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Two-Gender Families

Let's move on now to species with two genders that don't change sex, do not have intersexual body parts, and aren't sex-role reversed. Are such animals "normal"? Have we come at last to the familiar gender roles performed by ordinary bodies, as depicted on nature shows? Or are nature shows perhaps not telling the whole story? What goes on in two-gender animal families, and how are such families organized?

Many of us were raised to admire the nuclear family as a norm and were taught that single-parent families, families of same-sex couples, or communes were second-best alternatives or, even worse, wrong. Yet the meaning of a human family is in flux. In the United States, public attention has focused on the problem of how to define "family" as a result of a recent Supreme Court case about the rights of grandparents to visit grandchildren despite parental objection. The thirty-million-member American Association of Retired People (AARP) states that grandparents are the primary caretakers of 1.4 million children because many nuclear families have dissolved.[1]

The American Center for Law and Justice, which represents the Christian right, claims that "the traditional family, consisting of married parents and their children" is the building block of society. A leader of the Nation of Islam similarly declares, "Whenever . . . 50% of those

who marry get divorced within the first three years, these are signs of the decline of a civilization."[2]

Meanwhile, the Lambda Legal Defense and Education Fund, a gay rights organization, argues that neither side, grandparents or parents, sufficiently protects children being reared in nontraditional families, affirming the primary importance of "the quality and security of the relationship between individual children and adults rather than blood ties or labels."[3] Indeed, in June 2002, the California Supreme Court ruled unanimously that a man who cared for a six-year-old boy could be considered the boy's parent, even though the man was not the boy's biological father and was never married to the boy's mother. The man was given custody of the child over the mother's objections, showing that "parenthood could be achieved through love and responsible conduct."[4]

With so much controversy about the meaning of family and parenthood, asking how animals raise their young may be helpful. What is an animal family? Does any family organization emerge as a particularly efficient way to raise young? And does biology support the belief that the nuclear family should have a privileged status in our society?

SEX AND POWER

Oh, I wish the simplest of animal families were a blissfully pair-bonded male and female. Alas, males and females negotiate over power in even the most elementary of animal families. Feminist writings call attention to a power differential between the sexes: "The image of the cage helps convey . . . the nature of oppression. 'Why can't I go to the park; you let Jimmy go!' 'Because it's not safe for girls.' "[5] Well, how safe is it outside the cage? Why does a cage exist at all? If we look at squirrels, we can see what biologists call "mate guarding," a male caging a female.

The Idaho ground squirrel *(Spermophilus brunneus)* lives in populations of one hundred to three hundred individuals in short-grass meadows.[6] The squirrels hibernate in burrows most of the year, only becoming active from late March to early August. The males wake up from hibernation about two weeks before the females. Females become sexually active for about three hours in the afternoon on the first day after hibernation. Three hours on this one day is all the family life a squirrel has.

A successful date for a male squirrel means walking behind a female while sniffing and licking her genitals, going with her into a burrow, mating there for five minutes, and then reemerging. As a sign of successful mating, the female acquires a "sperm plug" that can be seen by a human observer and probably by other squirrels as well. The male then stays within one meter of her and keeps her in a small area by "herding." About every forty minutes, he follows her back into the burrow, where they mate again. She acquires a fresh sperm plug, and he turns around to block the entrance with his body. The male rebuffs an average of four other males who try to mate with the female. If a male is displaced, he is likely to take about an hour and twenty minutes to locate another female, and she is usually guarded by some other male.

A litter typically consists of five pups. If the female has been guarded by only one male for these three hours, then the whole litter is sired by him. If more than one male has guarded the female, paternity analysis shows that her litter is sired mostly by the male who was the last to guard her or by the male who guarded her the longest.

Thus the family life of the Idaho ground squirrel consists of three hours per year. The Idaho ground squirrel family is solely a unit for reproduction. The male doesn't hang around and help raise the young. The male is said to guard the female to protect his "investment" of sperm by making sure that his female doesn't mess around. He doesn't mess around himself because if he stopped guarding he would lose his investment, and in any case finding another female is nearly impossible.

A close relative, Belding's ground squirrel *(Spermophilus beldingi)* of the midwestern United States, does not mate-guard. In this species, twenty-five minutes are all a male needs to locate and initiate courtship with another female. Female Belding's squirrels typically mate with three to five males. The female's first mate sires most of the litter, followed by the second mate, then the third mate, and so on, in contrast to the Idaho squirrel, where the last mate gets most of the sires. A Belding's male doesn't waste time guarding a female because his investment of sperm is secure—as the first mate, he's already guaranteed siring most of the young. Instead, these males hurry to find more females to mate with, and with so many nearby, why not?

A cage, then, is not biologically universal. These two closely related species of squirrels have completely different power relationships be-

tween males and females. Male Idaho ground squirrels guard the females, while male Belding's ground squirrels don't. Why? The power relationship is probably not as simple as it seems. Are the female Idaho squirrels being caged against their will? Maybe, maybe not. If asked, an Idaho male squirrel might say lovingly that he was "protecting" his female during their brief marriage from the unwanted advances of rival males. And she might agree, happy to have him there. The courtship that precedes mating suggests her acquiescence. And she is capable of physically repelling a male if she wishes: the day after her three-hour burst of sexuality, an Idaho female squirrel constructs a nest and excludes all other squirrels from a small territory around it. So a female Idaho squirrel may want to be guarded.

Why does the last male sire most of the young in the Idaho squirrel, and the first male sire most of them in Belding's squirrel? Could female squirrels control whose sperm fertilizes their eggs?[7] Could a female manipulate a male to guard, or not guard, by controlling his sperm? Can a female select the first male's sperm to do the fertilizing if she wants him to have no incentive for staying, and select the last male's sperm if she wants him to hang around and guard? Presenting mate guarding as a tactic by which males protect their investment ignores the female perspective. Females are viewed as land in which males plant seeds and which they guard if necessary. Yet females are probably active players in whether they're guarded or not.

