cal manipulations in an environment in which a broad range of responses is possible.

The creation of naturalistic environments involves transposition by homology, a direct duplication of some environmental structure, or transposition by analogy. In the analogous case, certain ecological challenges are re-created, and the emphasis is placed on biobehavioral outcome and not on the structure used to produce it. Increasing the complexity of the cage environment with perches, poles, and partitions; introducing the challenges of foraging and tool using; and providing social companionship are clearly effective in broadening the range of species-normative behavior shown by primates in captivity. Moreover, by housing primates in naturalistic settings, we take definitive steps toward promoting their health and well-being. This effect is not limited to wild primates who are now maintained in captivity, but extends to primates born and then raised in a variety of ways in the laboratory. Even rhesus monkeys reared with limited social experience show a remarkable ability to adapt to seminatural and natural settings and to exhibit complex patterns of social organization, which are characteristic of free-ranging monkeys.

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17

Environments for Endangered Primates

THE FALL OF THE WILD

We tend to think dichotomously about animal environments, contrasting naturalistic with nonnaturalistic, free-ranging with enclosed, indoor with outdoor, and wild with captive. Our work with the endangered golden lion tamarin (*Leontopithecus r. rosalia*) has led us to question these dichotomies. Animal environments instead fall on a continuum (Beck, 1980) from that in which a species evolves—for example the eastern coastal rainforest of Brazil for the golden lion tamarin—to small restrictive enclosures that allow control of both primate and extraneous variables for experimentation.

The "wild" for golden lion tamarins is currently the 5000-hectare Poço das Antas Biological Reserve, as well as a nearby restricted military base and a handful of forest patches on private land in the wild. Our colleague James Dietz, who is conducting a behavioral ecology field study, estimates that about 400 tamarins remain in the wild. The region is heavily populated and is being developed rapidly for cattle ranches and citrus plantations. Cut trees are used for factory and household fuel. No surviving tamarin lives out of earshot of chainsaw and bulldozer. We have rescued tamarins huddled in terror under smoldering brush piles in freshly logged and burned clearings.

The Poço das Antas Reserve is a mosaic of secondary forest and old field. It is bisected by a railway and flanked by a highway. A new dam is altering the course and flood pattern of a bordering river. Fire periodically ravishes the fields and recolonizing tree seedlings; in February 1990 a fire burned over 30 percent of the reserve. Fighting fires and building fire breaks are prominent conservation activities. Gates and some fencing bar access at the most convenient entrances, but poachers, recreational motorcyclists, and squatters are common. The reserve's guard corp is too poorly manned, equipped, paid, and trained to provide total protection.

The behavioral ecology study began in 1983 as part of the Golden Lion Tamarin Conservation Program (Kleiman et al., 1986). Dietz has attempted to trap every wild tamarin. Each animal is brought to project headquarters and chemically anesthetized. It is weighed, measured, sampled for ecto-(parasites) and endoparasites, tattooed, and given a preventive dose of antibiotics. There are thirty-five to forty tamarin groups in the reserve, of which twenty are under current study (Baker et al., in press). Most groups have only one breeding male and one breeding female (Baker et al., in press); mean group size is about 7 (Peres et al., in press). Some animals in each group are radio-collared. Blood for genetic and virological studies has been drawn from many tamarins, and others have been radiographed. Tamarins with injuries have been medically treated. The groups are retrapped annually (the animals are so hungry that they will reenter traps for a bit of banana). Rescued or confiscated wild-born tamarins have been translocated into the Reserve and captive-born tamarins have been reintroduced. We have even discussed "reintroducing" gametes from zoo tamarins or "translocating" embryos to bolster genetic diversity.

LouAnn Dietz has conducted a conservation education project as part of the tamarin program. Most of this crucial work is conducted outside the Reserve, but classes are regularly brought in to see the tamarins and the forest from a special nature trail. The trail is actually a bit of a large trail system cut carefully through the Reserve for researchers and guards. This slight destruction is balanced by forest regeneration due to fire control, application of fertilizers, reduced cutting, planting of native tree seedlings, and translocation of bromeliads, but the trail system is clearly not natural. Even chartered tourist groups are occasionally allowed on the trail to see wild tamarins in exchange for a contribution that is used for Reserve management.

