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Reproductive Interference

Reproductive interference in laboratory experiments of interspecific competition

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Abstract Many studies that have researched interspecific competition in *Callosobruchus* (bean beetles), *Drosophila* (fruit flies), and *Tribolium* (flour beetles) have considered the major drivers of interspecific competition to be interspecific resource competition and intraguild cannibalism. These competition drivers have a density-dependent effect on the population dynamics. However, some studies have also detected a relative-frequency-dependent effect in the observed population dynamics. The most likely causal mechanism of this relative frequency dependence is reproductive interference, defined as any interspecific sexual interaction that damages female reproductive success. Reproductive interference has been overlooked by most laboratory studies in spite of the critical effect on the competition outcome. In this paper, I review laboratory studies of these insect genera from the perspective of reproductive interference and show that the reported results can be more reasonably interpreted by the joint action of reproductive interference and resource competition, including intraguild cannibalism. In addition, on the basis of results reported by a small number of related studies, I discuss the behavioral and evolutionary changes induced in those genera by reproductive interference.

Keywords *Callosobruchus* · *Drosophila* · Resource competition · *Tribolium*

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Interspecific competition

Interspecific competition is any interspecific interaction that reduces the population growth rate of one species as a result of resource exploitation or interference by another species (Post et al. 1999; Reznick et al. 2002; Cain et al. 2008; Begon et al. 2009). Interspecific competition is very important in ecological communities because it can affect species coexistence and cause various ecological changes in natural communities, such as habitat partitioning, food resource partitioning, and species replacement (Schoener 1983).

A characteristic feature of interspecific competition is a density-dependent effect on the population dynamics. In a competition between two species, the population growth rate of one species is reduced as the density of the other species increases. In the case of intraspecific competition, an increase in the population density of a species causes its own population growth rate to decrease (Fujita and Utida 1953; Hassell 1975). A simple often-used model is the Lotka–Volterra competition model (Lotka 1924). In this model, if two competing species have the same per capita growth rate, the competition outcome depends on the relative intensities of interspecific and intraspecific resource competition. To examine the theoretical predictions of this model, many laboratory experiments have been performed (e.g., Crombie 1947). The model organisms used include protozoa (*Paramecium* spp.) (Gause 1934), bean beetles (*Callosobruchus* spp.) (e.g., Utida 1953; Fujii 1965), fruit flies (*Drosophila* spp.) (e.g., Merrell 1951; Barker and Podger 1970; Budnik and Brncic 1974; Wallace 1974), and flour beetles (*Tribolium* spp.) (e.g., Park 1948; Park et al. 1964).

However, some results of these laboratory experiments are inconsistent with the theoretical predictions. The competition results between species of *Tribolium* are typical (Park et al. 1964). Park et al. (1964) studied the competition dynamics between *Tribolium confusum* and *Tribolium castaneum*, species that practice intraguild cannibalism, to estimate the intensity of interspecific competition (Park et al. 1964, 1965, 1970). They estimated the competition coefficient of *T. castaneum* on *T. confusum* to be 6.55 and that of *T. confusum* to *T. castaneum* to be 0.11, indicating that the effect of competition from *T. castaneum* on *T. confusum* is far greater than the effect from *T. confusum* on *T. castaneum*, but these values are inconsistent with the observed intensities of intraguild cannibalism (Park et al. 1965; Edmunds et al. 2003). Moreover, these estimated competition coefficient values cannot explain the competition outcome, in which the species with the higher initial density is likely to exclude the species with the lower initial density (Leslie et al. 1968; DeBenedictis 1977; Edmunds et al. 2003). Similarly, competition outcomes changed in *Callosobruchus* spp. with various combinations of the initial densities of competing species (Yoshida 1966; Bellows and Hassell 1984; Kishi et al. 2009).