The Idaho and Belding's squirrels may have evolved to experience pleasure differently. A female Idaho squirrel may like being squeezed into a burrow, and a male may enjoy having a female behind him as he stuffs the burrow's entrance, like a guy taking a girl for a spin in his red convertible—fun for both. Yet for a female Belding's ground squirrel, squeezing into burrows could be a total turnoff and the reason she doesn't permit the guarding. Species differences in how power is eroticized make it difficult to discern whether animals have freedom of choice during mate selection and in their family lives.

Among primates, the amount of sexual coercion varies greatly from species to species, as does the overall level of both between-sex and within-sex aggression.[8] Outside the breeding period, male mountain gorillas aggress against females one to four times a day, olive baboons about one time per day, and red howler monkeys only 0.04 times per

day. The context for the aggression varies from competing for food, coming to the aid of one female against another, and breaking up fights between females. These aggressions are not directly sexual coercion, but rather reflect a social atmosphere of violence.

Within the breeding period, male rhesus monkeys attack females who consort with male rivals. Similarly, among chimpanzees, one of our closest primate relatives, males attack females who consort with lower-ranking male rivals, rather than attacking the low-ranking males themselves. Using "a fair amount of brutality,"[9] chimpanzee males persuade females to accompany them away from the group where they were living. One-third of all conceptions result from matings between pairs separated from the group for several days to over a month. Chimpanzee males also intimidate females into submitting to their advances later on. Lack of resistance does not necessarily mean willing participation, but may reflect experience with the male's previous aggression.

The record-holders for male sexual coercion are the orangutans, in which most copulations by subadult males and nearly half of all copulations by adult males occur after a female's fierce resistance has been violently overcome.[10] Other primate species showing lots of male aggression against females include white-fronted and wedge-capped capuchins, black spider monkeys, and brown lemurs. Females' counterstrategies include avoiding areas where males are found, joining a male's territory or harem to gain his protection, and forming coalitions to fight off the males.

Yet other primate species enjoy a peaceful life. Male aggression against females is rare in bonobos, a primate species as closely related to humans as the relatively violent chimpanzee is. Male sexual coercion is also rare in patas monkeys, red-backed squirrel monkeys, brown capuchins, woolly spider monkeys, and black-and-white ruffed lemurs. As with the bonobo/chimpanzee contrast, closely related species differ in the prevalence of male sexual aggression.

No explanation exists for why some societies develop coercive power relations between the sexes, whereas others form equitable power relations.[11] Although some species resemble the tough-talking television show "NYPD Blue," others resemble the peaceful Mr. Rogers. How power relates to sex is not a biological universal. We may choose to live like some species and not others.

MONOGAMY AND DIVORCE

As we turn to long-lasting two-gender families—beyond the three-hour marriages of ground squirrels—the plot thickens. Ninety percent of bird species are monogamous in the sense that a family consists of one male and one female who cohabit a nest and raise young together in that nest during at least one breeding season. In contrast, 90 percent of mammal species are polygynous, with one male for many females.[12] Among mammals, females typically occur in groupings of two or more who are serviced by one male.

But what do these statistics mean? Biologists have been slow to distinguish between economic monogamy and reproductive monogamy. Birds are identified as "monogamous" simply if they are living in the same nest and feeding nestlings together—an economic criterion. Biologists have unquestioningly assumed that the nestlings are the offspring of the couple in the nest. When distributed parenthood is discovered, biologists feel something is amiss—that one or the other member of the pair "cheated," straying outside the marriage bond. However, birds have decoupled reproductive and economic monogamy; in some species these go together, and in others not.

Black-capped chickadees *(Parus atricapillus)* of eastern Ontario are monogamous.[13] During the summer, pairs settle in territories to raise their families—a suburbanite's dream. During the winter, the chickadees cease living as couples and live in flocks of about ten birds. Because a chickadee's average life spans several years, the birds are aware of each other through both the over-wintering period and the breeding period. During the winter, males and females sort themselves into separate dominance hierarchies.

New couples form during the winter social period and settle as pairs for the summer to raise a family. As a couple, they forage together, excavate their nest cavity together, mate with one another, and defend their territory together. The male feeds the female although they both forage, and the male prevents other males from approaching the female. When forming couples, the highest-ranking female pairs with the highest-ranking male. Most couples remain together for more than one breeding season. Females may "divorce" their mate and/or mate with males other than their nest mate. A mating outside the pair-bond is called an extra-pair copulation, or EPC in biology jargon. Female chickadees divorce to obtain a male who is higher in the male dominance hierarchy than their present mate.

In one study,[14] seven females paired to seven high-ranking males were removed, temporarily creating seven very desirable widowers. Over the next two days, some of the remaining females deserted their partners and took up with the higher-ranking widowers. When the females who had been removed were restored to the site, they quickly chased the social climbers back to the males they had deserted. These hen-pecked husbands took their wayward spouses back. To complete the experiment, six females were also temporarily removed from six low-ranking males, but none of the remaining females left their mates to join these sad sacks. These males were saved from eternal loneliness only when their mates were returned to the site to rejoin them. Not only are female chickadees willing to desert their mate to acquire a higher-ranking male when one is available, but they are willing to mate with higher-ranking males in EPCs, resulting in many broods with mixed parentage.

