Winner of the John Burroughs Medal for Natural History Writing and the Helen Bernstein/NY Public Library Award for Excellence in Journalism

THE SONG OF THE DODO

BY THE AUTHOR OF MONSTER OF GOD AND THE FLIGHT OF THE IGUANA

ISLAND BIOGEOGRAPHY IN AN AGE OF EXTINCTIONS

DAVID QUAMMEN

"Stunning."—BARRY LOPEZ, AUTHOR OF ARCTIC DREAMS

THE SONG OF THE INDRI

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THE PEOPLE of Madagascar know something about minimum critical size. They have an adage: *Ny hazo tokano tsy mba ala*. It means: One tree doesn't make a forest.

But if not one, then how many?

The years of debate over SLOSS, the years of empirical work at Lovejoy's Amazon site, the decades of research and discussion inspired by MacArthur and Wilson's theory—all that time and effort have yielded no simple answer. Instead of a simple answer, there has been complicated progress. Around 1980, the very terms of discourse began to change. Since then, island biogeography has split open like a chrysalis and a metamorphosed creature has emerged: the concept of population viability.

If the people of Madagascar have an adage that captures the essence of that concept, I haven't heard it. Like the rest of us, they're faced with the need to absorb a new way of thinking.

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THE FOREST reserve of Analamazaotra lies on the rugged eastern slope of Madagascar, sixty miles from Antananarivo. The road is bad and the rail line is sinuous, winding down off the plateau and then traversing the canyon-gouged face of the escarpment. Most visitors to Analamazaotra come down from the capital by train, which takes about five hours. It's a fast and comfortable trip by the standards of Madagascar (where travel can be difficult), notwithstanding two dozen stops in villages with unpronounceable names. About halfway along, the landscape changes from high savanna and rice paddies to rainforest. The forest is patchy, interrupted in more than a few places by swaths of naked earth where the hardwoods and tree ferns have been felled and burned. Hill rice grows sparsely on some of those charred slopes. Traveller's palm, a weedy Madagascan representative of the banana family, thrives on the edges of the disturbed ground. Eucalyptus plantations cover sizable stretches of terrain. Exotic to Madagascar, these eucalypti harbor virtually no wildlife and are good only for firewood and cheap timber. To ride the train from Antananarivo to Analamazaotra, then, is to view a diorama of ecological wreckage. The little forest reserve itself is surrounded by jeopardized, changing landscape. The rail line continues onward, down off the escarpment and onto the eastern coastal plain, where the topography is more suitable for dense human settlement and the native rainforest has long since been almost completely destroyed. The daily train pauses only briefly, near Analamazaotra, before heading on down. The station stop is a village known as Perinet.

It's a French name, left from the colonial period. The newer name that appears on train schedules is more authentically Malagasy, but the old one lingers because this is a famous place and Perinet is the name under which it's famous. Perinet is where people come, from all over the world, for a glimpse of the indri.

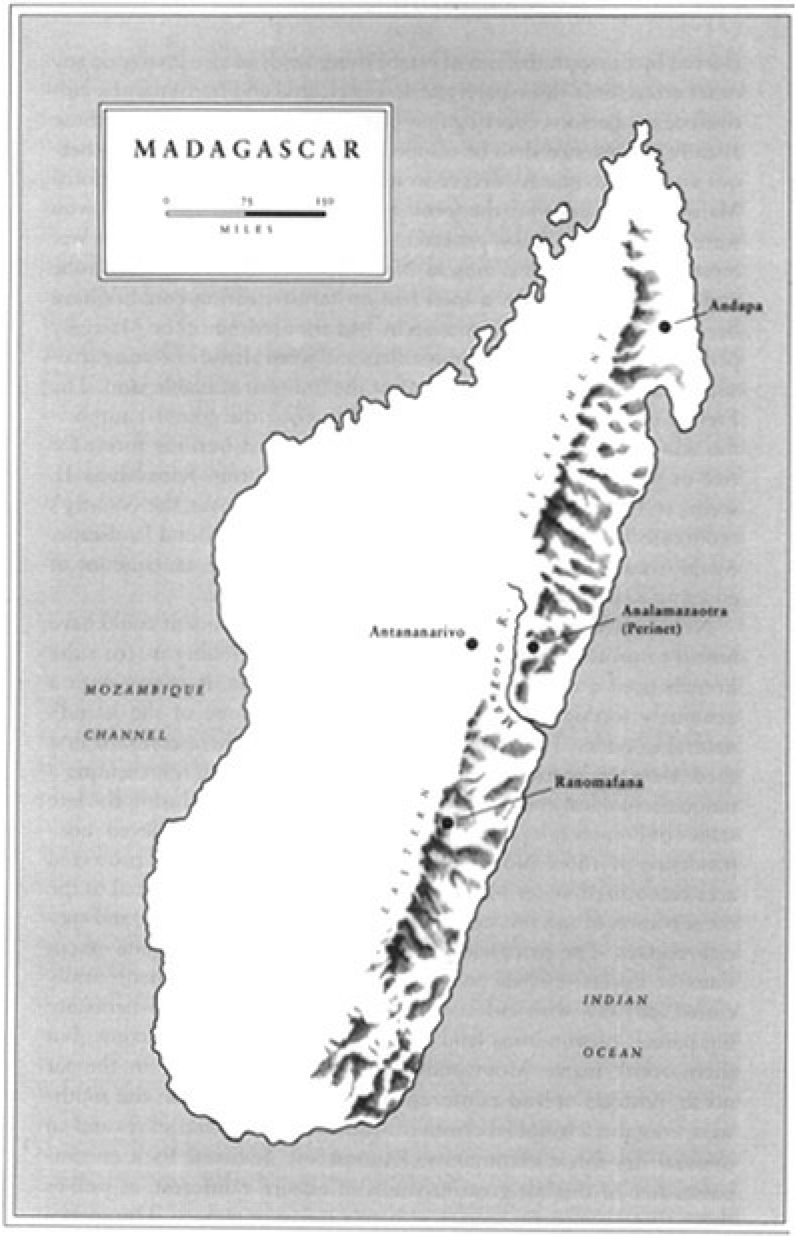
The Hôtel-Buffet de la Gare, true to its name, sits beside the tracks. Its back deck is the station platform. The hotel is another colonial vestige, a large building with a wide rosewood staircase leading up to the second-floor rooms and a spacious dining hall that serves also as lobby and bar. Half a mile from the hotel—a short stroll out the front door and down a narrow lane—stands the gate of the Analamazaotra reserve. The reserve isn't fenced and a person could walk into it anywhere, but dutiful visitors present themselves and their permits-of-entry at the gate. A sign there reads:

EAUX ET FORÊTS
RÉSERVE D'INDRI
BABAKOTO

Eaux et Forêts is the Department of Waters and Forests, charged with overseeing this reserve and others. *Babakoto* is the Malagasy name for the indri.

By one account, *babakoto* translates as "grandfather." By another account it's "little father," and by still another, "the ancestor." Madagascar has its own subtle protocols of denomination, its own shifty epistemological rules, and most things that are knowable here are known in multiple variants. That's especially true at Perinet.

The Analamazaotra reserve was established in 1970, but it belongs to a much older tradition. As early as 1881, in the twilight of the indigenous monarchy (which had been established by the powerful Merina tribe and lasted until conquest by the French), Queen Ranavalona II had seen fit to decree that the forest "may not be cleared by fire with the aim of establishing fields of rice, maize or any other crops; only those parts previously cleared and burnt may be cultivated; any persons effecting new clearings by fire or extending those already in existence shall be clapped in irons for five years." A generous view of the queen's decree would be that it reflected a traditional Malagasy reverence for the forest as "the robe of the ancestors" who were buried there. A less generous view would be that the decree was mostly a flexing of regal muscle. Notwithstanding the ancestors' robe and the queen's muscle, a total ban on forest clearing couldn't have been enforced, even if the monarchy had endured, since the Malagasy people resented such imperious edicts and were already exerting irresistible demographic pressure against the limits of available land. The French occupation began in 1895, and in 1903 the colonial authorities announced their own set of sanctions against burning forest for rice or pasture. This prohibition, like the one from Ranavalona II, seems to have been more about asserting control over the country's economic life and resources than about preserving natural landscape. Again it was a futile policy as well as a heartless one, tantamount to enacting a law against having babies and feeding them.



Neither a Merina monarchy nor a colonial government could have hoped to protect every hectare of forest, but beginning in 1927 the French tried a more modest approach—this time, it seems, with a genuinely foresightful concern for preserving some of the island's natural wonders. They established a system of nature reserves. At first there were ten, scattered throughout the country, each representing a unique ecological community. Two others were added during the late stages of French rule, and still others after the country achieved independence in 1960. Nowadays there are six categories of protected area recognized under Malagasy law, of which three are crucial to the conservation of species: strict nature reserves, national parks, and special reserves. The strict nature reserves are closed to everyone except Eaux et Forêts officials and approved researchers—or theoretically closed, anyway, with enforcement irregular. The national parks are big parcels of wondrous landscape in which anyone is welcome; but there aren't many. Montagne d'Ambre National Park, in the far north, protects upland rainforest. Isalo National Park, in the southwest, contains a weird labyrinth of sandstone gorges and spires and an unusual dry-forest community. Ranomafana National Park encompasses one of the last great expanses of eastern rainforest, as well as those three sympatric species of bamboo-eating lemurs. The special reserves, most of which are tiny compared to Isalo or Ranomafana, were each established for a narrower purpose—generally, to protect a particular species of animal or plant. Analamazaotra is a special reserve, and what makes it special is the indri.

The indri, largest of all surviving lemurs, is also the most spectacularly peculiar. Its neck is long, its limbs are lanky, its eyes glow yellow brown in a gawky black jackal-like face. Its ears are smallish and round, like a koala's. Although the dark-and-light pattern of its body fur suggests a giant panda, its shape is more gracile and humanoid. It appears to be built for basketball. Its legs are strong, its hands and feet are quick. It has almost no tail, just a nub, and that nub-tailed condition is unique among lemurs, unusual for any arboreal primate. Its scientific name, *Indri indri*, suggests nothing whatever except that the species is one of a kind. It won't live in captivity. It flees from humans and doesn't tolerate disturbance of its habitat. You could call it the ultimate wild animal.

It grows to the size of a small baboon but it moves through the forest without touching the ground—by making broad jumps from the trunk of one tree to another, sometimes twenty or twenty-five feet across gaps. This mode of locomotion is astonishing. With a great thrust from the legs, the indri leaps out; sailing horizontally through space, it turns; catching hold of the next tree trunk, it shoves that one aside and ricochets onward to the next, and the next, and the next, moving faster than a person can run. Perinet tourists of the more energetic variety sometimes try to keep up, stumbling along through the understory. Hopeless. But eventually the indri stops. It settles into a high fork of limbs and becomes virtually invisible, although with persistence, with binoculars, with help from a keen guide, a visitor can spot it again. And if timing is right and the visitor is lucky, the indri will sing.

