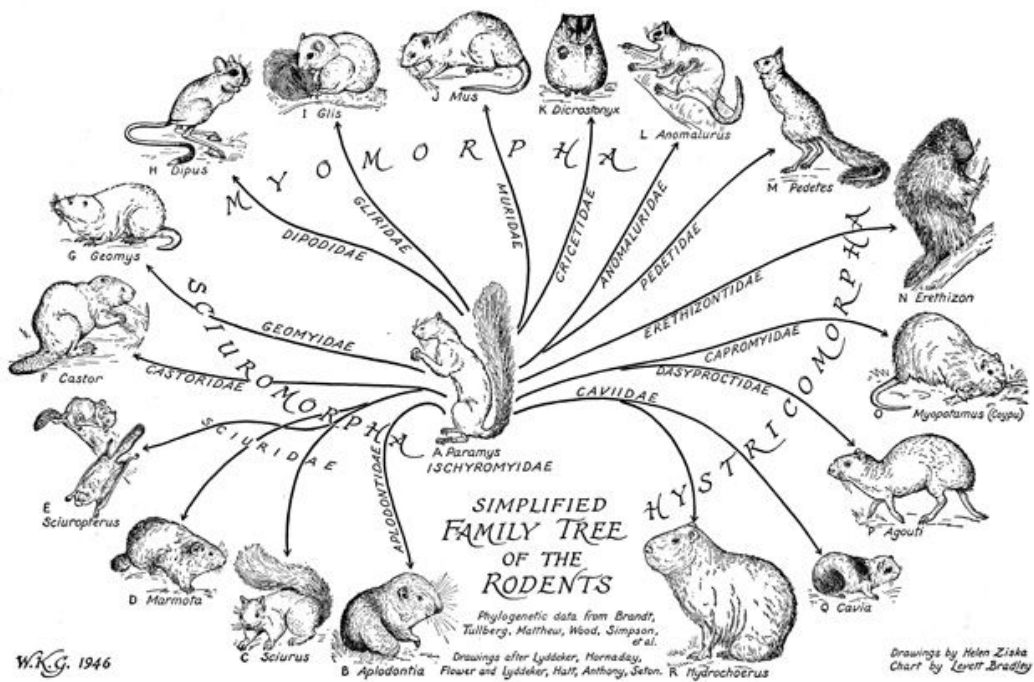


# Male Sexual Coercion and Female Counter-Tactics in Rodents

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## **Abstract**

Sexual coercion occurs in many species across multiple taxa, including humans. This coercive behavior is usually perpetrated by males against females, due to the difference in parental investment between the two sexes. Because this behavior can incur significant cost on females, they have evolved counter-tactics against coercive behavior. Here I define different forms of coercive behavior used by males and describe counter-tactics used by females. Next I explore different factors that affect the use of both coercive behavior and counter-tactics. Finally, I describe two examples in specific rodent species, describing how the interaction between environmental factors and behaviors of both sexes affects the use of coercive behavior and counter-tactics.

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Cover: **William King Gregory's 1946 tree of rodent relationships.**  
Gregory (1951). In: *Evolution Emerging: A Survey of Changing Patterns from Primeval Life to Man*. vol. 2, p. 757, fig. 20.33

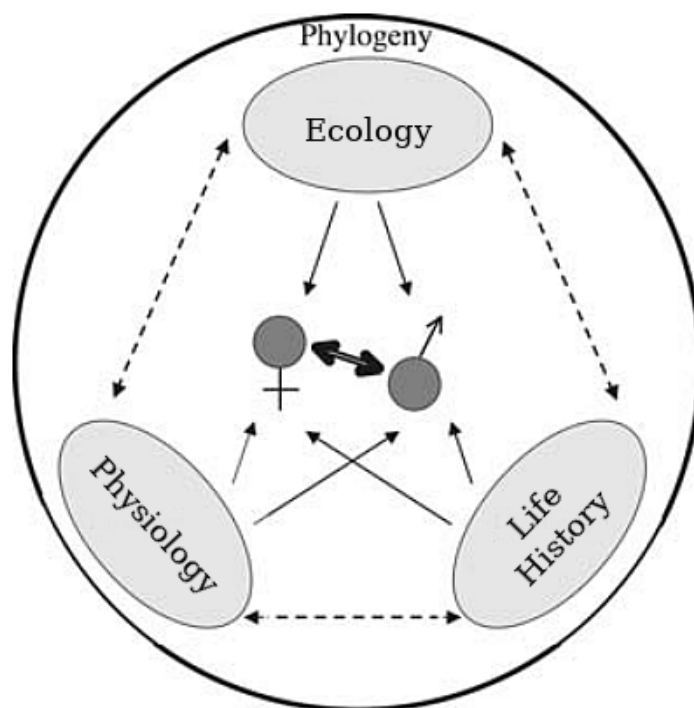
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# 1 Introduction

Sexual coercion has been observed in species across several taxa, including insects (Thornhill 1980), birds (Low 2005, Mineau et al. 1983), fish (Pratt 1979), reptiles (Shine et al. 2003), and many species of mammals (Clutton-Brock et al. 1992, Mesnick and Le Boeuf 1991, Poole 1989, Towers et al. 2018), including non-human primates (Baniel et al. 2017, Muller and Wrangham 2009, Smuts and Smuts 1993) and, most notoriously, humans (Muller and Wrangham 2009). In most cases, sexual coercion is used by males against females, although the opposite also occurs, if much more rarely (Prosen et al. 2004).

This is because it's generally in the interest of males to mate with as many females as possible, regardless of mate quality, while it's in the interest of the female to choose the best possible mate. Under these conditions, females are much more selective than males, and males may need a way to get an unwilling



**Figure 1:** Factors influencing the mating system of a species or population. The mating system (double solid line) is dictated by the influence of ecological, physiological, and life-history characteristics (single solid lines) on both males and females. In turn, ecological, physiological, and life-history characteristics are interrelated (dashed line) and have evolved within a particular phylogenetic framework. Edited from Kalcounis-Rüppell and Ribble (2007)

female to mate, leading to sexual coercion. In addition, females may try to mate with other, more preferable rivals. The male may then attempt to use coercion to keep her from mating with others.