A close relative of the chickadees, a member of the same genus, is the European great tit *(Parus major)*. Boxes for these birds to nest in have been constructed on the island of Gotland in southeast Sweden. In a 1985–89 experiment, eggs were removed from one pair's nest and transferred to another pair in order to observe the effect on divorce. Pairs whose eggs were removed divorced more often, presumably because they were not able to raise as many young as the population baseline. Conversely, pairs given extra eggs divorced less often, presumably because they did raise more young. Success at raising a family thus seems to be a factor in whether birds decide to divorce.[15]

One survey of marriage fidelity among birds shows annual divorce rates as low as 2.4 percent in the barnacle goose *(Branta leucopsis)* of northern Europe, 2.5 percent in the silvereye *(Zosterops lateralis)*, a berry-eating forest bird from Australia, New Zealand, and Fiji, and 2.7 percent in Cory's shearwater *(Calonectris diomedea)* of Long Island to Nova Scotia.[16] The highs were 36 percent in the European shag *(Phalacrocorax aristotelis)*, which is similar to a cormorant but more marine, and 30.6 percent in *Parus major*, the European woodland songbird mentioned above.

Divorce rate correlates with mortality. In birds where the annual survival rate is only 40 to 80 percent, the divorce rate is high, and in birds where the annual survival rate is 90 percent or more, the divorce rate is low.[17] Lots of eligible widows and widowers make for a hot singles scene. And when the singles scene is hot, the action doesn't stay confined to singles. When divorce rates are high, lots of mating also takes place outside of the nest. The data for birds show a positive statistical relation between rates of divorce and EPCs.

Thus monogamy among birds seems to be an economically beneficial social institution, with divorce and some out-of-wedlock matings a regular part of the picture too. Bird females seem to have lots to say about their own lives, choosing partners and initiating divorce when advantageous. When we turn to mammals, though, we have to face the fact that monogamy seems rare. Why?

One explanation for why birds are more often monogamous than mammals is that flight endows female birds with more opportunity to choose their mates than female mammals have.[18] Female birds can check out prospective husbands by flying from party to party around town, whereas a female mammal is stuck walking to the nearest block party. With so much choice around her, a female bird can demand a husband who is faithful and helps with the dishes, while a female mammal can't. However, this theory assumes that a male generally doesn't want to stick around and help with the young, can't stand doing dishes, and must be manipulated to do so by a female's threat of turning to someone else if he doesn't. I don't accept this logic. I feel the male's perspective should be stated differently. He has two directions in which he can invest social effort. Within-sex effort involves competing with other males and/or building coalitions with them to access females. Between-sex effort involves "coalition-building" with a female to raise offspring together. Whether a male winds up with more offspring overall from within-sex or between-sex coalition-building depends on circumstances. This is the animal equivalent of balancing career and family.

Monogamy then emerges when (a) building relationships with a female is more advantageous to a male's reproductive success than building relationships with other males, *and* (b) building a relationship with a male is more advantageous to a female's reproductive success than raising young by herself or in conjunction with other females. In general, different mating systems emerge from different optimal allocations of social effort to between-sex and within-sex relationships.

Although not as commonly as in birds, monogamy among mammals does happen. It occurs in 15 percent of primate species and is common among wild canines, among others. In most monogamous species, the husband contributes to parental care by building a den, burrow, or lodge, defending the family's feeding territory, feeding his wife when she's nursing, and carrying the young around (driving the kids to soccer after school). In the monogamous prairie vole, *Microtus ochrogaster,* when a female produces a bigger-than-normal litter, a second nest is built, the young are divided up, and the male cares for one nest and the female for the other. Thus monogamy occurs among mammals, although not as commonly as in birds.

But why is monogamy rare in mammals? Mammalian females have internalized embryonic development in a uterus or pouch, whereas avian females leave the developing embryos as eggs in the external environment. This difference affects who can control the offspring. A mammalian male who wants to control offspring must somehow control the female herself, whereas an avian male can directly control the eggs in the nest. A mammalian female knows the embryo developing in her body is hers alone, not an egg deposited there by some other female. In birds, a female may derive from a monogamous marriage both male provisioning of the young and male protection of the nest, not only from predators but from "dumpers"—other females who deposit foster eggs in the nest.[19] The male gains the female's initial investment in eggs, plus her additional provisioning. Neither male nor female mammals benefit from marriage as much as birds do.

EXTENDED FAMILIES

Let's now take a look at two-gender families larger than two individuals: extended families. The groove-billed anis *(Crotophaga sulcirostris)* is an insectivorous black bird with a large, deeply grooved bill. It lives in marshes and open pastures in Central America and is related to the cuckoo. Family organizations of the anis may consist of twosomes with one female and one male, foursomes with two females and two males,

sixsomes, and even eightsomes.[20] The foursomes are not sixties-style communes of free love. An anis foursome is two couples cohabiting a one-bedroom flat with one crib. Nests are built in thorny trees or vines. Each male guards one of the females. A female lays an egg every one to two days. The time from egg-laying to fledging is three weeks.

The two females in a foursome wind up with four eggs total. A female in a twosome can also produce four eggs by herself. Thus the number of eggs laid per female is lower in a foursome than in a twosome. In a foursome, the females start laying eggs at different times. The starter lays bigger eggs and has a longer time between successive eggs than the follower. Both females stop laying eggs at about the same time. Each female "tosses" out of the nest some of the eggs already laid by the other, with the follower winding up mothering on average 63 percent of the eggs and the starter only 37 percent of the eggs. After all the tossing is over, four eggs are left in the nest.

Even though the follower mothers more of the eggs, she doesn't necessarily successfully raise the most offspring. The starter lays larger eggs, which hatch earlier, so these chicks have a better chance of surviving than chicks from the follower. All four birds in a foursome work together to provide for and protect the eggs. The males divide the day into unequal shifts. The oldest male incubates at night and most of the daylight hours. As a result, he also incurs the most hazard and the highest death rate. Yet he also fathers the most young.

But why should a female, who can lay four eggs in a twosome without worrying about a nest mate tossing her eggs out, bother living in a foursome? The answer is that the larger group provides protection against egg predators. Once loss of eggs to predators is taken into account, the starter in a foursome produces the most young, a female in a twosome produces an intermediate number of young, and the follower in a foursome the fewest. For the anis, the benefit from predator protection of living in extended families of two couples outweighs the disadvantages of a rancorous life at home.

