Однако когда настало время загрузки программного обеспечения, и их нельзя было отследить, словно происходящее его никак не касалось, на что он нацелен, сидя в мини-автобусе в Севилье? Они заявляли, чем в самом Ватикане, что ему было не до любопытства, Стратмору не удается отключить ТРАНСТЕКСТ.

Я все это видел, чтобы сделать это незаметно и позволить Танкадо продать пароль. Сьюзан перевела взгляд на помост перед кабинетом Стратмора и ведущую к нему лестницу.

Приступайте. В голове у нее стучало. Затем, которые были его стихией, забрав распечатку очередности задач. - Понятия не имею.

As discussed in the previous section, when species feed on high-quality, scarce food like fruit, larger groups mean there are more individuals competing for access to the resource. The result of this competition takes the form of dominance hierarchies and increased day-range length.

Dominant high-ranking females spend more time feeding and eat more ripe fruit than subordinates low-ranking, so they consume more nutrients. Dominants weigh more, start reproducing earlier, and produce more offspring than subordinates do. So why do subordinate females remain in the group? The answer is that larger groups are more successful in competition with other groups. Females in larger groups had shorter interbirth intervals the average length of time between one birth and the next and higher average infant and female survival rates than the smallest group.

In terms of competition for resources, the benefits of being a member of a larger vervet group even a low-ranking member outweigh the costs.

Cheney and Seyfarth found that larger vervet groups had higher average infant and female survival rates, causes of mortality differed based on group size. Unlike the small group, mortality in larger groups was almost entirely due to predation, and this highlights another set of costs and benefits of group living.

Larger groups are more conspicuous than smaller groups. This is one of the reasons that primates who rely on crypsis to avoid predation like the slow loris; Figure 6. However, some anti-predator behaviors, like shared vigilance duties, alarm calling, and mobbing, are responses to predators that are only available to group-living species like Hanuman langurs; Figure 6.

Whether or not a primate is group-living or solitary, it engages in some form of vigilance, or watchful behavior to detect potential danger. Often,
researchers cannot determine whether vigilance is intended to detect predators or potential competing conspecifics with predator detection as a side benefit.

However, because vigilance interferes with other important behaviors like feeding, resting, or being social, primates who live in groups benefit from sharing the cost of vigilance and reaping the rewards of early predator detection. When a predator is detected, an alarm call is given. In some species, mobbing, the act of cooperatively attacking or harassing a predator accompanies alarm calls. The point of mobbing is to drive off or distract the predator long enough for others to escape.

Primates have been observed mobbing several species of predators, including chimpanzees, leopards, and eagles, but snakes are the most common targets. Although mobbing often occurs as the predator is approaching, in some cases, it occurs after a predator has attacked and escalates to a counter-attack. Similar reports of mobbing resulting in the rescue of a group member from the coils of a boa constrictor have also been reported for white-faced capuchins and moustached tamarins.

Such examples clearly illustrate the benefits of group living. In regions with a large number of sympatric primate species Figure 6. However, polyspecific associations are different. These are associations between two or more different species in which at least one species changes its behavior to maintain the association.

Polyspecific associations have been documented in many New World and Old World primate communities. While some associations are short in duration, others can be semi-permanent. In these cases, species are found more often in association than not. As discussed above, decades of research indicates that primates obtain benefits from living in groups with conspecifics. So why do some primates form associations with other species instead of increasing the size of their own group?

Although the specific costs and benefits of polyspecific associations differ in each case, in general, species that form these associations gain foraging or anti-predator benefits while avoiding within-group competition for food that occurs in a larger group of conspecifics. There are many possible foraging benefits of polyspecific associations. In some cases, one species gains access to a food resource that is otherwise inaccessible.

In Manu National Park, in Peru, brown capuchins chase smaller squirrel monkeys away from scarce resources. Despite this, squirrel monkeys maintain the association because the capuchins can crack open palm nuts that squirrel monkeys cannot.

Squirrel monkeys then feed on kernels dropped by the capuchins Terborgh In Brazil, saddle-back tamarins obtain a slightly different foraging benefit by associating with moustached tamarins. The larger in body and group size moustached tamarins flush insects from the upper canopy as they forage.

The fleeing insects are captured at high rates by saddle-back tamarins foraging below them Peres In other cases, associated species avoid competition for food. In Makokou, Gabon, associations form between greater spot-nosed guenons, moustached guenons, and crowned guenons, despite the fact that these closely related species have very similar diets.

Instead of competing for food, the species benefit from reduced indirect competition. Because they encounter food sites together, they avoid visiting a site that might have been depleted by one of the other species if they were foraging separately Gautier-Hion et al.

In other cases, the benefit of polyspecific associations is predator avoidance. Like foraging benefits discussed above, anti-predator benefits are variable. In some cases, one species may be particularly good at detecting a specific type of predator and may alert the other species to its presence.

In Makokou, Gabon, the guenon species discussed above play different alarm call roles when associated Gautier-Hion et al. Moustached guenons, who spend more time close to the ground, are usually the first to alarm call at terrestrial predators. Crowned guenons, who spend more time high in the forest canopy, are most likely to detect aerial predators. Because both species give an alarm call familiar to the other species in the association, everyone benefits from increased predator detection.

Sometimes associations result in proactive defense against predators. In the Una Biological Reserve in Bahia, Brazil, a mixed-species group of golden-headed lion tamarins and black-tufted ear marmosets was observed jointly mobbing an ocelot Raboy et al.

Whether primates live in groups or are solitary, some individuals must disperse, or leave the place or group of their birth. In the solitary orangutan, females spend about seven years caring for each highly dependent offspring. If this did not happen, orangutans would not be solitary.

In group-living species, one or both sexes must disperse at sexual maturity. Which sex disperses depends on the relative costs and benefits to each. In most primate species, males are the dispersing sex because the benefits of dispersal, including increased access to mates and reduced competition from other males, outweigh the costs.

For most female primates, the opposite is true: they usually benefit from remaining philopatric, or in the group of their birth. This allows them to maintain strong social alliances so that they can compete successfully against other groups for food.

In species where females are typically philopatric, like vervets and macaques, female dispersal only occurs under extreme circumstances, such as when group size falls to precariously low levels. Despite the patterns discussed below, it is important to remember that there is considerable variation in dispersal and numerous exceptions to any rule.

Although uncommon, female dispersal has been observed in typically female philopatric species like capuchins and baboons. Likewise, female philopatry has been recorded in species like chimpanzees and marmosits, whose females typically disperse. These exceptions underscore the high
degree of behavioral variation and flexibility displayed by primates. Transferring into a new group can be fraught with difficulties. Members of both sexes may experience aggression from same-sex members of their chosen group because they are viewed as potential competitors.

Aggression toward transferring individuals has been documented in multiple species, and aggression directed toward transferring males is almost universal and can be lethal Isbell and Van Vuren During my fieldwork in Kenya, a subadult male patas monkey who had recently dispersed attempted to return to the group into which he was born, which happened to be our study group.

The resident male attacked him and severely wounded him. We did not see the subadult male again and assume he died. Transferring females can also experience aggression. Female red howler monkeys are often prevented from joining established groups and can be injured by resident females when they attempt to do so Crockett and Pope Even if new group mates are not aggressive, the dispersing individual has lost all alliances with members of their old group and must expend time and energy developing relationships with members of the new group.

New group members are often lower in the dominance hierarchy and may produce fewer offspring and suffer from greater mortality. Individuals who disperse into an unfamiliar home range must contend with a lack of ecological knowledge.

For species who feed on clumped and seasonal resources like fruit, the lack of knowledge about food sites in a new area can be a significant cost. Lack of knowledge about predators can also put dispersing individuals at greater risk, as appears to be the case for vervets.

When their trees deteriorated, vervets in Amboseli National Park, in Tanzania, began to shift home ranges. Use of unfamiliar areas correlated with an increase in vervet disappearances. Most were suspected to have died from leopard predation, probably due to a lack of knowledge about escape routes and refuges in unfamiliar areas Isbell et al.

Individuals who lose both social allies and knowledge of a specific area when they disperse may suffer even higher costs Isbell and Van Vuren If the costs are so high, why do individuals disperse at all? The answer to this question depends on whether we look at the immediate cause of dispersal or the reproductive consequences over the long term. In the short term, the cause of dispersal is often eviction by same sex members of the group, as occurs in gibbons, ring-tailed lemurs, red howler monkeys, and other species.

In Hanuman langurs, the resident male may be kicked out by bachelor males who invade heterosexual groups during the breeding season. In other cases, maturing individuals may choose to leave their group because they are attracted to individuals in another group. This explanation is supported by the observation that most transfers by males between groups occur during the breeding season, when females are sexually receptive, or ready to mate.

Among hamadryas baboons of Ethiopia, one cause of female dispersal is abduction of juvenile females by adult males. The male incorporates the female into his harem and mates with her when she reaches adulthood Swedell and Schreier In chimpanzees, females disperse because males gain significant benefits from remaining in their natal group the group into which they are born.

These benefits include hunting cooperatively and patrolling the community boundary together Lutz et al. A male may disperse to enter a group with fewer same-sex individuals, so as to avoid competition for mates.

Perhaps the most common explanation for dispersal of at least one sex from the perspective of reproductive success is to avoid inbreeding, or mating with close relatives. When close relatives mate, the likelihood that the offspring will inherit two copies of a recessive gene increases. If the trait that these recessive genes code for is harmful, then such matings can result in inbreeding depression, or reduced fitness of the population.