The dominant hypothesis is that this difference in selectiveness is due to the difference in parental investment between the two sexes, where females usually invest more into their offspring than males (Arnqvist and Rowe 2013, Robert 1972), both during pregnancy and after, as long as young are still dependent on their parent(s). This is especially true for mammals, since only the mother can provide milk. In addition, males can sire several offspring with multiple partners, while females can only produce one offspring or set of offspring at a time, and often only with one partner (Arnqvist and Rowe 2013). In species where males care for young, or females can produce more than one (set of) offspring, females are expected to use coercion against males (Arnqvist and Rowe 2013, Kempenaers 1995).

Sexually coercive behavior can impose significant costs on the female, including physical injury, loss of offspring, and even death (Arnqvist and Rowe 2013). To prevent or at least reduce these costs, females have developed a host of counter-tactics, both behavioral and physiological (Muller and Wrangham 2009). The mating system of a species or population, including the occurrence and types of sexual coercion and counter-tactics, is largely influenced by its ecology and social structure, as well as its evolutionary history (**figure 1**). In this essay, I aim to give an overview of the influence of different ecological and social factors on coercive behaviors and counter-tactics in rodents.

Rodents should be an ideal subject for this kind of investigation (Wolff and Sherman 2007). They are a large and diverse group of species, with a wide range of habitats, social organizations and physiologies. Much research has been done on different species of rodents, thanks to the ease with which they can be kept in a laboratory environment. Finally, they are relatively short-lived, making it much easier to assess long-term effects of behaviors.

## 2 Defining Sexual Coercion

Smuts and Smuts (1993) define sexual coercion as "use by a male of force, or threat of force, that functions to increase the chances that a female will mate with him at a time when she is likely to be fertile, and to decrease the chances that she will mate with other males, at some cost to the female". In addition to providing criteria to determine whether aggressive behavior constitutes sexual coercion, this definition also suggests a distinction between direct and indirect forms of sexual coercion, where direct coercion increases the male's mating success, and indirect coercion decreases rivals' mating success.

Muller and Wrangham (2009) further clarify this distinction, defining direct coercion as "the use of force to overcome female resistance to mating". They use the second part of Smuts and Smuts' definition to define indirect coercion: "[the use of force] to decrease the chances that [a female] will mate with other males". In other words, direct coercion serves to increase the mating opportunities of the perpetrator, while indirect coercion serves to limit the mating opportunities of the victim. Different types of direct and indirect coercion are defined in **sections 2.1** and **2.2**. They further recognize infanticide as a third form of sexual coercion.

## 2.1 Direct Coercion

Clutton-Brock and Parker (1995) define three distinct types of direct coercion: forced copulation, harassment and intimidation. These types are mainly defined by the intensity of aggression and duration of the behavior.

**Forced copulation** Forced involves "violent restraint, resulting in immediate mating". This form of coercion is the most violent, but is also the fastest.

**Harassment** Harassment involves "repeated attempts to mate that impose costs on females, inducing eventual female submission". This behavior is less intense, since the male aborts his attempts to mate if the female resists. It also lasts longer, since the male keeps trying repeatedly.

**Intimidation** Intimidation involves "physical retribution against female refusals to mate, increasing the likelihood of submission to future advances". This behavior varies in intensity, depending on the species. Intimidation takes place over longer periods of time, even affecting subsequent estrous cycles.

## 2.2 Indirect Coercion

Muller and Wrangham (2009) distinguish three types of indirect coercion (coercive mate guarding): herding, punishment and sequestration. These three types can also be defined by their time frame, but this distinction is harder to make. They are best defined by how far in advance they anticipate female attempts to mate with other males.

**Male herding of females** Herding is a short-term tactic that involves "aggression directed toward females to induce immediate separation from rival males and to restore proximity to the guarding male". This behavior takes place shortly before the female might attempt to mate with a rival male.

**Sequestration** Sequestration is more long-term and involves "forceful separation of females from a social group, particularly during periods of maximal fecundity, to prevent copulations with rival males". This tactic is used long before a female can attempt to mate with rival males.

**Punishment** The time-frame of punishment is the hardest to define. It involves "physical retribution against female association or copulation with other males, decreasing the likelihood of these behaviors in the future". On the one hand, punishment only takes place in the short term, after the female has already interacted or even mated with a rival male. On the other hand, this serves to prevent the same behavior in the long term, and so at the same time also takes place long before her next attempt to mate.

### 2.3 Infanticide

Infanticide involves a male killing the young of a female in order to create a mating opportunity for the perpetrator. Although this could be considered a form of direct coercion, there are two distinct differences between other forms of direct coercion and infanticide. First, infanticide involves the use of violence against offspring and not the female. Second, although infanticide accelerates mating opportunities for the perpetrator, it does not necessarily increase his chances of mating with the mother.

### 2.4 Criteria for Sexual Coercion

While direct coercion is easily recognized, indirect coercion is harder to identify. Male aggression against females can occur for other reasons than sexual coercion, such as competition for food or status (Muller and Wrangham 2009). So how do we identify sexual coercion? In order for aggressive behavior to be defined as sexual coercion, it needs to meet several criteria.

First, if aggressive behavior is meant to increase male mating success, it should mostly target those females most likely to conceive. Cycling females should experience more aggression than those that are immature, pregnant, or lactating. Second, it should be associated with increased mating activity between the perpetrator and the victim. Third, aggressive behavior should impose a cost on the female. If this aggression is as an indication of mate quality, the advantages of mating with an aggressive male may be greater than the costs of the aggressive behavior.

Like aggression against females, infanticide is not always a form of sexual coercion (Ebensperger and Blumstein 2007, Hrdy 1979). It can also be a way to acquire resources like food or nesting space, or to avoid misdirected parental

care. In order to function as sexual coercion, infanticidal behavior should meet the following criteria: (1) the male should not kill its own offspring, (2) killing a female's offspring should shorten the time until she is fertile again, and (3) the male should have a chance to mate with the mother of the killed offspring.