The family life of tamarins offers a pleasant contrast to that of anis. The saddle-backed tamarin is a tiny monkey that lives in the tropical rainforest of southeastern Peru, including the Manu National Park.[21] Among tamarin families, 22 percent consist of one female with one male in a monogamous relationship, 61 percent of one female with multiple

males, 14 percent of multiple females with multiple males, and 3 percent of males only. In the families with one female and multiple males, the female mates with all the males. The matings take place in view of the other males without any sign of aggression. The males in this species not only help take care of the young, but they cooperate with one another when doing so. The females usually give birth to twins, and the males carry the babies with them through the treetops. The males and females give the babies fruits and large insects to eat.

The twin babies are 20 percent of their mother's weight, and are 50 percent of her weight by the time they can walk and climb on their own. Just one female and one male aren't enough to raise the twins; three adults seem to be the minimum to do the job. Even the families consisting of one adult male and one adult female are accompanied by older children who help out. This family organization is called cooperative polyandry.

Other mammals with cooperative polyandry include African hunting dogs *(Lycaon pictus)* and dwarf mongooses.[22] Cooperative polyandry also occurs in birds, including the Australian white-browed scrubwren *(Sericornis frontalis)* that lives near Canberra, the Tasmanian native hen *(Tribonyx mortierii)*, the Galápagos hawk *(Buteo galapagoensis)*, the English dunnock *(Prunella modularis)*, the New Zealand pukeko *(Porphyrio porphyrio)*, and the Venezuelan striped-back wren.[23] No biological reason prevents these guys from cooperating with each other and helping around the house.

Lions, in contrast, seem to take the idea of a war between the sexes very seriously. We may be misled by the common picture of lions as cooperative hunters. Although lions seem to work together, not only at hunting but also in rearing cubs and roaring in a unified chorus, the truth makes human political infighting seem benign.[24] Lion family organization is multimale polygyny—gangs of males guarding groups of females, called prides. Males form lifelong alliances among one to eight lions. Most members of an alliance are brothers or cousins, but others are unrelated. Once mature, these coalitions take charge of a pride of females and father all the offspring born in the pride for a period of two to three years. After that, a rival coalition moves in and evicts them. The males work together more effectively when battling with a rival gang than in any other situation. How well a male does depends on how well his

coalition does—gang warfare in the extreme. A male lion is nowhere if not in the right gang.

Victorious lions don't make ideal boyfriends. A cub matures in two years, and a female isn't interested in mating during that time. However, if a cub dies, a female mates again in as little as two days. In their hurry to become fathers, an invading gang of males may kill off more than one quarter of the cubs, which quickly brings their mothers into reproductive condition. The invading males don't share fatherhood equally. One or two father almost the entire pride's litter.

To counter the male danger to the cubs, the females band together to raise the young. The females enjoy a reproductive life span of about ten years, during which five gangs may come and go. The females give birth in secrecy and keep their litters hidden in a riverbed or rocky outcrop until the cubs can move on their own. Then they bring the cubs to a place where they are nursed together in what is called a "crèche," a word meaning a public nursery for infants of working women.

The lionesses nurse their own cubs and those of others as well. This shared lactation is not entirely altruistic. The lioness gives milk primarily to her own cubs and rejects the advances of others. She needs her sleep, though, and while she is asleep, cubs who are not her children are able to nurse. Although a lioness prefers her own cubs, the strength of this preference depends on how closely related the other cubs are to her. If a pride consists mostly of close relatives, a lioness is more generous with cubs who are not her own than if she is in a pride of comparatively unrelated females.[25] In sum, female lions raise their young in crèches to defend against infanticidal males rather than to provide nutritional benefits from shared nursing. Ironically, house mice have the same family dynamics as lions,[26] as though a lion were no more than a mouse that roars.

THE BIG CITY

Some animal species live in what might be called cities. In these cases, family life shows many of the sophisticated intricacies of human urban living. Consider the vampire bat. Your first impulse may be to shudder at the terrifying vision of vampire bats, in the dead of night, swooping

down to drink the blood of an unsuspecting victim. Yet vampires have a wonderful story to tell of social cooperation.[27]

The vampire bat *(Desmodus rotundus)* is a rather small bat, not much bigger than a plum. A vampire can hang by its feet from the hair of a horse's mane and bite the horse's neck. It doesn't suck the blood; instead, it removes a small patch of flesh with its razor-sharp incisors and laps up the blood flowing from the wound. A vampire's saliva has an anticoagulant to keep the blood from clotting. After one bat has drunk its fill, another continues at the same spot. Horses can dislodge feeding bats by tossing their heads, swishing their tails, or rubbing against trees.

Life as a vampire is hard. Bats are warm-blooded and, without feathers or fur, lose lots of heat. Their requirements for energy are huge. A vampire bat consumes 50 to 100 percent of its weight in each meal. Yet up to one-third of the bats may not obtain a meal on any given night. Going without a meal is dangerous. A vampire dies after sixty hours without food because by then its weight has dropped 25 percent, and it can no longer maintain its critical body temperature. To survive, vampire bats have developed an elaborate buddy system for sharing meals. The sharing takes place between mother and pup, as well as between adults.

One study of vampires on a ranch in Costa Rica focused on a population divided into three groups of a dozen females. The members of a group often stay together for a long time, twelve years in some cases, and get to know one another very well. The group of a dozen adult bats is a family unit from a vampire's standpoint. Most of the group consists of females, each of whom usually cares for one pup. A female pup stays in the group as she matures, whereas a male pup leaves. The females in a group span several generations. Group membership is not entirely static, however. A new female joins the group every two years, so at any time the females in the group belong to several lineages, called matrilines.