The song of the indri is an unearthly sound. It carries through the forest for more than a mile. It rings in the air back at the Hôtel-Buffet de la Gare. It has been said to be one of the loudest noises made by any living creature. It's a sliding howl, eerie but beautiful, like a cross between the call of a humpback whale and a saxophone riff by Charlie Parker. Biologists speculate that it may be useful for territorial spacing between adjacent indri groups (the basic social units, each consisting of a mated pair with one or two offspring), and possibly also for passing other sorts of information (about breeding availability of young adults, for example) across greater distances. It could be a threat, then, or a warning cry, or a way of advertising for new genes. The significance of the song is an unsolved mystery, one of many in connection with the indri. The most thorough study within recent decades was done by a young biologist named Jon I. Pollock, but even Pollock didn't claim certainty for his findings.

Pollock's study and others have supplied a bare outline of indri ecology and behavior. The species survives only in remnants of northeastern rainforest, from around the town of Andapa southward as far as the Mangoro River. (The forest at Ranomafana, which looks like good habitat but lies south of the Mangoro River, has no indri.) Before the centuries of human disturbance, it ranged wider. It feeds on leaves and fruit from many different tree species, but despite the dietary versatility it doesn't attain high population density in any given region, as some versatile herbivores do. It reproduces slowly: a single birth every three years, sexual maturity at about age six. Not many mammals, not many animals of any sort, have such low reproductive potential. And the song itself, according to that hypothesis about territorial spacing, may be a tool for ensuring that indri groups are few and far between. By mandates of its own ecology, the species remains rare, with all the jeopardy that rareness entails.

The mated pairs seem to be monogamous, though extended fidelity is unproven. An indri infant rides aboard its mother for much of the first year, as if stuck to her pelt with Velcro. Females are the dominant gender. They take precedence over males for feeding and grooming, and they don't tolerate being bullied in the matter of mating. Besides the song, there's also another sort of vocalization: a short, sharp bark (*coup de klaxon*, in the nice phrase of one French biologist) that functions as a warning against predators and noisome human observers. It seems that an indri's hearing is exceptionally acute, at least for detecting the song of another indri. Each animal possesses "a large membranous laryngeal sac" that, by Pollock's best guess, might be used in producing the song. Otherwise the indri's anatomy and physiology are poorly known; few scientists have laid hands on a dead specimen, let alone a living one. It *is* clear, though, that the indri's slow rate of reproduction and its low population density make the species especially vulnerable to extinction. Probably its body size does too, since larger animals tend to have larger needs. The dozen or so species of lemur that have gone extinct since humans colonized Madagascar were all large-bodied animals, generally much bigger than the lemur species that have survived. If that trend holds, the indri will be next.

Jon Pollock did his fieldwork at Analamazaotra and two other sites. For slightly more than a year he followed certain family groups, gathering data about their population structure and their behavior, charting their dietary preferences, mapping their territories, recording their strange music. That was two decades ago. Eventually he published a handful of papers, which today account for much of what is known about the species, since almost no one else has studied it. Pollock may still be the world's leading authority. I can think of only one other person in recent years who knew the ways of the indri intimately, and that person died young without leaving any of his knowledge in print.

"Forests inhabited by *Indri* resound each day to loud modulating calls emitted by two to four members of each group either spontaneously or in response to other groups' calls," Pollock wrote. "The song of an *Indri* group, which consists of a discrete succession of these loud calls, lasts for between 40 sec and 4 min, occurs usually during the morning, is emitted at least once on most days, and can be detected by the human ear up to 2 km from its source under optimal conditions." Pollock examined the acoustical structure of several recorded songs, using a Kay sonograph and a real-time soundspectrum analyzer, whatever those are. His report on the acoustical work, lumpishly titled "The Song of the Indris (*Indri indri*; Primates: Lemuroidea): Natural History, Form, and Function," was published in the *International Journal of Primatology*. "The song consists of a series of calls, each lasting from 1 to 4 sec, whose main energy lies from 500 to 6000 Hz, separated by short pauses of up to 3 sec," he wrote. "Pure tones of the call appear with up to four harmonics and may be modulated by as much as 2000 Hz within each call." This captures some of the physics but none of the soul.

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ON THE FIRST evening of my first visit to Perinet, several years back, I heard about a Malagasy teenager named Joseph, recommended by the hotelier as the finest of the local guides. Joseph knows the Analamazaotra reserve better than anyone, I was told. Yes yes, Joseph knows the ways of the indri. Intimately. Joseph grew up in the forest, he loves all the animals, even the plants, he has made himself *expert*. The hotelier himself was a gracious Malagasy of early middle age whose unassuming dignity inspired trust, and I was happy to take the recommendation. Later that evening I was introduced to his protégé, his star guide, this Joseph.

A laconic and serious young man. He looked about eighteen. Spoke a little English. Seemed to possess a steady, internalized confidence. He wasn't shy, he wasn't brash, merely focused. A professional who cherished his work. It turned out that Joseph was just his French name, convenient for tourists to remember. Like the indri, he had more labels than one, and his comfortable name, his Malagasy name, was Bedo.

I asked Bedo whether he'd be willing to lead me on a long quiet hike through the forest. Yes, of course. When? I asked. Whenever. I had already spent an afternoon in the reserve with another guide, a precociously cynical youngster who presumed that I'd tip him well for manhandling the boa constrictors and chameleons into photogenic poses. Bedo seemed promisingly different. For one thing, he would gladly take me through Analamazaotra by night, when the nocturnal lemurs were at large.

The indri itself is diurnal. It lays up at night and feeds by day; it does most of its singing (though not all of it, I would discover) in the morning. I knew that much and, although *Indri indri* is what mainly had brought me to Perinet, my time there was short and I didn't want to waste a good evening. I'd go looking for the indri the next day, I thought. Meanwhile, tonight there was a chance to see such shy little spooks as the greater dwarf lemur.

We started walking an hour after dark. Bedo carried a powerful battery beam and I had my dinky flashlight. The forest rustled and hooted with invisible life. I was comfortable in the knowledge that it's a benign forest: no jaguars, no tigers, no rhinos, no poisonous snakes that I'd heard about and, at least on this evening, no leeches or mosquitoes. We hiked for about four hours, crisscrossing the reserve on a network of steep trails. It was an overcast night with hardly a trace of moon, and the footing was tricky. Bedo set a brisk pace. He knew these jungle paths like an American kid knows the shortcut to the neighborhood ball diamond. After the first hour I put away my light, preferring to walk in his tracks and peer into the trees along his beam. Too bad I couldn't see with his eyes. There, he would say. Huh, what, where? *There there*, and he would point with the light. Ninety feet away in a high crotch of limbs, a pair of orange dots would glimmer back. His vision was impressive, but his effectiveness as a guide involved much more than just sharp eyesight; it involved knowledge and intuition and the intensity of his attention. He showed me the greater dwarf lemur, yes, and the brown mouse lemur, little animals squatting in high branches where I never would have noticed them even in daylight. He found four different species of chameleon, some miniature and some giant, all of them slow-moving, swivel-eyed, and camouflaged—but not sufficiently camouflaged to elude Bedo. His attunement to the ecosystem seemed preternatural. To me he paid little notice, as long as I kept the pace and appreciated the animals after he spotted them. He was no cynic, pandering to the predictable tourist impulses, angling for tips. He was a naturalist, inexhaustibly intrigued by his subject and tolerant of the innocent twit who chose to tag along. At one point, while we paused on a hilltop, waiting for my breath to catch up with us, from far in the distance came a high, mournful wail. Another. Sliding notes, harmonies, graceful razor slashes of sound.

Indri.

Bedo said nothing. He listened. This was something he didn't need to identify, not even to such an ignoramus as myself. His face lit in a special way. His face lit, I think, with love.

Finally, on a trail that had looped over several ridges and left me disoriented, he brought us down. We emerged from the reserve along one of its far borders and trudged back to the hotel on a village path. It was nearly midnight. I was sweaty and tired and I had missed dinner. While a grumpy waiter went foraging to the kitchen on my behalf, Bedo sat on a bar stool paging idly through a looseleaf binder. Are you hungry, Bedo? He shrugged.

Over his shoulder, I saw that the binder held mimeographed pages of typewriter print and rough illustrations. It was a quick-and-dirty draft of a taxonomic key to Madagascar's chameleons. Some visiting herpetologist had taken notice of Bedo's interest and left a copy of this treasure in his hands. Here, Bedo said, showing me *Chamaeleo brevicornis*. Pen sketch of a wonderfully ugly reptile with funnelshaped eyelids and a rhinoceros nose. And here, *Chamaeleo parsoni*, the big one. And here, *Chamaeleo nasutus*. Bedo browsed on through the binder. He seemed immune to hunger and weariness. The pages were dog-eared from an excess of careful fondling.

Later, in my notebook, I referred tersely to this "amazing guide." If I had known more of his history and had foreseen his future, I would have scribbled a thorough portrait. But I didn't expect to revisit him as a subject or a person. I was simply struck with a strong sense that if there was justice in life, then this young man might be discovered and nurtured by someone from the larger world. I didn't know that he already had been. I didn't know that Bedo of Perinet was the same teenage naturalist who had helped Pat Wright track and photograph the golden bamboo lemur at Ranomafana.

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MADAGASCAR'S special reserves, the group that includes Analamazaotra, are more numerous and generally smaller than the two other categories of protected area. Currently there are about two dozen special reserves, most of them established in the 1950s and 1960s, when no one in Madagascar or anywhere else was discussing the notion of minimum critical size. The special reserve of Nosy Mangabe encompasses only 520 hectares, not much more than one of Tom Lovejoy's isolated patches of forest. The Mangerivola reserve is slightly bigger, at 800 hectares, and the Cap Sainte Marie special reserve runs to all of 1,750 hectares. These are not immense parcels of landscape. For a standard of comparison from the United States, consider that Bryce Canyon National Park—which, according to William Newmark's work, seems too small to support a population of red fox—covers 14,400 hectares. The special reserve of Analamazaotra, at 810 hectares, is one of the smallest. You could walk its perimeter in a morning.

The perimeter is crisply demarcated. You could walk it in street shoes, and you wouldn't need a machete. Hell, you could rollerskate a good part of the way.

Along one side of the Analamazaotra reserve, from the hotel to the entrance gate, runs a blacktop road. The road isn't broad or busy, but it represents a significant boundary. The gap in the forest canopy is wide enough to prevent, say, an indri from jumping across. Along another side runs a bigger road, a national highway, recently built as an aid project by the Chinese. No chance of an indri crossing that. A third stretch of perimeter is bounded by the village of Perinet and the rail line—again, an impassable zone for an oversized lemur with an arboreal style of travel and a fear of human ruckus. The rest of the boundary of Analamazaotra is marked only by a path. But outside the path is unprotected forest, degraded by woodcutting and clearing for hill rice. There's also a eucalyptus plantation, which can't support lemurs of any kind, let alone indri.

My point is this: The Analamazaotra reserve is no sample within a vast tract of wilderness. It's much closer to being an isolate. If it isn't already insularized, so far as lemurs are concerned, it probably soon will be.