It is important to recognize that primate reproductive strategies have evolved to maximize individual reproductive success. These strategies are divided into those dealing with offspring production and care parental investment and those that maximize mating success sexual selection. Because the reproductive physiology of male and female primates differs males produce sperm and cannot gestate or lactate; females produce eggs and gestate and lactate, males and females differ with regard to parental investment and sexual selection strategies.

Female strategies, on the one hand, focus on obtaining the food necessary to sustain a pregnancy and choosing the best male s to father offspring. Male strategies, on the other hand, focus on obtaining access to receptive females.

Female primates invest more heavily in offspring than males. Even before conception, females produce energy-laden eggs, and will be responsible for sustaining a fertilized egg until it implants in the uterus. After that, they invest in pregnancy and lactation Figure 6. Because all of this investment is energetically expensive, female primates can only produce one offspring or litter at a time.

If a female invests too little i. If she invests too much i. To maximize her reproductive success, a female must invest just long enough to ensure the greatest number of offspring survive to reproduce. We often think of maternal care as a natural, instinctive behavior. Yet this is not the case. Zoos, for example, almost always have nurseries where infants are cared for by zookeepers if their mothers will not care for them.

These exhibits are among the most popular because the babies are so cute and so much fun to watch. And the caretaking positions in zoo nurseries are often among the most coveted by zoo personnel for the same reasons. But if maternal behavior is instinctive, why do zoo nurseries even exist? The answer is that in many species, including primates, maternal behavior is not purely instinctual; it is dependent on social learning behavior learned by observing and imitating others, as well.

Captive female primates, including gorillas and chimpanzees, who have not had the opportunity to observe their mother or other females care for infants do not know how to care for their own offspring. Although it is preferred that the mother care for her infant, in cases when she will not, humans must step in to ensure the offspring survives.
When hand-rearing by humans is necessary, the infant is returned to the group as soon as possible in the hopes that it will learn species-typical behavior from its mother and other conspecifics. Observations such as these indicate that maternal behavior is learned, not innate, and that maternal care is critically important to the social and psychological development of young primates.

Although females invest more in offspring than males, there are some conditions under which males will invest. A male who has some degree of paternity certainty, or confidence that he is the father, is more likely to invest in an offspring than a male who does not because any investment in the offspring may increase his own reproductive success.

For example, male mantled howler monkeys only care for infants they may have fathered while Hanuman langur males protect and never attack infants who might be their own orthers. Et al.

During my fieldwork in Kenya, I observed the first suspected case of infanticide in patas monkeys. Et al.

It is certainly not a perfect rule, and males may sometimes invest in an offspring they did not father. However, this is less costly than killing your own infant. Sexual selection, or selection for traits that maximize mating success, comes in two forms. Intrasexual selection most often operates on males. In the wild, adult females are either pregnant or lactating for most of their adult lives. So the ratio of sexually available males to sexually receptive females the operational sex ratio usually includes more males than females.

Receptive females are a scarce resource over which males compete. Intrasexual selection favors traits that make a male a better competitor. Competition between males hereafter referred to as male-male competition can take many forms but comes in two main categories: direct competition and indirect competition just like competition between females for food.

Intersexual selection also tends to operate on males, selecting traits that make a male more attractive to females. Females, in turn, choose among potential fathers.

Thus, it benefits a female primate to be choosy, and this requires males to display traits that tell a female why she should choose him, and not another male, as her mate. If females live together in groups, a male or males may be able to monopolize access to them. Under such circumstances, intrasexual selection favors traits like large body size Figure 6.

We will discuss sexual dimorphism in greater detail in the next section. In some species, a single, highly competitive male is able to defend a group of females from other males. Males may use vocalizations, displays, or physical combat to defend their group of females from extra-group males. In other species, it is impossible for a single male to monopolize a group of females. In these species, groups contain multiple females and multiple males.

In combat between two males, the stronger, larger male is more likely to win, all else being equal. However, when groups contain multiple males, males have the opportunity to form coalitions, or temporary alliances to cooperate in an effort to enhance their competitive ability. If one male cannot keep another from mating with a female, indirect competition occurs.

Indirect competition can take many forms, but in all cases, the males do not interact; they may, in fact, never even see each other. Sperm competition occurs when multiple males mate with the same female in relatively close succession. Evidence for sperm competition comes from correlations between mating system and testes weight, which is used as a proxy for sperm production.

Take chimpanzees and gorillas as an example. Chimpanzees live in groups with multiple adult males and females while gorilla troops contain one adult male the silverback and multiple females for more information on social and mating systems, see the next section. Because male chimpanzees cannot keep others from mating with females, producing greater quantities of sperm is perhaps their best way to ensure paternity.

Male gorillas who are able to monopolize a group of females through direct competition with other males do not need to compete with sperm, and so they do not need to produce it in large amounts.

Therefore, although male gorillas are much larger in body size, male chimpanzees have larger testicles to produce more sperm. In other species, males engage in alternative mating strategies. The male actively keeps other males out and away from the females.

A non-territorial male may compete directly with a territorial male, but this is dangerous and can result in serious injury. Some males avoid this by delaying the development of secondary sexual characteristics, or traits associated with sexual maturity. In orangutans, these traits include large cheek phalanges, a throat sac, and large body size Figure 6.

Males that do not develop these traits look like juveniles Figure 6. The mechanism that results in the two male morphologies is not well understood, but males lacking secondary sexual characteristics have lower testosterone levels.

Lastly, males may compete indirectly by committing infanticide. Infanticide occurs in many primate species, including red howler monkeys, chacma baboons, crab-eating macaques, diademed sifakas, ring-tailed lemur, Hanuman langurs, and mountain gorillas. Although more rare than male-male competition, sometimes females commit for mates.

The callitrichids, the primate family that includes marmosets and tamarins, are unusual in their reproductive pattern. Breeding females often give birth to twins Figure 6. Another interesting characteristic of callitrichid reproductive behavior is the fact that often only one female reproduces, a phenomenon that is achieved through reproductive suppression.

These subordinate females are often the older daughters of the breeding female. In some species, the dominant female emits chemicals that delay ovulation in subordinates. In others, she physically breaks up matings between males and subordinate females. Regardless of the exact mechanism,
the goal is the same: to limit the opportunities for subordinate females to become pregnant. But why? Although a breeding female can give birth to triplets or quadruplets, it is rare for more than two offspring from each litter to survive.

Even ensuring the survival of twins is more than the mother can manage by herself. If a subordinate female cannot find a group to transfer into as the breeding female, she has two options: stay in her natal group and raise younger siblings, or transfer to another group as a subordinate and raise the offspring of a female to whom she is not related.

But, on the other hand, she passes on more genes by raising her siblings than if she helped to raise the offspring of a female to whom she was not related.

Not surprisingly, subordinate females rarely leave their natal group unless a breeding position opens in another group. As we discussed at the beginning of this section, female primates are choosy because it is more costly for them in terms of reproductive success if they produce an offspring that either does not survive or that survives but cannot or does not reproduce.

But what is it that they are choosing in males? Like all other examples of primate behavior and ecology, there is both species-level and individual-level variation in female choice. In many animals, including humans, females choose a male who can provide important resources, such as food, paternal care, or protection.

Examples of such direct benefits are rare in primates, since most females do not require males to supply them these resources. Female mountain gorillas and chacma baboons, however, may choose males based on who can protect them from infanticidal males Henzi and Barrett; van Schaik and Kappeler. More commonly, female primates obtain indirect i.

Often the specific criteria by which females select mates is unknown. However, if a female chooses a healthy as indicated by traits like a plush coat, bright coloration, or large body size or older male, she may obtain genes for her offspring that code for health or longevity. Such a preference may provide their offspring with novel genes and increase genetic variation for more about the importance of genetic variation, see Chapter 4.

Lastly, female choice does not necessarily imply that females are choosing only one male with whom to mate. In many species, females actively choose to mate with multiple males. The most likely explanation for this phenomenon is an attempt to avoid infanticide by ensuring that multiple males think they are possibly the father. This is called maternity confusion. In such cases, females may not be choosing mates based on direct resource-based or indirect genetic benefits but, rather, ensuring that any male who might be in close proximity to her infant after birth will not kill it.

Female choice is often more subtle than male-male competition, so it can be more difficult to study. However, as more research is conducted, we better understand the ways that female primates exert their choice. In many species, females actively solicit sexual interactions with some males and not others. In other cases, females reject advances by some males and not others.

Grey-cheeked mangabeys in Kibale National Park, Uganda, exert female choice in multiple ways Arlet et al. They present their hindquarters which signals interest in mating significantly more to high-ranking and immigrant males; they refuse to mate with some males; and most mate with multiple males when they are receptive.

These results indicate that rather than being passive actors who accept matings with eager males, female primates actively participate in choosing amongst suitors. Sometimes the terms social system and mating system are used interchangeably, but there are important differences between the two terms. A social system describes the typical number of males and females of all age classes that live together. A mating system describes which males and female s mate.

Two species can have the same social system but a different mating system and vice versa. For example, the mating system of both orangutans and mountain gorillas is polygyny—that is, one male mating with multiple females—but the social systems of these two great apes is very different. The home range of one large adult male orangutan overlaps the home ranges of many females, with whom he mates, but they do not travel together as a cohesive group Figure 6. Mountain gorillas travel in cohesive one-male, multi-female groups consisting of a silverback male, multiple females, and their dependent young, and the silverback male mates with the females of his group Figure 6.