## 2.5 Mating plugs

One final male tactic I want to mention is the use of mating plugs, also called copulatory plugs (Hartung and Dewsbury 1978, Koprowski 1992, Murie and McLean 1980). I mostly found this mentioned as a form of male-male competition, but I feel it could also be classified as a form of sexual coercion, since it can limit the female's options. However, the criteria are somewhat hard to pin down. One problem is that mating plugs have multiple possible functions, which are not mutually exclusive. In addition, the function and efficacy of mating plugs in any particular species can change over evolutionary time, or they can even disappear completely, due to antagonistic co-evolution between the sexes.

Four potential uses for mating plugs have been proposed (Schneider et al. 2016): (1) gradual release of sperm, (2) enhanced sperm transport, (3) coital stimulation and (4) prevent or delay female re-mating. There is currently little evidence to support the first hypothesis, but enough for the other three to make them plausible explanations for the use of mating plugs. In experiments with male mice who could not form plugs, ejaculate from these males was shown not to migrate to the cervix properly, reducing their fertility (Dean 2013, Kawano et al. 2014). Dean (2013) also showed that 57% of females mated to males who could not form plugs gave birth to a litter, compared to 82% of females mated to males that could, despite the fact that both types of males did fertilize eggs. This suggests that males without a mating plug were less able to provide the stimulation needed to prepare the uterus for implantation.

The fourth hypothesis is most relevant to us, but also the hardest to prove. One reason, as mentioned before, is that the different functions are not mutually exclusive. Another is that mating plugs are not always effective at preventing female re-mating, although it can reduce or prevent fertilization by rival males. Nonetheless, there is evidence that mating plugs can secure a male's paternity. Mating plugs have proven effective in preventing female re-mating in guinea pigs (Martan and Shepherd 1976). In a study on mice, Mangels et al. (2016) found that when a female mated with two males, if the first male could not form a plug, he lost almost all paternity to the second male, who could form a plug. They further found that this pattern remained even if first-to-mate males were vasectomized, indicating that this difference was due to the presence of the plug, rather than timing of ovulation or reduced fertility in males who did not form plugs. Mating plugs could also prevent re-mating by making the female less



attractive to rival males. Ramm and Stockley (2014) found that male house mice were less likely to mate with recently mated females due to this first-male advantage, and the presence of a visible mating plug is a potential indicator of female mating status.

Since there is some evidence that mating plugs can function to reduce (successful) female re-mating, we have satisfied one of the conditions to classify mating plugs as sexual coercion. This leaves us with two more: (1) the use of force or threat of force and (2) cost to the female. The first one is a bit complicated, since depositing a mating plug is not a violent act, and so doesn't feel like a form of force. However, the female has no choice as to whether a plug is deposited or not. As for the second, there is clearly a cost to the female, since she loses mate choice if she cannot successfully mate with other males. In addition females of several species remove mating plugs (see **section 3.1**), indicating there is some cost she wants to reduce. Given this information, mating plugs should be classified as a form of sexual coercion in those cases where they are used to reduce female re-mating, namely an alternative form of mate-guarding.

### 3 Female Counter-Tactics

Coercive behavior by males imposes both direct and indirect costs on females (Arnqvist and Rowe 2013, Muller and Wrangham 2009, **table 1**). Direct costs include physical injury and loss of young, while indirect costs include increased levels of stress and reduced foraging time. To prevent or reduce these costs, females use a range of counter-tactics, both behavioral - less costly but also less effective - and physiological - more costly but also more effective. Which tactics are used depends on the type and intensity of coercive behavior, where less costly behavioral tactics are used first, adding more costly physiological tactics when these prove insufficient (Muller and Wrangham 2009). Since direct coercion seems to be relatively rare in rodents, most of these tactics are used to deter forms of indirect coercion, especially infanticide.

#### 3.1 Behavioral Tactics

**Territory defense** The most basic tactic for females to avoid coercive males is to simply keep their distance. In a number of rodent species, females have their own territories. One of the functions of female territoriality is probably to avoid infanticidal males. In several species, territoriality is highest during lactation, when infanticide is most likely to occur (Ebensperger and Blumstein 2007).

**Fleeing** Another option is to flee from coercive males. During mating bouts of several species of tree squirrels, females flee from groups of pursuing males, in order to avoid mating in dangerous locations, or to promote mate choice (Koprowski 2007).

**Resistance** When avoiding males is not feasible or unsuccessful, one final option is to try and resist the coercive male. Resistance is costly and has a high risk of injury. Female rats reduce this risk by adopting a more defensive form of resistance, which is less likely to trigger retaliation from the male (Blanchard et al. 2001). Accordingly, although male sexual aggression against females is common, this rarely results in injury.

**Table 1:** Costs of male coercive behavior, as well as examples of rodent species where this behavior occurs.

<b>Coercive behavior</b>	<b>Costs to female</b>	<b>Occurrence in rodents</b>
Forced copulation	Physical injury, loss of mate choice, heightened stress	Tuco-tucos <sup>1</sup>
Harassment	Physical injury, increased chance of predation, heightened stress	Tree squirrels <sup>2</sup> , laboratory mice <sup>3</sup>
Intimidation	Physical injury, heightened stress	Laboratory mice <sup>3</sup>
Herding	Reduced mate choice	Tree squirrels <sup>2</sup>
Sequestration	Increased chance of predation, reduced mate choice	Tree squirrels <sup>2</sup> , prairie dogs <sup>4</sup>
Punishment	Physical injury, reduced mate choice	
Infanticide <sup>5</sup>	Loss of young, physical injury	House mice, rats, tree squirrels, arctic ground squirrels
Mating plugs <sup>6,7,8</sup>	Loss of mate choice	Hamsters, mice, gerbils, rats, ground squirrels, tree squirrels

Sources: <sup>1</sup>Fanjul and Zenuto (2017); <sup>2</sup>Koprowski (2007); <sup>3</sup>Canastar and Maxson (2003); <sup>4</sup>Hoogland (2007); <sup>5</sup>Ebensperger and Blumstein (2007); <sup>6</sup>Hartung and Dewsbury (1978); <sup>7</sup>Murie and McLean (1980); <sup>8</sup>Koprowski (1992)

**Convenience polyandry** A far more feasible tactic is convenience polyandry. In this case, the female simply gives in to male mating attempts to avoid (further) aggressive behavior. Many species of rodent have methods to express post-copulatory mate choice (see **section 3.2**), making this a preferable option to resistance in these species. Unfortunately, it can be difficult to distinguish between convenience polyandry and polyandry for other reasons, as polyandry can have several other benefits (Thom et al. 2004, Thonhauser et al. 2013), some of which are explained below.

