An Invasion of Cheats:
The Evolution of Worthless Nuptial Gifts

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Summary

Nuptial gifts are food items or inedible tokens that are transferred to females during courtship or copulation [1–3]. Tokens are of no direct value to females, and it is unknown why females require such worthless gifts as a precondition of mating. One hypothesis is that token giving arose in species that gave nutritious gifts and males exploited female preferences for nutritional gifts by substituting more easily obtainable but worthless items [4]. An invasion of such behavior would require that females accept the substitute gift and copulate for a period of time similar to that with genuine gifts. We show that both these prerequisites are met in the dance fly *Rhamphomyia sulcata*, in which females normally accept a nutritious gift. We removed the gift from copulating pairs and replaced it with either a large or small prey item or inedible token. We found that although pairs copulated longest with a large genuine gift, the tokens resulted in copula durations equivalent to those with a small genuine gift. We also observed that males that returned to the lek with tokens re-paired successfully. These findings suggest that female behavior in genuine gift-giving species is susceptible to the invasion of male cheating on reproductive investment.

Results and Discussion

Nuptial feeding occurs in a diverse array of taxa [1, 2, 5] and may serve to attract mates, help to protect the ejaculate, [4, 6] or act as parental investment [7, 8]. In the empidid dance flies, there is an enormous diversity of nuptial gifts, which include nutritious prey items, dried insect fragments, and inedible tokens such as a fragment of leaf or twig, a seed tuft, or a silk balloon [9–11]. Some species are polymorphic in gift giving, and males give both prey items and inedible tokens [1, 9]. The diversity of mating plans in the empidids is considered a textbook example of an evolutionary progression toward ritualized courtship acts [11–13]. The proposed evolutionary sequence sees a decline in male investment in mating effort from a prey item, to a silk-wrapped dried insect fragment, to a silk balloon [11, 13]. The development of sexual conflict theory [14–17] suggests a simpler model, such as that proposed by Sakaluk [4], in which all types of inedible gifts are a consequence of males reducing their reproductive investment from

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costly gifts to less valuable items. Both models, however, are dependent upon the successful invasion of male cheating. Nuptial gift size is a large determinant of copula duration in many species [1, 18], including empidids [19]. If males switch to providing worthless gifts, the invasion of this behavior is dependent upon females accepting the worthless gift and copulating long enough for sperm transfer. Females have been shown to terminate copulations when gifts are distasteful or provide inadequate resources [18], suggesting that inedible tokens should be rapidly rejected. Female crickets [4] and spiders [20], however, have been shown to accept foreign nuptial gifts.

We conducted a gift manipulation experiment to address whether cheating could invade in a species in which males provide valuable nuptial gifts. We utilized the dance fly *R. sulcata*, in which all males provide a prey item as a nuptial gift, and pairs mate on the vegetation where the female eats the gift (Figure 1A). We removed mating pairs' gifts, replaced them with either a large or small genuine gift or a large or small worthless gift (cotton ball), and timed the duration of the copulation. We chose to use cotton as the inedible token because it is very similar to the lightweight and bright wind-blown seed tufts of token-giving empidids [9]. The copula duration in pairs that were given a large genuine gift was significantly longer than that of pairs that were given the other types of gift (Figure 2). It is important to decouple the influence of the nuptial gift on copula duration from the influence of the male that produced, caught, or collected the gift. In *R. sulcata*, large males carry large gifts [21], and it may be expected that in many species male morphology and quality covary with gift quality or size. By manipulating gift size, we have disentangled the influence of the gift on copula duration from any other variable that may have been correlated with gift size. This methodology powerfully establishes the role of the nuptial gift in increasing copula duration.

Our experiment showed that worthless tokens were of equivalent value to males in terms of copula duration as small genuine gifts. Pairs that were given the worthless gifts copulated for the same time period as those given a small genuine gift (Figure 2). The copula duration for pairs with large tokens (mean = 104.3 ± 12.33 s) was also well within the range of natural copulations (mean = 159.19 ± 13.3 s; within 25%–50% quartile, 93–152 s). Presumably, these shorter natural copulations result in adequate sperm transfer for some fertilization success because selection will act strongly against males that feed females for no reproductive return. If these shorter copulations resulted in no sperm transfer, then males with tokens would be unsuccessful at invading the population. It seems highly improbable, however, that males would bear the cost of capturing even a small prey item and lekking with this nuptial gift if they were to obtain no fertilization success from this behavior.