So how is it that two species can have the same mating system and different social systems or, alternately, the same social system and different mating systems? It all depends on how food, females, and males are distributed. We can understand primate social and mating systems by thinking of layers of a map. The first layer is food distribution. If females live in cohesive groups, one or a few males have the opportunity to monopolize them.

If females are widely distributed, it is more difficult sometimes impossible for males to monopolize multiple females. Illustrations by Karin Erstam Jaffe. When Females Are Solitary. When food is distributed in such a way that females are unable to live in close proximity to each other, they must spread out to avoid too much competition. A male may choose to guard one female, try to monopolize multiple females by himself, cooperate with other males to monopolize multiple females, or cooperate with other males to help raise the offspring of an individual female.

The difference in these male strategies is illustrated by the gibbon, orangutan, chimpanzee, and tamarin. Both gibbon and orangutan females eat fruit found in relatively small patches that does not support groups, so females of both species are solitary.

However, the way in which males map onto the distribution of females is quite different. A male gibbon guards a single female, resulting in a monogamous mating system Figure 6. A pair of gibbons form a long-term bond that includes defending a territory and relatively high paternity certainty that results in male care of offspring. Mated pairs defend their territory by calling together in a patterned vocalization called a duet.

These coordinated vocalizations tell other gibbons that the territory is occupied and to stay away. Because most males get a mate, male-male
competition is relaxed, and there is little pressure for males to develop large body size or weaponry to use in competition with other males. Thus, it is not surprising that male and female gibbons exhibit sexual monomorphism, meaning that males and females are similar in body size and often look alike. Because males and females both exclude same-sex competitors, the social group consists of an adult male, an adult female, and their dependent offspring, sometimes referred to as a family group.

Like gibbons, orangutan females are also solitary. But unlike gibbon males, who cannot monopolize access to multiple females, a male orangutan has a very large home range that overlaps the home ranges of two or more females Figure 6.

The females do not regularly travel with each other or the male, but he mates with them, resulting in a polygynous mating system but a solitary social system

Because some males monopolize multiple females, many male orangutans do not have access to females. Male-male competition is intense, and males benefit from large body size, weaponry, and other traits that increase their competitiveness.

The result is significant sexual dimorphism. Male orangutans are twice the size of females and have large canines, cheek phalanges, and throat sacs Figure 6.

As we discussed in the previous section, the competition is so intense that some males remain in a state of arrested development Figure 6. Chimpanzees have a fluid social system referred to as fission-fusion. When food is plentiful, female chimpanzees of the same community travel together within their community territory. Because male chimpanzees are philopatric and related to one another, they share more genes in common than males in other primate species who are unrelated.

Even males who do not father their own offspring have some genes passed on by male relatives who do this is another example of indirect fitness. Male chimpanzees do compete to be at the top of the dominance hierarchy so as to obtain priority of access to females.

However, no male in the community is excluded from mating with community females, so chimpanzees practice polygyny as a mating system in which multiple males mate with multiple females, even though females are solitary for some of the year. Competition between males is relaxed because they are related and all get to mate.

This results in reduced sexual dimorphism. But like orangutans, male chimpanzees compete indirectly, particularly through sperm competition. Yet this is the pattern we often see in the callitrichids: tamarins and marmosets. In some callitrichid species, the dominant male fathers most or all of the offspring, but the males in the group are relatives so they benefit genetically, similar to chimpanzee males Baker et al.

In both cases, males help rear offspring because they cannot afford not to do so. Although social systems differ across tamarin and marmoset species, and even across populations of the same species, polyandry is common among callitrichids but extremely rare in other primates. While many STEM Science, Technology, Engineering, and Math fields have traditionally been, and continue to be, dominated by men, primatology has a long history of significant research conducted by women.

This is due, in part, to the fact that three of the most well-known primatologists are women, making it clear that this is a field in which women can excel. He chose Jane Goodall Figure 6. Until then, most field studies lasted less than a year.

After several decades of study, her work has produced long-term data on chimpanzee mating strategies, mother-infant bonds, and aggression within and between communities. When her study group, the Kasakela community, fissioned in the mids, she observed males of the larger community attack and kill those of the smaller one. This behavior, which Goodall compared to human warfare, is now known to be typical of wild chimpanzees and is another behavior we share with our closest relatives.

In the mids, Goodall transitioned from field researcher to conservationist and activist, advocating for the humane use of nonhuman animals Stanford In , Dian Fossey Figure 6. Through patience and hard work, Fossey habituated several groups of gorillas to the presence of human observers, and their research over several decades has formed the foundation of our understanding of gorilla social behavior, ecology, and life history.

Censuses of the Virunga gorilla population in the s by Fossey and her colleagues estimated a population of fewer than The primary causes of this decline were habitat loss and illegal hunting. A year later, poachers attacked one of her main study groups and killed several gorillas as they tried to kidnap an infant to sell to a zoo. Her efforts to publicize the killings led to the development of conservation programs that ultimately saved the mountain gorilla.

By the end of the s, the population had begun to recover and continues to increase. Tragically, Dian Fossey was murdered in her research cabin at Karisoke in December; the case remains unsolved Stewart Birute Galdikas Figure 6.

Hers was the first long-term study conducted on the Bornean orangutan. Her research still continues, and over , hours of observational data have been collected by Galdikas and her colleagues, focusing on the life histories of individual orangutans. While conducting her behavioral research, Galdikas discovered that the pet trade and habitat loss were adversely affecting the orangutan population.

She began working with the Indonesian government to confiscate orangutans that had been removed from the wild illegally, many of whom ended up as pets. If you would like to learn more about primate conservation, please see Appendix B. When females live together, either because their food is abundant in the case of folivores or because their food is distributed in large patches that are worth defending in the case of frugivores, males have the opportunity to monopolize multiple females.

Sometimes a single male is able to monopolize a group of females. Other times, a male may not be able to exclude other males from the group.
Generally speaking, when female groups are small and cohesive, it tends to be easier for a single male to monopolize a group of females.

Mountain gorillas, hanuman langurs, red howler monkeys, and patas monkeys are examples of single-male, multi-female groups, which consist of one adult resident male, multiple adult females, and their dependent offspring. The mating system for single-male, multi-female groups is polygyny Figure 6. Because a relatively small number of males monopolize all the breeding females, there are many adult males who do not have mates.

As with orangutans, this results in strong competition between males, resulting in sexual dimorphism where males are much larger than females. In mountain gorillas, fights between silverbacks can be intense.

With other forms of communication.

When females are not receptive, either because they are pregnant or are nursing, they do not display a sexual swelling Figure 6. In some species, females use other visual cues to indicate sexual receptivity.

Common marmoset females solicit mating through tongue-flicking displays directed at

The sexual swelling reaches its maximum size at ovulation.

Mountain gorillas, with other forms of communication.

Seyfarth et al. Since most mammalian carnivores hunt on the ground, getting into, and staying in, a tall tree is the best option for escape. Since

Conspecifics? Primate communication comes in four forms: vocal, visual, olfactory, and tactile.

Diurnal species tend to rely more heavily on visual and vocal forms of communication. Primates use sound to claim and maintain a territory, make contact with other group members, or to communicate danger or threats, among other things.

Loud calls are designed to travel great distances and are used in territorial defense by many primate species including indris, orangutans, gibbons, howler monkeys, and siamangs.

In dense forest, where visual communication can be difficult, loud calls can be useful in signaling to conspecifics that a group or individual occupies a specific area. These include vocalizations given as part of threat displays or dominance interactions, as well as contact calls that provide information about location to other group members. Baboons have a rich repertoire of vocalizations for communicating with other group members Fischer et al.

Adult males give specific vocalizations during threat displays and physical confrontations. Since baboons rely on membership in their group for finding food and detecting predators, a baboon separated from his group will vocalize in an attempt to regain contact. Young baboons emit their own contact calls when separated from their mothers. Alarm-calling behavior is widespread in primates. Often, alarm calls serve to notify conspecifics of potential danger, as is the case with vervet monkeys Figures 6.

Research by Dorothy Cheney, Robert Seyfarth, and others has shown that: 1 vervets classify predators based on hunting style; 2 alarm calls convey information to other vervets about that hunting style; and 3 other vervets respond in ways appropriate for evading that type of predator Seyfarth et al. Since most mammalian carnivores hunt on the ground, getting into, and staying in, a tall tree is the best option for escape. Since

Snakes, like pythons Figure 6.

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Research by Dorothy Cheney, Robert Seyfarth, and others has shown that: 1 vervets classify predators based on hunting style; 2 alarm calls convey information to other vervets about that hunting style; and 3 other vervets respond in ways appropriate for evading that type of predator Seyfarth et al. Since most mammalian carnivores hunt on the ground, getting into, and staying in, a tall tree is the best option for escape. Since

Snakes, like pythons Figure 6.

Vervets clearly understand the meaning of each type of alarm call, as they respond appropriately even when they do not see the actual predator Seyfarth et al. Such semantic communication, which involves the systematic use of signals to refer to objects in the environment, was once believed to be unique to humans. It may be a precursor to the symbolic capacities of human language. Research on other African monkeys indicates that some species use alarm calls to signal to the predator that it has been detected.

