Sexual Conflict in White-Faced Capuchins

It's Not Whether You Win or Lose

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Introduction

This inquiry into the nature (the how and why) of male-female conflict in primates begins with the conundrum of the white-faced capuchin male as a social creature. Is he best characterized as a "new age sensitive male" or an "aggressive, despotic abuser" of females and their offspring? Our several decades of observing these male monkeys have shown us the many facets of their paradoxical social attributes. Within his group, a capuchin male will tolerate playful infants bouncing on his head while he is resting, he will try to retrieve an infant from the grasp of a predator, allow it to suckle from his nonfunctional nipples, carry it through the trees and present his body as a bridge when the gap between branches is too wide for the infant to cross. But when he changes groups, this same capuchin male may snatch a small infant from its mother's body and kill it with canine punctures to its skull or body, despite the efforts of the mother and others to protect it. Capuchin males routinely supplant females from preferred feeding locations, causing the females to avoid and cower away from them. But alpha males also readily form coalitions with coresident females against other group members and outsiders. A capuchin male will sit pressed up against another adult male, grooming him and gently placing the other's fingers in his mouth; he will hurdle around the forest giving lost calls until he locates a "missing" male who has moved far away from his group and then engage in an affiliative reunion display that is very similar to the courtship display for this species. Or conversely, he will gang up with other males to slash a rival male with his large, sharp canines until the victim dies of his wounds. What could be the source of such apparently contradictory
behavior on the part of capuchin males, how do females respond to it, and why would females live with such volatile social partners?

These are the questions that underlie this chapter, in which we will describe how evolutionary biologists are increasingly identifying sexual conflict (conflict between the sexes for the control of reproduction: Arntqvist & Rowe, 2005; Chapman, Arntqvist, & Rowe, 2003; Clutton-Brock & Parker, 1995; Eberhard, 1996; Parker, 1979) as the driving force behind many of the variable behavior patterns we observe during social interactions (e.g., Gowaty, 2004; Muller & Wrangham, 2009; Smuts & Smuts, 1993; Stumpf, Martinez-Mota, Milich, Righini, & Shattuck, 2011). To exemplify the general points we make about the probable chain of adaptations and counteradaptations that led to the behaviors we observe in male and female capuchin monkeys today, we will use our findings from nearly 30 years of studying a Costa Rican population of wild, white-faced capuchin monkeys (Cebus capucinus) in the Santa Rosa Sector of the Área de Conservación Guanacaste.

Starting Points: Anisogamy, Sexual Selection, and Parental Investment

Explanations of sex roles and of conflicts between males and females usually begin with anisogamy (sexual reproduction via the union of two dissimilar gametes) and with Bateman's Principle (1948)—the theory that because eggs are larger, less mobile and more resource-rich than sperm, females initially invest more in reproduction than do males and therefore females are the limiting resource over which males compete for access. Bateman's experiments with fruit flies demonstrated that males exhibit greater variance in mating success than do females, which, following Darwin (1871), Bateman attributed to the indiscriminate eagerness of males to mate versus the discriminating choosiness of females regarding their mates. Williams (1966), Parker (1979), and Trivers (1972) all extrapolated from anisogamy and Bateman's work to develop theories of sexual conflict. Parker and Williams focused on sexual selection (male-male competition and female choice) as resulting from the original unequal investment made by females in eggs and males in sperm. Trivers focused on asymmetrical parental care patterns (females typically provide more care of their offspring than do males) as arising from anisogamy and as resulting in choosy females and competitive, promiscuous, males.

These very influential evolutionary models of sexual reproduction and their successors have typically portrayed females, both implicitly and explicitly, as the "losers" when the reproductive interests of males and females diverge. The traditional depiction of females as losers in sexual conflict is based mainly on the assumption that the initial higher investment of females in their gametes forces them to continue to invest more in their offspring than do males. This "constrained-by-prior-investment" argument is carried even further in assumptions about sexual
conflict in mammals. Because female mammals gestate and lactate for their young, they are seen by many evolutionary biologists to invest more than males in the rearing of their young; to be more constrained than are males in the quantity of young they can produce in their lifetimes; and, unlike males who have only invested sperm, to be largely constrained by prior investment from the option of abandoning their costly offspring (Trivers, 1972).

There have been many criticisms of Bateman’s experiments and conclusions (e.g., Dewsbury, 2005; Snyder & Gowaty, 2007; Tang, Martinez, & Ryder, 2005) and of the assumption that females are constrained in their options by their initial high investment in eggs (e.g., Dawkins & Carlisle, 1976; Kokko & Jennions, 2008a; Trillmich, 2010). A common misapprehension about optimal decisions (the “Concorde Fallacy”) is that investment strategies should be based on prior costs (what micro economists call “sunk” or lost costs) rather than future benefits. Named after the construction of the Concorde jet on which the governments of Britain and France lost so much money, the Concorde Fallacy is the mistaken assumption that large prior costs justify continued investments, when it is in fact the likelihood of future benefits that justify investment (see Kokko & Jennions, 2008a for detailed review). Some researchers (e.g., Hrdy, 1986; Kokko & Jennions, 2008b) have also called into question the assertion (originating with Darwin) that females are coy in their choice of mates whereas males are indiscriminate. And there have been counterarguments made to the assertion that females are the losers in sexual conflict (e.g., Arnvist & Rowe, 2005; Gowaty, 2004; Green & Madjidian, 2011). Over the course of this chapter, we will return to these assumptions and outline some of the criticisms and counterarguments. We now turn to what is arguably for many animal species another important starting point for conflict between males and females over reproduction: internal fertilization.