Under current conditions, a recklessly venturesome indri might still wander in or out, crossing through the damaged forest or the inhospitable eucalyptus. When the eucalyptus has been harvested, when the damaged forest has been leveled for rice, the possibility of such crossings will disappear. Birds and bats will still enter and leave. But to its population of indri, the Analamazaotra reserve will be a separate and circumscribed world. Whether that population remains viable over time will depend on a number of factors, most of which are more complicated than a sheer-area measurement of 810 hectares.

The list of factors starts with: How big is the Analamazaotra population of indri?

Pat Wright, who worked there for a season before shifting her focus to Ranomafana, suspects that the number may be as high as two hundred. Probably she's being optimistic. She admits her uncertainty, noting that no careful census has ever been done at Analamazaotra. Nor can any decent estimate be made of indri numbers throughout the whole country, she adds. Although everyone agrees that the species has declined as its habitat has been fragmented and destroyed, no one can claim to know how many indri remain. "There may be more than we think, there may be less," Wright says. "What we think we know is just a dream." Jon Pollock, focusing his own fieldwork on a few family groups, apparently never tried to count the full population at Analamazaotra. But his published data on average group size and population density make possible an informed estimate. Assuming that Pollock's numbers were accurate, Analamazaotra at the time of his study contained about eighty indri.

Two decades later, the figure may be less. The population has more likely shrunk than grown. Let's make the hopeful assumption that it has stayed about constant. If so —if the population has held constant at eighty for the past twenty years, and if it continues to hold at that level into the immediate future—the indri of Analamazaotra are in trouble. Virtually all recent work on the concept of population viability tells us that eighty animals just aren't enough.

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IN THE LATE 1970s, a few ecologists began using a pregnant new term: *minimum viable population*. It could be traced back to a journal paper that two researchers in Australia had published, in 1971, on the ecological requirements of certain species of Macropodidae, the marsupial family that includes wallabies and kangaroos. The researchers, A. R. Main and M. Yadav, had studied macropod distribution on small land-bridge islands offshore from western Australia. For each island under scrutiny, they noted the presence or absence of various macropod species, the island's size, and its diversity of vegetation. Main and Yadav were proceeding in parallel to the fashionable new school of island biogeography, rather than as part of it. They didn't mention the species-area relationship—not by that label, anyway—although it overshadowed their whole study. They didn't mention the equilibrium theory. The sources they drew on, and the context in which they wrote, were almost completely Australian. They referred to their study animals with informal Aussie names, some of which sound as fantastic as creatures from Tolkien: quokka, tammar, euro, boodie. Main and Yadav were interested in macropod conservation, not theory.

They addressed a practical question: How much area was necessary to "adequately satisfy the ecological requirements" of each of these species? Ecological requirements would include sufficient habitat not just for one animal or a few but for a self-sustaining population. How much landscape was needed to support a population of quokka? How much landscape for a population of euro? Could the minimum area requirement of each species be deduced from its presence or absence on those variously sized coastal islands? Some of the smaller islands held only a single macropod species, the tammar or the rock wallaby. Larger islands supported more species and bigger-bodied species. The biggest macropod, the red kangaroo, didn't exist on any of the islands. Main and Yadav gathered the sort of data that would have allowed them to draw a species-area curve for their collection of islands and to explain the irregularities of that curve in terms of habitat diversity. Just as marsupials had evolved in isolation from other mammals, though, their work seems to have evolved in isolation from the influence of MacArthur and Wilson.

They took a further analytical step that made their paper unusual for its time. They calculated the density at which each macropod species populated its habitat. For instance, one animal per hectare for the quokka; one animal per ten hectares for the (bigger-bodied) euro. Then, by multiplying the density of a given species by the area of the smallest island on which that species survived, they produced an interesting set of numbers. "When these data are extrapolated to small island situations," they wrote, "it is possible roughly to estimate minimum viable population sizes."

That seems to have been the first use of the phrase "minimum viable population." Actually it's more than a phrase; it's an important idea. Although several earlier biologists had written vaguely about "minimal populations" and "viable populations," Main and Yadav had said something new. But there wasn't much immediate response.

Main and Yadav also implied but didn't emphasize a point that would later be recognized as significant—that the minimum viable population might differ from one species to another. Still, their results for the tammar, the euro, and the red kangaroo all fell within a narrow range. In the last sentence of their paper, they added: "The minimum viable population (defined as the population size likely to persist indefinitely) appears to lie between two and three hundred animals."

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SEVEN YEARS later, a graduate student in the Department of Forestry and Environmental Studies at Duke University submitted his dissertation. It was an analysis of the task of determining minimum viable population sizes, as illustrated with the case of the grizzly bear. The student's name was Mark L. Shaffer.

Shaffer at that time had never set eyes on a grizzly in the wild. He had grown up in western Pennsylvania, attended college there, and gone off to the University of Pennsylvania for a master's program in land-use planning. But he had found himself more interested in how wildlife uses landscape than in how humans do. He transferred to Duke and started fresh toward a different kind of degree. He took some classes in computer modeling. Also, like so many other biologists of his generation, he became fascinated with island biogeography. When the equilibrium theory began being applied to conservation issues by Diamond, Terborgh, Wilson, and others, Shaffer followed that work in the literature. He read the SLOSS arguments. He was concerned about the worldwide destruction of habitat, the fragmentation of what remained, and the loss of species. He formulated his concern in terms that rang faintly of his earlier work in land-use planning.

He recalls thinking: "We've got a finite amount of land. We're in competition for it with nature. So the question is always, How much do you set aside?" It was the same question that Tom Lovejoy was asking, but Shaffer's route toward an answer was different.

He knew that inside the question *how much?* lurked the question *how many?* That is, he knew that the minimum critical size of an ecosystem was a less fundamental measurement than the minimum critical population of each constituent species. When any species becomes too rare within an isolated patch of habitat, that species can't survive. It isn't viable. It goes extinct. But how rare is too rare?

This question leads to a battery of others. What's the numerical threshold of viability? Is there a single magic number for all species, or does the viability threshold differ for different species? Does it differ for the same species in different contexts? If so, what accounts for the differences? Is the determination of viability threshold a purely scientific task, or does it also involve sociocultural values? Can the sociocultural element be quantified? Shaffer had picked a doctoral topic with some meat.

He chose the grizzly bear as his exemplary case for two reasons: because it was a large-bodied animal at the top of its food chain, and because field biologists had already studied it closely. Of the first reason, he says, "If you focus on things on top of the food chain, and save enough land for them, then probably you're saving enough for the whole food chain." The second reason was relevant because his analysis would depend on types of data available only for an exceptionally well-studied species.

Shaffer would need information about longevity, causes of death, age at first reproduction, average litter size, sex ratios within various age classes of the population, social structure, and breeding system. That sort of information didn't exist for wolves or mountain lions. For grizzlies, thanks largely to a pair of biologist brothers named Frank and John Craighead, it did. The Craigheads had studied the grizzlies of Yellowstone National Park between 1959 and 1970, and had published much of their data.

The Yellowstone grizzlies offered one other advantage. The greater Yellowstone ecosystem is a vast area of woodland and meadow and mountain slopes and river drainages encompassing not just Yellowstone National Park and Grand Teton National Park but also contiguous portions of seven national forests, several wildlife refuges, part of the Wind River Indian Reservation, and some Bureau of Land Management holdings, as well as bits of private and state land, most of it still wild enough to be hospitable to grizzly bears. Despite the patchwork of ownership status, these various pieces constitute a single ecological whole. Because the ecosystem is surrounded by developed terrain (including farms, ranches, barbed wire, towns, suburbs, highways, railroad tracks, irrigation canals, power lines, airports, golf courses, guardrails, trailer parks, malls, lumber mills, movie theaters, gas stations, gun shops, pizza parlors, parking lots, picket fences, barking dogs, traffic lights, stop signs, and concrete lawn ornaments), terrain that *isn't* so hospitable to them, the grizzlies of greater Yellowstone are effectively insularized. They stand discrete as a population, on a discrete ecological fragment. So the Yellowstone grizzlies became Shaffer's empirical paradigm.

The first chore he faced, before considering the specifics of that population, was to define the term announced in his title: "Determining Minimum Viable Population Sizes: A Case Study of the Grizzly Bear *(Ursus arctos* L.)." What exactly is meant by "minimum viable population"? Main and Yadav had defined it as "the population size likely to persist indefinitely," but that was vague. How probable is "likely" and how long is "indefinitely"? Main and Yadav hadn't committed themselves to specificity on these parameters, nor in the meantime had anyone else. Shaffer did. Admitting that his choices were arbitrary, he specified a ninety-five percent likelihood and a time period of one hundred years. If a population of some given size had a ninety-five percent chance of surviving for as long as a century, then by his proposed standard it could be called viable.

Inserting precise numerical values in place of the vaguely worded expectations allowed him to construct a framework of assessment. Another important service that Mark Shaffer performed, before launching into his prognosis for the Yellowstone grizzlies, was to clarify the matter of what generally brings about extinction among small populations.

The causes are multifarious but they can be divided into the two types I mentioned earlier, deterministic (human-generated) factors and stochastic (accidental) factors—or, in Shaffer's preferred language, "systematic pressures" and "stochastic perturbations." Systematic pressures are those that can be predicted and controlled, such as sport hunting, bounties, pesticide applications, destruction of habitat. Stochastic perturbations are those that elude human prediction and control, either because they are genuinely random or because they result from nonhuman causes so intricate and obscure as to *seem* random. Stochastic perturbations introduce uncertainty into the fate of a population—and the smaller the population, the greater the uncertainty. So the study of uncertainty and its consequences is crucial to the conservation of rare species.

Systematic pressures, important as they may be, were outside the purview of Shaffer's project, he explained. He wasn't writing a polemic against bear hunting. What he was concerned with were those stochastic perturbations. How would they affect small populations? At what population threshold would the effects become fatal?

"In general, there are four sources of uncertainty to which a population may be subject," Shaffer wrote. He listed them: demographic stochasticity, environmental stochasticity, natural catastrophes, genetic stochasticity. Behind the jawbreaker terminology were some easily digestible ideas.

Demographic stochasticity means accidental variations in birth rate, death rate, and the ratio of the sexes. Say you have an extremely rare species—make it another hypothetical beast, call it the white-footed ferret. Only three individuals survive, a female and two males. The female breeds with one male, gives birth to a litter of five, then dies. By an unfortunate chance, the newborn ferrets are all males. Demographic stochasticity. Now you have seven white-footed ferrets but no females, and extinction is inevitable.

Environmental stochasticity means fluctuations in weather, in food supply, and in the population levels of predators, competitors, parasites, and disease organisms with which your jeopardized species must cope. Say you have eighteen white-footed ferrets, with a balanced sex ratio, but the prairie dog colony on which they depend for food and shelter is being killed off by a virus. Your ferrets are not susceptible to the virus. Still, without enough prairie dogs to eat, they begin starving. They die back to a mere handful. A three-year drought makes their lives miserable, each long dusty summer adding stress to their situation; then comes a ferociously hard winter. Environmental stochasticity. Hungry, inadequately sheltered, the ferrets go extinct.

Neither of these two types of uncertainty could destroy a large population of animals. There's safety in numbers. But a small population is vulnerable to a gentle nudge.