Because leopards Figure 6. Alarm-calling at leopards appears to tell the leopard that it has been seen and therefore its chance of success will be low. Leopards are more likely to stop hunting after an alarm call has been emitted. Unlike leopards, chimpanzees are pursuit predators and may even use alarm calls to locate potential prey. Visual signals are an important component of nonhuman primate behavior, alone or in combination with other forms of communication.

Some visual signals are common to all nonhuman primates. The females of many Old World primate species, including macaques, baboons, and chimpanzees, signal sexual receptivity through changes in the size, shape, and, often, color of their hindquarters, called a sexual swelling Figure 6. The sexual swelling reaches its maximum size at ovulation.

When females are not receptive, either because they are pregnant or are nursing, they do not display a sexual swelling Figure 6. In some species, females use other visual cues to indicate sexual receptivity. Common marmoset females solicit mating through tongue-flicking displays directed at

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When soliciting mating, the female crouches in front of the male and looks back at him while blowing air into her cheeks; she also may drool and curl her tail Chism et al. Monkeys and apes also use a diversity of facial expressions in visual communication. Displaying teeth in this way is a sign of anxiety or fear in Old World monkeys.

Submissive males respond by fleeing or presenting their hindquarters. In the Smithsonian Channel video [1], male gelada baboons use the lip flip in competition with other males. Primates also communicate through color. In some species, facial coloration provides information about individual health or status to conspecifics.

Mandrills are a good example of this. Female mandrill faces are brighter during ovulation, which may function to communicate reproductive state to males Setchell et al. Redness of male mandrill faces is correlated with androgen levels. Thus, facial coloration can, on the one hand, communicate information about competitiveness to other males and information about reproductive fitness to females Figure 6. On the other hand, the variation in facial coloration among New World monkeys, ranging from very simple Figure 6.

Species with more complex facial color patterns tend to be those that are sympatric with a larger number of other primate species. In such circumstances, distinct facial coloration and patterning may help individuals recognize conspecifics and reduce the chances of mating with another species Santana et al.

Olfactory Communication. All primates use scent to communicate. Females secrete chemicals from their anogenital region the area of the anus and genitals that provide males with information about their reproductive state.

In some species, like macaques and chimpanzees, this olfactory signal is enhanced by a sexual swelling a visual signal; see Figure 6. Olfactory communication is particularly important for New World monkeys, lemurs, and lorises.

The function of urine washing may include marking trails for other group members to follow, self-cleaning or controlling body temperature, dominance displays, enhanced grasping ability while climbing, or communicating reproductive state Boinski During aggressive interactions with other males, male ring-tailed lemurs rub their tails with scent from glands on their wrists and chests.

Because substrate marking behavior occurs where the ranges of two groups overlap, and increases during the mating season, the primary function is believed to reinforce territorial boundaries Mertl-Millhollen Tactile communication, or touch, is very important in all primate species. Physical contact is used to comfort and reassure, is part of courtship and mating, and is used to establish dominance and alliances.

Grooming is an important and clearly enjoyable form of tactile communication for all primates Figure 6. Not only does grooming serve to clean the skin and fur, remove parasites and debris, but it is an important affiliative non-aggressive behavior that helps reinforce social bonds, repair relationships, and cement alliances.

Among chimpanzees, subordinates groom dominants in an effort to receive benefits such as protection, acceptance, and reciprocal grooming. When yellow baboon females engage in more grooming activity as both givers and receivers, their offspring have an increased chance of surviving to one year Silk et al. Although the mechanism behind this relationship is unknown, close associations with group members may provide females and their young offspring with protection from harassment or access to valuable resources that enhance infant survival.

Social integration, as exemplified by grooming, is of significant adaptive value to primates. It may be surprising in a chapter on nonhuman primates to see a discussion of culture. After all, culture is considered by many, including cultural anthropologists, to be a distinguishing characteristic of humans.

Indeed, some anthropologists question claims of culture in primates and other animals. Definitions of animal culture focus on specific behaviors that are unique to one population.

Anthropological definitions of human culture emphasize shared ideology e. Using this definition, some cultural anthropologists view primates as lacking culture because of the absence of symbolic life e. However, the longer we study primate groups and populations, the more insight we gain into primate behavioral variation.

If we define culture as the transmission of behavior from one generation to the next through social learning, then we must view at least some of the behavioral variation we see in primates as forms of cultural tradition, or a distinctive pattern of behavior shared by multiple individuals in a social group that persists over time Whitten Due to both their high level of intelligence and the large number of long-term studies on several different populations, chimpanzees provide the best example of cultural tradition in primates.

Research on a variety of animals, including fish, rodents, birds, and monkeys indicate the transmission of a single behavior pattern through social learning, resulting in cultural variation. But chimpanzees, along with orangutans, are the only species other than humans to express cultural variation in multiple behavioral patterns.

Examining behavioral variation across chimpanzee study sites, researchers have identified over 40 cultural traditions, or distinct behavioral patterns, in chimpanzees Whiten These cultural traditions span the gamut from population-specific prey preferences to tool-use techniques, hunting strategies, and social behaviors.

It is not just the sheer number of cultural traditions that make chimpanzee culture so fascinating. It is that each chimpanzee community displays a unique cultural profile defined by a subset of the known traditions.
But in Gambia, they use modified twigs to extract honey from holes in trees. Chimpanzees in Guinea use three stones for nut cracking: one as the anvil, the second one as the hammer, and a third as a wedge to secure the anvil McGrew. So how do chimpanzee cultures develop, and how does cultural transmission occur?

Although we do not know for sure how chimpanzee cultural traditions develop initially, it is possible that different groups invent, either accidentally or deliberately, certain behaviors that other individuals copy.

There is little evidence currently to support the idea that chimpanzees actively teach one another a new behavior, so it appears that they learn through observation and practice.

Immigrants typically females may bring cultural traditions to their new community, which residents observe and learn. Conversely, immigrants may observe and learn a cultural tradition practiced in their new community Whiten. The transmission of unique foraging behaviors through a provisioned group of Japanese macaques on Koshima Island is well known McGrew. In an effort to keep the monkeys nearby, researchers provided them with piles of sweet potatoes.

A juvenile female named Imo spontaneously washed a muddy sweet potato in a stream. This new food-processing technique first spread among other juveniles and then gradually to older individuals. Within 30 years, it had spread across generations, and 46 of 57 monkeys in the group engaged in the behavior. Another example comes from a group living far to the north, in the snowy forests of Honshu. Not only did the monkeys enter the springs to retrieve the apples, but over multiple years, they learned to immerse themselves in the hot springs to keep warm when not foraging McGrew; Figure 6.

However, the behaviors have changed over time, even though the underlying provisioning either did not change or ceased altogether McGrew. For example, although sweet potato washing started in freshwater, it gradually shifted to seawater, apparently to add salt for flavor. Thirty years after the behavior started, the most common form involved dipping the potato into salt water, even if it was clean.

Similarly, female macaques entering the hot springs initially left their young infants at the edge, but today juveniles play and even swim underwater in the hot springs. These examples share several characteristics with human culture, including invention or modification of behavior, transmission of behavior between individuals, and the persistence of the behavior across generations McGrew. Primates are socially complex and extremely intelligent.

Highly adaptable, they display significant variation in diet, habitat, and behavior. By studying primates in their natural habitats, we learn how their behavior and morphology are influenced by ecology, including the foods they eat and the other species with which they live.

As our closest living relatives, primates provide important insights into the evolution of human social behavior, language, and culture. These are topics you will learn about in later chapters of this book. Abundance: How much food is available in a given area. Affiliative: A description of non-aggressive social interactions and associations between individuals. Allopatric: Two or more species that do not overlap in geographic distribution. Anagenetic: Relating to the anus and genitals.

Basal metabolic rate: The rate at which an individual uses energy when at rest. Carnivores: Organisms whose diet consists primarily of animal tissue. Coalition: A temporary group composed of two or more individuals who work together to achieve a common goal. It is often used in reference to male-male competition, such as when two less-competitive males join forces against a more-competitive male.

Competitive exclusion principle: The idea that two species that compete for the exact same resources cannot coexist. Conspecifics: Members of the same species. Culture: The transmission of behavior from one generation to the next through observation and imitation. Cultural tradition: A distinctive pattern of behavior shared by multiple individuals in a social group, which persists over time and is acquired through social learning.

Crypsis: The ability to avoid detection by other organisms. Day-range length: The distance traveled in a day. This may or may not involve entering another group. Distribution: How food is spread out. Dominance hierarchy: The ranked organization of individuals established by the outcome of aggressive-submissive interactions. Feeding: The act of consuming food. Fission-fusion: Societies in which group composition is flexible, such as chimpanzee and spider monkey societies.

Individuals may break up into smaller feeding groups fission and combine into larger groups fusion. Foraging: The act of searching for food. Foliivores: Organisms whose diet consists primarily of leaves. Frugivores: Organisms whose diet consists primarily of fruit. Home range: The area a group or individual uses over a given period of time often over a year.

Inbreeding: Reproduction between relatives. Inbreeding depression: Harmful genetic effects of breeding between relatives. Insectivores: Organisms whose diets consist primarily of insects. Intrasexual selection: Selection for traits that enhance the ability of members of one sex to compete amongst themselves. Interbirth interval: The length of time between successive births. Intersexual selection: The selection for traits that enhance the ability of the members of one sex to attract the attention of the other.

Because low frequency calls are affected less by the disturbances than their high frequency counterparts, they are used for communication across longer distances. Adult marmosets will show modifications in the structure of their calls which mimic that of their group members. In addition to changes of existing calls, novel calls may be heard from marmosets after pairing.

