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The effects of age and relatedness on mating patterns in thornbug treehoppers: inbreeding avoidance or inbreeding tolerance?

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Abstract The social environment of many species includes synchronous maturation of siblings in family groups, followed by limited dispersal of adults from their natal site. Under these conditions, females may experience high encounter rates with same-age siblings during mate searching, increasing their risk of inbreeding. If inbreeding depression occurs, mating with a sibling is often considered maladaptive; however, in some contexts, the inclusive fitness benefits of inbreeding may outweigh the costs, favoring females that tolerate some level of inbreeding depression. We evaluated mating patterns in the treehopper *Umbonia crassicornis*, a semelparous species in which females encounter same-age siblings during mate searching. A female *U. crassicornis* that mates with a brother suffers from inbreeding depression. We used a free-choice mating design that offered females simultaneous mating opportunities with three groups of males: siblings, same-age nonsiblings, and older nonsiblings. These groups represent the types of males typically encountered by females during mate searching. Our goal was to assess whether mating patterns were influenced by inbreeding avoidance by evaluating two hypotheses: kin discrimination and age-based mating (older males cannot be siblings in this species). There was no difference in the proportions of females mating with siblings vs nonsiblings, suggesting an absence of kin discrimination. However, females mated with a greater proportion of older vs younger males. Given that females do not avoid siblings as mates despite a cost to

inbreeding, our results provide a possible example of inbreeding tolerance. We also discuss some factors that may have contributed to the mating advantage of older males.

Keywords *Umbonia crassicornis* · Social environment · Kin discrimination · Courtship · Mate choice

Introduction

In species characterized by synchronous maturation of siblings in family groups, followed by limited dispersal of adults from their natal site, individuals often face an increased risk of inbreeding when they begin searching for mates (Bateson 1983a; Pusey and Wolf 1996; Lambin et al. 2001). This kind of social environment is found across a diverse group of taxa, including some insects (Wood 1993; McKamey and Deitz 1996; Tallamy and Schafer 1997; Lihoreau et al. 2007), spiders (Riechert and Roeloffs 1993; Aviles and Bukowski 2005), copepods (Palmer and Edmands 2000; Windsor and Innes 2002), and amphibians (Waldman and McKinnon 1993). In many species where inbreeding depression occurs, behavioral mechanisms that reduce inbreeding can be found (Thornhill 1993). However, in some cases, the inclusive fitness benefits to females of mating with a brother may outweigh the costs, in which case selection may favor females that tolerate some level of inbreeding depression (Parker 1979; Bateson 1983b).

Recently, Kokko and Ots (2006) developed a series of theoretical models that outlined the conditions under which inbreeding tolerance might evolve. They also offered some solutions to the apparent discrepancy between their simulations, which suggest inbreeding tolerance should be common, and the lack of examples of inbreeding tolerance

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in animals. Aspects of the social environment experienced during mate searching, such as encounter rates and whether choice occurs from sequential or simultaneous evaluation of mates, can have significant effects on the evolution of inbreeding tolerance. In many contexts, the selection for inbreeding avoidance may be weak, and there may even be selection for mechanisms that bias matings towards kin. Accordingly, although there are many empirical examples of inbreeding avoidance (see Pusey and Wolf 1996; Keller and Waller 2002), inbreeding tolerance may be more prevalent than is currently thought.

In the treehopper *Umbonia crassicornis* (Hemiptera: Membracidae), females frequently encounter their brothers during mate searching. Siblings mature synchronously in family groups, and although individuals begin to disperse as they reach sexual maturity, most only disperse a few meters (Wood and Dowell 1985). When sibling mating does occur, it results in significant inbreeding depression. In a population in Costa Rica, females mated to their brothers suffered a 32% reduction in adult offspring survival, compared with females mated to nonbrothers (Masters 1997). Even though *U. crassicornis* females mate only once, and mating with a brother can result in an approximately 1/3 reduction in a female's direct fitness, kin selection may still favor sibling mating (Parker 1979). However, given that inbreeding depression may be higher during harsh conditions (Kokko and Ots 2006), and that the natural history of mate choice and mating opportunities in *U. crassicornis* is incompletely known, it is not possible on the basis of this number alone to predict whether selection will favor inbreeding avoidance, inbreeding tolerance, or preference for sibling matings.