The ability of males bearing inedible tokens to exploit female sensory biases was also evident in our experiment. We observed occasionally that when the manipu-
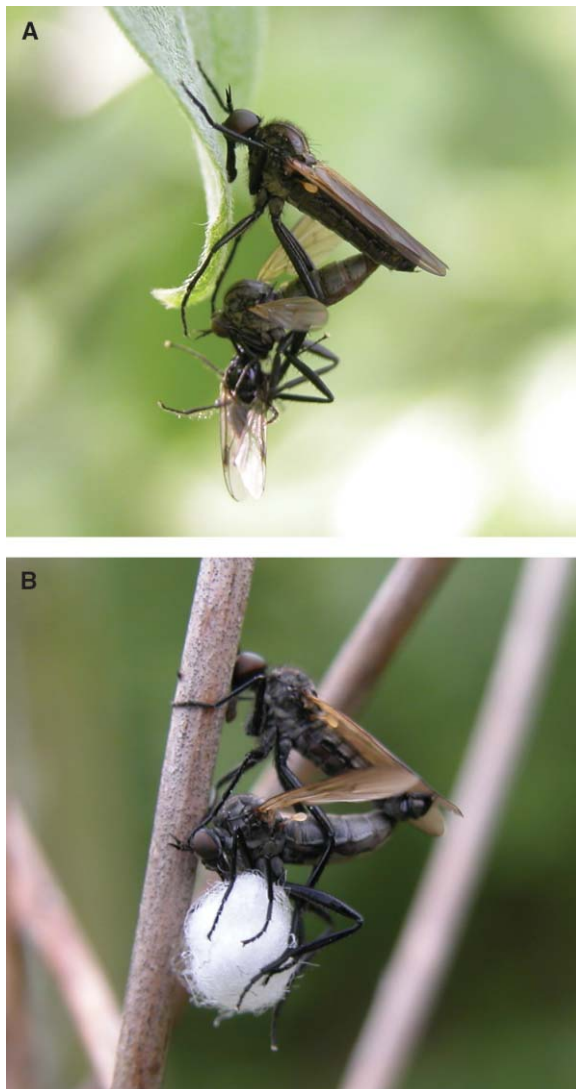
Figure 1. Pairs of *R. sulcata* Copulating on the Vegetation

(A) The female is feeding on a prey item provided by the male.
(B) The female is holding a large token (cotton ball) that was switched with the pair's original nuptial gift.

Figure 2. The Relationship between Gift Treatment and Copula Duration ($\pm$ the Standard Error) in *R. sulcata*

Copula duration is the estimated marginal means from a GLM (gift type $F_{3,24.8} = 3.28$, p = 0.038; date $F_{6,17.8} = 4.10$, p = 0.009; gift type*date $F_{17,69} = 1.86$, p = 0.038). There is a significant difference in the copula duration for large gifts compared with all other gift types (small genuine, p = 0.04; large token, p = 0.01; small token, p = 0.001). The small nuptial gift did not increase copulation time when compared with either of the tokens (large token, p = 0.99; small token, p = 0.75). There was no difference in copulation time between pairs with large or small tokens (p = 0.92). Significance values are adjusted with the Sidak method for multiple comparisons.