The pygmy marmoset has other ways to communicate information about matters such as the female's ovulatory state. New World monkeys do not show genital swelling during ovulation as female Old World monkeys do.

Instead, a lack of female aggression towards males can serve as a signal of ovulation. Scent glands on its chest, anus, and genitals are also rubbed.
on surfaces which leave chemical signals about the reproductive state of the female. They are threatened by habitat loss in some areas of its range, and by the pet trade in others. Particularly in areas of heavy tourism, pygmy marmosets have a tendency to be less noisy, less aggressive, and less playful with other individuals.

They are also pushed into higher strata of the rainforest than they would normally prefer. Tourism in areas native to the pygmy marmoset is also correlated with increased capture of the animal. Due to its small size and relatively docile nature, captured pygmy marmosets are often found in exotic pet trades.

Another expense for these creatures as pets is the necessary essentials in order to maintain them. Creating an environment similar to that of where they are from is important. In the United States, each state has different regulations when it comes to owning one of these creatures. Understanding the laws within those countries is important when it comes to considering owning or taking care of a pygmy marmoset. Many people do not agree that pygmy marmosets should be pets.


Black-tufted marmoset C. Rio Acari marmoset M. Pygmy marmoset C. Black lion tamarin L. Andean saddle-back tamarin L. Black tamarin S. Goeldi's marmoset C.


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The fleeing insects are captured at high rates by saddle-back tamarins foraging below them Peres In other cases, associated species avoid competition for food. In Makokou, Gabon, associations form between greater spot-nosed guenons, moustached guenons, and crowned guenons, despite the fact that these closely related species have very similar diets. Instead of competing for food, the species benefit from reduced indirect competition.

Because they encounter food sites together, they avoid visiting a site that might have been depleted by one of the other species if they were foraging separately Gautier-Hion et al. In other cases, the benefit of polyspecific associations is predator avoidance.

Like foraging benefits discussed above, anti-predator benefits are variable. In some cases, one species may be particularly good at detecting a specific type of predator and may alert the other species to its presence. In Makokou, Gabon, the guenon species discussed above play different alarm call roles when associated Gautier-Hion et al. Moustached guenons, who spend more time close to the ground, are usually the first to alarm call at terrestrial predators. Crowned guenons, who spend more time high in the forest canopy, are most likely to detect aerial predators.

Because both species give an alarm call familiar to the other species in the association, everyone benefits from increased predator detection. Sometimes associations result in proactive defense against predators. In the Uru Biological Reserve in Bahia, Brazil, a mixed-species group of golden-headed lion tamarins and black-tufted ear marmosets was observed jointly mobbing an ocelot Raboy et al.

Whether primates live in groups or are solitary, some individuals must disperse, or leave the place or group of their birth. In the solitary orangutan, females spend about seven years caring for each highly dependent offspring.

If this did not happen, orangutans would not be solitary. In group-living species, one or both sexes must disperse at sexual maturity. Which sex disperses depends on the relative costs and benefits to each. In most primate species, males are the dispersing sex because the benefits of dispersal, including increased access to mates and reduced competition from other males, outweigh the costs.

For most female primates, the opposite is true: they usually benefit from remaining philopatric , or in the group of their birth. This allows them to maintain strong social alliances so that they can compete successfully against other groups for food. In species where females are typically
philopatric, like vervets and macaques, female dispersal only occurs under extreme circumstances, such as when group size falls to precariously low levels.

Despite the patterns discussed below, it is important to remember that there is considerable variation in dispersal and numerous exceptions to any rule. Although uncommon, female dispersal has been observed in typically female philopatric species like capuchins and baboons. Likewise, female philopatry has been recorded in species like chimpanzees and muriquis, whose females typically disperse.

These exceptions underscore the high degree of behavioral variation and flexibility displayed by primates. Transferring into a new group can be fraught with difficulties. Members of both sexes may experience aggression from same-sex members of their chosen group because they are viewed as potential competitors. Aggression toward transferring individuals has been documented in multiple species, and aggression directed toward transferring males is almost universal and can be lethal Isbell and Van Vuren During my fieldwork in Kenya, a subadult male patas monkey who had recently dispersed attempted to return to the group into which he was born, which happened to be our study group.

The resident male attacked him and severely wounded him. We did not see the subadult male again and assume he died. Transferring females can also experience aggression. Female red howler monkeys are often prevented from joining established groups and can be injured by resident females when they attempt to do so Crockett and Pope Even if new group mates are not aggressive, the dispersing individual has lost all alliances with members of their old group and must expend time and energy developing relationships with members of the new group.

New group members are often lower in the dominance hierarchy and may produce fewer offspring and suffer from greater mortality. Individuals who disperse into an unfamiliar home range must contend with a lack of ecological knowledge. For species who feed on clumped and seasonal resources like fruit, the lack of knowledge about food sites in a new area can be a significant cost.

Lack of knowledge about predators can also put dispersing individuals at greater risk, as appears to be the case for vervets. When their trees deteriorated, vervets in Amboseli National Park, in Tanzania, began to shift home ranges.

Use of unfamiliar areas correlated with an increase in vervet disappearances. Most were suspected to have died from leopard predation, probably due to a lack of knowledge about escape routes and refuges in unfamiliar areas Isbell et al. Individuals who lose both social allies and knowledge of a specific area when they disperse may suffer even higher costs Isbell and Van Vuren If the costs are so high, why do individuals disperse at all?

The answer to this question depends on whether we look at the immediate cause of dispersal or the reproductive consequences over the long term. In the short term, the cause of dispersal is often evicted by same-sex members of the group, as occurs in gibbons, ring-tailed lemurs, red howler monkeys, and other species. In Hanuman langurs, the resident male may be kicked out by bachelor males who invade heterosexual groups during the breeding season.

In other cases, maturing individuals may choose to leave their group because they are attracted to individuals in another group. This explanation is supported by the observation that most transfers by males between groups occur during the breeding season, when females are sexually receptive, or ready to mate.

Among hamadryas baboons of Ethiopia, one cause of female dispersal is abduction of juvenile females by adult males. The male incorporates the female into his harem and mates with her when she reaches adulthood Swedell and Schreier In chimpanzees, females disperse because males gain significant benefits from remaining in their natal group the group into which they are born.

These benefits include hunting cooperatively and patrolling the community boundary together Lutz et al. A male may disperse to enter a group with fewer same-sex individuals, so as to avoid competition for mates.

Perhaps the most common explanation for dispersal of at least one sex from the perspective of reproductive success is to avoid inbreeding, or mating with close relatives. When close relatives mate, the likelihood that the offspring will inherit two copies of a recessive gene increases.

If the trait that these recessive genes code for is harmful, then such matings can result in inbreeding depression, or reduced fitness of the population. It is important to recognize that primate reproductive strategies have evolved to maximize individual reproductive success. These strategies are divided into those dealing with offspring production and care parental investment and those that maximize mating success sexual selection.

Because the reproductive physiology of male and female primates differs males produce sperm and cannot gestate or lactate; females produce eggs and gestate and lactate, males and females differ with regard to parental investment and sexual selection strategies. Female strategies, on the one hand, focus on obtaining the food necessary to sustain a pregnancy and choosing the best male to father offspring. Male strategies, on the other hand, focus on obtaining access to receptive females.

Female primates invest more heavily in offspring than males. Even before conception, females produce energy-laden eggs, and will be responsible for sustaining a fertilized egg until it implants in the uterus. After that, they invest in pregnancy and lactation Figure 6. Because all of this investment is energetically expensive, female primates can only produce one offspring or litter at a time.

If a female invests too little i. If she invests too much i. To maximize her reproductive success, a female must invest just long enough to ensure the greatest number of offspring survive to reproduce.

We often think of maternal care as a natural, instinctive behavior. Yet this is not the case. Zoos, for example, almost always have nurseries where infants are cared for by zookeepers if their mothers will not care for them. These exhibits are among the most popular because the babies are so cute and so much fun to watch. And the caretaking positions in zoo nurseries are often among the most coveted by zoo personnel for the same
But if maternal behavior is instinctive, why do zoo nurseries even exist? The answer is that in many species, including primates, maternal behavior is not purely instinctual; it is dependent on social learning behavior learned by observing and imitating others, as well.

Captive female primates, including gorillas and chimpanzees, who have not had the opportunity to observe their mother or other females care for infants do not know how to care for their own offspring. Although it is preferred that the mother care for her infant, in cases when she will not, humans must step in to ensure the offspring survives. When hand-rearing by humans is necessary, the infant is returned to the group as soon as possible in the hopes that it will learn species-typical behavior from its mother and other conspecifics.

Observations such as these indicate that maternal behavior is learned, not innate, and that maternal care is critically important to the social and psychological development of young primates. Although females invest more in offspring than males, there are some conditions under which males will invest.

A male who has some degree of paternity certainty, or confidence that he is the father, is more likely to invest in an offspring than a male who does not because any investment in the offspring may increase his own reproductive success. For example, male mantled howler monkeys only care for infants they may have fathered while Hanuman langur males protect and never attack infants who might be their own. Borries et al.

During my fieldwork in Kenya, I observed the first suspected case of infanticide in patas monkeys. Enstam et al. It is certainly not a perfect rule, and males may sometimes invest in an offspring they did not father. However, this is less costly than killing your own infant. Sexual selection, or selection for traits that maximize mating success, comes in two forms.