Poço das Antas is still a wild place, with rare orchids, brightly colored birds, coral snakes, and ocelots. But it is not pristine. The drone of cars, trucks, trains, and planes rivals that heard around any urban zoo. Animal traps, anesthetic drugs, antibiotics, fecal samples, tattoos, radiographs, blood samples, fire control, locked gates, trails, signs, and tours, all tools of the zoo manager, are essential for the continued survival of the golden lion tamarin. And if the tamarin can be saved, so too will be the less endearing species at lower trophic levels. That is, if the tamarin is saved, its environment is saved as well. But is it a naturalistic or nonnaturalistic environment? Are the tamarins free-ranging or enclosed? Are they wild or captive? These questions pertain not just to Poço das Antas and golden lion tamarins. Every national park is becoming increasingly insularized and penetrated by human influence that far exceeds the long-evolved subsistence uses that were sustainable only a century or two ago (Altmann and Muruthi, 1988).

CAPTIVE ENVIRONMENTS

The continuum of tamarin environments is being compressed from the other end as well. We know of no biomedical or behavioral program that keeps a golden lion tamarin for long periods in a small cage or restraining chair. Such settings may be necessary for essential research using nonthreatened primates, although one could argue that there are no nonthreatened primates or that scientific progress never justifies such loss of reproductive opportunity or the stresses of physical confinement and social deprivation. Some endangered primates are designated as surplus to captive breeding populations because of genetic overrepresentation or sex-ratio inbalances. But to use these individuals in invasive research would discourage the search for and use of management techniques that would preclude surplus animals.

But some conservation-driven work by our colleagues David Wildt and Steve Monfort does require temporary housing of golden lion tamarins in small metabolic cages for urine collection. Wildt and Monfort track urinary hormonal metabolites to noninvasively pinpoint ovulation. The data will coordinate artificial insemination and embryo transfer should these technologies be needed in zoos or in the wild for tamarin propagation. The results also provide physiological measures of sexual receptivity. Following the work of French and Stribley (1987), Wildt and Monfort study receptivity when a female lives alone, with other females in the absence of a male, with only a male, and with other females and a male. This provides better understanding of the mating systems of wild tamarins, and may reveal possibilities for increasing reproductive output. The subjects in this research live in conventional cages but are trained to enter the metabolism cages. The National Zoo's animal care and use committee determined that the potential yield of scientific information important for the conservation of the species justified the temporary separation of a few individuals.

The Golden Lion Tamarin Management Plan, a model for later plans for other endangered species, stipulates a cage size of at least 3 x 2 x 2.5 meters. That is roughly the size of a shower stall, but it is in such cages that the captive golden lion tamarin population has grown from about 70 in 1973 to over 550 today. The key was not the size of the physical environment but the suitability of the social environment. Kleiman et al. (1986) discovered that this species breeds best in captivity when kept as monogamous pairs, and when offspring are allowed to remain with their parents to assist in the raising of subsequent litters. Nest boxes, climbing networks, elevated feeding stations, and the addition of meat protein to the diet also contributed by simulating or substituting for essential resources of the natural environment. But the research and breeding that made the propagation program for golden lion tamarins so successful took place in small, inexpensive, easily maintained, notably unaesthetic cages in more than 50 zoos around the world.

Some zoos are now housing tamarins in large naturalistic habitats. Zoo habitats tend to be stage sets (Robinson, 1988) with artful rock work, artificial trees, vines, lichens, pools, waterfalls, rainstorms, theatrical lighting, and auditory surrounds. Live vegetation can be included with tamarins since they do not eat leaves (although locomotion will take a toll). South American rodents and sloths are appropriate cagemates. But habitats do little for the tamarin within. Their strength is that they delight and comfort the zoo visitor outside, who hopefully becomes more sympathetic toward and knowledgable about the preservation of biological diversity.