In most aquatic animals, the sperm unites with the egg external to the body of the reproducing individuals after the male and female release their gametes into their watery surroundings. Internal fertilization, which occurs in land dwelling animals, is thought to be a reproductive adaptation that evolved to protect eggs and sperm (and ultimately the zygote) from desiccation. Most mammals carry this pattern of protecting the zygote even further by gestating the young internally, rather than secreting fertilized eggs as do birds and reptiles. In the same way that anisogamy may have originally evolved for selective reasons (competition among gametes) but then had a side-effect on male-female conflict, it is possible that the process of internal fertilization evolved to protect the gametes from drying out but also set off a chain of reactions from males and then subsequent reactions from females. This is because an important epiphenomenon of internal fertilization is that it created the possibility of cryptic conception and increased the ability of the female to exert female choice.

Thus, we could say that the widespread pattern of internal reproduction has benefits for females as well as the costs identified by Trivers (1972) and others. Indeed, if we return to the traditional winner/loser metaphor of most evolutionary
models of sexual reproduction, one could make the argument that females hold the trump card in the game of competing with males for control of reproduction. Females may not be capable of producing as many offspring as the males of their species, although it is important to remember that many male animals are not reproductively successful whereas almost every female that reaches adulthood produces some offspring. And because of gestation and lactation costs, female mammals may invest more energy in rearing their offspring than do males. But for viviparous females, their offspring are guaranteed to be their own and thus the possibility of cuckoldry does not act on females as a powerful selective force as it does on males, driving the latter to engage in costly and dangerous competitive/coercive measures. Evolutionary biologists maintain that the ultimate purpose of life is to reproduce one's own genetic material. Thus, from an evolutionary point of view, paternity uncertainty imposes a serious constraint on a male's life purpose and is believed to set off an entire chain of events (an "arms race" as some have called it, e.g., Dawkins & Krebs 1979; Mulder & Rauch, 2009; Palombit, 2010) in which males behave in a strategic manner and/or evolve morphological and physiological features that not only improve their reproductive success in comparison to other males but also reduce ambiguity about which offspring they have truly sired. And females respond with countermeasures that maintain paternity uncertainty and that protect themselves and their offspring from the features that males have evolved to improve their reproductive success (Hrdy, 1974, 1977, 1979).

Sexual selection theory and its applications (going all the way back to Darwin and up through recent papers) have been criticized for assuming that conventional Western gender roles apply to animals (e.g., see critiques in Chilton-Brock, 2007; Fausto-Sterling, 1997; Gowaty, 1982, 1997; Martin, 2008; Roughgarden & Akçay, 2010). Green and Madjidjian (2011) wondered whether researchers of sexual conflict, like those of sexual selection, approach their topic with a preconceived view of how the sexes should act. Thus, they carried out a quantitative analysis of the terminology used in publications on sexual conflict. These authors found that in the literature on sexual conflict, researchers use many terms to describe how males and females respond to one another (28 in total) but that male behaviors are consistently described with terms implying action and female behaviors with terms implying reaction. When a male responds to a problem presented by the environment or by female patterns, it is called an adaptation. When a female responds, it is labeled resistance or counteradaptation. Green and Madjidjian argue that the use of these sex-stereotyped terms implies that the male has the upper hand (the male adapts and the female resists or counteradapts). Furthermore, they found that theoretical models are focused almost solely on costs for females even though costs for both sexes must occur in any coevolutionary process. They conclude by arguing that anthropomorphic stereotyping of sex roles seriously constrain rather than enhances our understanding of sexual conflict, but that nonetheless, it is difficult to avoid the trap of conventional terminology.
In this review of sexual conflict in capuchins, we will try to interpret our findings on male and female interactive patterns more neutrally as a chain of actions and reactions or a sequence of problems set and solutions developed/evolved, without making assumptions about which sex has the upper hand, the first move, or the fewest costs. We choose to enter the chain of actions and reactions with the advent of, and responses to, the process of internal fertilization. Other researchers might start at another point in the sequence.

White-Faced Capuchins and Sexual Conflict

White-faced capuchins occur across Central America from Honduras in the north down to Panama and into limited areas of northwestern Ecuador and Colombia in South America (Pragaszy, Visalberghi, & Fedigan, 2004). Like other members of the genus Cebus, white-faced monkeys are arboreal omnivores with an eclectic diet consisting of fruit, insects and small invertebrates. They live in social groups made up of kin-related adult females and their offspring (“matrilines”) associated with temporarily resident adult males. Group size averages 15 members, ranging from 3 to 40 individuals, with approximately equal numbers of adult females and adult males residing together (Fedigan & Jack, 2011, 2012). Males disperse from their natal groups into neighboring groups at around 4.5 years of age, well before being capable of reproducing (6 years; Hakeem, Sandoval, Jones, & Allman, 1996) or attaining full adult body size (10 years; Jack, Sheller, & Fedigan, 2011). After this initial move from the birth group, males continue to change groups repeatedly over the course of their adult lives at approximately 4-year intervals (Jack & Fedigan, 2004b). Females, with a few exceptions, remain in their natal groups and first give birth around 6 years of age and then produce additional infants approximately every 2 years after that. Female white-faced capuchins copulate with the multiple resident males of their groups and then gestate their young for 5.5 months before giving birth and suckling their infants for approximately one year (Carnegie, 2011).