**Soliciting of multi-male mating by females** Multi-male mating (MMM), can occur for several reasons, but the most prominent in mammals is to avoid infanticide. This works through two possible mechanisms, which are not mutually exclusive. In several species, the act of mating inhibits infanticide in males (see sources in Ebensperger and Blumstein 2007, p. 276). In addition, MMM can cause paternity confusion, reducing the likelihood that males will commit infanticide. In these cases, males are unable to recognize their own offspring (Ferkin 1990, Mateo 2003), meaning they risk killing their own young if they kill those of a female they previously mated with.

**Maternal aggression** Another risky tactic, aggression is used by females in some species in an attempt to prevent infanticide. Aggression is a risky tactic both because of high energy expenditure and risk of injury. In addition, females are not always successful in preventing infanticide. Accordingly, females should be selective in their use of aggression. Maternal aggression is highest when pups are most vulnerable (Ebensperger and Blumstein 2007, Parmigiani et al. 1989, Sgoifo et al. 1992). Female mice can distinguish between infanticidal and non-infanticidal males, and are more aggressive toward the former (Elwood et al. 1990). They are also more aggressive when pups are present in the nest, thereby avoiding unnecessary risk when they have no pups to protect.

**Preferring dominant males** Females can also choose to mate preferentially with dominant males. This can have three reasons, again not mutually exclusive. First, if dominant males are more likely to commit infanticide or be coercive, mating with him is likely to protect both her and her pups. Second, if males protect their own offspring, dominant males are more likely to be successful than less dominant ones, and other males are less likely to attempt infanticide. Male house mice successfully defend their offspring from intruders (Mainardi et al. 1996, Pflanz 2002), and females prefer dominant males (Drickamer 1992, Hayashi 1990). Third, dominant males are better able to protect her from other, coercive males.

**Cooperation with other females** If males don't defend their offspring, another option is to cooperate with other females, usually kin. Females of a number of rodent species nest together with other females (Hayes 2000), and cooperating female house mice and Belding's ground squirrels are known to successfully chase off intruders (Maestriperi and Rossi-Arnaud 1991, Sherman 1980).

**Removal of mating plugs** In species where males form mating plugs, females can choose to remove mating plugs themselves (Koprowski 1992) or, if the plug is loose, mate with subsequent males until the plug is dislodged (Dewsbury 1984, Murie and McLean 1980).

### 3.2 Physiological Tactics

**Ovulation synchronicity** In species where females are spontaneous ovulators (meaning they ovulate on a cycle), they can synchronize their cycles so they ovulate around the same time (Muller and Wrangham 2009). This makes it harder for males to monopolize females, especially when females are only fertile for a short period. This can also be used to enhance the effects of paternity confusion and cooperation with other females; removing a way for males to identify their own offspring, and allowing females to defend and care for all of their pups at the same time. Gunnison's and Utah prairie dogs breed more synchronously than black-tailed prairie-dogs, which seems to be one of the reasons mate guarding is more common in black-tailed prairie dogs, and multi-male mating less common (Hoogland 2007).

**Manipulating ovulation** While some rodents are spontaneous ovulators, in other species ovulation is triggered by the act of mating (Milligan 1982). There are even species of spontaneous ovulators where mating can cause the female to ovulate earlier, or to release more eggs (Eberhard 1996). The chance of any of these things happening increases with things like mating duration or number of intromissions (Solomon and Keane 2007). Females can use this to their advantage to reduce the costs of multi-male mating and convenience polyandry, by mating with a male long enough to use these tactics, but not so long that ovulation is triggered, so she doesn't have to sacrifice her mate choice.

**Manipulating implantation** Like ovulation, preparation of the uterus for implantation can also be triggered by mating, likelihood of successful implantation is also dependent on duration of mating or number of intromissions, and it can be exploited in the same way. In Norway rats, for instance, the likelihood of successful implantation depends on the number of intromissions (Chester and Zucker

1970), and dominant males achieve more intromissions than subordinate ones (McClintock et al. 1982), suggesting females allow preferred dominant males to mate longer, increasing their odds of paternity.

**Manipulating fertilization** In rodents, semen is not directly delivered to the site of fertilization. Instead, semen is transported after mating, which requires a certain amount of time. Females can again use this fact to reduce the costs of other counter-tactics, for instance by mating with a non-preferred coercive male, then mating with another, preferred male before sperm from the first mating is fully transported (McClintock et al. 1982).

**Abortion of pregnancy** One potential tactic that is still under debate is abortion of pregnancy, usually called the Bruce effect, where pregnant females terminate the pregnancy when exposed to an unfamiliar male. They do this to prevent investing further in offspring that is unlikely to survive. There is some debate on both the cause of this behavior and its occurrence in the wild. Stokes and Sandel (2019) provide evidence for two possible theories. In most rodent species that exhibit the Bruce effect, males commit infanticide, but also provide paternal care. Thus, the appearance of an unfamiliar male could mean that infanticide is likely, but could also be a sign that the previous will not return to provide paternal care. Either way, his future offspring is unlikely to survive, and any further investment in the current pregnancy is wasted. They also find limited evidence of the Bruce effect occurring in the wild, but conclude that it simply happens more frequently in captivity, due to the higher frequency of interaction.