The bats live in the hollows of trees. Imagine a hollow tree with an opening at its base and a long vertical chamber reaching up into the tree trunk. The females congregate at the top of the chamber. About three males hang out, so to speak, in the tree hollow. One male assumes a position near the top of the chamber, nearest to the females, and defends this location against aggressive encounters from other males. This dom-

inant male fathers about half of the group's young. Subordinate males take up stations near the base of the tree by the entrance. Other males are out of luck, roosting alone or in small male-only groups rarely visited by females.

The pattern of food-sharing is especially interesting. The food is transferred by one bat regurgitating into the mouth of another. (You wouldn't want to be a bat, would you?) Most (70 percent) of the food transfers are from a mother to her pup. This food-sharing supplements the mother's lactation. The other 30 percent involves adult females feeding young other than their own, adult females feeding other adult females, and on rare occasions, adult males feeding offspring.

Some adult females have a "special friendship" with females who are not their kin (males also have same-sex relations; see p. 141). This bond is brought about in part by social grooming. The bats spend 5 percent of each day grooming and licking one another. Some of this grooming is between special friends, and the remaining among kin. A hungry bat grooms one who has recently fed to invite a donation of food. To solicit food, a hungry bat licks a donor on her wing and then licks her lips. The donor may then offer food.

The mutual assistance is significant. If they didn't help each other, the annual mortality of vampires would be about 80 percent, based on the chance of missing a meal two nights in a row. Instead, the annual mortality is around 25 percent because food-sharing tides bats through their bad nights.

Biologists assume that animal species don't readily cooperate with each other. If natural selection is the survival of the fittest, shouldn't natural selection reward selfishness and discourage cooperation? Biologists suggest two forms of cooperation that can evolve by natural selection. The first is cooperation restricted to helping kin, and the second is cooperation restricted to helping special buddies—those who regularly reciprocate the cooperative acts.[28] Vampire bats help not only kin as do many species, but also unrelated friends—which is what makes vampires so interesting. This mutual helping, called "reciprocal altruism," takes place primarily between animals who have lived together and gotten to know one another. Each helps the other at various times, and each instance of helping benefits the recipient much more than it costs the donor.

Critics of the idea of reciprocal altruism have argued that natural selection favors the "cheater" who takes food without reciprocating. If cheaters are evolutionarily more successful than food-sharers, the altruism eventually disappears and all the animals wind up being selfish. The vampires solve the problem of cheaters by developing special friendships through what might be considered same-sex courtship. This involves continual mutual grooming and food solicitation using the bat equivalent of kissing, all of which reinforces the pair-bond and promotes long-term survival.

Other species have different tactics to exclude or retaliate against the selfish.[29] For instance, Rhesus macaques who find food sources and don't give food calls telling everyone else about it are subsequently targets of aggression.

Little is known about whether animals acquire a "reputation" that others use to decide whether to include them in cooperative activities. The idea of reciprocal altruism invites thinking in terms of pairs. Yet in my field studies of lizards, whenever I've seen two animals interacting with each other using head bobs, pushups, and color changes, all the other lizards in the vicinity were watching too. Do they remember what they've just seen? Probably. The lizards can probably remember who won or lost in a showdown over territory, and they can probably remember who cheated and who reciprocated in an instance of cooperation. Animals may talk about each other as well, indulging in animal gossip.[30] Animal interactions, from mating to territorial spats, to grooming and food-sharing, are often done out in the open, so that everyone can see and later discuss what happened. Animals with "nice" reputations may be included in cooperative activities and "meanies" left out. Reputations may provide a way for an animal to know whether another is likely to reciprocate, without having to learn the hard way.

Similarly, little is known about animal "generosity." A social system effective at excluding cheaters promotes evolution of the desire to share. Generosity depends on society's promise that what goes around comes around. If vampires someday prove to be among nature's most generous creatures, future children's comic books may feature vampires as friends rather than foes.

The gold medal for cooperation between mammals is held by small, almost hairless rodents that live underground in parts of Kenya, Ethiopia, and Somalia. Their subterranean families consist of certain in-

dividuals specialized for reproduction and others who routinely groom, feed, and protect the offspring. If this society sounds like a colony of bees, with a reproductive queen surrounded by the workers, you're right. These mammals, called naked mole-rats *(Heterocephalus glaber)* because of their exposed smooth skin, are the vertebrate counterparts of the social insects.[31]

A family of naked mole-rats typically consists of about one hundred individuals. Naked mole-rats are underground all the time. Their only aboveground signs are volcano-shaped mounds about one foot high, created by ejecting loose soil from their burrows. Naked mole-rats make these mounds when excavating tunnels, primarily at dawn and dusk, and during the winter rainy season. To find food, the naked mole-rats dig until they bump into a juicy root. The rats can't see or smell through the dirt, so finding a root is like a miner striking a vein of gold. Because naked mole-rats are so difficult to study in the field, most observations are based on captive colonies in the lab.

Naked mole-rat families are really close—more than 80 percent of the matings occur between brothers and sisters or between parents and offspring. Typically one female and one to three males do the breeding. The breeding female is aggressively dominant over other females. A breeding female gives birth every two to three months, producing a litter of about ten pups. A female produces thirty to sixty offspring per year. Nonbreeding naked mole-rats are not sterile. If a breeding male or female dies or is removed, a nonbreeding mole-rat of the same sex steps up to take his or her place.

Breeding is a demanding occupation. Although the breeding female typically remains the largest and heaviest animal in the extended family during her tenure as chief breeder, the breeding males lose weight after they become breeders, quickly shedding 17 to 30 percent of their weight, and appear emaciated after several years. Meanwhile the breeding female becomes not only heavier but also longer, adding vertebrae to her spinal column.

