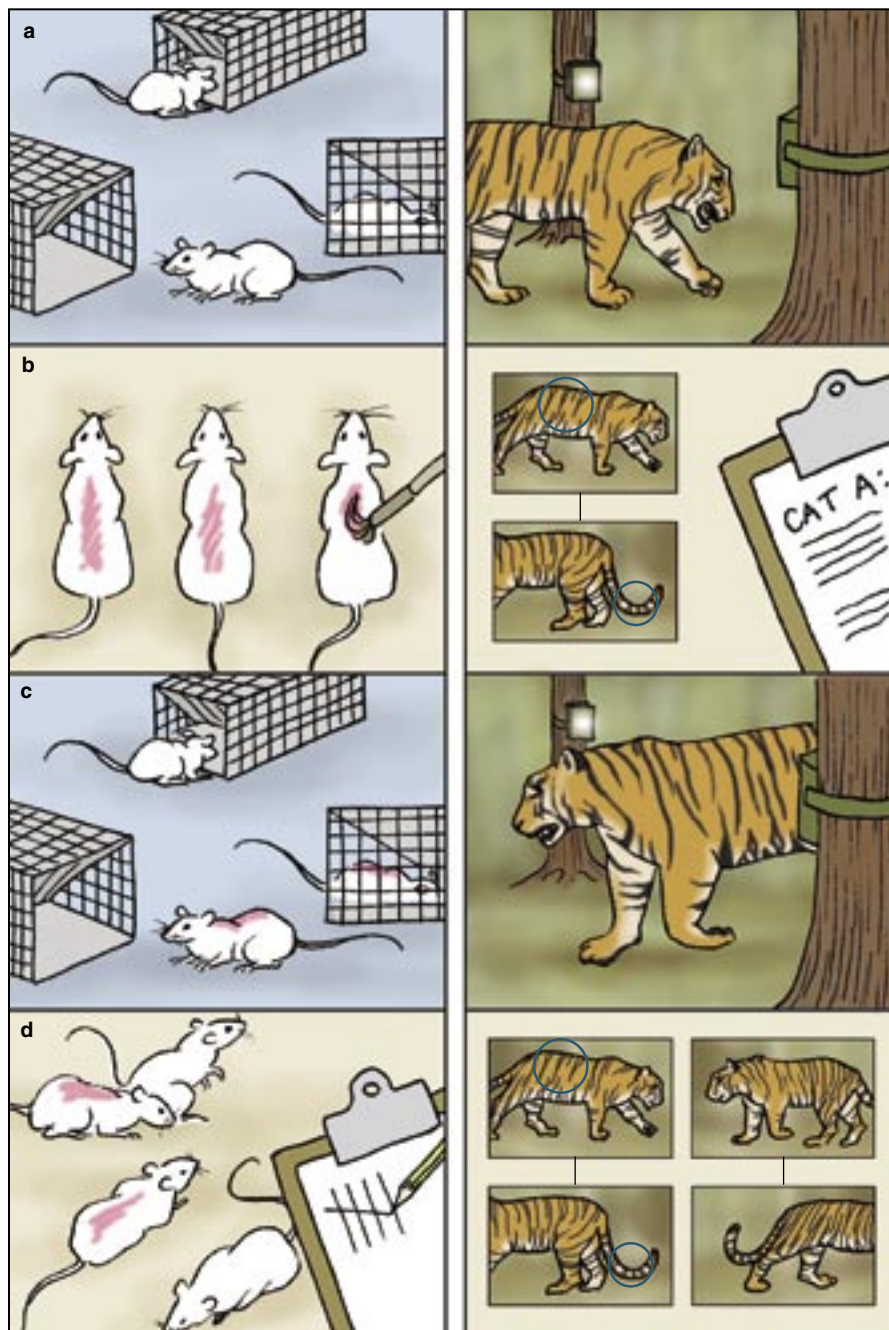

Figure 5. A classic "mark-recapture" analysis is often used to gauge population density *(panels at left)*. In such studies, animals are captured *(a)*, marked in some way (here with splotches of paint, *b*) and then released. A second round of trapping *(c)* then allows the total number of animals to be inferred by tallying the proportion marked *(d)*, assuming that the newly captured ones constitute a representative sample of wild population. Exactly the same type of analysis can be done using camera traps when individuals can be identified from their markings *(right)*.

pose you found that m_2 were marked with paint. You could reasonably expect that the ratio of marked animals captured on the second day (m_2) to the total number animals captured on the second day (n_2) equals the ratio of marked mice available for capture (which equals the number you marked on the first day, n_1) to the total population of your basement, which then works out to $(n_1 n_2)/m_2$.