Some studies of competition in *Drosophila* have also reported that the per capita growth rate (i.e., female fecundity) of a species depends on its initial relative frequency (Narise 1965; Ayala 1971; Ayala et al. 1973; DeBenedictis 1977). For example, Narise (1965) reported that the relative frequency of *Drosophila simulans* to *Drosophila melanogaster* in the parental generation correlated with their relative frequency in the progeny generation, indicating that the per capita growth rate of each species depended on its initial relative frequency, and the species with the higher initial density was likely to win the competition. These observed relative-frequency-dependent outcomes, however, are not fully examined in most studies of interspecific competition.

Reproductive interference

Reproductive interference, which is any interspecific sexual interaction that reduces female reproductive success, can cause a relative-frequency-dependent effect on the population dynamics, in which the per capita growth rate of one species increases with the relative frequency of one species to another species (Kuno 1992; Gröning and Hochkirch 2008). This relative frequency dependence is the main feature that differentiates reproductive interference from interspecific resource competition (Kuno 1992; Yoshimura and Clark 1994), though reproductive interference can also have a density-dependent effect (Hochkirch et al. 2007). For example, the female fecundity of *Callosobruchus maculatus* is reduced by mating attempts by *Callosobruchus chinensis* males, and the magnitude of the fecundity reduction depends on the relative frequency of *C. chinensis* males to *C. maculatus* females (Kishi et al. 2009; Kyogoku and Nishida 2012). Another example is found in dendrobatid frogs when a female frog searching for a conspecific male is surrounded by the louder calls of heterospecific males. As the relative frequency of heterospecific males to conspecific females increases, a female spends longer time on searching, (Amézquita et al. 2006, 2011). The relative frequency dependence of reproductive interference makes the outcome initial frequency-dependent of each species, and thus a priority effect (Kuno 1992; Yoshimura and Clark 1994). Reproductive interference is more likely to lead to species exclusion or niche partitioning than interspecific resource competition (Kuno 1992; Ribeiro and Spielman 1986). In fact, in nature, reproductive interference can be a major driver of habitat and food resource partitioning between closely related species, and of replacement of one species by another (reviewed by Gröning and Hochkirch 2008). Thus, both resource competition and reproductive interference are possible mechanisms that can drive interspecific competition to species exclusion.

During interspecific interaction between closely related species, it is reasonable to assume that both reproductive interference and interspecific resource competition occur concurrently (Kishi and Nakazawa 2013). We analyzed a mathematical model incorporating both reproductive interference and interspecific resource competition, and found that the effects of these two mechanisms on the competition dynamics are not additive but synergistic. Furthermore, the model analysis predicts that the more critical driver of the dynamics is reproductive interference, whereas the role of interspecific resource competition is subordinate (Kishi and Nakazawa 2013). Then a possible situation is that, when one species is superior in reproductive interference and the other species is superior in resource competition, the first species can coexist with, or even exclude, the latter species (Kishi and Nakazawa 2013). This situation may have been observed in some of the laboratory experiments of interspecific competition mentioned in the previous section.

This article reviews some published laboratory studies of interspecific competition from the perspective of reproductive interference. For this review, I selected experiments performed with *Callosobruchus* spp. (bean beetles), *Drosophila* spp. (fruit flies), and *Tribolium* spp. (flour beetles). These insect genera have been used in many laboratory experiments of interspecific competition, so a large body of literature is available. Furthermore, the competition results obtained with these insect models constitute an important basis of current concepts of interspecific competition (Cain et al. 2008). Therefore, by showing that those results can be better explained if reproductive interference is taken into account, this review has the potential to have a large impact on the current conceptual framework of interspecific competition.