Because capuchin females conceive via internal fertilization and mate with multiple males, it is difficult for the researcher, and presumably for the male capuchin, to be certain who sires the resultant infant. (The researcher’s solution to paternity uncertainty is to collect fecal samples from mothers, infants, and potential sires and subject the samples to DNA relatedness analyses.) As described earlier, the replication of one’s genetic material (in this case, the production of viable offspring) is believed by evolutionary biologists to be the driving force of living forms. Therefore, an adult male monkey has a good evolutionary reason to invest effort and energy in the survival of his own offspring but not in the offspring of unrelated males. Thus, the lack of assurance that he is the sire sets up a problem for the male monkey to which we believe he has adapted various solutions: competition with other males for access to a female; the offering of benefits to a
female that increase the chances she will choose him as a mate; and male coercion of a female to the same ends.

Male Solutions to the Uncertainty Problem Set by Internal Fertilization

Male-Male Competition

All male animals compete for opportunities to inseminate eggs, and capuchin males are no exception. Since female capuchins reside in permanent, kin-related social groups, males compete for the opportunity to immigrate into and retain residency within these groups, which is where the mating occurs (we have only rarely observed females to mate with outsider males during brief periods of group instability). To gain entry into groups, small parties of males periodically attempt to take over the positions of resident males, via physical intimidation and fighting with the male members of the group (Fedigan & Jack, 2004; Jack & Fedigan, 2004a, 2004b; Jack et al., 2011). If successful, these invading males become resident and then cooperatively attempt to keep other males out of the group. This pattern of male-male competition for residency within the established groups of related females results in the complete replacement of adult males in our study groups approximately every 4 years. Either before or during the takeover process, or once in the group, immigrating males sort themselves into a dominance hierarchy, after which relationships among group males are generally tolerant and cooperative in nature. Indeed, once in a group, overt male-male competition over mates is rare; we observe all resident males of a group to mate with females, regardless of male rank, and the top-ranking (alpha) male of the group does not overtly harass or interrupt the copulations of subordinate males. Despite these behavioral observations suggesting that overt mating competition does not occur among coresident males, genetic paternity tests (Jack & Fedigan, 2006; Muniz et al., 2010) find that alpha males sire most of the offspring (70–90% in our Santa Rosa study groups). This suggests that even though reproductive competition is high (as evidenced by high reproductive skew), it is not manifested aggressively among coresident males. Although female choice is not as conspicuous in our species as in brown capuchins (e.g., Janson, 1984), it is possible that female white-faced capuchins allocate their receptive and proceptive behaviors in such a way that they mate more often with alpha males when they are ovulating and with subordinate males when they are not receptive (Izar, Stone, Carnegie, & Nakai, 2009). It is also possible that male mating competition is occurring at an inconspicuous level (e.g., sperm competition or subordinate male avoidance of mates sought by the alpha male).

Knowing that alpha males are more reproductively successful than subordinate males, has helped us understand the frequent movement of males between social
groups. Male white-faced capuchins are truly only transient members of any one group, continually dispersing throughout their lives. In some years these changes in male group members occur through aggressive evictions, when outsider males cooperatively take over a group by evicting resident males, while in other years the male changeovers occur voluntarily. In these latter cases, subordinate males are usually the first to go, often leaving the alpha male on his own to defend the group (from predators and would-be immigrants) while they seek out residency in a new group. In such circumstances, it is only a matter of time before a lone alpha male will be challenged by a coalition of extragroup males looking to take over the group in which he resides (and the mating opportunities that go along with it). Sometimes the resident alpha male is actually killed by invaders, other times he joins a neighboring group, and sometimes he simply disappears. This pattern of frequent male dispersal enables subordinate males to increase their dominance rank and, in the process, increase their reproductive chances (Jack & Fedigan, 2004b).

Male Benefits to Females (Influencing Female Mate Choice)

Alpha male capuchins have exaggerated secondary sexual characteristics (i.e., pronounced jaw line and brow ridge) and are in a permanent state of piloerection, making them look larger and more impressive than the other males of the group (Perry, 1998a). These traits likely result from their heightened testosterone levels compared to those of subordinate males (Schoof & Jack, 2009). Alpha males are conspicuously active in defending their groups against predators, neighboring groups, invading males, and anthropogenic disturbances. And they will do so to the point of being sometimes fatally wounded during aggressive interactions with outsiders (e.g., by nonresident males, large carnivores, angry humans, and passing vehicles). From an ultimate or adaptive perspective, we suspect that the females choose the alpha male to sire their young, because along with his fighting strength, the alpha male offers special benefits to the adult females of the group. Top-ranking males spend more time than other group members monitoring the surrounding environment and are often the first to alert the group to danger and to rush to its defense (Gould, Fedigan, & Rose, 1997; Jack, 2001; Rose & Fedigan, 1995). They are also more likely than subordinate males to perform impressive arboreal displays that involve a swaggering walk, exaggerated leaps through the trees and heavy landings onto tree limbs, causing large branches to sway violently or crash to the ground. All males in the group will court females (and/or respond to female courtship) via whirling "dances" that include distinctive body movements, facial expressions, and vocalisations. And all resident males will respond to the distress call of an infant in their group by hurrying to retrieve it, but alpha males are particularly prone to do so (Fragaszy et al., 2004; MacKinnon, 2002). These behavioral patterns (protection of females, their young, and their resources; male courtship displays; and "ornamental" features) are all believed to entice females to
accept these males as residents in their group (Rose, 1994) and to preferentially choose alpha males as their copulation partners when the female is ovulating.