Natural catastrophes (floods and fires, typhoons and hurricanes, earthquakes and volcanic eruptions) can deliver a nudge that isn't gentle. Such catastrophes aren't totally random, in that they do have physical causes; but the causes are so complex as to be virtually unplumbable, the timing is unpredictable, and therefore these events loom as another sort of uncertainty. Your small population of ferrets might endure the hunger, the droughts, and the hard winter, building themselves steadily back up to a population of three or four dozen—only to be eradicated, blotto, when some catastrophic flood puts their home under water.

Then there's genetic stochasticity. This refers to the vagaries by which certain alleles become more common or more rare within a gene pool, irrespective of the influence of natural selection. The vagaries can be costly in two ways. First, helpful alleles can become so rare—by that random process I described earlier, genetic drift—that they disappear accidentally. Second, harmful alleles that are recessive, rare, and (because of their rarity) ordinarily carried only in the heterozygous situation can become just common enough within a small population that they occur homozygously. Inbreeding increases the chance of homozygosity, by pairing family-carried alleles with themselves. And when recessive alleles occur in the homozygous situation, they achieve expression. If they're harmful recessives, what they express is harm.

The sum total of harmful recessive alleles, within any given population, is known as the genetic load. In a large population, the load can be carried almost without consequence; a few recessive alleles, shuffled among many dominant alleles, produce no effects. In a small population, the load can be more burdensome. Since small populations are often forced toward inbreeding, they frequently suffer from the expression of those harmful recessive alleles. The result is called inbreeding depression. If a given population carries a substantial genetic load and that population suffers an abrupt reduction in size, inbreeding will become more likely, and inbreeding depression may cause trouble.

Another form of genetic stochasticity that affects small populations is the founder effect. Remember the founder effect? Remember the flamingo pink socks? When a small number of individuals become isolated from a larger population (either because those individuals have founded a new colony or because they are sole survivors, the larger population having died away), the small population will contain only a meager sample of the larger population's genetic diversity. To some degree that genetic sample will be random. Rare alleles—whether they're harmful, neutral, or helpful—will have been lost. Even losing the neutral alleles, let alone the helpful ones, may eventually have negative consequences. How? Consider the sock drawer again. When you pack hastily for a trip, groggy in the early morning darkness and grabbing socks at random, you're likely to miss the one flamingo pink pair. But what if your plane makes an unscheduled stop in Las Vegas on Halloween? Of course you'll wish you had them. The founder effect deprives small populations of rare and seemingly useless alleles that might later, under changed circumstances, turn out to be useful.

Genetic drift compounds the founder-effect problem, stripping a small population of the genetic variation that it needs to continue evolving. Without that variation, the population stiffens toward uniformity. It becomes less capable of adaptive response. There may be no manifest disadvantage in uniformity so long as environmental circumstances remain stable; but when circumstances are disrupted, the population won't be capable of evolutionary adjustment. If the disruption is drastic, the population may go extinct.

Environmental stochasticity can deliver just such disruption. So can a natural catastrophe. In fact, all four of Shaffer's stochastic perturbations can interact in a dire feedback cycle by which a small population spirals down to extinction.

Imagine, again, your population of white-footed ferrets. Imagine you have a slightly more reassuring abundance—say, eighty. They live as resident predators within two separate prairie dog colonies, one on a gentle plateau and one beside a river. Comes a catastrophic flood, a once-in-a-century event, unpredictable and unavoidable. It covers your riverside colony and drowns every animal. You still have forty other ferrets on the plateau, but two droughts and then a tough winter reduce that number to twenty. Suddenly you're worried. And you should be. Several of the remaining females, for lack of other options, breed with their sons. Several males breed with their sisters. As a result of inbreeding, some of the offspring are born sterile, and as those animals reach adulthood the overall birth rate goes down. Other offspring of incestuous matings are born without resistance to a bacterial disease; that disease hits the colony, and it kills them. Still others, also victims of inbreeding depression, are born with a general lack of vigor. Nothing is specifically wrong with these ferrets, nothing you can point to, but they don't have the robustness of a heterozygous individual. Another harsh winter, and they die. Now you're down to seven ferrets, and by the sorry breaks of the game only two of your seven are female. One female is too old to give birth. The other female produces a litter of five healthy young, then a coyote eats her. The five young are all males. Final tally? You have eleven white-footed ferrets, consisting of ten males and an elderly female. Your species is history. Take a picture and kiss it goodbye.

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WHAT DESTROYED your population of ferrets? Well, let's suppose that poisoning by government agents and loss of habitat to wheat farming were partly responsible. But those systematic pressures didn't deliver the final blow. Poison and habitat loss merely reduced a once abundant species to a last beleaguered eighty. After that, the four kinds of uncertainty were enough to carry your ferret to its doom.

Mark Shaffer's dissertation, like William Newmark's, turned out to be more than a journeyman's academic exercise. Shaffer provided the first orderly discussion of those four kinds of uncertainty, and he took the significant step of offering a meaningful (though unabashedly tentative) definition of minimum viable population:

> A minimum viable population for any given species in any given habitat is the smallest population having at least a 95% chance of remaining extant for 100 years despite the foreseeable effects of demographic, environmental, and genetic stochasticity, and natural catastrophes.

In a later publication Shaffer would propose a revised definition with higher numbers, based on his feeling that a five percent chance of extinction was too much and that a century of security was too little. He would also add the important insight that creating any such definition, upon any numerical standard, involves society's values as well as biology's powers of prediction. He would recognize that cultural and political questions, as well as scientific ones, will always be part of the process. How much do we care? How badly do we want to preserve white-footed ferrets? What degree of security do we demand?

Species all over the world, reduced to small populations in fragments of habitat, are jeopardized by the four types of uncertainty. Your ferrets might be anywhere. They might be this animal or that plant. They might be the grizzlies of Yellowstone, the snow leopards of Annapurna, the mountain gorillas of central Africa. Or imagine them on a tropical island. Imagine them with the face of a jackal, yellow brown eyes, black-and-white fur like a giant panda's. Imagine you know them as *babakoto*. They sing. Imagine that the last eighty live in a little forest reserve called Analamazaotra.

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PAT Wright came to Analamazaotra in 1984. It was during her first visit to Madagascar, an exploratory trip for scouting the prospects of doing lemur research at various field sites. She and another primate ecologist decided to go down to that famous village, Perinet, for a glimpse of that famous big lemur, the indri. “Being tropical biologists, of course, we didn’t think we needed a guide,” she remembers. “As we were searching for the animals, suddenly this little boy appeared on the trail. And he said, ‘They’re over here.’ “The boy’s name was Bedo. “He was bright-eyed and cheerful, and he spoke a little French. We both liked him very much,” Wright says. “At the very beginning, he was an extremely charismatic personality.” And he led them, as promised, to a group of indri. Later, when Wright and her colleague set out on a longer walk, they took the boy along. “We could see right away that he really knew the forest well. He could point out various forest animals, birds and things, along the way. He had very good eyes.” Wright delivers this much in a flush of easy recollection.

“So,” she adds, with sadness and love in her voice, “that was the first time I ever met him.”

She returned to Analamazaotra a year later with one of her students from Duke University, David Meyers, and together they began making field observations on *Hapalemur griseus*, the close relative of her still undiscovered golden bamboo lemur. Little Bedo became their regular guide. He worked with them each day in the reserve, he shared their meals, he spent most of his waking hours with them. They lived like a family. Bedo was about fourteen then, Wright recalls. “He was really enthusiastic over everything about nature. There was nothing that didn’t interest him. He loved the snakes, he loved the smallest insects and the chameleons. And he was really good at the lemurs.”

He had grown up in a house just across the road, one child among many of a fisheries manager employed at the reserve by Eaux et Forêts, and so Analamazaotra had been his childhood playground. His forest skills derived from devotion, experience, empathy, and another attribute. “He had incredible eyes,” Wright repeats. “I’ve never seen anybody better.”

He was ingenuous but resourceful. Wright tells a story about Bedo’s efforts on behalf of a primatologist who needed fecal samples from the species of lemur he was studying. Bedo absconded with his mother’s cooking pot, stood under the animals for as long as it took to catch them defecating, and returned proudly with the pot full of lemur shit. He had character strength and integrity that was remarkable in a youngster, Wright says. It showed in his attitude toward nature and in his pious adherence to the traditional strictures of his tribe. Wright and David Meyers conversed with him mainly in French but began teaching him English. He was bright. When her work on the bamboo-eating lemurs took her away from Perinet—down to Ranomafana—Wright wanted Bedo to join her there and help with the field survey. But first he had to finish his school year. She left him money for the bus and explained how he should travel to Ranomafana, a daunting journey for a young village boy who had never been anywhere. She knew there was some uncertainty about this proposition. Would he decide to stay home, would he show up at Ranomafana, or would he set out on the trip and then get lost? She remembers the exact date when that question was answered, in late June, because it coincided with a national holiday. She had been out of camp for a long stretch of hours, tromping across the hillsides, bushwhacking away from the trails, following a group of lemurs. Suddenly, there was Bedo. "He not only had found Ranomafana, but he had found us, in the forest," she says. He carried a sleeping bag over his shoulder, and a small pack. He was ready to work.

Eventually he returned home to Perinet, left school, and started making good money (at least by Malagasy village standards) as the best and most-requested nature guide at the Analamazaotra reserve. Pat Wright still visited the village occasionally and stayed close to him as he grew through adolescence.

Once she brought him to the capital. He had never before seen Antananarivo. They took an elevator up to the roof of the Hilton Hotel and gawked at the view. "We were twelve stories high," says Wright. "Higher than any indri had ever been. It was just amazing to see him. He just couldn't believe it." Then he went back to the elevator and rode up and down, up and down, until he was sated with that thrill. Wright also showed him the spectacle of a large grocery store, and they strolled through the Zoma, the open-air market, on its busiest day. At first Bedo seemed enchanted by the whole urban spectacle. But then, Wright says, the enchantment paled. "I remember walking along the street, and I said, 'Well, Bedo, how do you like the big city?' He looked at me and said, 'There's no animals. I don't like it very much. There's no animals anywhere.' He said, 'You can't hear them, you can't see them. They're not here.' And it was just with such sadness."

About the same time, Bedo met a world-class nature photographer named Frans Lanting, who had come to Madagascar on assignment for *National Geographic*. Lanting recognized Bedo's skills and hired him as an assistant, first for work at Analamazaotra, later for some of the trips Lanting made to other parts of Madagascar. Intermittently over the course of a year they traveled together, finding and photographing wildlife. "I crisscrossed the island from east to west and from north to south," Lanting says, "and I never met another individual like him. He was exceptional. He moved through the forest like a lemur." While Lanting and a second helper wrestled with equipment, Bedo would track lemurs or scout ahead for other creatures. He would climb trees. He would notice chameleons. He would discover rare birds on their nests. Because of his agility, his forest sense, and his affinity for the animals, Lanting began calling him by a nickname: *Babakoto*. Little father, ancestor.

Indri.