In the following sections, I review published studies of interspecific competition in each of these model insect genera. I first review competition results obtained with *Callosobruchus* (including some of my own work). Second, I review studies of *Drosophila*. Although a relative frequency dependence has been reported in the competition dynamics between species of *Drosophila* (Narise 1965; Ayala 1971), this result has long been attributed to frequency-dependent selection, in which the frequency of one genetic strain relative to that of another strain increases when the first strain is more adaptive to the environment (Dobzhansky 1943; Ayala and Campbell 1974; Nunny 1983; Antonovics and Kareiva 1988). Here, I propose that the observed frequency dependence can be better explained by reproductive interference. Finally, I review a series of studies conducted with *Tribolium* spp. Several of these studies reported an initial-frequency-dependent competition outcome that cannot be explained by intraguild cannibalism. I suggest that although intraguild cannibalism may be the major driver of competition, reproductive interference is the causal mechanism of the initial-frequency-dependent outcome observed in *Tribolium*. In each section, I also discuss behavioral and evolutionary changes adopted as a response to reproductive interference, though studies addressing such changes are relatively scarce.

Callosobruchus

Callosobruchus spp. (bean beetles) have been used not only in studies of intraspecific and interspecific competition (e.g., Utida 1941, 1953; Fujii 1965) but also in studies of sexual conflict (e.g., Rönn et al. 2006; Eady et al. 2007; Arnqvist and Tuda 2010) and host–parasitoid interaction (e.g., Utida 1950, 1955; Tuda 1998). Two commonly studied species, *C. chinensis* and *C. maculatus,* are both worldwide pests. In Japan, *C. chinensis* occurs in both granaries and fields, whereas *C. maculatus* has been recorded only in granaries (Nagayasu and Matsushita 1981). In the laboratory, if provided with no water and food, each *C. chinensis* or *C. maculatus* female in her lifetime lays 60–80 eggs individually on the surface of adzuki beans (Umeya 1987). Most *C. chinensis* females mate once with a conspecific male, but *C. maculatus* females mate multiple times (Miyatake and Matsumura 2004). Mated females attached eggs on the surface of beans. Each hatched larva digs into a bean and completes larval and pupal stages for about a month inside the bean where it competes for resource with other larvae (Utida 1971).

Experiments in which *C. chinensis* and *C. maculatus* are placed together and the hatched larvae are allowed to compete have all resulted in species exclusion, but the winning species varied among the experiments (Utida 1953; Fujii 1965, 1967; Ishii and Shimada 2008; Kishi et al. 2009). Utida (1953) first reported that *C. maculatus* excluded *C. chinensis*. However, subsequent studies have reported the opposite result (i.e., *C. chinensis* excluded *C. maculatus*) (Yoshida 1957, 1966; Bellows and Hassell 1984; Utida 1998; Kishi et al. 2009). Several experimental conditions have been suggested as the factor affecting the competition outcome, including humidity, temperature, and ventilation of the experimental arena (Fujii 1965, 1967). These environmental conditions have been considered to affect the intensity of interspecific larval competition (Yoshida 1966; Bellows and Hassell 1984), in which a larva of *C. maculatus* bites and kills both conspecific and heterospecific larvae in a bean (Toquenaga 1993). However, even those studies that found *C. maculatus* to be superior in larval competition, reported that *C. chinensis* ultimately excluded *C. maculatus*.

Kishi et al. (2009) demonstrated that the competition outcome between *C. chinensis* and *C. maculatus* is determined by reproductive interference rather than by resource competition. In particular, they showed that *C. maculatus* females, but not *C. chinensis* females, are vulnerable to reproductive interference; the fecundity of a female *C. maculatus* decreases when housed with a heterospecific male, whereas the fecundity of a female *C. chinensis* is not affected when housed with a *C. maculatus* male (Kishi et al. 2009; Kyogoku and Nishida 2013). Experiments carried out over multiple generations confirmed that *C. chinensis* is likely to exclude *C. maculatus*, but the outcome depends on the initial relative frequencies of the two species. This vulnerability of *C. maculatus* to reproductive interference probably explains most previously reported results in which *C. chinensis* excluded *C. maculatus*. Yoshida (1966) not only reported that *C. chinensis* strongly excludes *C. maculatus*, he also reported data supporting the vulnerability of *C. maculatus*. Specifically, he showed that when *C. maculatus* females are housed with heterospecific males, not only their fecundity considerably decreased but their longevity is also decreased (Yoshida 1966).