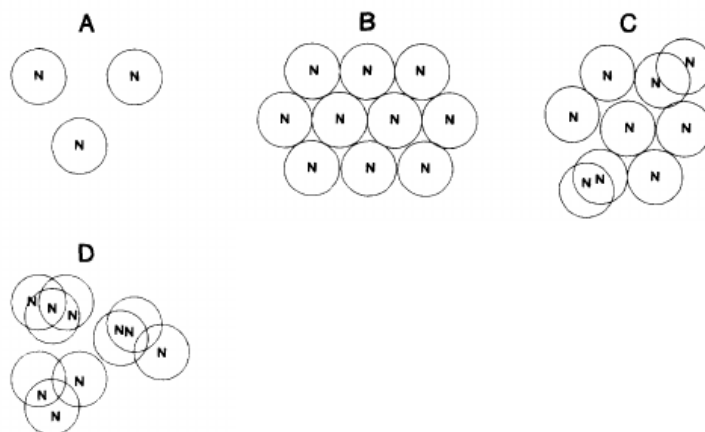
## 4 Factors Affecting Occurrence of Coercion and Counter-Tactics

There are many factors that can affect the occurrence of both coercive behavior and female counter-tactics. Here I look at some ecological and social factors relevant to rodents. I also consider the effect of some female counter-tactics on the types of coercive behavior used by males.

### 4.1 Vegetation

The presence and height of vegetation is one potential factor affecting the occurrence of certain coercive behavior. Higher vegetation makes it easier for females to hide, making it harder for males to harass them or keep them separated from other males. We can see the effect of vegetation in prairie dogs (Hoogland 2007).

The vegetation around black-tailed prairie dog burrows is generally longer than vegetation around burrows of Gunnison's and Utah prairie dogs. This makes it



**Figure 2:** Four alternative spacing patterns that have been recorded for female small rodents. N signifies nest location. Patterns B-D require territorial defense, pattern A does not. Edited version of Wolff (1993), figure 1.

**Table 2:** Predicted density-dependent effects on various aspects of the social behavior of rodents. After Krebs et al. (2007)

	<b>Low density</b>	<b>High density</b>
Territoriality	Territories large, widely spaced, mutual avoidance, low aggression, vacant space available	Territories small, considerable overlap, aggression high
Dispersal and philopatry	All males disperse relatively far, females disperse close to natal site, dams might bequeath maternal site to daughters	Delayed emigration, sons and daughters remain on natal site, extended families, cooperative and communal breeding of females
Age at sexual maturity	Sons and daughters mature at young age	Delayed sexual maturation for both sexes, cooperative and communal breeding for some species
Attempts at infanticide	High by males, low by females	Low by males, high by females

harder for female black-tailed prairie dogs to hide, and they are indeed far less likely to mate with multiple males than Gunnison's or Utah prairie dogs.

## 4.2 Risk of Infanticide

Risk of infanticide is an important factor affecting female counter-tactics. All tactics carry at least some costs, so females are less likely to use them if the risk of infanticide is lower, although some counter-tactics can have functions besides avoiding infanticide. The risk of infanticide, in turn, can be influenced by several factors.

### Seasonality of Breeding

Infanticide as a form of sexual coercion is far less likely in seasonal breeders, since the male is unlikely to get an opportunity to mate with the mother. Accordingly, infanticide by males is rare in Sciurid rodents (11-14 out of ~280 species; Ebensperger and Blumstein 2007), most of whom are seasonal breeders. One exception to this is when infanticide improves the female condition in the next breeding season, as is the case for Arctic ground squirrels (McLean 1983).

### Length of Female Investment

In non-seasonal breeders, an important determinant for the risk of infanticide is the length of time a female invests in raising her young (Palombit 2015). In most rodent species, young are altricial (i.e. born with closed eyes and little or no fur), and therefore completely dependent on their mother. To prevent the cost of having to take care of two (sets) of dependent offspring, females with altricial young enter lactational amenorrhea (pausing of the estrous cycle while nursing). This makes infanticide a very attractive tactic in these species, since the female usually resume cycling after losing their young.

## 4.3 Escape Options

One important factor determining whether males can successfully guard their mate are the female's escape options. Returning to our earlier example of prairie dogs, mating in these species takes place underground, with the female primarily responsible for choosing the specific mating burrow (Hoogland 2007). After mating, males of all three species attempt to keep the female trapped inside, and rival males out. Their success rate differs depending on the number of entrances to the mating burrow. Mating burrows of black-tailed prairie dogs usually have two entrances, or occasionally three or four. Those of Gunnison's prairie dogs

have as many as five or six entrances, and Utah prairie dogs' have at least that, and can have as many as twenty or more. This is a third possible reason, besides vegetation height and synchronous breeding, that multi-male mating seems to be more common in the latter two species.

#### 4.4 Population Density

Population density influences both male and female behavior (**Table 2**). At low density, males rove around a large area, and are likely to encounter unfamiliar females with pups that they are unlikely to have sired. At high density, on the other hand, they are confined to smaller areas, overlapping with several female home ranges. Because familiarity with females inhibits infanticide, the rate of infanticide by males should be lower at high densities (Krebs et al. 2007, Wolff 1995).

In several species, males engage in mate guarding at low population densities, but switch to dominance hierarchies at high population densities (Waterman 2007). This switch is triggered by the increase of the cost of mate guarding with increasing densities of both rivals and potential mates. When a male uses coercive mate guarding, he must spend time and energy to defend females against rival males, and to keep mates separate from them. The cost of these defensive behaviors increases with the density of the related sex. In a dominance hierarchy, the male no longer has to constantly guard against rival males, only those that threaten his status. The cost of monopolizing females is also reduced, depending on how much females prefer dominant males. Dobson (1984) found that male ground-dwelling squirrels switched from territoriality to dominance hierarchies only when density of both females and males was high. He concluded that this was due to the combined cost of keeping away rival males and sequestering more females.

At least in small rodents, female spacing and territoriality varies with density (Wolff 1993, **figure 2**). At low densities, each female occupies an exclusive home range or territory (**figure 2A-B**). At medium densities, territories may overlap with those of close female kin (**figure 2C**). At high densities, female kin will form group territories, which are communally defended against intruders (**figure 2D**). This can include communal nesting and even breeding. In brush mice, there is significant home-range overlap between females at high densities (Kalcounis-Ruppell 2002), but not at low densities (Ribble and Stanley 1998).