PREPARING TAMARINS FOR REINTRODUCTION

We thought habitats would be better than cages for tamarins being prepared for reintroduction. Foraging skills could be facilitated because food could be distributed over a greater area and there would be a greater range of places to hide food. More important would be the greater locomotor opportunities afforded in a habitat than in a cage. Captive-born, cage-housed tamarins are reluctant to use slender flexible vegetation; indeed if their cage contains only a rigid climbing structure of milled lumber or plastic pipe, they are reluctant to use natural vegetation of any sort. We hypothesized that a habitat outfitted with vines and slender branches as the only means to reach nest boxes, resting sites, food, and water would predispose tamarins to acquire the locomotor skills essential for survival in the wild. Further, because tamarins living in cages with unchanging climbing structures develop habitual travel routes and are unable to spatially orient after reintroduction, we thought that dismantling and rearranging the naturalistic furniture in the habitat would facilitate spatial orientation. Training in locomotion and orientation was thought to be especially crucial, since a tamarin deficient in these skills would be seriously disadvantaged in finding food and shelter, avoiding predators, and maintaining normal intragroup and intergroup social behavior (Beck et al., in press; Fleagle, 1979; Garber, 1984). But the labor-intensive pretraining in a habitat conferred only short-lived postreintroduction advantages in foraging, locomotion, and spatial orientation (Beck et al., in press).

Further, ingenuity can provide equivalent experiences in small cages. For example, tamarin cages in Snowdon's laboratory are outfitted with "rubber perches," which are excellent simulations of slender natural vegetation (Snowdon and Savage, 1989). McGrew and McLuckie's (1986) flexible ducts allow a tamarin to leave its cage and explore a large area and neighboring tamarins. This facilitates orienting skills and provides opportunities for the animals to learn the "etiquette" of territorial encounters.

We know of no evidence that large, naturalistic habitats enhance the well-being or survival skills of tamarins. Functional (not necessarily naturalistic or aesthetic) simulation of critical features (or salient elements; see Glickman and Caldwell, chap. 14, this volume) of the natural physical environment (Fig. 17.1), and a natural social environment, are sufficient for health, longevity and reproduction, and for the expression of a broad sample of the behavioral repertoire. Further, functional simulation conserves the scarce resources available for captive breeding and research programs. Tasks requiring the tamarins to work for food, and thereby gain some control over feeding schedules, seem also to contribute to well-being (Kleiman et al., 1986; Markowitz, 1982; Molzen and French, 1989; Snowdon and Savage, 1989).

Figure 17.1. A klipspringer (*Oreotragus oreotragus*) on a rocky outcrop in east Africa. Photo by B. Beck.

We built habitats at the release sites of the golden lion tamarins that we reintroduced to the wild in 1984 and 1985. These habitats were wood and wire mesh cages, 15 meters long, 4.5 meters wide, and 3 meters high. The understory of the forest was bent in and down as the mesh was assembled around it; taller trees extended through the mesh at the top. Each habitat had a nest box. These habitats were built to allow the animals to acclimate to and become familiar with the release site, gain some locomotor and foraging experience in natural vegetation, encounter invertebrates and small vertebrates that came to the cage, and experience direct rainfall. Further, five of the six groups reintroduced in these years had been intensively trained in foraging and locomotion before being moved to these forest cages, where their training continued. In retrospect these habitats were a forgiveable conservatism, but

Figure 17.2. Klipspringers on rocks in the Frankfurt (Germany) Zoo. Though the enclosure is decidedly nonnaturalistic, the rocks functionally simulate outcrops, a critical habitat element for this species. Photo by B. Beck.

they did not serve their purpose. For reasons noted above, the tamarins, especially the adults, preferred to use the wood framing and wire mesh for locomotion. We documented that the animals recognized knotholes and rolled leaves as likely places to search for food, and that they would eat spiders, butterflies, and snakes if they could catch them. They seemed indifferent to rain, unless they had full bellies in which case they went into their nest box. But we do not think the tamarins actually learned much in these habitats; they clearly could not have survived in the forest without extensive human support over at least a year.

The moment of reintroduction was marked by opening a small door in the roof of the habitat. Fleet-footed field assistants with radio receivers were deployed around the area to follow the tamarins as they rushed back to nature. But the tamarins seemed reluctant to leave the habitat, venturing only 30 meters away and 20 meters high on the first day. They played on and in the 3-meter high habitat during the day, and slept inside in the nest box at night. Because the understory had been compressed into the habitat, tamarins on the roof were dangerously exposed to raptors. We had to dismantle the habitats shortly after release.