lated pairs terminated copulation, the male flew off with the token, reentered the lek and re-paired. For the manipulation with the large token, we observed this behavior twice on 2 different days. One of these males re-paired three times within 20 min with the cotton ball to attract females. The second male re-paired twice, the second time within 5 s of entering the lek. The size and brightness of the white ball may have made a clear signal to the female empidids that the male was carrying a gift. The average copulation time for these natural pairings with large tokens was 106.3 $\pm$ 45.15 s. There were similar occurrences with the small token for two males on 2 different days. Both of these males reentered the lek, and each returned once having re-paired; one of these copulations was 27 s (only one copulation could be timed). These observations indicate that female preferences for gifts are broad and include items as incongru-
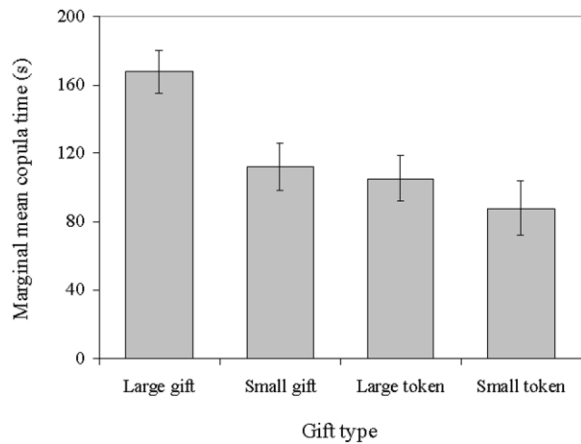
ous as a white cotton ball. The cotton fibers that we used as tokens have a similar appearance to the fibers of other seed tufts, and our results suggest that males who utilized seed tufts could attract females with such a gift. The evolution in empidids of silk balloons [22] and swollen projections on the forelegs [23], which give the appearance of a carried gift, suggest a considerable selection pressure on males to reduce an apparently costly investment in nuptial feeding. The prevalence of female ornamentation within this taxon, an occurrence that is rare across the rest of the animal kingdom, also suggests that gifts are of a high resource benefit to females and are, hence, a costly resource for males [10, 24, 25].

The extent to which worthless gift-giving behavior may invade would depend on how much cheaper tokens were to collect and carry and, hence, on the fitness benefits of more frequent, short copulations with tokens versus fewer, longer copulations with large genuine gifts. Inedible tokens such as wind-blown seed tufts are likely to be more readily available and less costly to collect than insect prey. Sexual selection in *R. sulcata* currently acts to decrease gift size, presumably because males are more maneuverable and flight efficient in the lek with a small gift [21]. Lightweight but large and, thus, presumably highly visible worthless gifts may allow males to provide a gift that is a large visual target to females while minimizing carrying costs.

During copulation, females appeared to be trying to feed from the inedible tokens because they turned the cotton balls over in their legs and probed them with their proboscis in a similar manner to females eating a genuine nuptial gift. This behavior with inedible tokens has also been observed in species that accept inedible

gifts [9, 11]. These observations suggest that in species where females accept inedible tokens, the males may have previously given nutritious nuptial gifts. We predicted that females would continue trying to obtain nutrition for longer from large tokens. There was, however, no difference in the copula duration of pairs with large compared to small tokens (Figure 2). These findings suggest there is a set 1–2 min time period after which females give up trying to obtain any nutrition from the gift, regardless of its size.

The dried and silk-wrapped insect fragments used in some species are more likely to be independent solutions to reducing male reproductive investment rather than intermediate behaviors in a progression toward silk balloons or other tokens. The occurrence in some empidid species of a polymorphism in gift giving, in which males give both prey items and tokens, may be the consequence of an incomplete worthless gift-giving invasion in which males with genuine gifts had sufficiently high fitness to persist in the population [9, 26]. Given the wider prevalence of prey item gift giving and the generality of predatory behavior for self-feeding, it would indeed seem most parsimonious that token giving has evolved from species that presented genuine gifts. We have shown here that males that provide worthless nuptial gifts could potentially invade a species that gives genuine gifts. Worthless-gift giving may have evolved through sensory exploitation of female preferences for edible nuptial gifts.

Experimental Procedures

Gift Manipulation Experiment
This study was conducted in May, 2004 on farmland in eastern Fife, Scotland, the United Kingdom. *R. sulcata* lek in small swarms between 2 and 10 m above the ground and alongside stands of vegetation. Pairs form in the lek and descend to mate on the surrounding vegetation. We have observed that either of the sexes can terminate copulation, and at termination, the gift is either dropped or is carried off by the male. If the female terminates copulation, she beats her wings and disentangles herself from the male. If the male terminates copulation, he releases his hold of the vegetation and lets the pair drop and split up. To obtain pairs for our manipulations, we observed pairing in the lek and followed the pairs to where they landed on the vegetation. We only used pairs that we had observed descending from the lek; in this way, we were confident of only using pairs that had just commenced copulation. Immediately after the pairs landed, one of us (N.R.L.) caught hold of the gift that the female was feeding on and slowly pulled the gift from the female's legs while simultaneously replacing it with one of the substitute gifts. The real gift was removed by pulling on the wing or leg of the gift with fine forceps. At all times, the female had hold of at least one of the gifts. If a female did not have hold of a gift, she immediately terminated copulation. Timing of the copulation began as soon as the female had accepted the substitute gift and ended when the pair split up.