Finally, density can also affect mating tactics, which can be coercive themselves but can also trigger additional coercive behavior in the other sex. In tree squirrels, dominant males chase and try to sequester females, while subordinate males adopt a satellite tactic (Koprowski 2007), where they wait on the sidelines to mate with females that manage to escape chasing males. At low population



densities however, chasing is the only tactic used by males. In many rodent species, mating system varies from monogamy to polygyny or promiscuity with increasing population density (Waterman 2007).

#### **4.5 Sperm Competition**

The intensity of sperm competition influences the size of mating plugs. Ramm et al. (2005) found that the accessory glands needed to produce the components that form the mating plugs are larger in rodent species with more intense sperm competition, as indicated by larger testes size relative to body size. Because these glands also produce products not related to mating plugs, they also analyzed variation in plug size, and found that species with more intense sperm competition indeed produced bigger mating plugs.

Sperm competition, specifically whether there is a first-male or last-male advantage, also affects mate guarding (Waterman 2007). If there is a first-male advantage, such as in Belding's ground squirrels (Sherman 1989), males should not mate-guard, but immediately resume searching for mates. If there is some measure of last-male advantage, such as in Idaho ground squirrels (Sherman 1989), it's worthwhile for the male to guard the female, either through active mate-guarding or a mating plug.

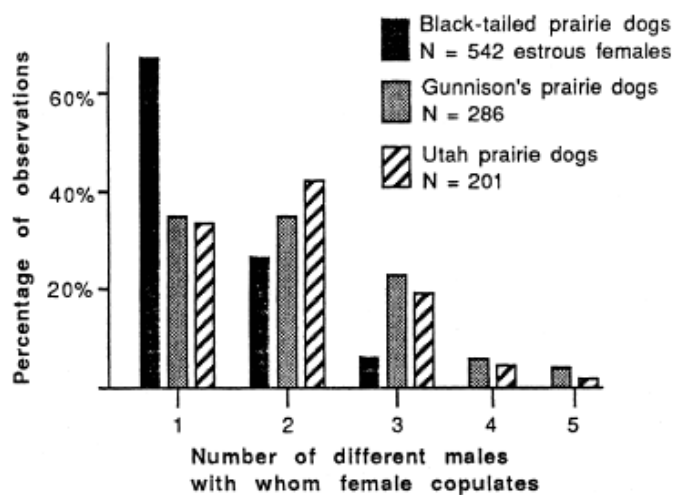
#### **4.6 Female Tactics**

Finally, I want to address the influence of female counter-tactics on coercive behavior. One thing I've noticed is that forms of direct coercion are relatively rare in rodents, while indirect coercion is far more common. I believe this is due to female counter-tactics, in particular cryptic mate choice and multiple mating. Males have little to gain by forcing the female to mate if she can prevent him from siring her offspring. Instead it's far more productive to keep her from mating with rival males, especially given the high incidence of multi-male mating in rodents (Solomon and Keane 2007).

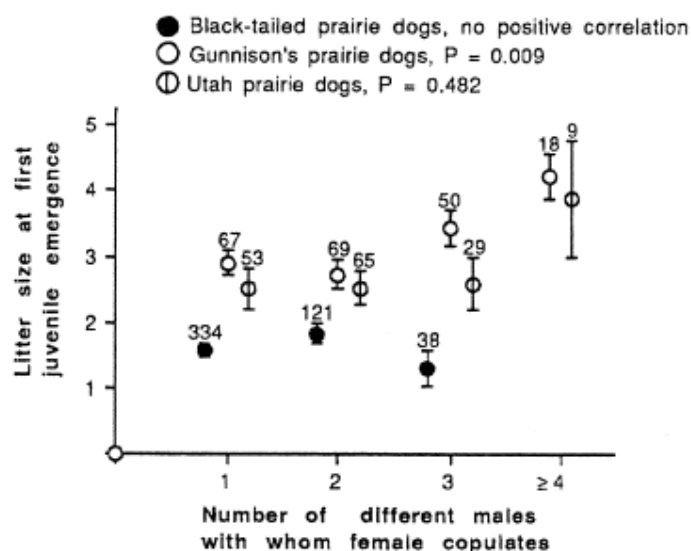
Female tactics can also affect male behavior in other ways besides making direct coercion less viable. The rate of multiple mating by females will increase the rate of mate guarding and mating plugs. Certain female tactics to deter infanticide, such as multi-male mating, if widespread enough, could lower the rate of attempted infanticide by males. On the other hand, if females prefer dominant males, subordinate males may respond by increasing their use of direct coercion. Female promiscuity, on the other hand, should reduce the rate of direct coercion, since females are less likely to refuse matings (Muller and Wrangham 2009).

## 5 Mate Guarding in Prairie Dogs

One group of species that is useful to compare, and have come up multiple times already, are prairie dogs. Hoogland (2007) compared mating behavior and



**Figure 3:** Occurrence of multi-male mating among female prairie dogs. After Hoogland (2007)



**Figure 4:** Litter size for prairie dogs versus mother's number of sexual partners. The number above each SE line indicates the number of females for which there is information on both number of copulations and litter size at first juvenile emergence. After Hoogland (2007).

alarm calling among black-tailed, Gunnison's and Utah prairie dogs. In all three species, multiple mating by females is common (**figure 3**). This does not seem to be a tactic to deter infanticide, since there is little evidence that infanticide by males is used as sexual coercion. Female prairie dogs only come into estrus once each year, so infanticide does not reduce the time until her next estrus. Instead, multiple mating seems to allow female prairie dogs to raise larger litters than if they had only mated with one male (**figure 4**).

Although males of all three species engage in vigorous mate-guarding, they are not equally successful. Multiple mating by females is more common in Gunnison's and Utah prairie dogs (65%) than it is in black-tailed prairie dogs (33%), and multiple paternity is more common in Utah prairie dogs (82%) than Gunnison's prairie dogs (77%). These differences in successful mate guarding seem to be caused by three factors: lower visibility of females, higher number of entrances per mating burrow, and higher reproductive synchrony of females (**table 3**).