The proximate mechanisms of reproductive interference causing the fecundity reduction of *C. maculatus* females may be indirect and direct mating interactions with *C. chinensis* males (Kishi et al. 2009; Kyogoku and Nishida 2013). Indirect behavioral interference by *C. chinensis* males occurs when a mated *C. maculatus* female searches for beans with fewer eggs. A mated *C. maculatus* female usually moves away to avoid a heterospecific male that attempts copulation, but a mated *C. chinensis* female does not (Kishi et al. 2009). The behavior in which the female tries to escape from heterospecific mating attempts may be induced by a traumatic mating with a conspecific male (Crudgington and Siva-Jothy 2000). As a possible direct mechanism it has been suggested that multiple matings with *C. chinensis* males may directly damage the sexual organs of *C. maculatus* females (Kyogoku and Nishida 2013).

Intensity of reproductive interference, like intensity of resource competition, can be altered by experimental conditions, genetic variations, or behavioral plasticity. As a result, the opposite outcome, in which *C. maculatus* excludes *C. chinensis*, is sometimes observed (Utida 1953; Ishii and Shimada 2008). For example, temperature may alter the intensity of reproductive interference by altering the intraspecific mating behavior of *C. chinensis* (Katsuki and Miyatake 2009) or *C. maculatus* (Fox et al. 2006). Genetic variation may also affect the intensity of reproductive interference. The competition winner varied when experiments were performed with different combinations of four strains of *C. chinensis* and four of *C. maculatus* (Fujii 1969). Genetic strains of each species differ in heritable life history traits, such as the development period and the total number of eggs laid by each female (Fujii 1968; Utida 1971; Takano et al. 2001), and in sexual traits (Harano and Miyatake 2005, 2007; Eady et al. 2007; Sakurai et al. 2012). For example, the female mating frequency differs between different genetic strains of *C. chinensis* (Harano and Miyatake 2005, 2007). Thus, genetic variation can reasonably explain some of the conflicting results obtained in experiments performed at the same temperature (30 °C) and humidity (70 %) (Utida 1953; Yoshida 1966; Fujii 1967; Bellows and Hassell 1984; Ishii and Shimada 2008).

Here, I show that the cost of reproductive interference to a *C. maculatus* female differs between three *C. chinensis* strains (jC, wild, and jC-S), comparing the intensity of reproductive interference on *C. maculatus* females. The jC strain is maintained in a laboratory at Kyoto University (Utida 1953; Kuno et al. 1995), the wild strain was collected in 2007 from an adzuki bean field at Kyoto University, and the jC-S strain is a branch of the jC strain that was established more than 30 years ago and has been maintained in a laboratory at the University of Tokyo (Ishii and Shimada 2008). In this experiment, 10 adzuki beans were placed in a small dish with a *C. maculatus* female that had mated once with a virgin conspecific male. Then a virgin male of each strain was added to the dish. In the control treatment, no male was added to the dish. Ten replications of each of these four treatments were performed. After 3 days, the total number of eggs laid by the *C. maculatus* female was counted. Other experimental conditions and methods were similar with those used by Kishi et al. (2009). As a result, analysis of variance showed a significant difference among treatments ($df = 3$, $F = 11.49$, $P < 0.0001$, Fig. 1). Post hoc test (Tukey's HSD test, $P < 0.05$) showed that the reproductive interference exerted by the jC and wild strains was significantly stronger than that exerted by the jC-S strain (Fig. 1). In fact, the jC strain of *C. chinensis* excludes *C. maculatus* (Kishi et al. 2009), but the jC-S strain is excluded by *C. maculatus* (Ishii and Shimada 2008; S. Kishi, unpublished data). Different strengths of reproductive interference might be caused by different culture conditions used in the laboratories, since handling methods and stock culture densities affect the intensity of intraspecific sexual conflict (Katsuki et al. 2013).