Male Coercion of Females

As described by Smut and Smuts (1993) and more recently explored in an entire volume (Muller & Wrangham, 2009), male primates may also attempt to coerce females to choose them as copulation partners. This pattern of males endeavoring to forcibly bend females to their own ends is widespread in the animal kingdom and can take a variety of forms (e.g., intimidation, harassment, and attempted sequestering or “guarding” of females as well as physical attacks on them and killing of infants sired by unrelated males). Smuts and Smuts (1993) argued that male coercion of females to mate with them is sufficiently common as to constitute a third mechanism of sexual selection (Darwin had originally outlined only two: male-male competition and female choice). Other researchers of sexual conflict have since agreed with Smuts and Smuts (e.g., Clarke, Pradhan, & van Schaik, 2009; Clutton-Brock & Parker, 1995; Stumpf et al., 2011; Watson-Capps, 2009). In many respects, sexual coercion is the place where male-male competition and female choice converge under the label of “sexual conflict”: males compete with one another for mating opportunities and the chance to influence female mate choice and sometimes they use force to override and/or influence this mate choice (often at the expense of not only female reproductive success but that of other males).

As mentioned above, once male white-faced capuchins have established themselves as residents within a group, we see few overt behavioral manifestations of mating competition among them and they rarely direct aggression against females residing in their group. Females mate with most or all group males with no interference or harassment from higher ranking males, even when they mate in full view of the alpha male. This means that forms of sexual coercion frequently observed in other primate species (e.g., sexual harassment and intimidation, reviewed in Palombit, 2010) are not common occurrences in our study species, although alpha males do groom and follow females when the latter are periovulatory, suggesting a mild form of mate guarding (Izar et al., 2009). Extreme forms of mate guarding or attempted sequestering of females would be difficult for any one male, including the alpha male, to achieve due to the dispersed nature in which our capuchins travel and forage, their rapid locomotor patterns and the often dense foliage in which they reside. We simply do not see alpha males in “hot pursuit” of periovulatory females, although the fact that they follow them more than they follow other females (and do so more than subordinate males) suggests that alpha males might have an enhanced ability to detect ovulation and/or the females may be providing them with cues (e.g., olfactory ones) that we have yet to document (Izar et al., 2009).

However, we do observe infanticide in our study groups, a manifestation of sexual coercion that has, by far, the most damaging consequences to female
reproductive success. To be sure, infanticide, specifically the killing of infants by adult males, is the number one cause of infant death in white-faced capuchins, and infanticide is only observed in the context of a changeover in male group membership or in the rarer instances of male rank reversals (i.e., when a resident male establishes himself as the group’s new alpha male) (Fedigan, 2003; Perry, 1998b; Perry, Godoy, & Lammers, 2012). In our study population, 82% of infants <12 months of age die following group takeovers, whereas during times of group stability, the mortality rate for infants is 12% (Fedigan, 2003). By killing the dependent offspring of group females, newly immigrant males (or new alpha males) can influence female reproduction by shortening her interbirth interval (i.e., causing her to resume cycling earlier than she would have if she raised her current infant to weaning age), thereby increasing that male’s mating opportunities and ultimately his reproductive potential. This behavior enables a male to influence the timing of female reproduction while at the same time decreasing the reproductive fitness of other males (by killing their offspring). In this way, infanticide is not only the ultimate manifestation of male sexual coercion of females but also of male-male mating competition.

Costs of Male-Male Competition and Coercion

The costs to females of male competitive and coercive patterns are large and extensive. Over the years of our long-term study, we have gathered ample evidence that the lives of female capuchins are enormously affected by the ubiquitous and persistent efforts of males to compete with other males for mating access and to gain some control over how, when, and with whom the females copulate/reproduce. First and most obvious is that the killing of infants by adult males is very costly to the female who has gestated and suckled that infant, in both an energetic and reproductive sense. Since infanticide usually occurs in the context of male invasions and takeovers of groups, this is a period during which all members of the group (females, juveniles, and males) are at risk of being wounded and also a time when group members expend a lot of energy either fighting off the invaders (in the case of resident males) or avoiding them (in the case of females and their young) (Fedigan, 2003; Fedigan & Jack, 2004).

It is sometimes the case that the characteristics selected for in male-male competition (large size, aggressive behaviors, and “armaments”; Darwin, 1871) can also be directed at females and their young to improve a male’s control over reproductive outcomes. Furthermore, females may suffer collateral damage simply if they are present when males compete with other males for reproductive access (Watson-Capps, 2009). In capuchins, takeovers generally occur over a period of weeks, during which time the group is highly destabilized in its social patterns and disrupted in its ranging and feeding patterns. Cortisol levels of adult females are significantly elevated during and after takeovers, indicating heightened
stress levels and energy expenditure (Carnegie, Fedigan, & Ziegler, 2011). Even though female capuchins exhibit strong and stable linear dominance hierarchies (Bergstrom & Fedigan, 2010), we have been unable to demonstrate that higher ranking females are more reproductively successful than subordinate females. We suspect this is because frequent male takeovers and infanticide confound the effects of female-female dominance relations on reproductive success (Fedigan, Carnegie, & Jack, 2008) and particularly affect higher ranking females who are more central to the group and easier for invading males to locate and target for aggression than the more subordinate, peripheral females.