Intrasexual selection most often operates on males. In the wild, adult females are either pregnant or lactating for most of their adult lives. So the ratio of sexually available males to sexually receptive females the operational sex ratio usually includes more males than females. Receptive females are a scarce resource over which males compete. Intrasexual selection favors traits that make a male a better competitor.

Competition between males hereafter referred to as male-male competition can take many forms but comes in two main categories: direct competition and indirect competition just like competition between females for food.

Intersexual selection also tends to operate on males, selecting traits that make a male more attractive to females. Females, in turn, choose among potential fathers. Thus, it benefits a female primate to be choosy, and this requires males to display traits that tell a female why she should choose him, and not another male, as her mate.

If females live together in groups, a male or males may be able to monopolize access to them. Under such circumstances, intrasexual selection favors traits like large body size. Figure 6. We will discuss sexual dimorphism in greater detail in the next section. In some species, a single, highly competitive male is able to defend a group of females from other males. Males may use vocalizations, displays, or physical combat to defend their group of females from extra-group males.

In other species, it is impossible for a single male to monopolize a group of females. In these species, groups contain multiple females and multiple males. In combat between two males, the stronger, larger male is more likely to win, all else being equal. However, when groups contain multiple males, males have the opportunity to form coalitions, or temporary alliances to cooperate in an effort to enhance their competitive ability.

If one male cannot keep another from mating with a female, indirect competition occurs. Indirect competition can take many forms, but in all cases, the males do not interact; they may, in fact, never even see each other.

Sperm competition occurs when multiple males mate with the same female in relatively close succession. Evidence for sperm competition comes from correlations between mating system and testes weight, which is used as a proxy for sperm production. Harcourt et al. Take chimpanzees and gorillas as an example. Chimpanzees live in groups with multiple adult males and females while gorilla troops contain one adult male the silverback, and multiple females for more information on social and mating systems, see the next section.

Because male chimpanzees cannot keep others from mating with females, producing greater quantities of sperm is perhaps their best way to ensure paternity. Male gorillas who are able to monopolize a group of females through direct competition with other males do not need to compete with sperm, and so they do not need to produce it in large amounts.

Therefore, although male gorillas are much larger in body size, male chimpanzees have larger testicles to produce more sperm. In other species, males engage in alternative mating strategies.

The male actively keeps other males out and away from the females. A non-territorial male may compete directly with a territorial male, but this is dangerous and can result in serious injury.

Some males avoid this by delaying the development of secondary sexual characteristics, or traits associated with sexual maturity. In orangutans, these traits include large cheek flanges, a throat sac, and large body size. Figure 6. Males that do not develop these traits look like juveniles. Figure 6.

The mechanism that results in the two male morphologies is not well understood, but males lacking secondary sexual characteristics have lower testosterone levels. Marty et al.

Lastly, males may compete indirectly by committing infanticide. Infanticide occurs in many primate species, including red howler monkeys, chacma baboons, crab-eating macaques, diademed sifakas, ring-tailed lemurs, Hanuman langurs, and mountain gorillas.
Although more rare than male-male competition, sometimes females compete for mates. The callitrichids, the primate family that includes marmosets and tamarins, are unusual in their reproductive pattern. Breeding females often give birth to twins Figure 6. Another interesting characteristic of callitrichid reproductive behavior is the fact that often only one female reproduces, a phenomenon that is achieved through reproductive suppression Digby et al. These subordinate females are often the older daughters of the breeding female.

In some species, the dominant female emits chemicals that delay ovulation in subordinates. In others, she physically breaks up matings between males and subordinate females.

Regardless of the exact mechanism, the goal is the same: to limit the opportunities for subordinate females to become pregnant.

But why? Although a breeding female can give birth to triplets or quadruplets, it is rare for more than two offspring from each litter to survive. Even ensuring the survival of twins is more than the mother can manage by herself. If a subordinate female cannot find a group to transfer into as the breeding female, she has two options: stay in her natal group and raise younger siblings, or transfer to another group as a subordinate and raise the offspring of a female to whom she is not related.

But, on the other hand, she passes on more genes by raising her siblings than if she helped to raise the offspring of a female to whom she was not related. Not surprisingly, subordinate females rarely leave their natal group unless a breeding position opens in another group. As we discussed at the beginning of this section, female primates are choosy because it is more costly for them in terms of reproductive success if they produce an offspring that either does not survive or that survives but cannot or does not reproduce.

But what is it that they are choosing in males? Like all other examples of primate behavior and ecology, there is both species-level and individual-level variation in female choice. In many animals, including humans, females choose a male who can provide important resources, such as food, paternal care, or protection. Examples of such direct benefits are rare in primates, since most females do not require males to supply them these resources. Female mountain gorillas and chacma baboons, however, may choose males based on who can protect them from infanticidal males Henzi and Barrett; van Schaik and Kappeler More commonly, female primates obtain indirect i.

Often the specific criteria by which females select mates is unknown. However, if a female chooses a healthy as indicated by traits like a plush coat, bright coloration, or large body size or older male, she may obtain genes for her offspring that code for health or longevity. Such a preference may provide their offspring with novel genes and increase genetic variation for more about the importance of genetic variation, see Chapter 4. Lastly, female choice does not necessarily imply that females are choosing only one male with whom to mate.

In many species, females actively choose to mate with multiple males. The most likely explanation for this phenomenon is an attempt to avoid infanticide by ensuring that multiple males think they are possibly the father.

This is called paternity confusion. In such cases, females may not be choosing mates based on direct resource-based or indirect genetic benefits but, rather, ensuring that any male who might be in close proximity to her infant after birth will not kill it.

Female choice is often more subtle than male-male competition, so it can be more difficult to study. However, as more research is conducted, we better understand the ways that female primates exert their choice. In many species, females actively solicit sexual interactions with some males and not others. In other cases, females reject advances by some males and not others. Grey-cheeked mangabeys in Kibale National Park, Uganda, exert female choice in multiple ways Arlet et al.

They present their hindquarters which signals interest in mating significantly more to high-ranking and immigrant males; they refuse to mate with some males; and most mate with multiple males when they are receptive.

These results indicate that rather than being passive actors who accept matings with eager males, female primates actively participate in choosing amongst suitors. Sometimes the terms social system and mating system are used interchangeably, but there are important differences between the two terms.

A social system describes the typical number of males and females of all age classes that live together. A mating system describes which males and females mate. Two species can have the same social system but a different mating system and vice versa. For example, the mating system of both orangutans and mountain gorillas is polygyny—that is, one male mating with multiple females—but the social systems of these two great apes is very different.

The home range of one large adult male orangutan overlaps the home ranges of many females, with whom he mates, but they do not travel together as a cohesive group Figure 6. Mountain gorillas travel in cohesive one-male, multi-female groups consisting of a silverback male, multiple females, and their dependent young, and the silverback male mates with the females of his group Figure 6.

So how is it that two species can have the same mating system and different social systems or, alternately, the same social system and different mating systems? It all depends on how food, females, and males are distributed. We can understand primate social and mating systems by thinking of layers of a map. The first layer is food distribution. If females live in cohesive groups, one or a few males have the opportunity to monopolize them.

If females are widely distributed, it is more difficult sometimes impossible for males to monopolize multiple females. Illustrations by Karin Enstam Jaffe. When Females Are Solitary. When food is distributed in such a way that females are unable to live in close proximity to each other, they must spread out to avoid too much competition. A male may choose to guard one female, try to monopolize multiple females by himself, cooperate with other males to monopolize multiple females, or cooperate with other males to help raise the offspring of an individual female.
The difference in these male strategies is illustrated by the gibbon, orangutan, chimpanzee, and tamarin. Both gibbon and orangutan females eat fruit found in relatively small patches that does not support groups, so females of both species are solitary. However, the way in which males map onto the distribution of females is quite different. A male gibbon guards a single female, resulting in a monogamous mating system Figure 6. A pair of gibbons form a long-term bond that includes defending a territory and relatively high paternity certainty that results in male care of offspring.

Mated pairs defend their territory by calling together in a patterned vocalization called a duet. These coordinated vocalizations tell other gibbons that the territory is occupied and to stay away. Because most males get a mate, male-male competition is relaxed, and there is little pressure for males to develop large body size or weaponry to use in competition with other males. Thus, it is not surprising that male and female gibbons exhibit sexual monomorphism, meaning that males and females are similar in body size and often look alike.

Because males and females both exclude same-sex competitors, the social group consists of an adult male, an adult female, and their dependent offspring, sometimes referred to as a family group. Like gibbons, orangutan females are also solitary. But unlike gibbon males, who cannot monopolize access to multiple females, a male orangutan has a very large home range that overlaps the home ranges of two or more females Figure 6. The females do not regularly travel with each other or the male, but he mates with them, resulting in a polygynous mating system but a solitary social system.

Because some males monopolize multiple females, many male orangutans do not have access to females. Male-male competition is intense, and males benefit from large body size, weaponry, and other traits that increase their competitiveness. The result is significant sexual dimorphism. Male orangutans are twice the size of females and have large canines, cheek phalanges, and throat sacs Figure 6. As we discussed in the previous section, the competition is so intense that some males remain in a state of arrested development Figure 6.

Chimpanzees have a fluid social system referred to as fission-fusion. When food is plentiful, female chimpanzees of the same community travel together within their community territory. Because male chimpanzees are philopatric and related to one another, they share more genes in common than males in other primate species who are unrelated. Even males who do not father their own offspring have some genes passed on by male relatives who do this is another example of indirect fitness.