Limiting the sampling to two consecutive nights helps ensure that the population size being estimated is fixed—that is, one can reasonably assume that there are no significant additions of mice (through birth or immigration) or losses (though death or emigration). But sampling for a few more nights would help reduce the level of uncertainly. And the analysis only gets a little more complicated.
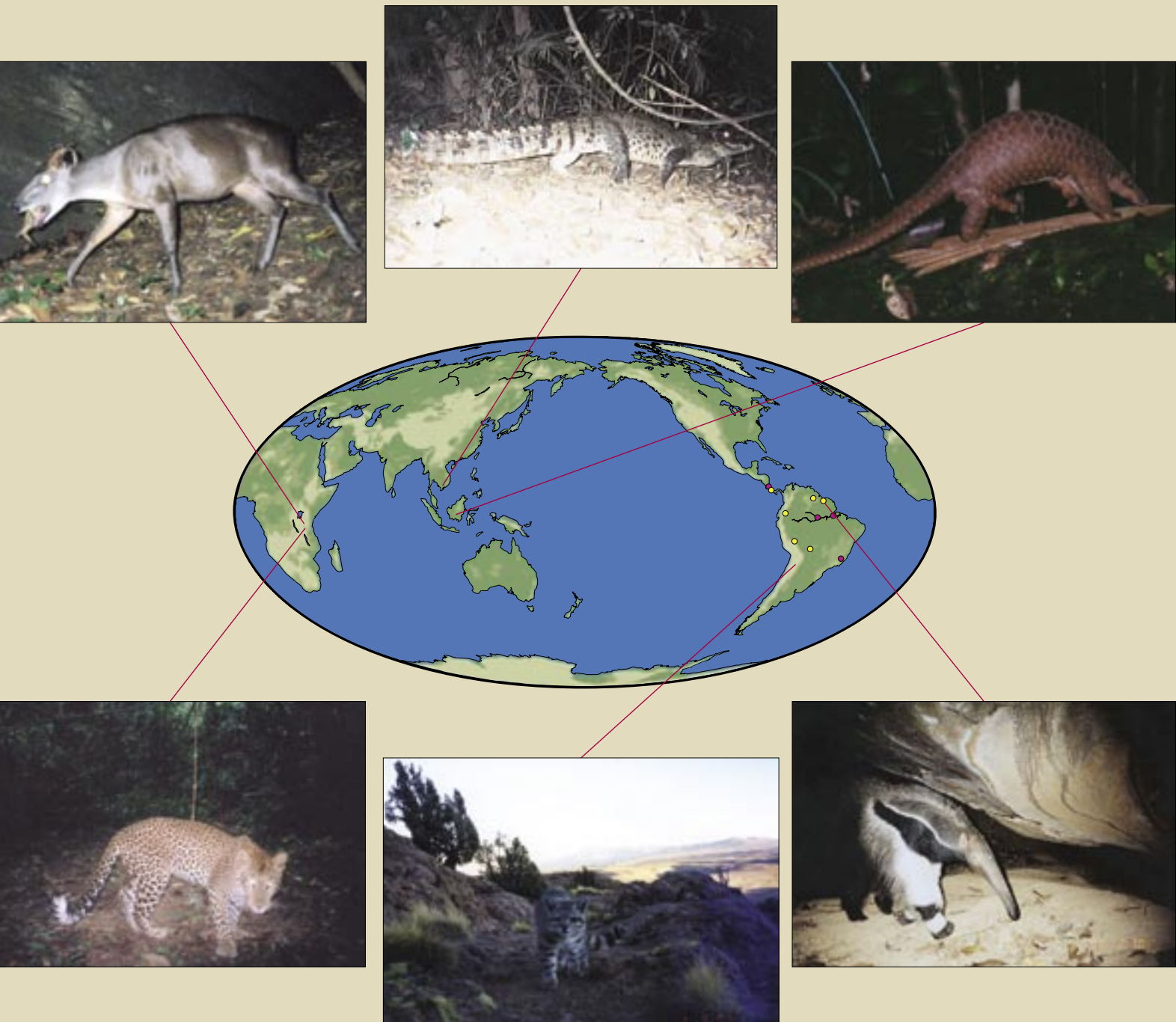
Figure 6. Workers at Conservation International's Center for Applied Biodiversity Science and their overseas colleagues have so far established four permanent monitoring stations in Central and South America *(purple dots on map)*. Six other monitoring sites are in the process of being set up *(yellow dots)*. Camera-trap photos from these locales and others around the world have confirmed the presence of many rare animals including (clockwise from upper left) Abbott's duiker *(Cephalophus spadix)*, Siamese crocodile *(Crocodylus siamensis)*, pangolin *(Manis javanica)*, giant anteater *(Myrmecophaga tridactyla)*, Andean mountain cat *(Oreailurus jacobita)* and leopard *(Panthera pardus)*. (Images are, respectively, courtesy of Francesco Rovero and James Sanderson; Anthony Simms; Rupert Ridgeway and James Sanderson; Kamajna Panashekung, Kupias Tawadi and James Sanderson; Lilian Villalba, Elisea Delgado and Juan C. Esquivel; Francesco Rovero.)