One aspect of the work was especially hard for Bedo. Although Lanting is a conscientious man with his own passionate devotion to untrammeled nature, even he found a small bit of trammeling to be professionally necessary. With some of the more elusive species, he resorted sometimes to capturing animals in order to photograph them. Later the captives would be released; nonetheless, Bedo didn't like it. He chafed. When an animal was caged, he suffered an empathic sense of spiritual imprisonment. "That's what made him one of the wild creatures of the forest," says Lanting. Mostly they photographed the animals as they found them, under circumstances that demanded more patience but less compromise—at large in the forest. "That's where he was happiest."

Lanting too recognized that Bedo was bright, and that his extraordinary love of the natural world was an important resource in a country so troubled and precious as Madagascar. Clearly, such a gifted young man deserved to be cultivated toward some larger possibility than simply guiding tourists through the Analamazaotra reserve for quick cash. Bedo would never be a scholar, he lacked the disposition for long years of training as a scientist, but he might make a wonderful educator, Lanting thought. Maybe Bedo could share his enthusiasm and his knowledge with impressionable Malagasy children, not just with affluent Western visitors. So Lanting tried to help, involving himself in the boy's education. "And that's where things became frustrating," he says. Bedo was an adolescent, after all. In his case the eternal adolescent afflictions of confusion and headstrong impatience were exacerbated by his life at the Hôtel-Buffet de la Gare. Elsewhere he was just another poor village boy, but at the hotel he was a celebrated guide, fawned upon and well paid by foreigners. His schoolboy existence, in contrast, seemed dull and pointless. He became truant. He started to flunk out. Lanting wanted to help pay for Bedo's schooling, as did Pat Wright, but the effort was futile if Bedo didn't attend. Lanting visited the school principal, hoping to arrange some framework of support and accountability that would encourage Bedo to persevere. Couldn't there be, Lanting wondered, a structure of expectations and incentives? Couldn't the principal send him some sort of modest, regular report as to how Bedo was doing? But structure, incentives—these were alien concepts that could be translated only loosely. Establishing a framework of accountability proved impossible. "In that sense," Lanting says, "Madagascar's like quicksand."

Not long after Bedo left school, I arrived at Perinet for my own first visit, becoming another of the foreigners who fawned on him, paid him well, and made his work as a guide seem more promising than further education. On the night he led me through Analamazaotra, I wasn't aware of his connections with Wright and Lanting. I had no inkling that he was already Madagascar's most famous young naturalist, admired not just by tourists but by a number of eminent foreign biologists who had either done fieldwork at Analamazaotra or at least stopped there to see and hear the indri. I knew nothing about the tension in his life between school and forest. I knew nothing about his travels to Ranomafana and elsewhere. I certainly didn't appreciate that his quiet charm, his confidence among English- and French-speaking clients at the hotel, his expertise, his earning power, his emergence as a minor celebrity, might make him resented in his own village. I didn't begin learning any of this until later, back in the United States, when Pat Wright told me by telephone that Bedo had been murdered.

The details were still indeterminate, Wright said, but there was no doubting the basic fact. His body had been found. In a voice dry and heavy with sorrow, she reminded herself and me, "He had the best eyes."

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MARK Shaffer's dissertation, discussing the four kinds of uncertainty that jeopardize small populations, was submitted in 1978 but not published. His first journal article on the subject didn't appear until 1981. Meanwhile two other scientists, Ian Franklin and Michael Soulé, working independently, tackled the same question: How rare is too rare?

Although neither Franklin nor Soulé used precisely the same phrase—minimum viable population—as Shaffer had, they each analyzed some of the factors that determine such a threshold. They even dared to suggest certain tentative numbers. Whereas Shaffer had looked mainly at the demographic aspect of uncertainty (because that was what presented itself in the grizzly bear data he was using), Franklin and Soulé both considered the genetic aspect. They published their analyses, in 1980, as separate chapters of a volume titled *Conservation Biology: An Evolutionary-Ecological Perspective*. Soulé himself was one of the book's editors, and he had invited Franklin to contribute. Their individual treatments converged on one remarkably similar conclusion, which gave a sense of reliability to what they both said.

Franklin was a quantitative geneticist. He discussed how genetic variation is lost in a small population (by the founder effect and genetic drift) and how the consequences of that loss (including inbreeding depression and loss of adaptability) affect both the short-term and the long-term prospects for survival of the population. In the short term, the main concern is inbreeding. "There will be a minimum population size, depending on the species, at which the population will be able to cope with the inbreeding effects," he wrote. Below that minimum population size, inbreeding depression will be problematic. Harmful recessive alleles will tend to turn up homozygous (like snake eyes in craps) among the offspring, and the population will become genetically maimed. Intrepidly, Franklin offered a generalized estimate of this minimum size in relation to inbreeding. Based on the collective experience of domestic-animal breeders and on some other evidence, he suggested the number fifty. If the population barely exceeds that minimum, if it escapes the dangers of inbreeding and manages short-term survival, then the gradual loss of genetic variation over the long term becomes a concern.

The long-term prospects depend on a balance between two counterpoised factors: mutation and genetic drift. What one giveth, the other taketh away. In any population, genetic drift tends to eliminate the rarest alleles from being passed down between generations. The mutation process, in the meantime, adds a sprinkling of new variation to the gene pool.

Some mutations will be potentially harmful, some will be neutral, some will be helpful—and even those that are neutral under present ecological conditions may turn out to be helpful when conditions change. So the phenomenon of mutation shouldn't be thought of as necessarily bad. It supplies fresh possibilities for adaptation and evolution.

In a large population, the rate of mutation will more than compensate for the rate of loss, and genetic drift will be no issue. But a smaller population will experience fewer mutations. In a very small population, Franklin explained, the losses by drift will be greater than the gains by mutation, and the richness of genetic potentiality will leak away. How small is too small to maintain a positive balance? Franklin again offered a bold estimate. Based on laboratory work on *Drosophila*, he placed the balance point at five hundred. Below that number, a population will have less adaptability and diminished prospects of long-term survival with each passing generation.

These estimates became famous as "the 50/500 rule": for short-term avoidance of inbreeding, fifty; for maintaining long-term adaptability, five hundred. Being specific, the numbers were destined to attract criticism. Some biologists considered them deplorably simplistic and misleading. The 50/500 rule also caught the attention of park planners and wildlife managers, including those Costa Rican officials who (as Dan Simberloff told me) felt obliged to give up on their harpy eagles and jaguars, since the populations at issue were below fifty. Why did the numbers carry such force? Because they were plausible, because they were based on evidence (though only a small amount) as well as on sound theoretical argument, and because people were hungry for answers. This isn't to imply that the 50/500 rule was a pernicious mirage. Even if Franklin's numbers weren't accurate, they certainly helped to sharpen the focus of the discussion.

Another valuable service of Franklin's chapter was that it clarified the crucial distinction between *census population* and *effective population*. The census population is the sheer number of living individuals. The effective population is a number derived mathematically, reflecting the patterns of breeding participation, gene flow, and loss of genetic variation. Among sexually reproducing animals and plants, the effective population will almost inevitably be smaller than the census population. But how much smaller? That depends, Franklin explained, on how many females within the population are reproductively active, how many males win a chance to mate with those females, how much difference in fecundity distinguishes one female from another, how much imbalance exists in the ratio of effective females to effective males, and how much the population size fluctuates from one generation to the next. In a herd of elk, where a few great bulls gather harems and the younger males get little or no chance to mate, the effective population will reflect that inequity of opportunity. Franklin offered a few simple equations relating the various relevant factors to effective population size. The general message of his algebra is that, depending on reproductive habits and demographic history, the effective population may be drastically smaller than a mere head-count of individuals would suggest.

Why is this important? Because any minimum population threshold pertains to the effective population, not the census population. In other words, the precautionary wisdom of population genetics tells us that eighty indri aren’t actually eighty indri.

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MICHAEL Soulé, in his own chapter of *Conservation Biology*, divided the genetic issue into three concerns: first, inbreeding depression over the short term; second, loss of adaptability over the longer term; third, the danger that significant evolutionary change among vertebrate species was "coming to a screeching halt" throughout a large part of the planet. He discussed the first and the third concerns, pointing back to Franklin's chapter for a consideration of the second.

Like Franklin, Soulé had been reading the animal-breeding literature as well as the records of experimental genetics. He described a brothers-and-sisters mating experiment that had been conducted with a breed of swine known as Poland China, yielding various symptoms of inbreeding depression after just two generations. The average number of Poland China piglets per litter fell sharply; the survival rate among newborn piglets fell sharply; and the sex ratio of newborns shifted toward males, resulting in a shortage of young sows. Soulé had also investigated cases involving guinea pigs, poultry, mice, and Japanese quail. He cited obscure agronomic papers such as "Inbreeding as a Tool for Poultry Improvement" and "Influence of Inbreeding on Egg Production in the Domestic Fowl." Pragmatic animal breeders, he reported, had discovered by trial and error just how much inbreeding is tolerable to a line of domestic stock before the poor creatures start going weird. "Their rule of thumb is that the per generation rate of inbreeding should not be higher than two or three percent," Soulé wrote.

Among wild creatures the situation would be somewhat different. A line of domestic animals, with its centuries-long history of manipulated breeding by humans, is generally less vulnerable to inbreeding depression than most wild species, because in a domestic line many of the harmful recessive alleles have already been bred out. So Soulé proposed a slightly lower limit as the safe standard for conserving wild populations: one percent inbreeding per generation. At that modest rate, a small population in the wild would probably be spared from inbreeding depression over the short term—for five or ten generations. How does it translate into population size? For the inbreeding rate to be held to one percent, Soulé calculated, the effective population size must be at least fifty. So, by his own path, he had come to the same numerical conclusion as Franklin. A rock-bottom minimum of fifty, as effective population, should be considered necessary for the avoidance of inbreeding depression over the short term.

Soulé labeled it "the basic rule." The word "rule" sounds more urgently persuasive than "recommendation" or even "warning," and probably Soulé's label is what encouraged other biologists later to speak of "the 50/500 rule" in reference to his work and Franklin's. Of course, both these numbers represented early and tentative attempts, by a pair of daring thinkers, to give some provisional quantification to a concept that was still in the process of being defined.

Soulé's third concern was bigger and more worrisome.

"This century will see the end of significant evolution of large plants and terrestrial vertebrates in the tropics," he wrote. The end of evolution? Yes—although what he meant, more precisely, was the end of speciation. Existing species of trees and of vertebrate animals might continue to evolve incrementally within a single lineage, but they would no longer split into new and distinct lineages. This is a damned serious claim, since such splitting constitutes one of the main sources of biological diversity. Soulé's logic was based on the worldwide attrition of wild landscape as well as on the biogeography and genetics of speciation. Because of habitat destruction and fragmentation throughout the tropics, he argued, and because the nature reserves that humanity grudgingly sets aside will be too small, we should expect a time in the near future when vertebrate and tree speciation virtually stop. Each species will have barely enough habitat (at best) to maintain itself as a viable population, but not enough to allow it to split into several divergent populations. Each reserve will offer inadequate area, inadequate topographic relief, inadequate pockets of geographical isolation, to foster allopatric speciation among large creatures. As species are lost to extinction, the losses won't be counterbalanced by new species, and Earth will grow gradually impoverished of large-bodied animals and plants. The invertebrate animals and simpler plants—those creatures that are generally much smaller and more numerous—may not be so sorely affected. But for the overall diversity of large vertebrates and trees, if Soulé is correct, the consequences will be severe. Species of rare ape will disappear, and no new ape species will arise. Species of feline will go extinct, and no new felines will evolve. Species of dipterocarps, the great hardwoods of Asian rainforests, will be lost and not gained. The world will be an emptier, lonelier place. Still, we humans can probably look forward to sharing the future with a fair number of beetles, tapeworms, fungi, tarweeds, mollusks, and mites. Dandelions and silverfish are also a good bet.