Masters (1997) tested for inbreeding avoidance through kin discrimination in a Costa Rican population of *U. crassicornis* and found that females did not discriminate between siblings and nonsiblings as mates. In contrast, she did find kin discrimination in the closely related *U. ataliba*, in which females preferred to mate exclusively with brothers and exhibited outbreeding depression when mated to nonsiblings. In another study, Wood and Dowell (1985) found that, in a Florida population of *U. crassicornis*, females were courted significantly more by older than by younger males. Masters (1997) argued that the lack of kin discrimination in *U. crassicornis*, coupled with the courtship advantage of older males from the Wood and Dowell (1985) study, meant that any inbreeding avoidance occurred through mating with older males, and not through kin discrimination per se. However, in Masters' (1997) study, mating trials were conducted under conditions that females were unlikely to experience in the field. The lack of kin discrimination, therefore, may not have accurately reflected mating patterns that would be expressed in a complex natural setting (Jennions and Petrie 1997). In Wood and

Dowell's (1985) study, it was not determined whether the females that were courted by older males eventually mated with them. Furthermore, in a field study, it is difficult to determine the age structure of the available pool of mates. As a result, it was unclear whether females were courted by a larger proportion of older males than expected based on their representation in the mating pool. Finally, even if older males have higher mating success, this may be due to a relationship between male age and mate quality (Brooks and Kemp 2001) rather than to the relationship between male age and relatedness (in this species, an older male cannot be a sibling; see "Materials and methods" section below). What is needed, therefore, is a study with known proportions of available mates, where female mating decisions can be evaluated under conditions that reproduce the social environment of mate choice in the field.

We tested for the presence of kin discrimination and age-based mating concurrently, as both factors may influence the outcome of mate choice in *U. crassicornis*. We used a free-choice mating experiment that offered females simultaneous mating opportunities with males differing in age and relatedness. Our experimental design incorporated key aspects of the social environment of *U. crassicornis* critical for our assessment of female mating patterns: (1) the onset of sexual maturity of siblings while still aggregated in their family group, (2) the close spatial proximity of different family aggregations, and (3) the presence of courting older males while females are still sexually immature. This study was designed to measure the outcome of mate choice under seminatural conditions, in which females encounter the types of males typically present during mate searching (Wood 1974; Wood and Dowell 1985), rather than to isolate particular mechanisms of mate choice. However, we also monitored courtship activity, as the relationship between courtship and mating success may suggest whether male behavior (initiation of courtship) or female choice (differential mating success once courtship is initiated) is responsible for observed mating patterns.

Materials and methods

The study organism

Umbonia crassicornis ranges from Colombia to Mexico, with naturalized populations as far north as southern Florida (Mead 1962). Individuals use a variety of host plants, primarily in the Mimosaceae (McKamey and Deitz 1996). Females mate only once, and lay only a single clutch of eggs in their lifetime (Wood 1974). Females care for their eggs and nymphs by making feeding slits on the host plant and protecting them from predators until they reach adulthood (Wood 1976; Cocroft 1996). Multiple family

groups are often found on the same plant within 1 m of each other or on separate plants that are within 2–3 m of one another (Cocroft RB, unpublished data; Masters 1997; Wood and Dowell 1985). All of the 50–80 siblings in a family eclose to adulthood within 2–3 days of one another (Wood and Dowell 1985), then remain aggregated for 15–20 days before dispersing from their natal plant (Wood 1974). Males and females reach sexual maturity in about 10 and 20 days, respectively, after eclosing to adulthood. Males disperse earlier than females: approximately 25% of males and 50% of females remain in their aggregation by the time females reach sexual maturity (Wood and Dowell 1985). Average dispersal distances for males and females are 6 and 3 m, respectively (Wood and Dowell 1985). Older post-dispersal males are often found at aggregations of younger individuals during the period when females reach sexual maturity (Wood and Dowell 1985). The lifespan of adults in the field is unknown, but in our greenhouse population, adult males and females live to a maximum age of about 60 and 100 days, respectively (PA De Luca, unpublished data). In order for father–daughter matings to occur, a male would have to live to about 85 days, which is well beyond the maximum age recorded for males, even under greenhouse conditions. Thus, father–daughter matings do not occur.