Who becomes a breeder (either male or female) seems to be determined by conflict among the aspiring females. Upon the death of the female breeder, the would-be successors not only attack one another but also target specific males, shoving and biting them. Of seven fights started by females against males, five fights led to the death of the male.[32]

The males attacked were either mates of the previous breeding female or were pair-bonded to rival females, as indicated by courtship activities such as frequent anogenital nuzzling.

The nonbreeding males and females provide parental care to the offspring of the breeders. From shortly before the pups are born until they're weaned, the nonbreeders huddle with the pups in the communal nest to provide a stable thermal environment, a warm nursery. The nonbreeders regularly nudge, handle, and groom the young; retrieve pups that fall out of the nest; transport pups when the family moves to a new nest site; and evacuate pups from the nest during a disturbance. The nonbreeders also provide food to the pups in the form of caecotrophies, partly digested fecal pellets. The pups routinely solicit and obtain these morsels of candy from the nonbreeders of both sexes, but not from the breeders themselves. After the pups are fully weaned, they are able to eat food that has not been preprocessed. Nonbreeders also defend, maintain, and extend the family's system of tunnels. They collect and transport food through the tunnels back to the nest, where they feed other family members, including the breeders.

The distribution of reproductive activity throughout a group is called its reproductive skew. A social group where everyone reproduces has low skew. High skew occurs in the naked mole-rats because only two to four individuals in the entire group of one hundred or more reproduce. The reproductive skew in an animal society is the most fundamental attribute a society has from an evolutionary standpoint—the index of a society's reproductive equity. Little is known about what determines a society's reproductive skew to begin with, but once in place, the skew sets a baseline for how each individual in the society structures a life plan for reproductive success.

Cliff swallows *(Hirundo pyrrhonota)* are perhaps our closest cousins when it comes to life in the big city.[33] Swallows live as monogamous pairs in colonies. Their nests, which look like small pitchers, are arranged side by side. Up to five thousand birds form what amounts to a city of mud huts. Not all swallows live in the big city, though. Some live in small villages of twenty or so nests, and some males hang out outside of town without any nests.

Cliff swallow life includes many features of our own city life—a hot real estate market, trespassing, robbery, hanky-panky with the neigh-

bors, plus presumably some compensations. Nonetheless, most observers of cliff swallow life emphasize the problems, perhaps because the birds live in the countryside, where the virtues of city living are underappreciated. The nests are packed in so densely that occasionally a bird is trapped inside and dies when a neighbor's construction project blocks its entrance hole. Even worse, the droppings from a nest above may clog up and bury a nest below—swallows seriously need expertise in civil engineering. Swallows also have a major public health crisis. The colony density promotes the growth of bugs that harm the chicks and adults.

Birds occasionally "trespass" into one another's nests by either barging in on the owner unannounced or following the owner in before he or she can turn around and block the entrance. Seventy-five percent of the trespassers are males. Of nest entries considered "successful," 14 percent of the time, the trespasser stole grass used to line the nest; 9 percent of the time, a male trespasser forced himself on his neighbor's wife; 7 percent of the time, the trespasser stole some still-wet mud before it had dried; 3 percent of the time, a female laid an egg, or transferred an egg, into her neighbor's nest; 1 percent of the time, the trespasser tossed one of the neighbor's eggs or chicks out the window; and in 0.3 percent of the cases, the trespasser evicted the owner. Enough intrigue for a new TV drama, "Cliff Swallow Vice."

Females congregate in flocks while gathering mud and grass to make nests. "Surplus" males hang around mud holes waiting for females to alight. The males circle above and then pounce, "forcing" copulation as the pair flails about in the mud. Nonetheless, some males may be innocent of evil intent, traveling to a mud hole for regular ol' mud, where they encounter a female who "elicits a forced copulation." Also, "females did not always appear to struggle with the males attempting to copulate with them at a mud hole. Some females clearly allowed successful cloacal contact."[34] Indeed, 86 percent of the extra-pair copulations (EPCs) at the mud hole appeared to "achieve" cloacal contact.

What do husbands back at the nest do about all this? They are "suspected of dealing with the threat of cuckoldry by frequently copulating with their mates." Indeed, "the male copulated with his mate virtually each time she returned to the nest," leading to conjugal love "dozens" of time in a single morning.

Biologists have observed which males are "perpetrators" of illicit romance. Among thirty-eight male birds observed in EPCs, one male "committed" twelve copulations, another eleven, the next eight, and so forth. Thirty percent of the EPCs involved the top three, with the numbers trailing off to those who had only one dalliance apiece. Thus only a few males commonly "engaged in this behavior," whereas most "did it" casually or not at all.

EPCs lead to extra-pair paternity, or EPP—that is, to eggs in the nest fathered by a male other than the male tending the nest. Females place eggs in one another's nest, leading to varied egg maternity in the nest too. Extra-pair maternity, or EPM, refers to eggs mothered by females other than the female tending the nest.

Females either lay eggs in their neighbor's nest or transfer eggs laid in their own nest to other nests by carrying them in their bills. Females transfer eggs primarily to nests nearby, within five nests of their own. The transfer typically happens when the recipient nest is left unattended. In several cases, though, a male nest owner allowed a neighboring female to enter his nest and lay an egg there while he was present. The female does not toss an egg already there to make room for hers; she simply adds her own egg to those already there. Around 15 percent of the nests wind up with one or more eggs with extra-pair maternity.

Biologists call transferring eggs "brood parasitism"; the bird owning the recipient nest is called a "host"; and the bird delivering the egg, a "parasite." Host birds lay 71 percent fewer eggs than parasite birds, implying that parasites are somehow taking advantage of the hosts. However, the parasites are themselves often parasitized, as they leave their own nest unguarded.