In a nutshell, each night (after the first one) provides one estimate of the total population—derived as before by equating the ratio of marked animals caught to total animals caught with the ratio of marked animals in the population to total population. One then averages over these results to obtain the best overall estimate of total population and to determine the size of the error bars.

Are such procedures really that useful? Indeed they are. One of us (Trolle) once conducted an intensive three-month mammal survey in the Pantanal wetlands of Brazil and during that time made only one direct observation of an ocelot. Had this been the only datum, little could have been said about the size of the local population. Yet during the same period, camera

traps emplaced in these wetlands returned 55 pairs of photos of ocelots. Because their spots differ from animal to animal, Trolle and Marc Kéry of the U.S. Geological Survey Patuxent Wildlife Research Center were able to identify individuals, of which there were nine. Of course, the number of ocelots that eluded the camera traps was unknown. To estimate that, Trolle and Kéry did a capture-recapture analysis.

Each of nine ocelots had a unique "capture history," that is to say, a record of when it was photographed. Such a set of capture histories can be succinctly summarized in the form of a binary matrix where each row corresponds to an individual ocelot and each column represents a "camera trapping occasion": a fixed number of days (in this case, a week) during which an individual ocelot was either recorded or not by any or all of the camera traps. If, for instance, ocelot number 7 was photographed at least once during the third camera-trapping occasion, one would record a 1 in the seventh row and third column of the capture-history matrix. Even if this ocelot was recorded multiple times or by multiple cameras during that time, it would still only rate a 1 in this column of the matrix. If no camera snapped its picture, this element would be set to 0.

Feeding this matrix into standard capture-recapture software produced a population estimate of 10 ± 4. In this case, Trolle and Kéry knew there were at least nine ocelots (having identified that many in the photos), so the range on the population size was in fact between 9 and 14. To convert this result into population density required an estimate of the amount of ocelot territory being sampled. The area spanned by the cameras (9.3 square kilometers) was easy enough to calculate. What was trickier was accounting for the fact that some ocelots had home ranges that extended well beyond this core area.

Fortunately, Trolle and Kéry could readily work out how far these ocelots moved around by determining the maximum distance between photos of each of the nine animals and averaging over the whole set. They then added a strip around the core area of the camera traps that was one half of this distance wide. This addition brought the total range being sampled up to 17.7 square kilometers. Dividing the population size by this area gives a density of a little over half an ocelot per square

kilometer. This result not only showed that the technique Karanth and Nichols had used for Indian tigers worked for another cat species, it also revealed that the ocelot population in these Brazilian wetlands is considerable.