Pair formation is facilitated by substrate-borne vibrational signals produced by males, and female reply calls elicit searching behavior by males (Cocroft and McNett 2006). Once a female is located, courtship occurs when a male climbs onto one side of the female's body (Wood 1974) and emits a series of vibrational signals while attempting genital contact (PA De Luca, unpublished data). A female will often reject a courting male by shaking him off and walking away. Mating follows courtship only when a female raises the distal end of her abdomen to expose her genitalia. Female cooperation during all stages of the mating sequence (i.e., mate attraction, courtship, and mating) is, thus, necessary for a male to achieve a copulation.

Insect maintenance

The individuals used in this experiment were third–fifth-generation greenhouse-reared descendents of insects collected in Miami and Key Largo, FL, in 2003 and 2004. Individuals were collected from the field as late-instar nymphs or teneral adults that were still aggregated in their family group. A total of 19 different families (each family comprising ~50–80 individuals) was collected over both years. Families were kept in a greenhouse at the University of Missouri and maintained on their own potted *Albizia julibrissin* (Mimosaceae) host plant isolated within a screen cage. When a family eclosed to adulthood, the sexes were separated after about 10 days and placed on their own host plants. The colony was maintained through selective mating

of unrelated individuals from different families every generation (~3–4 months).

Study design

We conducted the experiment within a greenhouse at the University of Missouri. We used two cages, each measuring 183×122×76 cm (L × W × H). Within each cage, we placed five potted *A. julibrissin* plants (approximate height, 70 cm). Three groups of adults were placed into each cage, with each group set on its own *A. julibrissin* plant. The three plants containing insects were placed in the middle of the cage, set at a distance of 50 cm from one another in a triangle. The proximity of the three groups of insects relative to one other falls within the range of interfamily distances measured in the field for *U. crassicornis* (RB Cocroft, unpublished data; Wood and Dowell 1985). The two unoccupied plants were provided as additional dispersal locations and were situated to the left and right of the three central plants at a distance of 50 cm. Greenhouse temperatures ranged between 25 and 30°C, and the photoperiod was set to a 13:11 light/dark cycle.

Each group of insects within a cage was drawn from a separate family (3 groups=3 different families in a cage). Two family groups were similar in age, with each composed of 10 male and 10 female siblings between 5 and 7 days old posteclosion. These individuals were randomly selected from their respective larger family group and reaggregated on their own *A. julibrissin* plant within the cage. Teneral adult *U. crassicornis* from the same family group under 10 days old can be reaggregated onto a different host plant without affecting their behavior (Wood 1974). The third family group was composed of only 10 sibling males, which were randomly drawn from a family that was 15–17 days old posteclosion. These males were mate-searching older males that had already dispersed, and thus, their sisters were not included with them. Females in each cage thus had free choice of three groups of potential mates in an equal ratio: 10 siblings, 10 same-age nonsiblings, and 10 older nonsiblings. Our experimental unit for statistical analyses was a group of three families within a single cage.

This experiment was replicated over three time periods in 2004 (July, September, and November), which provided a total of six experimental units. For each new study period, individuals were drawn from new sets of families and placed in each of the two cages as described above on a new set of potted *A. julibrissin* host plants. Cages were washed with a mild detergent soap between replicates to eliminate any potential chemical cues left by the previous groups of insects.

Individuals were uniquely marked with a 3-mm^2 numbered tag glued to the left side of the pronotum. Each study period commenced on the day both cages were stocked with insects. Hourly observations were conducted daily from 08:00 to 18:00. We ended a study period once all the females in both

cages mated. Study periods lasted 12 (July), 15 (September), and 17 (November) days. During observations, we recorded the date, plant location, and individual identities of insects engaging in courtship and mating behavior.

Quantifying male courtship behavior and female mating patterns

To compare the number of courtships exhibited by the three different groups of males (siblings, same-age nonsiblings, and older nonsiblings), we included in our analysis only those courtships that were observed occurring from the day the first female in each cage mated. This standardized our comparisons of the different groups of males in each cage relative to the onset of female mating. This was done because, in natural populations, mate-searching older males arrive at aggregations and begin courting females several days earlier than sibling males. Thus, our analysis focused on relative differences during the period of female sexual receptivity. A courtship event was scored when a male was observed positioned on the side of a female. In some cases, females were courted by two males simultaneously. When this occurred, each male was scored as having performed a courtship event. After mating, females were allowed to remain in their cage so as not to disturb the natural behavior of the insects during the course of the study periods.