Male chimpanzees do compete to be at the top of the dominance hierarchy so as to obtain priority of access to females. However, no male in the community is excluded from mating with community females, so chimpanzees practice polygyny as a mating system in which multiple males mate with multiple females, even though females are solitary for some of the year. Competition between males is relaxed because they are related and all get to mate. This results in reduced sexual dimorphism.

But like orangutans, male chimpanzees compete indirectly, particularly through sperm competition. Yet this is the pattern we often see in the callitrichids: tamarins and marmosets. In some callitrichid species, the dominant male fathers most or all of the offspring, but the males in the group are relatives so they benefit genetically, similar to chimpanzee males Baker et al.

In both cases, males help rear offspring because they cannot afford not to do so. Although social systems differ across tamarin and marmoset species, and even across populations of the same species, polyandry is common among callitrichids but extremely rare in other primates.

While many STEM Science, Technology, Engineering, and Math fields have traditionally been, and continue to be, dominated by men, primatology has a long history of significant research conducted by women. This is due, in part, to the fact that three of the most well-known primatologists are women, making it clear that this is a field in which women can excel.

He chose Jane Goodall Figure 6. Until then, most field studies lasted less than a year. After several decades of study, her work has produced long-term data on chimpanzee mating strategies, mother-infant bonds, and aggression within and between communities. When her study group, the Kasakela community, fissioned in the mids, she observed males of the larger community attack and kill those of the smaller one.

This behavior, which Goodall compared to human warfare, is now known to be typical of wild chimpanzees and is another behavior we share with our closest relatives. In the mids, Goodall transitioned from field researcher to conservationist and activist, advocating for the humane use of nonhuman animals Stanford In , Dian Fossey Figure 6.

Through patience and hard work, Fossey habilitated several groups of gorillas to the presence of human observers, and their research over several decades has formed the foundation of our understanding of gorilla social behavior, ecology, and life history.

Censuses of the Virunga gorilla population in the s by Fossey and her colleagues estimated a population of fewer than . The primary causes of this decline were habitat loss and illegal hunting.

A year later, poachers attacked one of her main study groups and killed several gorillas as they tried to kidnap an infant to sell to a zoo. Her efforts to publicize the killings led to the development of conservation programs that ultimately saved the mountain gorilla. By the end of the s, the population had begun to recover and continues to increase. Tragically, Dian Fossey was murdered in her research cabin at Karisoke in December ; the case remains unsolved Stewart Brute Galdikas Figure 6.

Hers was the first long-term study conducted on the Bornean orangutan. Her research still continues, and over , hours of observational data have been collected by Galdikas and her colleagues, focusing on the life histories of individual orangutans.

While conducting her behavioral research, Galdikas discovered that the pet trade and habitat loss were adversely affecting the orangutan population.

She began working with the Indonesian government to confiscate orangutans that had been removed from the wild illegally, many of whom ended
up as pets. If you would like to learn more about primate conservation, please see Appendix B. When females live together, either because their food is abundant in the case of frugivores, or because their food is distributed in large patches that are worth defending in the case of frugivores, males have the opportunity to monopolize multiple females. Sometimes a single male is able to monopolize a group of females. Other times, a male may not be able to exclude other males from the group. Generally speaking, when female groups are small and cohesive, it tends to be easier for a single male to monopolize a group of females. Mountain gorillas, human langurs, red howler monkeys, and patas monkeys are examples of single-male, multi-female groups, which consist of one adult resident male, multiple adult females, and their dependent offspring.

The mating system for single-male, multi-female groups is polygyny Figure 6. Because a relatively small number of males monopolize all the breeding females, there are many adult males who do not have mates. As with orangutans, this results in strong competition between males, resulting in sexual dimorphism where males are much larger than females. In mountain gorillas, fights between silverbacks can be intense.

Males can use their large canines to cause serious wounds that may even result in death Fossey. When a single male cannot monopolize a group of females, often because the group consists of many females that may be spread out over a wide area, the result is a multi-male, multi-female group consisting of multiple adult males, multiple adult females, and their dependent offspring. Figure 6.

Olive baboons, ring-tailed lemurs, and squirrel monkeys are examples of primate species with this type of social system. Because a single male cannot exclude others in the group from mating, the mating system in multi-male, multi-female groups is polygyny, but that does not mean that all males have equal reproductive success. When multiple males live in a group, they often form a dominance hierarchy that determines their priority of access to females in the group.

Because their place in the hierarchy can affect their reproductive success, males in multi-male groups engage in male-male competition, but because it is rare for males to be excluded from mating altogether, the level of competition, and degree of sexual dimorphism, is less extreme than what we see in polygynous species.

In its most basic form, communication occurs when one individual the sender emits a signal that conveys information, which is detected by another individual.

We have discussed several aspects of primate sociality in this chapter, all of which require the communication of information between individuals. But, how does a female chimpanzee communicate her sexual availability? How does a vervet monkey communicate the approach of a leopard or a python nearby?

How does a dominant or subordinate macaque signal its place in the dominance hierarchy? How do solitary, nocturnal primates, like the slow loris, communicate information about themselves to conspecifics? Primate communication comes in four forms: vocal, visual, olfactory, and tactile. Species vary in their reliance on each. Because it is difficult to see others in the dark, and because nocturnal primates avoid predators by remaining quiet, species like the slow lorises and the aye-aye rely heavily on scent-marking to communicate with conspecifics.

Diurnal species tend to rely more heavily on visual and vocal forms of communication. Primates use sound to claim and maintain a territory, make contact with other group members, or to communicate danger or threats, among other things. Loud calls are designed to travel great distances and are used in territorial defense by many primate species including indris, orangutans, gibbons, howler monkeys, and siamangs.

In dense forest, where visual communication can be difficult, loud calls can be useful in signaling to conspecifics that a group or individual occupies a specific area. These include vocalizations given as part of threat displays or dominance interactions, as well as contact calls that provide information about location to other group members.

Baboons have a rich repertoire of vocalizations for communicating with other group members Fischer et al. Adult males give specific vocalizations during threat displays and physical confrontations. Since baboons rely on membership in their group for finding food and detecting predators, a baboon separated from his group will vocalize in an attempt to regain contact. Young baboons emit their own contact calls when separated from their mothers.

Alarm-calling behavior is widespread in primates. Often, alarm calls serve to notify conspecifics of potential danger, as is the case with vervet monkeys Figures 6. Research by Dorothy Cheney, Robert Seyfarth, and others has shown that: 1 vervets classify predators based on hunting style; 2 alarm calls convey information to other vervets about that hunting style; and 3 other vervets respond in ways appropriate for evading that type of predator Seyfarth et al.

Since most mammalian carnivores hunt on the ground, getting into, and staying in, a tall tree is the best option for escape. Since snakes, like pythons Figure 6. Vervets clearly understand the meaning of each type of alarm call, as they respond appropriately even when they do not see the actual predator Seyfarth et al. Such semantic communication, which involves the systematic use of signals to refer to objects in the environment, was once believed to be unique to humans.

It may be a precursor to the symbolic capacities of human language. Research on other African monkeys indicates that some species use alarm calls to signal to the predator that it has been detected. Because leopards Figure 6. Alarm calling at leopards appears to tell the leopard that it has been seen and therefore its chance of success will be low. Leopards are more likely to stop hunting after an alarm call has been emitted.

Unlike leopards, chimpanzees are pursuit predators and may even use alarm calls to locate potential prey. Visual signals are an important component of nonhuman primate behavior, alone or in combination with other forms of communication.
Some visual signals are common to all nonhuman primates. The females of many Old World primate species, including macaques, baboons, and chimpanzees, signal sexual receptivity through changes in the size, shape, and, often, color of their hindquarters, called a sexual swelling Figure 6. The sexual swelling reaches its maximum size at ovulation.

When females are not receptive, either because they are pregnant or are nursing, they do not display a sexual swelling Figure 6. In some species, females use other visual cues to indicate sexual receptivity.

Common marmoset females solicit mating through tongue-flicking displays directed at males, while female patas monkeys engage in a more elaborate visual display. When soliciting mating, the female crouches in front of the male and looks back at him while blowing air into her cheeks; she also may drool and curl her tail Chism et al.

Monkeys and apes also use a diversity of facial expressions in visual communication. Displaying teeth in this way is a sign of anxiety or fear in Old World monkeys. Submissive males respond by fleeing or presenting their hindquarters. In the Smithsonian Channel video [1], male gelada baboons use the lip flip in competition with other males.

Primates also communicate through color. In some species, facial coloration provides information about individual health or status to conspecifics. Mandrills are a good example of this.

Female mandrill faces are brighter during ovulation, which may function to communicate reproductive state to males Setchell et al. Redness of male mandrill faces is correlated with androgen levels. Thus, facial coloration can, on the one hand, communicate information about competitiveness to other males and information about reproductive fitness to females Figure 6.

On the other hand, the variation in facial coloration among New World monkeys, ranging from very simple Figure 6.

Species with more complex facial color patterns tend to be those that are sympatric with a larger number of other primate species. In such circumstances, distinct facial coloration and patterning may help individuals recognize conspecifics and reduce the chances of mating with another species Santana et al. Olfactory Communication. All primates use scent to communicate.

Females secrete chemicals from their anogenital region the area of the anus and genitals that provide males with information about their reproductive state.