Shiras's Legacy
Shiras was interested in more than photographing wildlife: He was also intent on protecting it. In 1904, this Pennsylvania congressman introduced a bill to allow the federal government to regulate the conservation of waterfowl. That bill failed to pass, but 14 years later a more expansive measure was enacted to protect all migratory birds. That law came too late to help the migratory passenger pigeon (which went extinct the following year), but clearly the national mind-set was beginning to turn toward conservation.

Writing in 1927, Shiras's fellow phototrapper Chapman expressed concern about people's actions disturbing natural systems:

A satisfactory study of the relation of an animal to its surroundings, physical and organic, can be made only when these surroundings are essentially natural. The removal of but a single species may affect the entire fauna. The introduction of a species may be followed by equally far-reaching results. In other words, the origin of structure and habit, the function of form and color, should be studied where the conditions of life have been undisturbed.

Such unspoiled areas must be identified now while there is still time to call attention to them so that they can be set aside and protected for posterity. Although few people will ever visit these sites, and the ones that do will not stay long, carefully placed camera phototraps can provide a glimpse of the rich goings-on inside. The views of animals these automatic devices return are ones that even seasoned field biologists, including those of us who work regularly in some of the most remote and undisturbed places on the planet, will likely never experience directly. Such photographs will increase scientific understanding and, despite their often haphazard composition, should boost people's appreciation of nature, just as they did for viewers of Shiras's wildlife photographs a century ago.

Bibliography
Balmford, A., R. E. Green and M. Jenkins. 2003. Measuring the changing state of nature. *Trends in Ecology and Evolution* 18:326–330.

Chapman, F. M. 1927. Who treads our trails? *The National Geographic Magazine* 52:330–345.

Debinski, D. M., and P. S. Humphrey. 1997. An integrated approach to biological diversity assessment. *Natural Areas Journal* 17:355–365.

Hellawell, J. M. 1991. Development of a rationale for monitoring. In *Monitoring for Conservation and Ecology*, ed. B. Goldsmith. London: Chapman and Hall.

Henschel, P., and J. Ray. 2003. *Leopards in African rainforests: Survey and monitoring techniques.* New York: Wildlife Conservation Society.

Kremen, C., A. M. Merenlender and D. D. Murphy. 1994. Ecological monitoring: A vital need for integrated conservation and development programs in the tropics. *Conservation Biology* 8:388–397.

Karanth, K. U., and J. D. Nichols. 1998. Estimation of tiger densities in India using photographic captures and recaptures. *Ecology* 79:2852–2862.

Karanth, K. U., J. D. Nichols, N. S. Kumar, W. A. Link and J. E. Hines. 2004. Tigers and their prey: Predicting carnivore densities from prey abundance. *Proceedings of the National Academy of Sciences of the USA* 101: 4854–4858.

Lambeck, R. J. 1997. Focal species: A multi-species umbrella for nature conservation. *Conservation Biology* 11:849–856.

Lawler, J. J., D. White, J. C. Sifneos and L. L. Master. 2003. Rare species and the use of indicator groups for conservation planning. *Conservation Biology* 17:875–882.

Shiras, G. III. 1906. Photographing wild game with flashlight and camera. *The National Geographic Magazine* 6:387–446.

Shiras, G. III. 1913. Wild animals that took their own pictures by day and by night. *The National Geographic Magazine* 7:763–834.

Shiras, G. III. 1915, Nature's transformation at Panama. *The National Geographic Magazine* 8:159–194.

Trolle, M. and M. Kéry. 2003. Estimation of ocelot density in the Pantanal using capture-recapture analysis of camera-trapping data. *Journal of Mammalogy* 84:607–614.

Yoccoz, N.G., J. D. Nichols and T. Boulinier. 2001. Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution* 16:446-453.

For relevant Web links, consult this issue of *American Scientist Online*:

http://www.americanscientist.org/ IssueTOC/issue/701