Patterns of male-male competition and male-female coercion (as well as male-female benefits) are also not without costs to the males. First of all, there are considerable energetic investments made by males during these interactions. Alpha males have higher testosterone and, for the most part, higher cortisol levels than do subordinates (Schoof & Jack, 2009). These higher cortisol levels indicate greater amounts of stress experienced by alpha males and the higher testosterone levels are hypothesized to be associated with greater male vulnerability to parasites and other forms of infections (Poulin, 1996; Schalk & Forbes, 1997). Furthermore, the strategy of male dispersal to neighboring groups, thought to be an adaptation to increase their chances of copulating with fertile females (Jack & Fedigan, 2004b), also comes with very high costs. These males must move to new and unfamiliar ranges, which increases their risks of starvation, dehydration, and predation, along with the high probability that they will be wounded while battling their way into new groups. Janson, Baldovino, and Di Bitetti (2011) report 38% mortality for males of dispersing age in the closely related brown capuchin (Cebus apella nigritus). Mortality for dispersing males of our species of capuchin is likely lower because our males disperse in cohorts (Jack & Fedigan, 2004a, 2004b; Perry et al., 2012) rather than alone, as is the case for brown capuchins. However, aggression from unknown conspecifics nonetheless poses a real threat to dispersing males. We have observed many cases of males being seriously injured in the course of takeovers, and this aggression can sometimes be lethal, either immediately or from infections of the wounds they incur (Gros Louis, Perry, & Manson, 2003). Even the behaviors engaged in by males in their attempts to influence female mate choice are not without costs; alpha males expend more time and energy engaged in vigilance behaviors and often put themselves directly into harm’s way in their attempts to protect females and infants from predators or aggressive conspecifics.

Female Solutions to the Problems Set by Male-Male Competition and Male Coercion

The literature on sexual conflict indicates that female animals have evolved many mechanisms that lower the costs imposed on them by male-male competition and male coercion; in other words, patterns that help the females to exert and
maintain some control over their reproductive lives (e.g., Gowaty, 2004; Mulder & Rauch, 2009; Stumpf et al., 2011; Watson-Capps, 2009). We will briefly describe some of these patterns here (typically referred to as “female counteradaptations” in the sexual conflict literature) and indicate which ones we have documented in our white-faced capuchin females.

Polyandrous, Nonconceptive, and Post-Male-Takeover Mating

Females in many primate species mate with multiple males (polyandry, or polygynandry in the case of multiple females residing and mating with multiple males). It has been shown in several studies that male primates are more favorably disposed toward females with whom they have mated (Clarke et al., 2009; Palombit, 2010), so that even if males are unable to make a conceptual association between copulation and siring an infant (which is probably the case), they are predisposed to be protective and nonaggressive toward the infant of a female with whom they have recently consorted. If a female mates with several males, this exacerbates the paternity uncertainty already imposed by internal fertilization and predisposes several males instead of just one to be protective. So we can understand why there would be selection for female primates who live in groups with multiple males to mate polyandrously and this is what we have commonly seen in our capuchins.

Furthermore, we have hormonal evidence that female capuchins mate with males when they are not cycling reproductively and continue to mate with them after they have already conceived (Carnegie, 2011; Carnegie, Fedigan, & Ziegler 2005, 2006; Manson, Perry, & Parish, 1997; and see below on female choice). Additionally, we have observed females to mate with newly resident males who have recently invaded and taken over the group, even when these females are already pregnant. This may represent a form of “situational receptivity” (Clarke et al., 2009; Hrdy, 1979) in which females initiate mating and/or respond positively to male sexual initiations (whether or not the females are concepitive) in order to predispose the new males to be nonaggressive toward future infants.

Female Mate Choice, Concealed/Unpredictable Ovulation, and Cryptic Female Choice

Female brown capuchins exhibit very obvious proceptive behavioral patterns and actively pursue males sexually over a period of days (Fragaszy et al., 2004; Janson, 1984). Although females of our study species do sometimes initiate sexual behavior with distinctive proceptive behaviors, these are much more subtle, fleeting signals than those exhibited by brown capuchins, and mating in white-faced capuchins is just as likely to be initiated by males as females. As noted by Kappeler and van Schaik (2004), there is surprisingly little direct evidence for female choice in free-living primates. This is in large part because field conditions limit our ability to perform experiments of the type typically performed on invertebrates to
sort female choice from male-male competition and coercion. However, there is considerable indirect evidence for female choice in wild primates, such as our capuchins, some examples of which we just described—females choose to mate polyandrously, postconceptively, and after takeovers ("situationally"), all of which increase paternity uncertainty in the males and helps females to counter male attempts to control reproduction.