Behavioral plasticity of females is also expected to affect the intensity of reproductive interference. If females can avoid or mitigate the cost of reproductive interference by changing their behavior, they can reduce the fitness costs imposed by reproductive interference. For example, we have observed that *C. maculatus* females housed with *C. chinensis* males hid in gaps between adzuki beans to avoid mating attempts by the males (Kishi and Tsubaki 2014). This avoidance behavior of the females, in combination with larval resource competition, resulted in resource partitioning even within the confines of a small dish. This result suggests that behavioral plasticity against reproductive interference can be a key factor in the initiation of resource partitioning, and once the partitioning is initiated, evolutionary adaptation to specific resources is possible. Fujii (1970) reported that fewer *C. maculatus* females use oviposition sites where *C. chinensis* individuals were present. Such avoidance behavior of *C. maculatus* females would likely delay extinction under interspecific competition, particularly if there are many hiding places (bean gaps) available in the experimental arena. Thus, the habitat structure can affect the intensity of reproductive

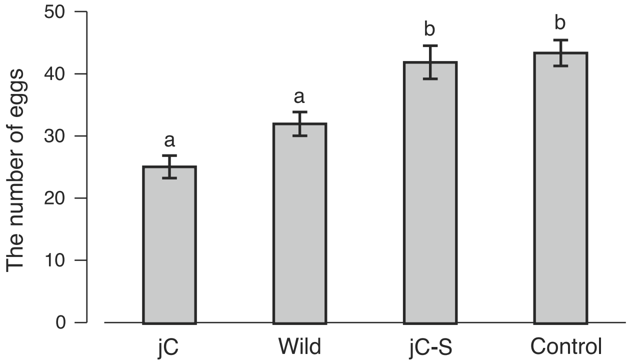

Fig. 1 The average number of eggs laid by a *C. maculatus* female over 3 days when housed with a *C. chinensis* male of the jC strain (jC), wild strain (Wild), or jC-S strain (jC-S), or when housed without a male (Control). *Different letters* above the *bars* indicate a significant difference between the treatments (Tukey's HSD test). The *bars* show standard error

interference via behavioral avoidance of females, and then can affect the competition dynamics via reproductive interference. Further investigations should examine the potential of behavioral plasticity to weaken reproductive interference to a greater extent.

Drosophila

Drosophila spp. (fruit flies) have been popular model organisms used in many areas of biology, particularly evolutionary biology and genetics (Powell 1997), since Morgan (1910) first used them for genetic experiments. Worldwide, genus *Drosophila* comprises more than 3000 species, with more than 250 species in Japan alone (Hotta and Okada 1989). In *D. melanogaster*, a female mates multiple times and each mating takes about 20 min. When provided with water and food and kept at 25 °C, a mated female lays about 50 eggs per day for a total of more than 2000 eggs in her 2-month lifespan (Hotta and Okada 1989). At 25 °C, the development period from egg to adulthood is about 10 days. Courtship behaviors of sexually mature adults vary among species (Ewing and Bennet-Clark 1968; Spieth 1974; Ewing 1983; Greenspan and Ferveur 2000). For example, the interval between the wing vibration pulses is longer in *D. simulans* males than in *D. melanogaster* males (Kawanishi and Watanabe 1981).

The main form of interspecific competition between *Drosophila* species has been considered to be resource competition, the intensity of which has been considered to vary with environmental conditions. For example, larvae of different species compete for food and adult females of different species compete for oviposition sites (Moore 1952; Miller 1964; Tantawy and Soliman 1967; Budnik and Brncic 1974). In larval competition, *D. simulans* larvae are superior to *D. melanogaster* larvae on a laboratory medium (Moore 1952; Barker 1971). In experiments in which female *Drosophila* compete for oviposition sites, *D. melanogaster* females lay more eggs at the edge of the medium and *D. simulans* females lay more eggs at the center of the medium (Moore 1952; Chess et al. 1990). Oviposition sites at the edge of the medium are more favorable, because the larval survival rate is higher at the edge where the medium is wetter than the crusty medium at the center. Thus, *D. simulans* females use more favorable oviposition sites than *D. melanogaster* females. The intensities of both the larval and the adult female competitions can be altered by environmental conditions, such as the habitat temperature and ethanol concentration of the medium (Moore 1952).