Statistical analyses

We used G tests to evaluate differences between the observed and expected proportions of females courted by, and mating with, (1) sibling vs nonsibling males and (2) younger vs older males. For each comparison, we first assessed whether the responses of females were homogeneous across runs and cages using replicated G tests (Zar 1984).

   To evaluate the proportions of females courted by, and mating with, siblings vs nonsiblings, we compared the observed data to the expected sibling: nonsibling ratio of 1:2 (i.e., 10 sibling/20 nonsibling males available for each female in a cage). To evaluate the proportions of females courted by, and mating with, older vs younger males we compared the observed data to the expected older/younger male ratio of 1:2 (i.e., 10 older/20 younger males available for each female in a cage). For all analyses, descriptive statistics are reported as the mean ± SE ($N=6$ experimental units).

Results

Courtship behavior

Older males moved from their plant and began courting females from both younger family groups on their respective plants on the first day of observations during all three study periods. Both groups of younger males started to disperse and court females 4.7±0.4 days later ($N=6$ experimental units). A total of 328 courtships were observed when we included only those that occurred from the day the first female in each cage mated. Older males performed 44±3.6% of the courtships, while sibling and same-age nonsibling males performed 24±2.2% and 32±3.2% of the courtships, respectively. Females began mating about 8 days after the start of observations (see "Female mating patterns" section below); thus, despite the difference in the onset of courtship behavior between older and younger males, females in each cage experienced courtship from all three groups of males for about 4 days prior to the onset of their sexual receptivity.

   The courtship data were homogeneous across experimental units, and thus, we used the pooled data: (1) sibling vs nonsibling males, heterogeneity $G=6.21$, $p=0.29$, df=5; (2) younger vs older males, heterogeneity $G=7.42$, $p=0.19$, df= 5. Nonsibling males performed significantly more courtships than expected (pooled $G=9.96$, $p=0.002$, df=1, Fig. 1a), and older males performed significantly more courtships than expected (pooled $G=20.76$, $p<0.0001$, df=1, Fig. 1b).

Female mating patterns

Females began mating 8.1±0.8 days after the start of observations. A total of 106 matings were observed. Older males obtained 44±4.5% of the matings, while younger sibling and nonsibling males obtained 28±6.5% and 28± 3.7% of the matings, respectively. Of the 14 females with no mating record, nine died before having mated. The other five females were observed sitting on a clutch of eggs at the start of a new observation day and so were inferred to have mated. Our observation regime was thus successful in capturing 95% (106/ 111) of the matings. Average age at mating for females was 21.6±0.3 days ($N=106$). Average age at mating for younger (siblings + same-age nonsiblings) and older males was 21.7± 0.2 ($N=41$) and 29.8±0.5 days ($N=30$), respectively.

   The mating data were homogeneous across experimental units, and thus, we used the pooled data: (1) sibling vs nonsibling males, heterogeneity $G=1.61$, $p=0.89$, df=5; (2) younger vs older males, heterogeneity $G=0.788$, $p=0.98$, df= 5. There was no significant difference between the observed and expected proportions of females that mated with siblings vs nonsiblings ($G=1.57$, $p=0.21$, df=1, Fig. 2a). However, females mated significantly more with older males than expected ($G=4.96$, $p=0.02$, df=1, Fig. 2b).

Discussion

Females of species like *U. crassicornis* that suffer from inbreeding depression have traditionally been expected to
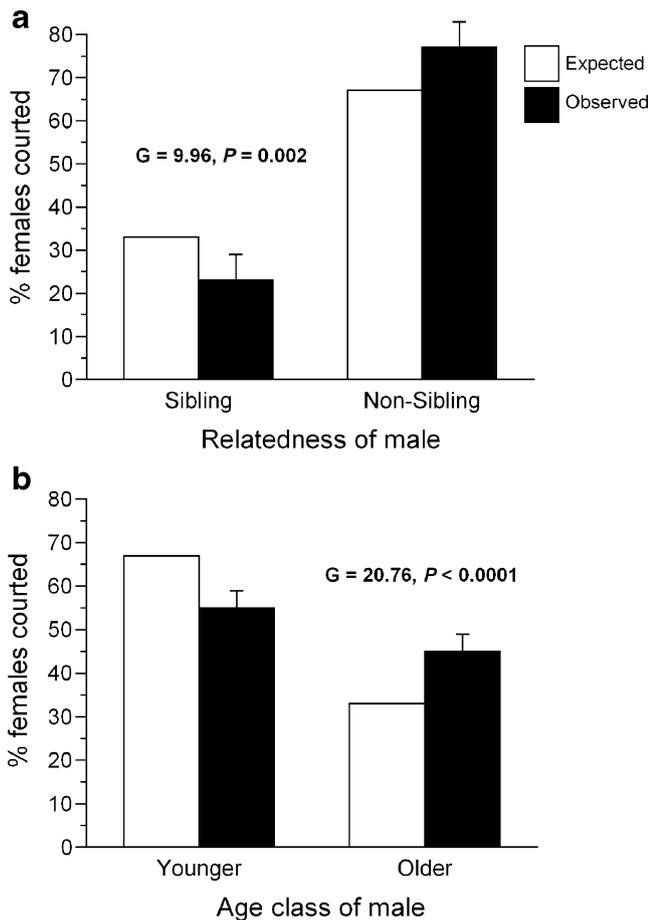
Fig. 1 Expected and observed proportions of females courted by **a** siblings vs nonsiblings and **b** younger vs older males. Observed proportions are provided as the mean ± SE (*N*=6 experimental units)