The fact that females can successfully encourage males to copulate when they are not in fact ovulating, suggests that their ovulatory phases may be concealed and/or unpredictable from the perspective of at least some of the males (Carnegie et al., 2006; Carnegie, 2011). One might argue that male capuchins are just always ready to copulate with any female at any time (i.e., the "indiscriminate eagerness of males to mate" identified by Bateman in fruit flies), but there is evidence that male primates do become sperm deleted and physically exhausted from multiple copulations (Dixson, 1998) and we know that capuchin males do sometimes reject female sexual advances (Fragaszy et al., 2004). Unpredictable/concealed ovulation has been argued to occur in many primate species where females show receptive and receptive behavior over periods of time that are much longer than their actual conception phases and where males readily mate with nonconceptive females (van Schaik et al., 2000). As noted by Strier (2010), there is little that females can do to alter their olfactory or physical cues, but many female primates are adept at modifying their behavior to stimulate sexual interest from males.

The fact that we see females mate with all the males of the group but our paternity tests indicate that alpha males sire 70-90% of the group's infants (Jack & Fedigan, 2006, see also Muniz et al., 2010), may indicate that alpha males are better at detecting cues to ovulation (see above) or it may also suggest that some form of "cryptic female choice" is operating in our study animals. "Cryptic female choice" is the term coined by Thornhill (1983) and a concept extensively developed by Eberhard (1996) to indicate the many different mechanisms by which a female can mate with a male but reject him as the sire of her offspring—and therefore exert female control over reproduction. Cryptic female choice typically refers to postcopulatory patterns by which females may preferentially use sperm from one male over that of another—via differential sperm storage and transport to the egg. Again, there is no direct evidence for postcopulatory female choice in primates, probably because of the invasive nature of the experiments required to document it (Birkhead & Kappeler, 2004), but there is some indirect evidence, for example the discrepancy between those male capuchins that we observe to copulate and those who actually sire the infants (see Schwensow, Eberle, & Sommer, 2008, for similar findings in grey mouse lemurs, Microcebus murinus).

Reproductive Synchrony

The pattern whereby the multiple females of a group all cycle simultaneously and/or give birth in the same season, is believed to be primarily an adaptation to the
seasonality of resources, but it can also function to decrease the ability of any
given male to monopolize mating opportunities. In our capuchins, we have dem-
onstrated that, although births do occur throughout the year, 44% of births occur
in the 3-month period (May–July) that immediately precedes the peak of food
availability (Carnegie, Fedigan, & Melin, 2011). The fruits eaten by these monkeys
are most abundant about 8 weeks after the peak in births (Carnegie, Fedigan, &
Melin, et al., 2011). Since we also know that lactation is the most energetically
costly part of female reproduction and that lactation costs peak when the infants
are 8 weeks of age (McCabe & Fedigan, 2007), we have concluded that reproduc-
tive seasonality in this species is geared toward enhancing maternal ability to lac-
tate for their young. Nonetheless, a side-effect of reproductive seasonality may be
that if many of the females of a group cycle more or less simultaneously, it is more
difficult for any one male to monopolize mating access to these females.

Female-Female Alliances and Female Avoidance of Nonpreferred Males

Female primates also exhibit a number of social behaviors that may function
to help them maintain control over their reproduction. It is possible that these
patterns originally evolved for other reasons, but proved adaptive in the con-
text of sexual conflict. In many (but not all) monkey species, females usually
remain throughout their lives in the groups and home ranges in which they
were born. This pattern is known as female philopatry and results in the stable
core of social groups being made up of matrilineally related females and their
offspring. If the males of the species commonly disperse between groups, then
adult males are only temporarily associated with each kin-related cohort of
devolve monkeys. Kinship is a powerful basis for permanent alliances, because
these females spend their entire lives together and because their inclusive fit-
ness is enhanced by protecting not only their own direct offspring, but also
those of their relatives.

Females who grow up and remain in their natal groups throughout their lives
have an intimate knowledge of their home range (e.g., where to find water and
food during low-resource seasons and drought years), which enhances their sur-
vival and their ability to "lose" newly immigrant males. Antiphonal calling (when
one individual's vocalization elicits answering calls from other members of the
group) is very common in capuchins. Group members typically forage in a highly
dispersed pattern in the dense canopy, but commonly vocalize back and forth to
one another. As well as near-distance antiphonal "contact calling," we have found
that group members respond to the long distance "lost calls" of individuals who
have become greatly separated from the group and are vocalizing loudly in an
apparent attempt to relocate their group (Digweed, Fedigan, & Rendall, 2007).
However, we have also observed that group residents may literally run away from
a newly immigrant male and then fall silent and fail to answer that male's lost
calls. In the long run, this does not appear to be a successful strategy to avoid
a group takeover, but it can temporarily protect females and their infants from agitated and aggressive newcomer males.

Invasions of immigrant males, and takeovers that result in the ejection of prior resident males, appear to be inevitable in white-faced capuchins—sometimes occurring despite the best efforts of females to support the resident males (Perry, 1997, 2008). While females do not have much choice as to which males ultimately join their groups, we have found in some cases that the females will disperse with the former alpha male when he is ejected from the group and will travel with him into a new group (Jack & Fedigan, 2009). Although capuchins are characterized by male dispersal and female philopatry, 14% of the adult females that have resided in our main study groups have been immigrants. Immigrating females are not readily accepted into established groups, they often receive aggression from resident females, and they are never very well integrated as group members, likely because they lack the kin network that is so important for females of this species (Perry, Manson, Muniz, Gros-Luís, & Vigilant, 2008). Immigrant females usually remain on the group’s periphery, occupy low dominance ranks, have low reproductive success, and often end up dispersing again. In our analysis of these immigrant females and females that emigrated or disappeared from our study groups, we found that female dispersal is much more common in years where takeovers occur than during times of group stability (Jack & Fedigan, 2009). Female dispersal is yet another (albeit costly) way in which females can exert female choice of their mates and it also demonstrates that females sometimes form relationships with males that are as strong as their alliances with their female kin.

