

ORIGINAL ARTICLE

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The evolution of empty nuptial gifts in a dance fly, *Empis snoddyi* (Diptera: Empididae): bigger isn't always better

Received: 29 December 1997 / Accepted after revision: 7 October 1998

Abstract Adaptive female choice is thought to have led to the evolution of nutritionally valuable nuptial gifts in many insect species. However, in several dance fly species, males offer and females accept “empty gifts” with no nutritional value. In the species studied here, *Empis snoddyi* Steyskal, males produce empty balloons comprised of hundreds of silk bubbles and form mating swarms that females approach to investigate males. Males within the swarm engage in agonistic interactions. The empty balloon has been hypothesized to be an indicator of male condition such that males with larger balloons are predicted to have higher mating success and be more successful in male-male interactions than males with smaller balloons. We examined the role of male body size and balloon size in the context of intersexual and intrasexual selection. We found that neither male body size nor balloon size affected the outcome of pairwise male-male interactions. Using multiple-regression techniques, we found significant linear selection for increasing male body size and decreasing balloon size associated with mating success, a surprising result given a positive relationship between male body size and balloon size. A visualization of selection showed the highest peak of male mating success for larger males with intermediate-size balloons. These results can be explained by a trade-off between long-range attraction of females using large balloons and close-range attraction of

females via improved flying efficiency associated with smaller balloons. Both male body size and balloon size are important components in determining male mating success; however, the empty balloon does not appear to play a typical role as a sexually selected ornament.

Key words Sexual selection · Mating behavior · Balloon flies · Selection analyses · *Empis snoddyi* · Nuptial gifts

Introduction

Males of many species perform a courtship feeding ritual involving the presentation of nuptial gifts to potentially receptive females (Thornhill and Alcock 1983; Zeh and Smith 1985). A nuptial gift often confers a nutritional benefit that represents a male's contribution to the female in addition to his sperm (Thornhill and Alcock 1983; Andersson 1994). In insects, nuptial gifts can be prey items (food items that provide nutrients to the female; e.g., Kessel 1955; Downes 1970; Thornhill 1976), seminal gifts (nutrients passed to the female with the male's sperm; e.g., Boggs and Gilbert 1979; Gwynne 1983), somatic gifts (specialized male organs eaten by the female during copulation; e.g., Dodson et al. 1983), or suicidal food transfer (the female consumes all or part of the male during copulation; e.g., Elgar 1992).

In some insect species, males offer and females accept items with no nutritional value, i.e., “empty” nuptial gifts. Empty nuptial gifts often play a similar role as nutritive nuptial gifts in the courtship rituals (Will and Sakaluk 1994 and references therein); however, it is not clear why empty nuptial gifts have evolved. Few studies have addressed the paradoxical phenomenon of truly empty nuptial gifts that play a crucial role in courtship displays but are not consumed by the female.

The Dipteran subfamily Empidinae (dance flies or balloon flies) provides a unique opportunity to investigate the selection mechanisms that may have led to empty nuptial gifts. Although most species of empidines

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provide nuptial gifts, the gifts range from intact prey to partially eaten and wrapped prey to empty balloons (Kessel 1955; Downes 1970; Cumming 1994). Nuptial balloons of species in the empidine family range from small balloons containing large prey items (e.g., *Empis aerobatica*, *E. bullifera*, *Hilara wheeleri*), to balloons stuck to inedible dried prey items (e.g., *E. geneatis*), to completely empty balloons made of silk or saliva (e.g., *H. sartor*, *H. granditarsis*, undescribed *Hilara* spp.; reviewed in Kessel 1955; Cumming 1994).

The empty balloon in the empidine mating system has been hypothesized to be an artifact from the nutritious nuptial gifts presented in ancestral empidine species. Empty balloons are thus seen as a ritualized behavior that has evolved from a food source to simply a sign stimulus in the empidine courtship (Kessel 1955; Downes 1969; Downes and Smith 1969). More recently, the empty balloon, like body size (reviewed in Andersson 1994), has been hypothesized to be an indicator of male fitness (Thornhill and Alcock 1983; Cumming 1994). Thornhill and Alcock (1983) hypothesize that the balloon indicates the male's physiological condition: it advertises the quality of the male by indicating his ability to obtain food resources. Both of these hypotheses suggest that females should prefer larger males or males with larger balloons.