One of the groups in the 1985 release received no formal training, although it did live for an equal time in the forest habitat before actual reintroduction. As noted above, this untrained group showed poorer food-finding and ranging after reintroduction, compared to a matched trained group, but this difference was only transient. After documenting the difference, we felt obligated to train the untrained group. This was of course possible since the animals had remained near the prerelease habitat site. Food was hidden in slots in a special platform, and the platform was moved farther and farther into the forest each day. The animals learned to search for food in the platform, and in natural sites that they encountered on their way to and from the platform. They also learned to locomote and orient in and through real natural vegetation. This seemed to be a more authentic method of training and it eliminated the need for costly "habitats in the wild" that were of limited value. We fundamentally revised our reintroduction strategy to make use of a new type of tamarin environment.

THE PSYCHOLOGICAL CAGE

The psychological cage depends less on containment than on attachment. A captive-born group of tamarins with a nest box and

a food supply, and without strange tamarins calling in the distance, is not motivated to move when released into the forest. Lack of locomotion and orientation skills compound the sedantism. Harking back to environmental dichotomies, they are surely "free-ranging" but they are actually "confined." We reasoned that tamarins could be more realistically and cost-effectively trained after release than before. We could do this safely since they would be in their psychological cage. Wim Mager, director of the Apenheul Zoo, independently converged on this idea, and uses it to mount unique primate exhibits (Mager and Griede, 1986). Several callitrichids and squirrel monkeys roam in their psychological cages at Apenheul. We set out to develop the concept by releasing a tamarin group in a fine stand of beech and oak forest in the heart of the National Zoo (Bronikowski et al., 1989). The zoo's animal care and use committee had a hard look at this proposal as well; letting animals out of cages is heretical to zoofolk.

We caught the tamarin group before it emerged from the nest box into its colony cage on the morning of the release. The box was taken to the release site, mounted in a tree, and the entrance opened. The feeding platform was hung just outside the entrance. The monkeys made brief cautious forays but were predictably reluctant to stray. On the second day they ventured farther, but then could not easily find their way back to the nest box. Some returned on the ground. Some had to be lured back with banana. Others fled and had to be trapped and carried back to the nest box tree; one was lost. Subsequently, none of the tamarins ventured farther than 100 meters from the nest box for the next three months (when the release was terminated due to cold weather). We repeated the experiment the following spring with the same group.

We strung stout ropes horizontally between mature trees in the immediate release area to compensate for the lack of the understory that wild tamarins seem to prefer. Food was again available in abundance. The animals did not "escape" from their psychological cage, but rather gradually expanded its edges. They visited trash cans and pop stands, and invaded the enclosures of bush dogs (which cowered), eagles (which cowered), bison (which charged), oryx (which seemed perplexed), and gibbons (which bit two tamarins severely, killing one). They had regular morning territorial encounters with another golden lion tamarin group in an outside habitat 200 meters away. They raised twins. The tamarins in this environment delighted and educated zoo visitors.

We were convinced that the psychological cage could be used to train reintroduced tamarins since we had learned that fully provisioned tamarins would slowly but surely begin to explore their environment, and in the process would learn to hunt effectively for "natural" food and to locomote and orient in "natural" vegetation. Jim Doherty (personal communication), General Curator, New York Zoological Society, has released ring-tailed lemurs in psychological cages on St. Catherines's Island with similar results. And we have subsequently used postrelease training in psychological cages in the reintroduction of more than 50 tamarins to the wild in Brazil. Although as we predicted, some animals initially fled and had to be recovered, they later expanded their territories around their nest boxes, had territorial encounters with neighbors, and reproduced. The notion of psychological cages holding reintroduced tamarins in Brazilian forest obliterates environmental dichotomies such as "captive" and "wild." That they willingly return to their nest box, and spend more than 12 hours per day inside the box in less than a cubic meter of space, obliterates the dichotomy between an "indoor" and "outdoor" environment, and tests our biases about minimum cage size standards.