evolve behavioral mechanisms to reduce inbreeding (Thornhill 1993; Pusey and Wolf 1996). In our study, offering females different choices of males using an approach that recreated their natural social environment enabled us to simultaneously evaluate the kin discrimination and age-based mating hypotheses. The only indication of kin discrimination was the finding that females were courted significantly more by nonsiblings than by siblings. It is unclear whether this difference occurred because males were less likely to initiate courtship with sisters or because females terminated courtship by brothers. However, the difference in courtship rates did not translate into a significant difference in mating rates, which suggests that females do not discriminate kin from nonkin.

The lack of inbreeding avoidance is consistent with the prediction of Parker (1979), and more recently by Kokko and Ots (2006), that females should tolerate moderate levels of inbreeding when choosing mates. Kokko and Ots (2006) showed that, under some social conditions and parental investment patterns, selection could favor incestuous matings even if inbreeding depression values reach as high

as 60%. Such high levels of inbreeding depression should be accepted by females because it increases the reproductive success of their brothers. Interestingly, their simulation for a semelparous species where females encounter sibling and nonsibling males simultaneously and at high rates (as occurs in *U. crassicornis*) predicted that females would tolerate an inbreeding level of about 30%, which is similar to the value of inbreeding depression reported for *U. crassicornis* by Masters (1997). Another prediction of the Kokko and Ots (2006) model, that males should have higher inbreeding tolerance than females, remains unclear. Fewer courtships were observed occurring between siblings compared to nonsiblings, which might suggest that males avoided courting their sisters. However, our observation protocol did not enable us to determine which sex was responsible for initiating courtship encounters. Thus, it remains possible that males may have initiated courtship with their sisters, in support of the prediction, but that females quickly rejected their brothers before the encounter was observed.
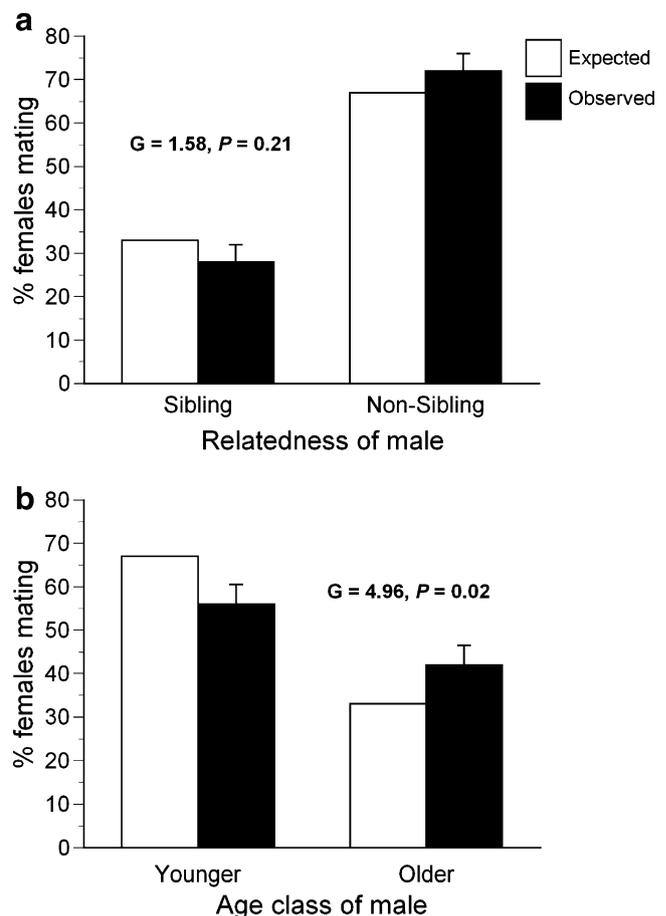