Just as some males are more likely to "perpetrate" an EPC, some females are more likely to be brood parasites. In one study 29 percent of the females labeled as parasites laid eggs in two or more nests, whereas other females laid eggs only in their own nests. Females did not brood-parasitize to get out of housework. The females labeled as parasites contributed just as much parental care and raised as many offspring in their own nests as did their hosts. The advantage to brood parasites is simply leaving more eggs in the nests of other females, not in lowering the size of their own nest. Just as certain females were more likely to lay eggs in another's nest, some females were more likely to receive the eggs of oth-

ers. Also, females sometimes transfer baby nestlings who have already hatched.

When EPCs and brood parasitism are taken into account, 43 percent of the nests are estimated to contain an egg unrelated to one or both birds tending the nest. Clearly, cliff swallows have decoupled economic monogamy from reproductive monogamy.

Both EPPs and EPMs lead to eggs in the nest unrelated to one or both of the paired birds at the nest. EPPs and EPMs are not symmetric, however, because an EPP implies that one gamete was transferred, whereas an EPM implies the transfer of two gametes, one from the mother and one from the father. In fact, a female transferring an egg may not be intending to get a free ride, but rather may be transferring the egg to the father's nest. So-called brood parasitism hasn't been demonstrated to be competitive at all.

The appetite for seeing theft and deceit everywhere has blinded biologists to other interpretations of what's going on. Swallows apparently have a distributed system for raising young. Throughout the colony the parenting workload is essentially parceled out to work teams of two adults apiece, which amounts to economic monogamy, even though the egg and gamete trading implies an absence of reproductive monogamy. Each team winds up tending about the same number of eggs and nestlings in its nest, and each clutch of nestlings contains offspring from the neighborhood. (For more on a system of distributed paternity in a closely related species, the tree swallow, see chapter 7.)

After fledging, the juvenile birds gather in flocks called crèches. The adults continue to feed their young for a few days after they have flown the nest by searching them out in these crèches and giving them food there. They can recognize their own offspring by listening for an individually distinctive signature in their calls. Some juveniles do not join the crèches, returning instead to the nests, much as an eighth grader might return to kindergarten for cookies. Called kleptoparasites, the juveniles block the nest entrance and intercept food destined for the baby nestlings inside. The parents "willingly" feed these juveniles. The adults never evict them as they routinely do other adults who trespass. Why? The parents are supposedly unable to recognize the juveniles as thieves and are duped into disgorging their food to someone other than their nestlings.

Why isn't the food given the juveniles considered a voluntary donation by the adults? Calling juveniles at the nest kleptoparasites criminalizes these birds and implies that the adults are incapable of knowing their own best interests. Indeed, any swallow who doesn't do what they're supposed to is criminalized. The males in EPCs are "perpetrators" of copulations, the females are "elicitors" of copulations, and females who place eggs in other nests are "parasites." Birds haven't been corrupted by sex and violence in the movies; shouldn't they be better behaved?

The plot thickens. Males sometimes copulate with other males at mud holes, described as "fights in the mud." In an experiment in which stuffed models of birds were placed near a mud hole, 70 percent of the copulation attempts were directed by males to the male models. The interpretation was that the males were "mistaken"; they were unable to distinguish the sex of the stuffed birds. Hmm . . .

Cliff swallows have a complex dynamic going. City life in these birds taxes the ability of biologists even to describe what's happening. But the pejorative language biologists have used so far undercuts the attempt to understand cliff swallow society in greater depth.

A DIFFERENT MODEL

Do animals really own anything? The assumption that they do naturalizes human property rights. Because of this assumption, animals can be described as stealing. Biologists are willing to impute ownership to animals, as though animals cared about property as much as people do. A biologist interprets a bird feeding another as wasting food. The bird is said to be incapable, too dumb, to know it's been duped into giving up hard-earned wages. Yet the same bird is acknowledged to be smart in so many other ways. Why is a bird smart in some ways and dumb in others? Time and again, biologists assume that ownership is well defined, and explain away the failure to be selfish as a limitation of ability, rather than as falsifying the assumption that selfishness is adaptive.

Close genetic relationship among individuals undercuts natural property. Imagine living in a place where you're closely related to everyone else. In a colony where every individual is related 50 percent to another, do you own half your things or half-own all your things? I don't know. The clarity of who owns what becomes fuzzy here. Reciprocal and dis-

tributed altruism also undercuts natural property. I live in San Francisco among the homeless. I often see people of limited means give to the poor on the streets. Hasn't someone told them to be selfish? Perhaps they, or their genes, have been there too. What goes around comes around.

Twenty years ago, Sandra Vehrencamp, an evolutionary biologist, introduced the theory that a society's reproductive skew was connected to what might today be called a "labor market" for cooperative effort within the society. Her focus was on insect colonies with multiple queens. The basic idea is that an animal helps another in exchange for access to reproductive opportunity.[35] Some individuals, the privileged, are envisioned to have control of reproductive opportunity, and to pay out some of this opportunity to others who do not have similar access. In return for this paycheck, the underprivileged contribute labor to assist the privileged in their reproduction.

The inequality of reproductive opportunity initially available to different individuals is called a "distributional inequity" by economists. Distributional inequity may reflect territories that vary in exposure to predators or availability of food, water, and a mix of sunny and shady spots. An animal's political connections may also give it control of resources. Distributional inequity may develop because of inheritance, age, abilities, and luck.

Exchanges of labor for reproduction are especially profitable between relatives, leading to the formation of an extended family wherein the individual who does the breeding is a parent of helpers who remain at the nest. The value to a helper of assisting its parent's reproduction depends on its genetic relationship to the parent's offspring. The highest value accrues to offspring who are full brothers or sisters—in this case a helper may not bother with reproducing at all but let the parent do all the work, called kin selection.[36]

An exchange of help for reproductive opportunity is possible even in the absence of a genetic relationship if the amount of access the helper is paid exceeds the reproductive opportunity the helper would have in the absence of supplying any labor. The reproductive opportunity granted by a privileged individual who employs an underprivileged individual is called a "staying incentive" because this payment leads the underprivileged individual to stay at the nest as a helper instead of leaving to start a new nest. Overall, the theory envisions the animal society as a political economy held together by transactions in the currency of reproductive opportunity.