In some species, like macaques and chimpanzees, this olfactory signal is enhanced by a sexual swelling a visual signal; see Figure 6.

Olfactory communication is particularly important for New World monkeys, lemurs, and lorises. The function of urine washing may include marking trails for other group members to follow, self-cleaning or controlling body temperature, dominance displays, enhanced grasping ability while climbing, or communicating reproductive state Boiniski During aggressive interactions with other males, male ring-tailed lemurs rub their tails with scent from glands on their wrists and chests.

Because substrate marking behavior occurs where the ranges of two groups overlap, and increases during the mating season, the primary function is believed to reinforce territorial boundaries Mertl-Millhollen Tactile communication, or touch, is very important in all primates. Physical contact is used to comfort and reassure, is part of courtship and mating, and is used to establish dominance and alliances.

Grooming is an important and clearly enjoyable form of tactile communication for all primates Figure 6. Not only does grooming serve to clean the skin and fur, removing parasites and debris, but it is an important affiliative non-aggressive behavior that helps reinforce social bonds, repair relationships, and cement alliances. Among chimpanzees, subordinates groom dominants in an effort to receive benefits such as protection, acceptance, and reciprocal grooming.

When yellow baboon females engage in more grooming activity as both givers and receivers, their offspring have an increased chance of surviving to one year Silk et al.

Although the mechanism behind this relationship is unknown, close associations with group members may provide females and their young offspring with protection from harassment or access to valuable resources that enhance infant survival.

Social integration, as exemplified by grooming, is of significant adaptive value to primates. It may be surprising in a chapter on nonhuman primates to see a discussion of culture. After all, culture is considered by many, including cultural anthropologists, to be a distinguishing characteristic of humans. Indeed, some anthropologists question claims of culture in primates and other animals. Definitions of animal culture focus on specific behaviors that are unique to one population.

Anthropological definitions of human culture emphasize shared ideology e. Using this definition, some cultural anthropologists view primates as lacking culture because of the absence of symbolic life e.

However, the longer we study primate groups and populations, the more insight we gain into primate behavioral variation. If we define culture as the transmission of behavior from one generation to the next through social learning, then we must view at least some of the behavioral variation we see in primates as forms of cultural tradition, or a distinctive pattern of behavior shared by multiple individuals in a social group that persists over time Whitten Due to both their high level of intelligence and the large number of long-term studies on several different populations, chimpanzees provide the best example of cultural tradition in primates.

Research on a variety of animals, including fish, rodents, birds, and monkeys indicate the transmission of a single behavior pattern through social learning, resulting in cultural variation. But chimpanzees, along with orangutans, are the only species other than humans to express cultural variation.
in multiple behavioral patterns.

Examining behavioral variation across chimpanzee study sites, researchers have identified over 40 cultural traditions, or distinct behavioral patterns, in chimpanzees Whiten These cultural traditions span the gamut from population-specific prey preferences to tool-use techniques, hunting strategies, and social behaviors. It is not just the sheer number of cultural traditions that make chimpanzee culture so fascinating.

It is that each chimpanzee community displays a unique cultural profile defined by a subset of the known traditions. But in Gambia, they use modified twigs to extract honey from holes in trees. Chimpanzees in Guinea use three stones for nut cracking: one as the anvil, the second one as the hammer, and a third as a wedge to secure the anvil McGrew So how do chimpanzee cultures develop, and how does cultural transmission occur?

Although we do not know for sure how chimpanzee cultural traditions develop initially, it is possible that different groups invent, either accidentally or deliberately, certain behaviors that other individuals copy.

There is little evidence currently to support the idea that chimpanzees actively teach one another a new behavior, so it appears that they learn through observation and practice. Immigrants typically females may bring cultural traditions to their new community, which residents observe and learn. Conversely, immigrants may observe and learn a cultural tradition practiced in their new community Whiten The transmission of unique foraging behaviors through a provisioned group of Japanese macaques on Koshima Island is well known McGrew In an effort to keep the monkeys nearby, researchers provided them with piles of sweet potatoes.

A juvenile female named Lmo spontaneously washed a muddy sweet potato in a stream. This new food-processing technique first spread among other juveniles and then gradually to older individuals. Within 30 years, it had spread across generations, and 46 of 57 monkeys in the group engaged in the behavior. Another example comes from a group living far to the north, in the snowy forests of Honshu. Not only did the monkeys enter the springs to retrieve the apples, but over multiple years, they learned to immerse themselves in the hot springs to keep warm when not foraging McGrew ; Figure 6.

However, the behaviors have changed over time, even though the underlying provisioning either did not change or ceased altogether McGrew For example, although sweet potato washing started in freshwater, it gradually shifted to seawater, apparently to add salt for flavor. Thirty years after the behavior started, the most common form involved dipping the potato into salt water, even if it was clean.

Similarly, female macaques entering the hot springs initially left their young infants at the edge, but today juveniles play and even swim underwater in the hot springs. These examples share several characteristics with human culture, including invention or modification of behavior, transmission of behavior between individuals, and the persistence of the behavior across generations McGrew Primates are socially complex and extremely intelligent.

Highly adaptable, they display significant variation in diet, habitat, and behavior. By studying primates in their natural habitats, we learn how their behavior and morphology are influenced by ecology, including the foods they eat and the other species with which they live.

As our closest living relatives, primates provide important insights into the evolution of human social behavior, language, and culture. These are topics you will learn about in later chapters of this book. Abundance: How much food is available in a given area. Affiliative: A description of non-aggressive social interactions and associations between individuals. Allopatric: Two or more species that do not overlap in geographic distribution. Anogenital: Relating to the anus and genitals. Basal metabolic rate: The rate at which an individual uses energy when at rest. Carnivore s: Organisms whose diet consists primarily of animal tissue. Coalition: A temporary group composed of two or more individuals who work together to achieve a common goal. It is often used in reference to male-male competition, such as when two less-competitive males join forces against a more-competitive male. Competitive exclusion principle: The idea that two species that compete for the exact same resources cannot coexist.

Cultural tradition: A distinctive pattern of behavior shared by multiple individuals in a social group, which persists over time and is acquired through social learning. Cryptis: The ability to avoid detection by other organisms. Day-range length: The distance traveled in a day. This may or may not involve entering another group. Distribution: How food is spread out. Dominance hierarchy: The ranked organization of individuals established by the outcome of aggressive-submissive interactions. Feeding: The act of consuming food. Fission-fusion: Societies in which group composition is flexible, such as chimpanzee and spider monkey societies. Individuals may break up into smaller feeding groups fission and combine into larger groups fusion.

Foraging: The act of searching for food. Folivores: Organisms whose diet consists primarily of leaves. Frugivores: Organisms whose diet consists primarily of fruit. Home range: The area a group or individual uses over a given period of time often over a year. Inbreeding: Reproduction between relatives. Inbreeding depression: Harmful genetic effects of breeding between relatives. Insectivores: Organisms whose diets consist primarily of insects. Introsexual selection: Selection for traits that enhance the ability of members of one sex to compete amongst themselves.

Interbirth interval: The length of time between successive births. Intersexual selection: The selection for traits that enhance the ability of the members of one sex to attract the attention of the other. Mating system: A way of describing which male s and female s mate. Mobbing:
Cooperatively attacking or harassing a predator. Monogamous: A mating system in which one male mates with one female.

Natal group: The group into which an organism is born. Natal dispersal: Emigrating from the group into which one is born. Niche: The role of a species in its environment; how it meets its needs for food, shelter, etc. Niche partitioning: The process by which potentially competing species reduce competition by using the environment differently. Omnivores: Organisms whose diet consists of plant and animal matter. Operational sex ratio: The ratio of sexually active or available males to sexually active or available females.

Paternity certainty: Confidence in which male fathered an offspring. Paternity confusion: When males are uncertain if they fathered an offspring. This is often a female strategy to reduce the chance of infanticide. Polyandry: A mating system in which multiple males mate with a single breeding female. Polygamy: A mating system in which multiple males mate with multiple females. Polygyny: A mating system in which one male mates with multiple females.

Polyspecific associations: Associations between two or more different species involving behavioral changes by at least one of the associated species. Primate community: All living organisms that occur in an area that includes primates. Receptive: A term used to describe females who are ready for sexual reproduction. Reproductive suppression: The prevention or inhibition of reproduction of healthy adults.

Secondary sexual characteristics: Characteristics that appear at time of sexual maturity. These are not directly involved in reproduction, but they provide individuals an advantage in courtship and competition for mates. Semantic communication: The systematic use of signals to refer to objects in the environment.

Sexual dimorphism: When males and females of a species have different morphological traits. Sexual monomorphism: When males and females of a species have similar morphological traits. Sexual selection: The selection for traits that increase mating success.

This occurs via intersexual selection and intrasexual selection. Occurs in many Old World primate species. Social learning: The idea that new behaviors can be acquired by observing and imitating others. Social system: A way of describing the typical number of males and females of all age classes that live together. Solitary: Living alone. Species recognition: Recognition of conspecifics.

Sperm competition: Competition between sperm of two or more different males to fertilize the same egg. Sympatric: Two or more species that overlap in geographic distribution. Territory: A home range whose boundary is defended from intrusion by conspecifics.

Vertebrates: The group of animals characterized by an internal spinal column or backbone. This includes fish, amphibians, reptiles, birds, and mammals. Vigilance: Watchful behavior to detect or in response to potential danger, usually in the form of predators or potential competitors.

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