Visibility of females within the home territory is mostly dependent on vegetation in the area. During the mating season, the home territory of black-tailed prairie dogs contains no vegetation over 15 cm tall. This makes it easy for males to see and mate-guard females. Home territories of Utah and Gunnison's prairie dogs, on the other hand, contain a lot of tall vegetation (>30 cm). This makes it easier for females of these species to hide, and harder for males to mate-guard.

In prairie dogs, mating takes place within a burrow (the *mating burrow*). After mating, the male attempts to keep the female trapped in the mating burrow, and rival males out. This delays remating, increasing sperm competition for the first male. Since the female enters first, she is mostly responsible for selecting the mating burrow. This gives her the opportunity to choose a burrow with a lot of entrances, maximizing her avenues of escape. Mating burrows of black-tailed prairie dogs generally have two entrances, and sometimes three or four, making these the hardest to escape. Those of Gunnison's prairie dogs have more, often

**Table 3:** Rates of multiple mating and multiple paternity among females in three different species of prairie dogs, and factors that influence the success of mate-guarding: height of vegetation, number of entrances to the mating burrow, and percentage of females that mated on the same day as at least one other female.

	<b>Black-tailed</b>	<b>Gunnison's</b>	<b>Utah</b>
Multiple mating	33%	65%	65%
Multiple paternity	5%	77%	82%
Vegetation height	<15 cm	>30 cm	>30 cm
Mating burrow entrances	2 - 4	5 - 6	5 - >20
Simultaneous matings	12%	27%	36%

five or six, increasing the female's escape opportunities. Utah prairie dog females have the best chance of escaping, as their mating burrows almost have at least as many entrances, and can even have up to twenty entrances or more.

This form of mate guarding is of course most effective if there is only one female to guard, and in prairie dogs this is often the case. Females are only sexually receptive for a few hours on one day each year, so the male only has a short window to mate with each female. Conversely, he only has to guard her for a short time. This is easy enough if only one female is receptive, but becomes harder when multiple are. The success of mate-guarding is thus affected by the level of reproductive synchrony among females. One way to measure reproductive synchrony is to calculate the percentage of females who mate on the same day as at least one other female. Hoogland (2007) did this for each species in different years, depending on which year had the most data available. Synchrony is lowest in black-tailed prairie dogs, where only 12% of females mated on the same day. Synchrony was higher among Gunnison's prairie dogs (27%) and highest among Utah prairie dogs (36%).

As we can see summarized in table 3, variation in all three factors match the variation in multiple mating and multiple paternity in these three species. All values are lowest for black-tailed prairie dogs, highest for Utah prairie dogs, and intermediate for Gunnison's prairie dogs. One final factor affecting the rate of multiple mating is the advantage for females. As we can see in **figure 4**, female black-tailed prairie dogs gain less additional fertility from multiple matings than Gunnison's and Utah prairie dogs. Since this is the case, they are probably less motivated to escape mate guarding than females of the other two species.

## 6 Monogamy in Prairie Voles

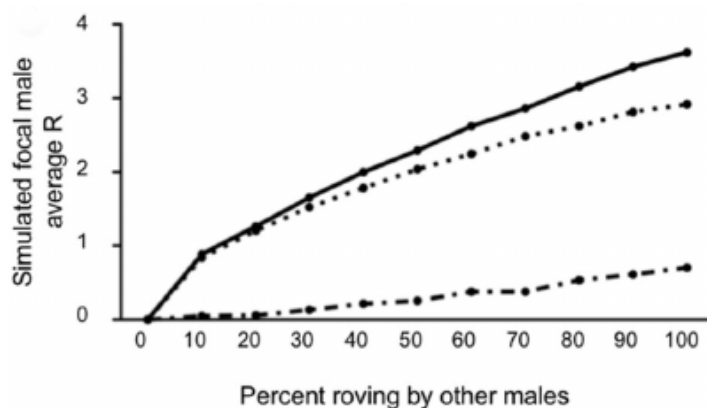
Prairie voles have long been described as a predominantly monogamous species (Getz et al. 1981, Getz and Hofmann 1986, Getz et al. 1987, Thomas and Birney 1979). However, more recent research has shown that the mating system of prairie voles is more complicated than simple monogamy. In fact, they can best be described as socially, but not genetically monogamous (Ophir 2017, Rice et al. 2018, Shuster et al. 2019). In both types of monogamy, males and females form exclusive bonded pairs, cooperating to raise their young. Genetic monogamy, they also mate exclusively with each other, while in social monogamy, one or both partners mate outside of the bonded pair.

Both male and female prairie voles employ two main mating tactics, wandering and residency, that they can switch between during their lifetime. Wanderers have a large home-range, do not defend a territory, and stay single rather than forming a pair-bond. They instead intrude on the territories of other voles to try

and gain mating opportunities. Only 20-35% of prairie voles adopt a wandering tactic, most of which are males (Getz et al. 1993, Ophir, Phelps, et al. 2008, Ophir, Wolff, et al. 2008, Solomon and Jacquot 2002, Zheng et al. 2013). The majority of prairie voles are residents. Residents form pair-bonds and defend a shared territory. Male residents provide parental care and use mate guarding to ensure paternity.

Male residents can be further subdivided into two types: true residents and roving residents, often simply called rovers (Madrid et al. 2020). True residents are genetically monogamous, only mating with their partner and always mate-guard. Rovers, on the other hand, are socially monogamous but not genetically monogamous. Although they do mate-guard, they also sometimes leave their mate to find additional mating opportunities. I found no mention of resident females showing roving behavior, but females readily mate with multiple males when given the opportunity (Wolff and Dunlap 2002, Wolff et al. 2002). Ophir, Phelps, et al. (2008) found evidence both for and against fitness benefits of multiple mating by females, but none for a loss of fitness. At worst fitness seems to be the same regardless of the number of partners, meaning there is no reason to actively look for additional matings, nor any reason to refuse them when an opportunity presents itself. Whether females are genetically monogamous thus depends on the tactic of their partner.