NATURALISM, STRESS, AND WELL-BEING

Even wild-born tamarins living totally at liberty in the Poço das Antas Reserve are not really free: "However paradoxical it may sound, the truth is actually this: the free animal does not live in freedom" (Hediger, 1964, p. 4). They engage in energy-consuming territorial encounters with neighboring groups (Peres, 1989), demarking for us researchers the unseen boundaries that surely constrain each group in a slightly different type of psychological cage. They roam their 40 hectare territories seeking the cryptic food that is distributed sparsely in space and time. Predators such as hawks, ocelots, and boas stalk the unwary. Nights are wet and surprisingly cold, and good nest holes are hard to find because there are few really old trees. Mosquitoes, ticks, and fly larvae feed on tamarins too. This hardly conforms to the romantic notion of the natural environment as a paradise, and serves as a reference for some thoughts on animal welfare, "psychological well-being," and stress.

Moberg (1985b) argues that stress can be measured in nonverbal animals by its prevention of normal reproduction, alteration of

metabolism so as to cause weight loss and interference with normal growth, suppression of the immune system so as to increase the likelihood of infection-related death, and hyperaggression or self-mutilation. If these effects can be observed in a captive animal, then that animal can be said to be stressed. The average captive-born adult golden lion tamarin, even one living in a shower stall, weighs 675 grams. The average wild adult weighs 600 grams (J. Dietz, personal communication). Captives are bigger as well as heavier. Captivity is certainly not interfering with growth or causing weight loss. Captive golden lion tamarins typically give birth to two litters per year; wild tamarins typically give birth to one. There is certainly no interference with reproduction. Hyperaggression and self-mutilation among captives disappeared after Kleiman's discoveries about keeping golden lion tamarins in monogamous pairs and allowing offspring to gain parental competence by helping to raise their younger siblings. Finally, the average longevity of zoo tamarins is now about 12 years. One has survived beyond 20! Dietz is not yet able to estimate life expectancies for wild tamarins, but their average longevity is certainly less than twelve. Further, preliminary data show that zoo-born reintroduced tamarins lose weight and have a birth rate like that of wild tamarins.

These comparisons suggest that "the wild" is far more stressful, and captivity (under good but not extravagant conditions) is far less stressful, than the more radical animal welfarists would have us believe. Recall that in our reintroduction program we gave golden lion tamarins the choice of being wild or captive: they chose to remain captive. Of course they may have chosen captivity out of familiarity, but remaining in captivity would nonetheless have been safer: at this time only 32 of 79 reintroduced tamarins (and 22 of their wild-born offspring) are still alive. Viral disease, exposure, intraspecific conflict, toxic fruits, predators, and theft by humans are documented or implicated as causes of loss. We would need to know age-specific mortalities of wild tamarins to compare this survival rate with that of a like-aged cohort of wild tamarins over a comparable period, and a like-aged cohort of wild-born tamarins brought into captivity. But we do know that if we had brought 79 wild tamarins into captivity since 1984, far more than 32 would be alive today. We must inescapably conclude that tamarin well-being is enhanced by good captive management; that stress is diminished in captivity; and that naturalistic environments do not necessarily promote health and reproduction. Indeed, effective preparation of captive primates for reintroduction requires environments that are more naturalistic—that is, that provide more stress and less well being (Beck et al., in press; Kleiman et al., 1991).

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CHARLES H. JANSON

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Naturalistic Environments in Captivity: A Methodological Bridge between Field and Laboratory Studies of Primates

Studies of animal behavior in the laboratory have traditionally focused on mechanisms of behavior: the neural, physiological, developmental, and psychological processes that give rise to behavior we observe in a given species. Conversely, studies of animal behavior in the field have usually emphasized evolutionary questions: understanding the natural context within which behaviors develop and are expressed, and the important forces that may have shaped those behaviors via natural selection (Tinbergen, 1963). Any complete understanding of the behavior of a given organism must encompass both approaches. In addition, however, it is argued here that a pure reliance on field studies to answer evolutionary questions and on laboratory studies to answer mechanistic questions in behavior necessarily leads to an incomplete understanding of either type of question. Laboratory and field approaches