The whole idea is profoundly gloomy, important, and persuasive. Even with that weighty message, though, Soulé's individual chapter in *Conservation Biology* was a less significant contribution than what he had done toward making the book itself happen. And behind the book was something larger still: a new branch of biological science.

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DURING THE LATE 1970s Michael Soulé was teaching biology at UC-San Diego. His early research specialty had been the genetic basis of morphological variation among reptiles, but he had grown steadily more worried about the larger problems of habitat destruction, habitat fragmentation, genetic deterioration of small populations, and extinction. He saw that many ecologists and population biologists were beginning to address these problems but that their efforts were mostly narrow and scattered. There was no coordination and not much cumulative effect. There was no common forum for scientists concerned with extinction and how to prevent it. Soulé felt that something had to be done. In 1978 he and a graduate student named Bruce Wilcox convened a gathering in San Diego. They called it, grandiosely and hopefully, the First International Conference on Conservation Biology.

Papers were presented by about twenty biologists, including Jared Diamond, John Terborgh, and the padrone of conservation-minded biologists, Paul Ehrlich. Soulé and Wilcox edited the papers into that compendious volume, *Conservation Biology: An Evolutionary-Ecological Perspective*, published two years later. The book's cover featured a brown-tinted negative image of African antelope, nicely suggesting the threat of negation by extinction. The brown tint turned out to be useful as a marker, since the phrase "conservation biology" would repeat itself on other publications and the subtitle, though descriptive, didn't roll off anyone's tongue. This volume became known, among cognoscenti within the field, as the Brown Book. Eventually there would be a rainbow of others.

It wasn't the first book to address the subject. Raymond Dasmann had published *Environmental Conservation* back in 1968, and David Ehrenfeld's *Biological Conservation* had appeared in 1970. But the Brown Book was something different: a collaborative effort by a broad group of scientists, many of whom had spent their professional lives under the influence of *The Theory of Island Biogeography*, all of whom agreed that the biological world was falling to pieces and that action had to be taken. These scientists were united by a bone-deep sense of ongoing loss. With each further hectare of ecosystem destroyed and with each additional species extinguished, they realized, the biological universe to which they had devoted themselves intellectually (and emotionally) became smaller. If the trend continued, the near future would see ecologists and field biologists increasingly supplanted by museum curators, paleontologists, and historians—people who could remind the public that once upon a time our planet had been graced with living elephants, bears, and lemurs.

In the book's introductory chapter Soulé and Wilcox defined the enterprise. "Conservation biology is a mission-oriented discipline comprising both pure and applied science," they wrote. On the pure side, it encompassed ecology, evolutionary biology, island biogeography, genetics, molecular biology, statistics, and a handful of other disciplines in the background, such as biochemistry, endocrinology, and cytology. On the applied side, it included economics, natural-resources planning, education, conflict-resolution techniques, and everything that island biogeography could teach regarding the design of nature reserves. Until recently, according to Soulé and Wilcox, academic snobbery had left many biologists unwilling to touch the subject, because those academics saw "applied" biology as the traditional province of lesser intellects trained in wildlife management and forestry. "But academic snobbery is no longer a viable strategy, if it ever was." The posture of superior detachment was a fatuous luxury that just couldn't be afforded anymore. "There is no escaping the conclusion that in our lifetimes, this planet will see a suspension, if not an end, to many ecological and evolutionary processes which have been uninterrupted since the beginnings of paleontological time." Personally, wrote Soulé and Wilcox, they hoped that it might be only a suspension. The purpose of the book, the purpose of conservation biology, was to prevent such an interruption from being permanent.

At least some of the anger and clarity in this statement came from Michael Soulé himself, an interesting man whose own career has tracked the historical progression of these scientific disciplines—from evolutionary biology to island biogeography to viable population theory and conservation biology—more closely than any other person's.

Soulé grew up in San Diego during the 1940s and early 1950s, when the city was still surrounded by small canyons full of chaparral vegetation and a boy could harvest abalone and lobster along the tide line below Sunset Cliffs. He played in the canyons; he collected butterflies; he looked at pond water through a microscope. He had a tolerant mother who let him keep snakes in his bedroom. Forty years later he's a professor at Santa Cruz, where I visit him in his office.

In his mid-teens, Soulé tells me, he belonged to a club of junior naturalists associated with the San Diego Natural History Museum. "It was sort of an informal group of nature-freak kids who would be called nerds, I suppose, these days," he says. "But we were all nature fanatics, and we'd go on field trips into the mountains and out to the desert, and go collecting marine invertebrates along the coast." They went down into Baja on one trip and even got out to some of the islands in the Gulf of California. It foreshadowed research expeditions that he would make later, to many of those same islands, while he was a grad student under Paul Ehrlich up at Stanford. That was the early 1960s, and by then Soulé had fallen under the spell of an exciting new theory, just published by two young rebels named MacArthur and Wilson.

During his years of doctoral work, he spent some time on the island of Angel de la Guarda and collected lizards at the Cañon de las Palmas site, where Ted Case more recently has been chasing chuckwallas. One of Soulé's earliest publications was a paper on reptile biogeography among the Gulf of California islands—a paper that owed much to MacArthur and Wilson. He and his co-author charted the distributional patterns and discussed the species-area relationship and the distance effect. Later, Soulé would do island work also in the Adriatic and the Caribbean. Still later, he would publish a paper describing ecosystem decay on insular fragments of chaparral habitat in San Diego County. The equilibrium theory was to him a stunningly useful tool, like the microscope through which he had once peered at pond water.

I ask him when he became aware of that theory.

"The day it was published," he says.

After finishing his doctorate and teaching for several years at a university in Malawi, in southeastern Africa, he came home and took a position at UC-San Diego. He continued his research on reptiles. Meanwhile he felt increasing concern about the conflict between human population growth and wild landscape. He had been sensitized to the population problem by his graduate advisor, Dr. Ehrlich (as had many Americans who knew Ehrlich only distantly, as author of *The Population Bomb)*, and in Malawi he had seen some of its consequences, both in terms of human travail and in terms of toll on the landscape. The surviving wildlife of Malawi wasn't nearly so abundant as the great game herds up in Kenya or Tanzania, and it was mainly restricted to a few small national parks. The changing landscape of southern California gave Soulé farther data, reminding him that habitat loss isn't solely accountable to starving Africans with machetes and plows.

"It was clear that San Diego was being destroyed," he says. The chaparral canyons were succumbing to urban sprawl. "They were paving paradise and turning it into a parking lot, as the song says. And when you see a place where you were born and raised being destroyed, it's very poignant. That probably creates a deeper—in *me* it created—a deeper degree of angst and concern than anything else. Yet, to be in a place long enough to see it go from either pristine to not pristine, or from tolerable to intolerable, before you are really moved to action …" His voice trails off. Michael Soulé was certainly moved to action, but apparently not as early as he wishes he'd been.

"Forgot what you asked me," he says.

"When you first became concerned about extinctions."

Oh yes. Well, it was gradual. It was a slow dawning. First there was that simpler worry about human population growth overwhelming the landscape. He was also aware of what Diamond and others were saying in the early 1970s about the implications of the equilibrium theory for small nature reserves: loss of species, relaxation to equilibrium, lower diversity on isolates than on samples. Then in 1974 he went on sabbatical to Australia. While he was there, an eminent wheat geneticist named Otto Frankel asked Soulé to come down and give a seminar in Canberra. He was interested in Soulé's work on islands, Frankel said, because he thought it might be relevant to a concern of his own, genetical conservation. "I'd never heard of genetical conservation before," Soulé recalls. And he knew beans about wheat. But he said sure, he'd be glad to give a seminar. The contact with Frankel led to a major collaboration that stretched across some years and yielded a co-authored volume, *Conservation and Evolution*. It's another of the milestones in the field.

Conservation and Evolution was published in 1981 with a green cover. The title isn't catchy, so it became known as the Green Book.

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SOULÉ'S OFFICE IS tiny, and we share the space with his bicycle. Something about California ecologists, I suppose—Ted Case also parks a ten-speed in his office. On the wall beside Soulé is a print of zebras. On another wall, a photo of the volcanic fires of Kilauea, in Hawaii. There's a file cabinet, a greaseboard for sketching ideas, a Christmas cactus in bloom on the desk, a Macintosh computer, and a cast of the skull of a sabertooth cat. I remember seeing the sabertooth skull in Ed Wilson's office and wonder passingly whether this is a runic token of membership in the elite of island biogeographers. Soulé is a lean middle-aged man in gym shoes, with a graying goatee. As we talk, he eats lunch: instant lentil soup from a cardboard cup. His life seems serious and compact, in a way that I find admirable, and he answers all my scientific questions and most of my biographical ones quite obligingly. Only a spirit of nosy mischief compels me to ask about his years at the Institute of Transcultural Studies, a Zen center in Los Angeles.

No mystery, he says. He was tired of the university scene. Burned out. The personal environment had come to seem stultifying. This was 1978, same year as the first conservation biology conference. He had had it with academic values and academic scuffles. So he resigned his tenured position at San Diego, went up to the center, and for a time functioned as its director. Helped with the medical clinic. Started a program of Buddhist studies. But he also continued with biology during that period. No, I shouldn't assume that he had despaired of studying nature or laboring to conserve it. He had just gotten a bellyful of the professorial life. At the Zen center he finished his work on two collaborative volumes—the Brown Book, from the conference, and the Green Book, with Frankel—and he wrote several papers. Did some international consulting on conservation genetics. Also, there was that essay titled "What Do We Really Know About Extinction?" with his list of eighteen contributing factors, which appeared in a volume called *Genetics and Conservation* (later to be known, by chromatically inclined insiders, as the Gray Book). It was a reason ably productive time, the Zen period, even in scientific terms, Soulé explains.

Yes, evidently so. I had pictured five years of ethereal meditation in a saffron toga. As I turn the conversation back to other topics, it occurs to me that considering the significance of those publications as well as their sheer quantity, the Institute of Transcultural Studies must have offered a work environment that other biologists might do well to consider.

On the strength of those early writings, Soulé emerged as one of the pioneer theorists on population viability. Then, in 1982, the ambit of theory intersected the ambit of practice when he got a call from a man named Hal Salwasser, who held the position of national wildlife ecologist for the U.S. Forest Service.