Here we report the first study of the mating system and sexual selection in *E. snoddyi* (Steyskal 1969), a North American empidine. Similar to other species where males produce empty nuptial gifts, males of this dance fly produce balloons comprised of hundreds of individual bubbles (Cumming 1994). Interactions between males and between males and females, as described below, suggest that sexual selection should be important in this species. Our goal was to determine if male balloon characteristics as well as male morphological characteristics were important factors in intrasexual and/or intersexual selection in the *E. snoddyi* mating system. We focused on two male characteristics of *E. snoddyi*: (1) male body size; measured as wing and femur length, and (2) male balloon size, quantified as balloon volume.

Methods

Our research was conducted in the Great Smoky Mountains National Park (N.C. and Tenn.) from 29 May to 7 July 1996. Our study focused on approximately ten swarms that were part of a population of *E. snoddyi* located at Indian Gap (1646 m elevation) along the Appalachian Trail. J.A. Sadowski made all field measures.

Individuals were collected with an insect net each morning; flies and balloons were rarely damaged during the collection process. Each fly was placed into an Eppendorf tube and put on ice for approximately 2 min to allow handling. Four morphological characters of both males and females were measured using digital calipers: right wing length, left wing length, right hind femur length, and left hind femur length. Balloon length and width were measured using digital calipers. Balloons are oblong so volume was quantified as the volume of a cylinder ($\pi r^2 h$) from length and width measures made on each balloon. After measurement, each fly was marked with a unique combination of paint dots by placing three

dots on the dorsal surface of the thorax with a toothpick. Model paint was used as it dried quickly, was permanent, and had no apparent toxic effects on the flies which were sometimes recaptured on subsequent days (see below). The fly was held for 2 min to ensure that the paint was fully dry and was then released.

Repeatability of morphological and balloon measures was estimated to determine the reliability of multiple measures performed on the same individual. Repeatabilities were calculated using variance components from a one-way analysis of variance (ANOVA; Sokal and Rohlf 1981; Lessells and Boag 1987). Repeatability of morphological measures was calculated based on three measurements per individual ($n = 30$ individuals). To calculate repeatability of balloon measures, the length and width of every balloon was measured twice on 370 males. Male morphological measures and balloon volume measures were highly repeatable (wing length: $r = 92\%$, femur length: $r = 79\%$, balloon volume: $r = 99\%$). To determine if assortative mating of males and females had occurred, we examined correlations between female body size (wing length and femur length), male body size (wing and femur length), and male balloon size (balloon volume).

Male-male interactions

To examine male characteristics in the context of intrasexual selection, we compared males engaged in pairwise male-male interactions. Male-male interactions, which are described in detail below, involve males chasing each other out of the swarm. In many interactions, there are clear dominant and subordinate relationships between pairs of males. We deem dominant males as those males who chase subordinate males out of the swarm for a distance of 3 m or greater. Only interactions in which there were no reversals in dominant and subordinate status of the two males were used in our analyses.

To examine whether male body size or male balloon size influences the outcome of pairwise male-male contests, we collected 87 pairs of males involved in pairwise interactions in the mating swarms. After a pair of males interacted, each male was captured in a separate net, then balloon size and body size measures for both males were recorded. The differences in male body size and balloon size between dominant and subordinate males were analyzed using a pairwise *t*-test. The dominant and subordinate males collected were a random subset of the population (i.e., did not reflect extremes within the total population of males we collected from the swarm and measured). After measuring, males were marked and released back into the swarm.

Male-female interactions

To examine male characteristics in the context of intersexual selection we compared males who did and who did not obtain mates. Each morning both copulating and non-copulating males were randomly collected throughout the entire swarming period. We equate mating success with intersexual selection because surrounding males do not appear to interfere with male-female interactions. This definition of intersexual selection may potentially confound previous effects of male-male interactions (Halliday 1983) but the intersexual interactions nevertheless clearly represent a separate episode of selection. Therefore, we refer to the second episode of selection as intersexual selection to clearly differentiate it from selection that occurs as a result of male dominance interactions.

To examine whether male body size or balloon size influence male-female interactions, we collected 24 copulating pairs and measured male balloon size and morphological characters of males and females and compared them to males who did not obtain copulations. A multiple regression was performed to determine which factors influence male mating success (Brodie et al. 1995). We regressed relative male mating success on (1) male body size and (2) male balloon size. The first variable, right wing length, was used as a measure of male body size because it was the morphological measure with the highest repeatability. The second variable, residuals from the regression of balloon volume on relative hu-

midity, was used as a measure of balloon size because daily relative humidity was significantly correlated with balloon volume ($R = 0.17$, $P = 0.006$, $n = 245$). Using residuals provides a measure of balloon volume uncorrelated with humidity. Male mating success or male fitness was determined by the number of mates a male obtained (0, 1). These measures were then converted to relative mating success by dividing each male's mating success by the average number of mates the entire population of males obtained (see Brodie and Janzen 1996).