The percentage of prairie voles that choose to adopt wandering, residency or roving seems to largely depend on the type and distribution of vegetation, as well



**Figure 5:** Reproductive success for a simulated roving focal male at a population of 1,000 mated pairs with 10% wandering males and 10% unpaired females. Average R gained via extra-pair copulations ( $\bar{E}$ , solid line), average R lost via cuckolding ( $\bar{C}$ , dotted line), and total change in R ( $\Delta R$ , dash-dotted line) for the simulated roving focal male as the percentage of roving in the population increases. After Rice et al. (2018), figure 6C

as population density. Streatfeild et al. (2011) compared the social and genetic mating systems of two populations of prairie voles, one in Kansas and one in Indiana, and found higher rates of both social and genetic monogamy in Kansas than Indiana. Comparison of the different habitats showed that the different rates of social monogamy were best explained by differences in vegetation, and rates of genetic monogamy by differences in population density.

In Indiana, vegetation was higher, providing more protection against predators. This makes wandering less risky, and thus a more viable tactic. In addition, the habitat in Indiana had a higher density of dicot plants, which provide high quality food for reproduction. This reduces the extra fitness gained by providing parental care, which is an important motivating factor for social monogamy. Finally, vegetation in Indiana was more aggregated than in Kansas. When resources are highly aggregated, the cost of defense by females is likely to be higher than the benefits gained. This results in overlapping home-ranges and aggregation of females. This makes it easier for wandering males to encounter females, again making this tactic more attractive.

The different rates of genetic monogamy were best explained by differences in population density, although this conclusion is complicated by the fact that low density only occurred in Kansas, and high density only in Indiana. Nonetheless, genetic monogamy was more common at low density than at high density. This is probably due to the higher encounter rate of opposite-sex individuals at higher population density. Similarly to aggregated resources, higher population density causes females to have more overlap of home-ranges, as well as being closer together. This makes it easier for both wanderer and resident males to find mating opportunities, making genetic monogamy less likely.

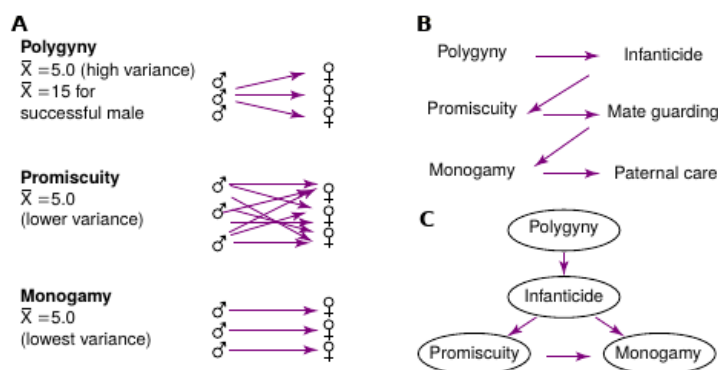
While population density can offer us an explanation for the actual occurrence of multiple mating, it tells us nothing about the decision to try to gain additional matings. Although extra-pair copulations are advantageous to resident males, they have to balance this with the risk of getting cuckolded by other males while they're away from their mate. Rice et al. (2018) used a model to determine under which circumstances resident males should choose to become rovers, and when they should remain true residents. They found that this mostly depends on the tactics of other males, particularly other residents. Specifically, the average fitness payoff of roving increased as more of the other males in the population rove. The tipping point for switching from true residency is around 50% rovers in the population. Around this point is when the fitness gained outweighs the potential fitness loss from cuckolding by other males. A higher percentage of wanderers, on the other hand, reduces the fitness gain of roving. This is because, while roving males open up opportunities for extra-pair copulations by leaving their mate unguarded, wandering males don't leave an unguarded female behind, and only increase the risk of being cuckolded. However, at numbers of wandering

males similar to those found in the field, the fitness gained through extra-pair copulations increases faster than fitness lost due to cuckolding (**figure 5**).

Of course, this model doesn't account for other factors that could affect the fitness payoff gained or lost by rovers, like risk of predation or less time spent on parental care. Nonetheless, it sheds light on an important factor that could affect the choice between roving or true residency. Although this model is purely theoretical, prairie voles do seem to have the ability to assess the social landscape, including the number of potential mates and rivals, and use this information to change their mating tactic accordingly (Ophir 2017).

## 7 Discussion

One interesting theory I came across is the idea that infanticide could be an important selective force in the evolution of mammalian mating systems (Wolff and Macdonald 2004, box 2). In this scenario, polygyny is the ancestral system, where one male mates with many females. In this system, subordinate males lack mating opportunities. They can then create these mating opportunities by



**Figure 6:** (A) Mean fitness ( $\bar{X}$ ) of a monogamous male can be similar to the average fitness of a promiscuous male assuming multi-male mating by females. Assuming that the mean litter size is five, variance is greatest for polygynous mating systems, with few males having high success and some males having none. Variance is lower for promiscuous matings and lowest for monogamous matings. Mean fitness is five for females in all cases. (B) Proposed evolutionary pathway from polygyny to monogamy. The current mating system (left) leads to the use of a new mating tactic (right), which leads to an alternative mating system, eventually leading to monogamy and paternal care. (C) Two alternative evolutionary pathways from polygyny to monogamy. If the threat of infanticide is great enough, males may switch straight to a monogamous mating tactic. After Wolff and Macdonald (2004), figure 1.

committing infanticide and mating with the female. The female can respond to this threat by mating with multiple males to confuse paternity, leading to a promiscuous mating system. Dominant males then develop coercive tactics to prevent multi-male mating and ensure paternity. In some cases, this could even evolve into monogamy and paternal care, depending on the differences in fitness between different mating tactics.

This is an intriguing avenue of research in the case of rodents, given the high risk of infanticide in many species, and the widespread occurrence of both multi-male mating and mate guarding. In addition, all the different mating systems mentioned in this theory occur in rodents, making them ideal for a comparative study on the subject. Unfortunately, despite the rather large body of research into rodent mating behavior, I had a hard time finding literature on coercive behavior outside of infanticide, especially pertaining to possible influences on the occurrence of coercive behaviors. I believe further research in this direction could prove valuable, given the great diversity in habitats and social systems found in rodents.



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