Several studies have reported that interspecific sexual interactions have frequency-dependent effects on the competition dynamics of *Drosophila* species (Narise 1965; Ayala 1971; Ayala et al. 1973; Moth 1974; Wallace 1974; Moth and Barker 1977, 1981; Pascual et al. 2000). Narise (1965) first reported a frequency dependence in the competition dynamics between *D. melanogaster* and *D. simulans*. Although his results were disputed by Putwain et al. (1967), subsequent studies have clearly demonstrated a frequency dependence caused by asymmetric reproductive interference between the two species (e.g., Moth and Barker 1981). The fecundity and longevity of *D. simulans* females decreases as the relative frequency of *D. melanogaster* to *D. simulans* increases, but the fecundity of *D. melanogaster* does not change (Moth 1974; Moth and Barker 1977). It has been consistently observed that *D. melanogaster* strongly excludes *D. simulans* (Moore 1952; Barker 1963, 1971; Aiken and Gibo 1979; Hedrick 1972). This asymmetric reproductive interference should have been caused by differences in the ability of males to discriminate between conspecific and heterospecific females, because female receptivity does not differ between the two species (Manning 1959). *Drosophila simulans* males strongly prefer conspecific females, whereas *D. melanogaster* males indiscriminately court the females of both species (Wood and Ringo 1980; Kawanishi and Watanabe 1981).

Behavioral changes have been observed during competition between *Drosophila* species that may reduce the effect of reproductive interference. For example, *D. simulans* males that have previously experienced courtship with *D. melanogaster* females reduce the duration of their courtship with *D. melanogaster* females, compared with naive males (Dukas 2004), although whether females show behavioral changes against reproductive interference is unclear. Evolutionary change and character displacement against reproductive interference have also been reported by several studies (Eoff 1975; Wasserman and Koepfer 1977; Aiken and Gibo 1979; Markow 1981; Izquierdo et al. 1992). In a multiple-generation experiment, the fecundity of *D. simulans* in the final generation was higher than that in the initial generation, but the fecundity of *D. melanogaster* did not change (Aiken and Gibo 1979). There are two possible explanations for this result: The *D. melanogaster* males may have evolved to discriminate and prefer conspecific females, or the *D. simulans* females may have evolved to avoid or mitigate the effects of reproductive interference by *D. melanogaster* males. Further researches should examine which of the evolutions occurs. *Drosophila* spp. can be the best materials for future studies of behavioral and evolutionary changes against reproductive interference.

Tribolium

The most famous textbook example of interspecific competition is a series of studies conducted with two species of flour beetles, *T. confusum* and *T. castaneum* (Begon et al.

2009; Cain et al. 2008). Both species are worldwide pests that infest both wheat flour and corn flour (Sokoloff 1972) although in nature they live beneath tree bark (Yoshida 1958). A mated female maintained in the laboratory at a temperature of 25 °C and a humidity of 70 % lays approximately 5 eggs per day and approximately 500 eggs in her 1-year lifespan (Park 1934). Hatched larvae grow from egg to adulthood in about 50 days at a temperature of 25 °C, feeding on wheat flour (Sokoloff 1972). When an adult male finds an adult female, he mounts the female dorsally and attempts copulation (Fedina and Lewis 2008). An adult female copulates multiple times (Fedina and Lewis 2008). Although interspecific copulations occur frequently, no hybrids have ever been reported (Serrano et al. 2000; Fedina and Lewis 2008).