Extended families form depending on supply and demand within the labor market. If demand for labor is tight—no jobs for youngsters outside of home—then even a small staying incentive will induce them to stay at home and join an extended family. With lots of opportunity outside of the home, even a large staying incentive will not persuade the youngsters from striking out on their own.

According to this thinking, family structure is fluid, changing when opportunities outside the nest vary and when the breeder changes mates (which devalues the genetic paycheck helpers receive for their labor). Great distributional inequity causes reproduction to concentrate in a few individuals by mutual agreement between breeders and helpers, resulting in a high reproductive skew that may amplify the initial inequity. If resources are evenly distributed, almost everyone breeds for himself or herself, and the social system has a low reproductive skew. Sandra Vehrencamp termed these extremes "despotic" and "egalitarian" societies.[37]

Let's see how this theory works in an actual case. White-browed scrubwrens of Canberra, Australia, fit the labor-market theory of family dynamics.[38] The social groups consist of a breeding female and one or more males (polyandry). In this case, the young males have to decide whether to stay and help mom and dad or to leave and set up a new home. Females build their nest alone and incubate the eggs alone. The males feed the female while she is fertile before the eggs are laid, and while she is incubating the eggs. The males and the females both feed the chicks while they are in the nest and up to eight weeks after they leave the nest. The males fight it out, leading to a dominance hierarchy, with the alpha male on top and the beta male as a subordinate. The question is what the alpha male should allow the beta male to do so that the beta male remains as a subordinate and doesn't strike out on his own. How does the alpha male hire the beta male as a helper? Four types of multimale families occur:

1. If the beta male is related to both the alpha male and the female, the beta male helps at the nest and doesn't father any of the nestlings himself. The alpha male is the sole male parent. Even

though the beta male is not the father, the eggs are very worthwhile to him because the eggs are his full siblings. When combined with limited outside opportunity, the beta male finds it reproductively profitable to stay, even without the incentive of sharing in some of the matings. This family has high reproductive skew.

2. If the beta male is related to the female but not the alpha male, the beta male again helps at the nest without mating, even though the eggs are not as valuable to him as they are when both the female and the alpha male are his relatives. Again the alpha male provides no staying incentive. This family too has high reproductive skew.
3. If the beta male is related to the alpha male but not the female, the value of the eggs is even less because the paternity of the eggs is uncertain. About 15 percent of the eggs are fathered by extra-group matings. From the beta male's perspective, any eggs the alpha male doesn't father have no value. As a staying incentive, the alpha male allows the beta male to sire about 20 percent of the brood by mating with the female. This family has moderate reproductive skew.
4. If the beta male is not related to either the alpha male or the female, the beta male sires about 50 percent of the brood himself. The alpha male has to share half of all matings, the maximal possible incentive, to keep the beta male as a helper. This family has zero reproductive skew.

Thus the alpha male can be viewed as allotting the beta male access to reproductive opportunity within the family group in whatever amount is necessary to induce him to stay as a helper. In situations 1 and 2, the beta male doesn't need any staying incentive at all. In situation 3, the alpha male allows the beta male to sire 20 percent of the brood, and in situation 4, to sire half of the brood.

Do you think these families are happy groups of individuals sticking together by mutual consent to fashion productive lives for all? Some biologists are critical, raising three objections.[39] The breeder, for one, may find the price of the staying incentives too high and not agree to pay. The helper would then abandon the nest and set forth alone. But the breeder might coerce the helper to stay anyway. However, the breeder might not be able to completely control the helper. The helper would therefore breed surreptitiously to whatever extent he could. This is not a peaceful home, but a family at war.

A second objection concerns whether the net effect of the "helper" is actually to help or to hurt. Does hanging around the nest and bringing in some food now and then yield a net benefit to the breeder? In naked mole-rats, the breeding female aggressively prods "lazy" workers, suggesting a tension between employer and employee.[40]

A third objection is that mutual consent is beyond what animals are capable of doing. Perhaps animals can't really negotiate labor contracts among one another when people can't even do this very well. But I believe that animals can do anything—I'm a hopeless animal chauvinist.

These objections are perhaps merely growing pains in the early stages of a new theory. The approach of looking at labor relations among family members seems promising to me. I'd like to see this theory become more dynamic and interactive. As it is, the breeder is assumed to know what the helpers are willing to accept and then offer that price. The breeder is what economists call a perfectly discriminating monopolist, a sole seller who has perfect information about what buyers are willing to pay. Economic theory also allows for price negotiation between seller and buyer, and competition among sellers and among buyers. Extending biological labor relations theory to include ongoing negotiations between breeders and helpers may solve the present limitations, and allow us to predict when societies will become peaceful or violent.

The take-home message from this theory is that reproductive inequity emerges from distributional inequity combined with genetic relationships. In animals, we have the counterpart of human democracies and dictatorships. We see in these biological theories the same issues that political scientists deal with in human societies. We see an even distribution of resources lead to widespread participation in breeding and a concentrated distribution of resources lead to power hierarchies, family feuds, and labor strife. We see economic markets for transactions of reproductive opportunity.

As we now move to social systems featuring multiple genders, the language biologists use to describe how animals behave becomes particularly loaded. The language always lauds the individuals who hold territories and possess mates, as though each male were biologically entitled

to a castle of his own, complete with princess. Words like stealing, parasitism, deceit, and mimicry dominate the discussion and distort the sophisticated reality of what really happens in societies that contain a biological diversity of participants. Instead, the theory of transactions of reproductive opportunity seems to extend nicely to family organizations with multiple genders.