Female-Male Alliances and Encouragement of Multimale Groups

Female primates may also react to attempted male coercion by forming close alliances with certain males, who protect them against others (“hired guns,” Cowlishaw, 1998). After newly immigrant capuchin males have settled into a group, they begin to actively protect the group from predators and defend its resources against neighboring groups. Once the aggressive, unsettled period of a takeover has calmed down, the infants sired by prior males are less and less in danger and indeed the males start to protect the young of the group. It is clearly in the interest of the females to form positive relations with these males through grooming and mating with them. Although females direct most of their affiliative behaviors to the new alpha male, they also groom, sit beside, and mate with subordinate males. We believe that female capuchins actively encourage multimale groups because groups with low ratios of adult males are at greater risk of takeovers and resultant infanticide (Fedigan & Jack, 2004). We have recently demonstrated that females in groups with higher proportions of adult males are more reproductively successful than those in groups with smaller proportions of adult males (Fedigan & Jack, 2011a). Interestingly, the same is not true for the males—their reproductive success is negatively associated with the proportion of
adult males in the group. The differential effect of adult sex ratios on reproductive success may be another example of sexual conflict in that male capuchins are better served by lower numbers of males in the group whereas females experience reproductive benefits from residing in groups with sex ratios skewed toward adult males.

Costs of These Female Adaptive Strategies

All of these female adaptive strategies to counter male-male competition and coercion involve some costs to the females. Perhaps the main one is feeding competition—by living with other females and their young as well as with multiple adult males, there is inevitable competition for access to food and water. As already mentioned, adult males commonly supplant adult females from preferred sitting/sleeping/foraging locations and food sources. In some groups, it is only the alpha male who is dominant to all the females but in others, many of the adult males are able to supplant individual females. On the other hand, coalitions of females (or of a female and a male) can evict almost any male from a feeding tree, and triadic forms of aggression are relatively common in our white-faced capuchins (Perry, Barret, & Manson, 2004).

There are also obviously costs of these female capuchin behaviors to the males of our study groups. Almost all of these patterns result in lowered ability of males to control the reproductive lives of females and they increase male levels of paternity uncertainty and their risk of caring for infants that are not their biological kin. Furthermore, along with the fact that alpha males need other males to defend their residency in groups (Fedigan & Jack, 2004), several of these female choice patterns force males to coreside in social groups and to cooperate with other adult males, which reduces their individual reproductive success (Fedigan & Jack, 2011).

Further Male Solutions to the Problems Set by Female Reproductive and Social Strategies

Some of the patterns we observe in male primates may be interpreted as reactions to the female patterns just outlined, especially to polyandrous mating, cryptic female choice, and female encouragement of multimale groups. For example, male chimpanzees, spider monkeys, and marmosets have large testes size relative to body size (Strier, 2010) and some primate males produce copulatory plugs (parts of their ejaculate harden and block the female vaginal tract, Dixon, 1998). Large relative testes and large ejaculate size (i.e., many sperm per ejaculate) are hypothesized to be forms of sperm competition in response to cryptic female choice.
Ejaculatory plugs help a male's ejaculate to remain in a female's vaginal tract, even if she mates with a subsequent male (Birkhead & Kappeler, 2004).

Male primates may also lower some of their reproductive costs of multimale social living, by residing in groups of related males. That way, even if their individual reproductive success is negatively affected by competing with the other males of their group to sire infants, their inclusive fitness will still be strong. We hypothesize that this is accomplished in white-faced capuchins by parallel dispersal behavior in which brothers or cousins immigrate into a new group together (Jack & Fedigan, 2004a, 2004b; Perry et al., 2012). Given that a single male (the group's alpha male) sires the majority of group infants, and that females residing in groups together are closely related, natal males born during the tenure of a single alpha male will be very closely related. Parallel dispersal of these closely related males may be why subordinate capuchin males are content, for at least a few years, to reside in groups where the alpha male (who is related to them) is experiencing greater individual siring success than their own and who also supplants them regularly out of their preferred feeding and resting spots! For his part, the alpha male does not harass the subordinate males in his group when they copulate, which can be interpreted as him "ceding" reproductive opportunities to them (Clutton-Brock, 1998; Henzi, Clarke, van Schaik, Pradhan, & Barrett, 2010). In capuchins, we have found that alpha males "need" the subordinate males to help ward off takeover attempts (Fedigan & Jack, 2004) and in chacma baboons, Henzi et al. (2010) found that alpha males showed restraint against copulating at every possible opportunity, which resulted in subordinate males having more mating opportunities. They also found that those subordinate males who had mated with group females acted as extra protectors of the infants.

Why Do Female Capuchins Live Year Round With Males?