Salwasser had a problem that he hoped Dr. Soulé might help solve. Back in 1976, Congress had passed the National Forest Management Act, amending the directives by which America's national forests were to be managed. Prior to that, a law dating from 1897 had dictated that managers should "protect and improve the forest," which was a sweet notion but too vague, leaving latitude for decades of excessive and ecologically damaging timber harvests. "Improving" the forest could be construed, and often had been, in a shamelessly reductionist sense. To carve logging roads through an old-growth wilderness, or to clearcut a mixed stand of trees and then plant seedlings of one fastgrowing species, might both be taken as improvements; if biological diversity was reduced in the process, well, tough splinters, that wasn't the Forest Service's mandated concern. But in 1976 the mandate had changed.

The new law made plain that increasing the standing stock of harvestable board-feet did not alone constitute protecting and improving a forest, and that managers were obliged also to "provide for diversity of plant and animal communities" within the forest boundaries. Furthermore, in the planning regulations associated with the new act, Salwasser found this command: "Fish and wildlife habitat shall be managed to maintain viable populations of existing native and desired non-native vertebrate species in the planning area." Viable populations of the native vertebrates? Fine, Salwasser was happy to try. But what exactly did it mean? What constitutes viable? He was calling with the hope that Soulé and Soulé's academic colleagues might share their thoughts toward an operational definition.

"I think it was a seminal event," Soulé says.

Soulé and Salwasser convened a workshop, under Forest Service sponsorship, that brought a small selection of viable-population theorists together with some of the agency people. It was held in Nevada City, California, in the foothills of the Sierra. Among those attending was Mike Gilpin, the aging triathlete with the nimble touch for computer programming, who remembers it vividly.

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"AND so I get invited to this meeting," Gilpin tells me during one of our many talks. A very small meeting, he explains, funded by the Forest Service and hosted by this fellow Hal Salwasser, an ecologist, who was charged with developing a new set of planning regulations. In addition to Salwasser and Soulé and Gilpin himself, the group included just three other Forest Service biologists, two other academics, and Mark Shaffer, who by that time held a job with the U.S. Fish and Wildlife Service.

"Now, I didn't know much of the background," says Gilpin, "but when Salwasser finally got around to closely reading his own National Forest Management Act of 1976, he saw the line in it that said, 'Each forest superintendent shall maintain viable populations of each vertebrate species in each national forest.' "It's a loose quote, rendered from memory, but there's no blurriness to Gilpin's recollection of the crucial two words. "So. One had to decide what a 'viable population' was."

Soulé had come up with the number fifty, Gilpin reminds me, as a rough approximation of the minimum population necessary for short-term avoidance of inbreeding depression. Ian Franklin had generated the other number that was currently in the air, five hundred, for long-term survival and adaptation. But how short was short-term? How long was long-term? How should a bunch of federal land managers construe that sticky phrase, "viable populations," which had somehow found its way into their planning regulations? If they went to the standard ecology textbooks, says Gilpin, they wouldn't find much help. The whole body of thought was too new. The ideas were just being invented.

"Anyway, we show up at this meeting," Gilpin recalls, "and, sort of the typical thing, you're sent some material in advance of the meeting, and you never read it. You figure you'll read it the night before, in the motel." That's what Gilpin had figured. But with circumstance and lassitude intervening, he had figured wrong. "So I got to this meeting not really knowing what they were talking about. I'd never read the National Forest Management Act and had not been interacting with any sort of real-world biologists for a long time." The Forest Service personnel turned out to be bright people who were eager to nudge their agency toward doing the right thing, if only some reputable scientific specialists would help them to say what that was. "We had this question read to us, and we sat around for two days dealing with the problem of population viability." Gilpin remembers the frustration that hit him—confident guy, agile mind, broad training—when he realized that he couldn't solve it.

"I was somewhat humiliated," he says. "I was also struck by the *reality* of this question."

He and his fellow theorists were being asked to make what seemed like a basic, uncomplicated forecast. "There's the species. You have some information on it—you don't have *enough* information, but you do have some information. Now," says Gilpin, casting himself in the managers' role, "tell me whether that species will be here, or not, fifty or a hundred years from now." It was a binary question: yes or no. If this branch of science had acquired any predictive capability whatsoever in the years since MacArthur and Wilson, here was a chance to deliver. "You didn't have to say the numbers, you didn't have to say what the genes were going to do. You just had to make the simplest possible prediction. Yes or no. Fifty years." Would the species survive for another half century or wouldn't it? When he realized that none of them—not himself or Soulé or the others—could offer a firm answer, Gilpin knew that their work hadn't come as far or made itself as useful as he had wanted to believe. Not yet, anyway. There was still too much uncertainty standing between population viability as an abstraction and the capricious empirical events of any particular case.

After the brush with reality at Nevada City, Mike Gilpin began giving the problem more thought.

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THEORY-HEADED wizards such as Gilpin and Soulé were unaccustomed to being asked for guidelines that a huge federal agency might actually put into practice. It was gratifying but also perplexing. It was probably a little scary.

The earlier rule-of-thumb numbers, fifty and five hundred, were obviously too general and absolute. A population of grizzlies in the greater Yellowstone ecosystem would not suffer precisely the same risks, nor react to them in precisely the same ways, as a population of spotted owls in western Oregon or a population of snail darters in Tennessee. The threshold of viability and the factors that determine it would vary from case to case. "The moral of this tale," Soulé wrote later, "is that the closer we approach reality, the more complex the problem appears."

Soulé himself had meanwhile emerged from the Zen center and reentered the academic world. Whether that carried him closer to reality or farther away is a matter of opinion about which even he seems to harbor ambivalence.

He took a position at the University of Michigan. Among the first things he did there was organize another small workshop on population viability. It was held at Ann Arbor in October 1984, with sponsorship by both the Forest Service and the Fish and Wildlife Service as well as support from several private organizations such as the New York Zoological Society. Mike Gilpin, Hal Salwasser, and Mark Shaffer participated again, joined now by more than a dozen select population biologists, evolutionary geneticists, and statisticians. This was the meeting, as Gilpin remembers it, that "definitely put all the pieces out on the table." From the table, those pieces went into a book. Soulé again served as editor, and the ideas brought to focus at Ann Arbor appeared eventually in *Viable Populations for Conservation*. The cover of that one is bright blue.

The Blue Book is thin in pages, dense in content. Math and computer modeling figure prominently. In their individual chapters, Gilpin and the others examined various implications of demography, genetics, effective-population size, spatial relationships among multiple small populations, and probability theory. They also discussed some practical realities: the genetic impoverishment of the California condor, the need for institutional cooperation in managing American grizzly bears, the cost-to-benefit ratio of forestalling the extinction of the Sumatran rhino, among others. The comprehensive overview, the voice of wisdom and synthesis, came from Soulé.

In an introduction and an epilogue he subsumed the technicalities and offered perspective. For instance:

> The problem that we address in this book is "How much is enough?" Put more concretely, it is: What are the minimum conditions for the long-term persistence and adaptation of a species or population in a given place? This

> is one of the most difficult and challenging intellectual problems in conservation biology. Arguably, it is the quintessential issue in population biology, because it requires a prediction based on a synthesis of all the biotic and abiotic factors in the spatial-temporal continuum.

Another instance, rather more pungent:

> There are no hopeless cases, only people without hope and expensive cases.

Soulé was the graybeard who could speak in these tones. He was the one who could trace the history of this scientific enterprise, which he and others now called conservation biology, backward through time—not just to David Ehrenfeld and Raymond Dasmann and Paul Ehrlich, not just to MacArthur and Wilson, not just to Frank Preston, but beyond them to a broader and longer intellectual and ethical tradition encompassing Rachel Carson and Aldo Leopold and Charles Elton and Gifford Pinchot and Theodore Roosevelt and Thoreau and Darwin and Saint Francis and Lao Tzu and a less familiar figure named Ashoka.

"Who was Ashoka?" I ask him when he has finished his soup.

The first Buddhist king of India, he tells me. "There was a period where Buddhism was the dominant religion—a short period of time—before the Mongol invasions of India. And Ashoka was a Buddhist king who issued a number of edicts called the Pillar Edicts. They were called that because they were written on pillars and put around the countryside. Like some of the prophets and kings of Israel, he recognized that it was possible to abuse and overexploit natural resources. So he issued rules about forestry and agriculture and the conservation of natural resources. They were one of the first sets of laws ever issued on conservation."

"What was the time period?"

"This was before Christ." Maybe about 100 B.C., Soulé says. But he's just guessing, he adds, don't hold him to it. He claims to have a bad memory. Keeping the dates of such-and-such a conference and such-and-such a workshop and so-and-so's important journal paper all straight in his head—that's hard enough, let alone ancient history like his boyhood in San Diego or the reign of Ashoka.

Our rambling conversation has already used up most of the time slot he promised me, so I let Ashoka drop. Dates can always be checked and corrected. There's another subject that interests me more. Since Michael Soulé has been such a pivotal figure—arguably, *the* pivotal figure—in the development of conservation biology and viable-population theory from its origins in island biogeography and elsewhere, I want to ask him at least one further question: about SLOSS. What I'm hoping, of course, is that he'll spill some gossip.

"Is it my imagination," I say, "or was that debate a little more heated than the average scientific disagreement?"

Soulé answers. His answer is discreet, statesmanlike, generous to all parties, and not for quotation.

So I back off, and come at the same subject again with a different approach. This approach is less gossipy and more decorous, unfortunately, but it's the best I can do. I ask Soulé about a curious journal paper that he published, in 1986, with Dan Simberloff as his co-author. I've read the thing three or four times, and though its scientific content is straightforward, I remain fascinated by its invisible political dimension. The pairing of authors seems odd. The SLOSS debate had long since grown truculent by 1986, with two factions fighting it out in the journals, and that truculence had been aggravated still further by the null-hypothesis controversy. Soulé was a close colleague of Mike Gilpin's, and his own record of work tended to identify him with the Diamond faction. Simberloff was the archenemy of that faction. If SLOSS was trench warfare, this paper seemed the equivalent of Lloyd George in a bear hug with Kaiser Wilhelm. What happened?

"I never met Dan Simberloff until I was in Moscow one time," Soulé says. They were both there as guests of an eminent Soviet biologist and they found themselves staying at the same hotel. They had dinner together one night and then did some sightseeing, in the course of which Soulé discovered that, God help him, he *liked* Simberloff. The guy was good company in a foreign land. "He's one of the most urbane and sophisticated people I've ever met. Extremely cultured and knowledgeable about music and art. It was wonderful for me to be able to hang out with him. And at the time, I had a manuscript with me …" Soulé's famously imperfect memory fails him again as he tries to recall how the manuscript had arisen in conversation. Maybe he had discussed it in a seminar, though he isn't sure. Anyway, the subject was on his mind and the manuscript was among his papers.

"It was about trying to resolve this dispute between Diamond and Simberloff. Those were the two key antagonists," he tells me unnecessarily. Then he corrects himself to a more emollient wording: "—protagonists."