Intraguild cannibalism is considered to be a major driver of interspecific competition between *T. confusum* and *T. castaneum* (Neyman et al. 1956; Park et al. 1965, 1970, 1974; Crenshaw 1966). Adults and larvae of both species prey on both conspecific and heterospecific pupae and eggs (Park et al. 1965, 1970, 1974), but the data show that *T. castaneum* prefers to prey on heterospecifics, whereas *T. confusum* preys indiscriminately on both conspecifics and heterospecifics. This asymmetric intraguild cannibalism predicts that *T. castaneum* should be the superior competitor, and in fact most studies have reported that *T. castaneum* excludes *T. confusum* (Park et al. 1964; I-nouye and Lerner 1965; Dawson 1966; Goodnight and Craig 1996). Environmental conditions, including food resources, temperature, humidity, and disease, are known to affect the competition dynamics (Park 1948, 1954; Dawson 1967; Sokoloff and Lerner 1967).

This asymmetric intraguild cannibalism, however, cannot account for the observed initial-frequency-dependent results, in which the species with the higher initial density excludes the species with the lower initial density (Leslie et al. 1968; Dawson 1970, 1977, 1979; Mertz et al. 1976; Edmunds et al. 2003). Asymmetric intraguild cannibalism predicts either that *T. castaneum* wins, or that the two species may coexist. In fact, however, *T. confusum* wins the competition when its initial density is higher relative to that of *T. castaneum*. This priority effect shows that the population dynamics are relative frequency dependent (DeBenedictis 1977).

Some reported data indicate that reproductive interference occurs between these two species in which *T. castaneum* is vulnerable to *T. confusum*. The fecundity of *T. castaneum* females is greatly decreased when housed with *T. confusum* males, compared with when housed with conspecific males, whereas the fecundity of *T. confusum* females is not affected when housed with *T. castaneum* males (Birch et al. 1951). Moreover, the fecundity reduction in *T. castaneum* females depends on the frequency of *T. confusum* males relative to *T. castaneum* females (Birch et al. 1951). Furthermore, the longevity of *T. castaneum* females is also decreased when housed with *T. confusum* males (Lloyd and Park 1962). Thus, between these two species, intraguild cannibalism and reproductive interference are both asymmetric and counterbalanced.

The asymmetric reproductive interference in the two species may be due to the asymmetric promiscuity of males of the two species. *Tribolium castaneum* males discriminate between females of the two species and prefer to attempt copulation with conspecific females, whereas *T. confusum* males indiscriminately attempt to copulate with females of both species (Serrano et al. 2000). This proximate mechanism of this differential promiscuity of males of the two species may be associated with their responses to volatile chemicals, including quinones, secreted by adults of the two species (Verheggen et al. 2007; Fedina and Lewis 2008). *Tribolium confusum* males are attracted to flour that has been conditioned with volatiles, and when they are kept in conditioned flour, they seek females, whether conspecific or heterospecific, more actively (Ghent 1963, 1966). In contrast, *T. castaneum* males avoid volatile-conditioned flour (Ghent 1963, 1966). As a result, interspecific mating between *T. castaneum* males and *T. confusum* females does not occur, but interspecific mating between *T. confusum* males and *T. castaneum* females occurs often (Graur and Wool 1985). Moreover, interspecific mating with *T. confusum* males damages the genitalia of *T. castaneum* females (Graur and Wool 1985). These results are consistent with the observed asymmetric reproductive interference, in which *T. castaneum* is vulnerable to *T. confusum*, but asymmetric reproductive interference is not consistent with the competition outcome that *T. castaneum* tends to exclude *T. confusum*.