Like most other primate species (and unlike most nonprimate mammals), capuchin males and females reside together year round. Given the conflicts that arise between the sexes, it begs the question of why females bother. Why do they put up with these rather volatile males that are capable of imposing enormous reproductive costs on them? Returning to the questions posed in the beginning of this chapter, we have shown that the apparently contradictory ("good cop/bad cop") behavior of male capuchins results in large part from their attempts to improve their reproductive success relative to other nonrelated males and to reduce ambiguity about which offspring they have actually sired—that is, to have as much control as possible over when and with whom females conceive their young. Male capuchins behave positively toward offspring likely to be their own, toward females who are likely or recent copulatory partners, and toward males who are their allies and relatives. These positive behaviors, however, change dramatically when males take up residency in a new group. It is at that time that we
see them behave aggressively toward male competitors and the latter's offspring. Female capuchins respond to competitive and coercive male patterns with a variety of behaviors that maintain or increase paternity uncertainty in the males and reduce male abilities to control them. They respond to beneficial male patterns, typically exhibited by alpha males, by concentrating their conception mating on those males.

In the long run, female capuchins cannot keep out males who are determined to live in association with their kin-related groups. However, they can and do exact numerous concessions out of them, which are costly to the resident males—vigilance, defense of resources, multimale social groups, and protection from predators, humans, and invading males.

**Metaphors of Sexual Conflict: Winners/Losers, Dialectics and More**

Because Parker (1979) used game theory to understand male and female mating strategies, he consistently referred to "winners and losers," as have many of his successors. Dawkins (1976) popularized the phrase: "battle of the sexes." However, as noted by Arnqvist and Rowe (2005), one sex does not win a conflict against the other in the way that some parasites may be said to win or lose a conflict with their hosts. That is, the average fitness of one sex in a population does not increase at the expense of the other, they are not independent. In this respect, sexual conflict is quite unlike antagonistic interactions between species (e.g., predator/prey or parasite/host interactions), where the fitness of one party (in this case, one species) can increase at the expense of the other. As succinctly said by Arnqvist and Rowe (2005, p. 221), what happens to the average fitness of one sex in a population also happens to the other.

If we insist on labeling one party as the winner and the other as the loser, then we should note that the actual "battle" for reproductive success is within each sex. A given male may exhibit a strategy that results in him having greater control over reproduction than does the female in a particular interaction (or vice versa)—but at the population level, males can only be as reproductively successful as the females. On the other hand, some females (as a result of genes, behavior, and a certain amount of serendipity) reproduce more successfully than do other females and some males reproduce more successfully than do others. Or as Gowaty (2004, p. 48) put it, although the contests over control of reproduction are between opposite sexes, the outcomes of these contests work to affect fitness variation within each sex.

Rather than perpetuating an anthropomorphic attribution of males as active winners and females as passive losers, researchers such as Gowaty (2004) have argued that sexual conflict is a form of dialectics, an ongoing dialogue between
two parties holding different points of view and that the dialogue in this case is about who holds control over reproduction. Mulder and Rauch (2009, p. 201) defined sexually antagonistic coevolution as "a chain of adaptations and counter adaptations during the struggle over sex-specific optimality in a given conflict trait." Gowaty (1997) has argued that sexually antagonistic coevolution occurs when each sex sets up problems that the other must solve in order to survive and reproduce. This vivid metaphor is one that we prefer because it is neither male- nor female-biased. "Problem setting and solving" is reminiscent of Newton's Third Law of Motion, that every action has an equal and opposite reaction, and even resembles the Buddhist view that envisions life forms as a vast net (Indra's Net) made up of jewels at every juncture (Kabat-Zinn, Watson, Batchelor, & Claxton, 2000). Each jewel represents a life form that is connected to the others such that a change in one is reflected in the others. Indra's Net seems an apt metaphor for socially cognitive animals such as primates, who are constantly negotiating and adjusting their lives and their reproductive success through a web of other individuals, similarly engaged.

Conclusion

Some primatologists (e.g., Snowdon, 1997; Sussman & Garber, 2004, 2007; Sussman, Garber, & Cheverud, 2005) emphasize the strong degree of cooperation found between males and females in many primate species, especially in relation to the rearing of their "joint investment," the infants. It is truly a joint investment since, as pointed out by Arnvist and Rowe (2005), every individual has one father and one mother. Snowdon (1997) notes that male primates may often assist during the female's lactation period to enhance infant survival and thus may make considerable, sometimes comparable, parental investments to those of females. There are, of course, many benefits of social living as well as the high frequencies of affiliative behavior and low frequencies of aggressive behavior that typify most primate societies. Indeed, resident adult and subadult male capuchins seldom direct physical aggression toward the females in their groups, and capuchins spend the vast majority of their social time in affiliative interactions.

Roughgarden (2009) has argued that evolutionary biologists emphasize intrasexual competition to the exclusion of recognizing the strong and widespread evidence for cooperation within and between the sexes. It is of course not possible to directly compare the importance of affiliation between the sexes to that of sexual conflict. Whether or not Roughgarden's assertion is justified, it is clear that the two main principles of sexual selection (male-male competition and female choice) need to be augmented by better consideration of the many ways in which male and female strategies conflict and coincide and by better understanding of how females and males affect, constrain, and enhance each other's lives and
ability to reproduce. It is also clear that both females and males play active roles in these interactions and adaptations.

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