The substitute gifts were assigned to the pairs in order; each type of gift manipulation was done on each of the trial days (except for the small tokens, which were not used on the first day). There were 7 trial days. Approximately one in five manipulations was successful. Manipulation failures were due to the researcher's catching hold of the empidid's leg instead of that of the prey item; this caused the female to terminate copulation immediately. The numbers of failures caused by pairs rejecting the substitute gift were negligible. If the prey item was successfully caught hold of, then virtually all pairs stayed paired with the switched gift. We appreciate that this random sample of pairs may be biased toward females that were more tolerant of disturbance, but because all females were manipulated,

this should not bias our findings. The average time taken for the manipulation, from the time the pair first landed until completion of the gift switch, was 22.96 ± 1.85 s (n = 26). The rate-limiting step in the manipulations was catching hold of the prey item; the time taken to present the substitute gift was equivalent across gifts and was very brief (2–3 s). In order to establish how long pairs would copulate without a nuptial gift, we removed gifts from pairs and did not substitute another gift. In all 20 attempts, the pair split before the researcher performing the manipulation could start the stopwatch. Pairs were never observed mating without a gift (n = 276) [21].

Pairs were given one of four types of substitute gifts: a large prey item (n = 27), a small prey item (n = 27), a large token (n = 23), or a small token (n = 19). We chose our experimental prey items on the basis of genuine nuptial gifts we observed males carrying in a previous study (n = 521) [21]. The largest prey item that was observed in natural pairs in 2001 was a female *R. sulcata* (prey area = 11.97 mm^2); hence, the large prey item that we used was also a female *R. sulcata* (mean area = 8.94 ± 0.52 mm^2). The head, wings, and legs of the female *R. sulcata* were removed to leave only the abdomen and thorax in order to maximize the food content of the maximum-sized gift that all the pairs could handle. The smallest prey item observed in 2001 had an area of 0.45 mm^2. To obtain a similarly sized gift, we used one-third of the cuticle of the abdomen of a male *R. sulcata* (mean area = 0.63 mm^2). Only the cuticle of the male abdomen was used, in order to minimize the amount of food within the gift and also to keep the gift as small as possible while maintaining a gift that could be handled by the experimenter. Both tokens were small hand-rolled balls of cotton wool (Figure 1B). The size of the largest token (mean area = 10.98 ± 0.47 mm^2) was of a similar size to the large genuine gifts. The smallest token (mean area = 1.23 ± 0.47 mm^2) was approximately the same size as the smallest genuine gifts. The suitability of the manipulated gifts as substitutes for nuptial gifts was borne out in that at the end of the copulations, on nine occasions for three of the different types of gift categories, the male flew off to the lek with the substituted gift and re-paired. The gift type for which we did not see males re-pair was the small genuine gift, but this gift type is also the most difficult to see.

We also collected data on natural copula durations for a complementary study. Timing for these copulations began from the time the pair first landed on the vegetation. In order to compare these natural copulation times with those of our manipulations, we took the average time of our manipulations (22.96 s) away from the natural copula duration.

Statistical Analysis
Data were analyzed with a general linear model (GLM). The gift manipulations were entered as a fixed factor, the date of manipulation as a random factor, and copula duration as the dependent variable. Date was included in the model because copula duration varied over the season. There was a significant interaction between date and gift type. The interaction showed that the magnitude of the difference between the treatments was not consistent across days. It may be that daily climatic variation alters the relative benefits of each of the different gift types or that variation in wind strength, for example, influences the ease with which the empidids can handle the large gifts. The main finding, however, of longer copulations with large gifts was consistent across days. We ranked the gift types in order of average copula duration for each day. The large genuine-gift treatment had the longest copulations for 5 out of the 7 days, and the second longest on the other 2 days. Ranks were randomly distributed for the three other gift types, indicating no difference between the copula durations for these treatments. Copula duration was square root transformed to meet the GLM assumptions of normality and homogenous variance. For clarity, the marginal means of untransformed values were used in Figure 2. The significance of the treatments within the gift manipulations was adjusted with the Sidak method for multiple comparisons.

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