Fig. 2 Expected and observed proportions of females mating with **a** siblings vs nonsiblings and **b** younger vs older males. Observed proportions are provided as the mean ± SE (*N*=6 experimental units)

What fitness benefits might *U. crassicornis* females derive from mating with older males? Many empirical studies have documented increased reproductive fitness from mating with older (or middle-aged) males. These advantages include both direct benefits (Zuk 1988; Cote and Hunte 1993; Mountjoy and Lemon 1996; Hasselquist 1998; Jones and Elgar 2004; Srivastava and Omkar 2004) and indirect benefits (Woodhead 1986; Conner 1989; Jones et al. 2000; Dickinson 2001). Determining if male age per se in *U. crassicornis* affects female reproductive fitness requires an experiment in which females are mated to unrelated males of varying ages and their reproductive success compared. The use of field-caught males (i.e., males of varying ages exposed to selection under natural conditions) in such an experiment would provide an interesting test of whether mating with older males confers fitness advantages to females in this species.

Two proximate factors may explain the mating advantage of older male *U. crassicornis*. First, older males are predicted to have increased levels of sexual advertisement (Kokko 1997; Proulx et al. 2002), and an older male courtship advantage has been observed in a range of species (Clutton-Brock and Albon 1979; Woodhead 1986; Le Boeuf and Reiter 1988; Marden and Wagge 1990; Otronen 1995; Plaistow and Tsubaki 2000; Kemp 2002; Felton et al. 2006). A field study of *U. crassicornis* in Florida found that older males performed significantly more courtships than younger males (Wood and Dowell 1985), and there was a similar result in our experiment. If female mate selection mechanisms in *U. crassicornis* favor males with high courtship rates, as appears to be the case, then older males would have an advantage over younger rivals.

Older males could also have benefited from sexual imprinting, whereby sexually immature females learn the cues of specific males in a population and then mate preferentially with them when they reach sexual maturity (Kendrick et al. 1998; Slagsvold et al. 2002; Hebets 2003). Recall that older *U. crassicornis* males are typically found courting unreceptive females at their natal aggregation for several days prior to the onset of female mating (Wood and Dowell 1985). In our study, females were still sexually immature during the period when only older males were courting; they might have imprinted upon older male courtship behavior and subsequently preferred them as mating partners. Sexual imprinting has recently been demonstrated in an invertebrate (Hebets 2003), but additional studies are required to determine whether sexual imprinting can explain the older male mating advantage in *U. crassicornis*.

Although there was a significant mating advantage for older males, age per se did not explain all of the variation in mating success. Females typically use multiple cues in mate choice (Candolin 2003; Hebets and Papaj 2005), and it is likely that variation in other male traits influences attractiveness independently of age. Additional studies with *U. crassicornis* are under way to determine other factors (e.g., mate-advertisement signals, courtship duration, and mate-searching behavior) that may contribute to a male's mating success. Also, females in this study were often courted simultaneously by two or more males, a situation that occurs commonly in natural populations (Wood 1974; Wood and Dowell 1985). Although we did not assess the extent of male competition in this study, the presence of several males competing simultaneously can affect a female's ability to effectively evaluate alternative male options (Jennions and Petrie 1997; Bateson and Healy 2005; Wong and Candolin 2005; Uetz and Norton 2007).

In conclusion, the social environment of *U. crassicornis* exposes females to inbreeding risk with their same-age brothers. The lack of kin discrimination during mate choice is consistent with the idea that inbreeding tolerance, rather than avoidance, may be occurring in this species. If this is true, then the increased mating success of older males is not the result of inbreeding avoidance, as suggested by Wood and Dowell (1985) and Masters (1997), but possibly from other factors such as higher levels of courtship activity, sexual imprinting, or male competition. Studies are under-way to identify the proximate mechanisms underlying the older-male mating advantage, as well as to assess the extent to which age-dependent variation in different aspects of male mate searching behavior affects mating success.

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