I infer from these findings that reproductive interference can reasonably explain the initial-frequency-dependent outcome, but that intraguild cannibalism is probably the more critical driver of competition dynamics in *Tribolium*. Cannibalism probably gives *T. castaneum* an advantage in the competition because *T. castaneum* prefers to prey on heterospecifics even when the densities of both species are relatively low. When the total population density increases, however, the individual cannibalism rate decreases because the crowding effect reduces the number of eggs laid (Rich 1956), while the incidence of reproductive interference increases. As a result, when the total density of the two *Tribolium* species is high, reproductive interference, rather than cannibalism, drives the competition outcome. Thus, cannibalism is the more critical driver when the total density is relatively lower, and reproductive interference is the more critical driver when the total density is relatively higher. Because this driver shift depends on the total population density, the first driver, intraguild cannibalism,

Table 1 Asymmetric reproductive interference and resource competition and their proximate mechanisms in three insect genera and the most likely competition outcome

Genus	*Callosobruchus*		*Drosophila*		*Tribolium*	
Species	*C. chinensis*	*C. maculatus*	*D. melanogaster*	*D. simulans*	*T. confusum*	*T. castaneum*
Reproductive interference	○		○		○	
	Female sensitivity		Male promiscuity		Male promiscuity	
Resource competition		○		○		○
	Competition among larvae		Competition among larvae, among adults		Intraguild cannibalism	
Competition outcome	○		○			○

Open circles indicate the superior species in each category

usually determines the competition outcome. Furthermore, it means that the competition outcome can be indeterminate (Neyman et al. 1956; Leslie et al. 1968; Dawson 1970; Mertz et al. 1976), particularly when the initial densities of the two species are both similar and relatively low (Neyman et al. 1956; Dawson and Lerner 1966; Dawson 1970). Because the frequency dependent effect of reproductive interference leads more quickly to species exclusion than the density dependent effect of cannibalism (Kuno 1992; Kishi and Nakazawa 2013), the time required for *T. castaneum* to go extinct is hypothesized to be shorter than that for *T. confusum*. In fact, Park (1948) reported that the average competition time of experiments that *T. castaneum* went extinct is shorter than the time that *T. confusum* did. Future studies should examine this hypothesis, in which cannibalism is the first driver and reproductive interference is the second driver, experimentally by using several genetic strains of each species, because the competition outcome between the two species is known to depend on the combination of genetic strains used (Park et al. 1961, 1964; Dawson 1967; Goodnight and Craig 1996).

In my review of the literature, I did not find any study reporting behavioral or evolutionary changes that mitigated reproductive interference by one *Tribolium* species on another. Although evolutionary changes in the cannibalistic behavior of *Tribolium* have been reported (Dawson 1979), future studies should perform experiments to investigate possible behavioral and evolutionary changes against reproductive interference in *Tribolium* species.

Summary

In this review, I have shown that reproductive interference occurred, and importantly affected the outcomes of laboratory studies investigating interspecific competition between species of *Callosobruchus*, *Drosophila*, and *Tribolium*. In each genus, reproductive interference was asymmetric between two competing species (Table 1). Remarkably, the asymmetry of reproductive interference was also counterbalanced by asymmetric resource competition or asymmetric intraguild cannibalism (Table 1). In *Drosophila* and *Tribolium*, the mechanism of the asymmetric reproductive interference is differential male promiscuity, and in *Callosobruchus* it is differential female receptivity. The importance of reproductive interference as a driver of the competition dynamics differed among these insect genera. In *Callosobruchus* and *Drosophila*, reproductive interference was the dominant driver over resource competition. In *Tribolium*, however, intraguild cannibalism was the dominant driver; nevertheless, reproductive interference was likely a key factor leading to initial-frequency-dependent outcomes and, probably, indeterminate outcomes. As shown by this review, these complicated results can be easily explained as the combined effect of reproductive interference and resource competition, including intraguild cannibalism. In addition, some studies have reported data indicating behavioral and evolutionary changes have occurred in *Callosobruchus* and *Drosophila* against reproductive interference, but in *Tribolium* no such data have been reported, probably because the possibility has yet to be investigated. Because our current conceptual framework of interspecific competition is based in large part on data obtained in these insect genera, it is clear that the conceptual framework should be modified to incorporate reproductive interference.

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