Before getting to know Simberloff, he says, "I considered myself more on the side of Diamond." His manuscript treated all the same issues of nature-reserve design that had troubled Tom Lovejoy and others, that had driven the SLOSS debate, and that had led to the entrenchment of the two factions. Soulé was now attempting to get past the old, polarized view of those issues by way of the more recent insights in viable-population theory. He was also hoping to make peace. There were so many powerful forces against which conservation biologists had to fight, he believed, that they just couldn't afford to fight against each other. "I gathered up my courage and I said, 'Dan, I want you to read this and see what you think of it.' "

Simberloff read the manuscript and thought enough of it to offer constructive criticism. He suggested some revisions and additions. Eventually, at Soulé's invitation, he signed on as co-author. The paper appeared in a good British journal under the title "What Do Genetics and Ecology Tell Us About the Design of Nature Reserves?" The word "Us" carried a bit of special significance, given the pair of authors: What points can we *all* agree on, Diamondites and Simberlovians both? But there weren't necessarily many. In the first sentence of the abstract, Soulé and Simberloff declared: "The SLOSS (single large or several small) debate is no longer an issue in the discussion about the optimal size of nature reserves." No longer an issue? Was that wishful thinking? I ask Soulé.

"Yes," he says.

Yes, but not entirely. Although some people continued fighting the old war, belaboring the old SLOSS dichotomy, others were moving into the new mode of thought. The more forward thinkers concerned themselves with population viability, not just with small areas versus large ones, and explored the notion of keystone species, meaning those plants and animals that might be especially crucial to maintaining the cohesion of an entire ecological community over time. Soulé and Simberloff emphasized keystone species and population viability as essential to the task of designing nature reserves. And they opined that if SLOSS wasn't a dead issue, it probably should be. With or without a little wishful thinking, the paper was a worthy effort.

I ask him about its effect. Did it help at all toward coaxing people out of the trenches?

"Who knows. I mean, my impression is that it did. But I don't have any direct evidence of that."

Soulé, the mediator, the synthesizer, is slow to claim credit and cautious about making leaps from fact to hypothesis. He's a good population biologist with a salubrious grounding in Zen and a strong sense of the probabilistic component of events. He knows that so much is always uncertain.

After two hours I thank him and prepare to clear out. While Soulé goes to find me a reprint of one of his more obscure articles (a gracious gesture that will spare me some library legwork), I notice an interesting small touch of his office decor. It's a photocopy of a newspaper clipping, taped inconspicuously to the side of a bookshelf. The headline says FACE OF CHRIST APPEARS IN TORTILLA AS IT FRIES.

When Soulé returns, I remark on it. Dan Simberloff's office door is upholstered with similar stories, I say. Was it Simberloff who sent this clip? Soulé can't recall. Possibly it was Dan, yes. In pen, at the bottom, someone has written: "Tickets on sale now!"

"He has a wild sense of humor," Soulé says.

I try to imagine that side of the complicated guy whom Soulé got to know in Moscow. Simberloff as incorrigible cutup. Simberloff as manic goofball, sending found comedy through the mail for the yuk of it. Um, okay, maybe. I still have a sense, though, that the tortilla thing represents more than pure silliness. I mention my own hypothesis about Simberloff pursuing the null-hypothesis argument by other means.

"Yes. He's a professional skeptic." Soulé gives me a tiny, dry smile. It's not as though the connection hadn't occurred to him. "I'm an amateur skeptic. But I do what I can."

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MARK Shaffer's contribution to the Blue Book was titled "Minimum Viable Populations: Coping with Uncertainty." It carried forward the line of thought that he had presented in his dissertation nine years earlier. Although systematic pressures inflicted by willful human activity can drive a species down to the margin of viability, Shaffer wrote, the terminal event—extinction—will generally involve an element of chance. Uncertainty is part of life, yes, but for small populations, uncertainty is the enemy of survival.

To that truth there are two corollaries, he added. "First, the smaller the population, the more likely extinction is in any given period of time. Second, the longer the period of time, the more likely extinction is for a population of any given size." The concept of minimum viable population is merely a formalized version of those corollaries, he explained, an effort to quantify the risk of extinction for any animal or plant population when it's sorely reduced in size. This formalized concept gives us the prerogative of deciding how much of such risk we, human society, are willing to accept. How badly do we want rhinos in Sumatra? How badly do we want elephants in Africa? How badly do we want grizzlies in Yellowstone? "Does a 95% probability of persistence for 100 years make extinction sufficiently remote," Shaffer asked, "or all too imminent?" He didn't supply an answer. He knew that it's a political question, not a scientific one.

But he made one dour prediction. His own rough estimates of viable population size led him to conclude that "the size and number of current nature reserves are likely insufficient to provide a high level of long-term security for at least some mammalian species, especially those that are large or rare."

He wasn't alone in this pessimism. Soulé and others were singing the same song.

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TWO MONTHS after Bedo's murder I return to Perinet, hoping to gather the facts. But there don't seem to be any facts, aside from the stark one that Bedo is dead. In lieu of facts, there is testimony. There are voices. The voices speak at me in French and in Malagasy and in English. Some of them are angry voices, some grief-weary, some defensive. I don't discover truth; I collect versions. It's *Citizen Kane* and *Absalom, Absalom!* all over again.

I call on Bedo's father, in the house just across from the Analamazaotra reserve. His name is Jaosolo. Because I am accompanied by Pat Wright and David Meyers, he welcomes me and begins talking about his son. Yes, Bedo loved the lemurs. The reptiles too, yes, all of the animals. Sometimes people would go to the forest and search for a rare species, and they wouldn't find it. When they went with Bedo, ah, they always found it. The grand professors from Europe would come, they would look up into the trees at a creature, and they would say: What's that? They wouldn't know. Bedo would look up, he would know. He would tell them the species. Always people would come, they would ask for Bedo. Where is little Bedo? Lately a Japanese group came to the hotel, just last month. They had arranged earlier that Bedo would guide them. They asked, Where is Bedo? He wasn't there. It wasn't his fault, but he wasn't there. I couldn't tell them why, says Jaosolo, his voice sounding tired and unsteady. *"Tous les visiteurs, professeurs ou autres, demandait toujours lui."* Bedo, he was the best.

Jaosolo has taken the loss hard. Barefoot, a small dignified man in the beret and uniform of Eaux et Forêts, he goes to a wooden cabinet and rummages there for mementos. The house is unlit and the windows, blocked with blinds, admit almost no sun. He puts on his delicate gold spectacles. He shows me a document stamped with a red seal, his official complaint over the death. He shows me a copy of *National Geographic* full of Frans Lanting's work as assisted by Bedo. He shows me snapshots. *"Ceci, c'est la dernière photo."* In this last picture, a strapping young Bedo stands surrounded by forest, wearing a T-shirt printed with lemurs.

I speak with the only eyewitness, a young friend of Bedo's named Solo. I speak with the gracious hotelier, Joseph Andriajaka, who watched Bedo grow up and encouraged his development as a guide, who recommended his services to so many Perinet visitors, including me. I sit near the railroad bridge across the little river that flows through the village, questioning Bedo's brother and sister. This is the murder site. Details are confused, but no one disputes the point that, whatever happened, it happened right here. The body was recovered, eventually, from the river. Bedo's brother has little to say. His sister speaks fiercely and vividly, telling me the tale. I stare at the muddy water. I ask heartless questions. Where exactly? How many days? What made the body so hard to find? Why did he go toward the river when he was attacked?

Later I talk with Alison Jolly, another eminent lemur biologist, who was in Perinet on the day of the killing. I talk with Jean-Marie de la Beaujardière, an honorary consul of Madagascar, who arrived the day after. Pat Wright and Frans Lanting and David Meyers share with me what they know—or, more accurately, what they have heard. I listen to accounts of the murder ten or eleven times, in three languages, with and without help from a translator. Each time it's different. In Madagascar, as Alison Jolly warns me, "things immediately move into the realm of myth. Usually within about a day."

I am variously told:

Bedo was killed with an ax. He was not killed with an ax. He was killed with a rock, thrown hard, which hit him in the temple. He drowned. His dead body was dropped into the river. He jumped into the river while trying to escape. No, his body could not have been in the river until just before it was found, days later, because the searchers wouldn't have missed it. Someone must have hidden his body, then later dumped it into the river. God knows who, God knows why. No, his body was there in the river the whole time, entangled in submerged branches. No, his body bore no signs of having spent days in the water. His belly was flat. He didn't drown. His wounds showed that he had been struck in the face with an ax. No, the ax belonged to an earlier stage of the altercation and it wasn't used on Bedo. He was hit with a rock. No, with four rocks. No, one rock, a regrettable accident that caused him to drown. No. He was murdered.

The incident occurred on a Sunday afternoon. No, it was Sunday night. Darkness. Broad daylight. One man did it. Two men, their names are the following. They are not natives of Perinet, they come from the city of Fianarantsoa, where they might or might not have been implicated in other grievous mischief, for which they might or might not have gotten off lightly. For killing Bedo, they have been sentenced to five years. No, the trial is yet to come. The two men are in jail in Ambatondrazaka. They are trying to blame it on each other. The prosecutor will be too lenient. They might receive life sentences.

The argument began at a party. Loud music and liquor. The liquor was a form of Malagasy moonshine known as *tokagasy*. Ordinarily it should be as clear as vodka; this batch was cloudy, so Bedo refused to drink. It might have been poisonous. No, he simply chose not to get drunk. No, he refused because he was haughty. He got into a fistfight with one of the hosts, who was outraged by Bedo's snub. Bedo won. No, Bedo was down on the ground, and his friend Solo brandished an ax to rescue him. Bedo and Solo then left the party. Near the railroad bridge, they were set upon. Bedo was hit—with the ax, no, with the rocks. He fell or was pushed or escaped into the water. He rose three times, the canonical number, then disappeared.

Why was he murdered? Because, in becoming the darling of foreign tourists, in earning so much fast easy money as a guide, he had provoked envy. Malagasy culture does not tolerate upstarts. Bedo spent his money on a punk haircut, a radio, flashy clothes. He had gotten abrasive and highfalutin. Some people hated him for it. No, he was just a young man groping toward maturity. Basically he was unassuming and sweet. He had great integrity. He was killed, perhaps, because his father and other officials from Eaux et Forêts had been trying to stop illegal cutting of hardwood from the Analamazaotra reserve. Illegal destruction of indri habitat. No. No, it was a meaningless village fight. He died because of alcohol and sudden anger, just like unfortunate souls in American cities every Saturday night.

According to Alison Jolly: "He was murdered for jealousy, and in a way it was we who were responsible." She means the foreign tourists and scientists who paid handsomely for his skills, disturbing the equilibrium of his world. This view has a certain logic.

By a contrary view, equally plausible, his death was a chance event.

At the time of my postmortem inquiries, Bedo lies buried in Perinet. But only temporarily. Later, I'm told, his body will be moved to the family's ancestral tomb in the north. If his family follows the Malagasy custom of *famadihana*, turning of the bones, that tomb will be reopened in a few years and Bedo's remains (among others) will be joyously rewrapped. Meanwhile, some of the scientists and conservation officials who knew him have begun talking about a different sort of commemoration: a scholarship fund, in Bedo's honor, for promising young Malagasy naturalists.

Frans Lanting mentions still another sort. "We called him *Babakoto,"* says Lanting, "and as long as there are these animals screaming in the forest, he'll be memorialized." But a point remains uncertain: How long is that?