The partial regression coefficients from the multiple regression of male traits on relative fitness provided measures of linear selection gradients of male balloon size and male body size (see Brodie et al. 1995). Selection gradients measure the direct effects of selection acting on a trait independent of other measured traits. Selection differentials were calculated by quantifying the difference in trait means between males who obtained matings and all males in the population sampled. We also calculated the intensity of selection of each of these characters by dividing each selection differential by the standard deviation of the population of males (Brodie et al. 1995). Selection intensities (standardized selection differentials) measure both direct and indirect effects of selection acting on a trait. A full regression model that included both squared and cross-product terms was also performed to measure the effects of correlational selection or stabilizing selection (Brodie et al. 1995).

Principal components analysis (PCA) was performed to uncouple male body size and balloon size and create uncorrelated variables. We do not use PCA as it is normally used; i.e., as a data reduction method. Instead, we used PCA to form uncorrelated composite traits. Because PCA works best with multiple variables, two different variables related to body size (male wing length and male femur length) and one balloon size measure (male balloon volume) were used. A selection analysis was performed using the PCA factors in a multiple regression on male mating success. All analyses were performed using SYSTAT 7.0 (Systat 1996).

The selection surface was visualized using a distance-weighted least-squares smoother (Wilkinson et al. 1996). This method is a non-parametric regression technique that allows complex functions and shapes. Schluter (1988; Schluter and Nychka 1994) has suggested that such non-parametric visualizations permit more intuitive descriptions of selection (Brodie et al. 1995). We used the distance-weighted least-squares smoother for its ability to handle three-dimensional plots and its flexibility in producing potentially complex surfaces (Systat 1996).

Results

E. snoddyi mating system

Males formed lek-like swarms of 5–15 individuals near a landmark (i.e., tree stump, bush, rock) each morning at daybreak for approximately 3 h while holding their balloons with their mid and hind pairs of legs. Male-male competition is vigorous in *E. snoddyi* and interactions among males within the swarm were agonistic. Male-male interactions often involved physical contact. Males often flew after each other, switching back and forth; eventually, the “dominant” male chased the “subordinate” male out of the swarm. Males could also grab each other, or grab each other's balloon, in midair while holding balloons. In the most extreme cases, midair grappling resulted in males falling to the ground, dropping their balloons, and tussling on the ground. Female *E. snoddyi* investigated potential mates by individually visiting each male, circling around the male, and chasing him out of the swarm for some distance. After pairing, the male passed the balloon to the female,

which she then held during copulation. The balloons were never eaten. The balloon was dropped after copulation ended but was never retrieved by the female or the male. Females were never observed mating with males who were not holding balloons. In 2 years of observations (1995 and 1996), males were never observed with a second balloon after their first balloon was discarded after mating. Thus, males apparently mate, at most, only once per day. However, we have observed males mating on subsequent days.

Male and female *E. snoddyi* are sexually dimorphic; males had significantly longer wings and longer femora than females (wing length: $t = -8.308$, $df = 381$, $P < 0.001$, femur length: $t = -7.937$, $df = 386$, $P < 0.001$). Coefficients of variation of male and female *E. snoddyi* wing and femur length measures were low; however, male balloon volume showed substantial variation (Table 1). There were no significant correlations, using a Bonferroni correction to control for multiple comparisons, between female body and male body size for mating pairs (Table 2). Within copulating pairs of males and females, male balloon size was not significantly correlated with female body size (Table 2).

Male-male interactions

Dominant and subordinate *E. snoddyi* males captured from pairwise male-male interactions were analyzed to determine if the outcome of pairwise aggressive interactions was related to differences in male body size or balloon volume. There was no significant difference in femur length between dominant (mean = 3.064 ± 0.019 mm) and subordinate males (mean = 3.047 ± 0.019 mm; pairwise t -test: $t = 0.748$, $df = 86$,

Table 1 Means, variances, and coefficients of variance for wing and femur lengths for male and female *Empis snoddyi* and balloon volume for male *E. snoddyi*

Sex	Character	Sample size	Mean (mm)	Variance	CV
Females	Wing length	26	5.327	0.140	0.070
	Leg length	27	2.770	0.026	0.058
Males	Wing length	357	5.830	0.085	0.050
	Leg length	361	3.056	0.033	0.059
	Balloon volume	312	66.790	601.393	0.367

Table 2 Bonferroni-corrected probabilities for correlations between female body measures (wing and leg length), male body measures (wing and leg length) and male balloon size (balloon volume). Wing and leg length were significantly positively correlated within an individual in females ($R = 0.75$, $P = 0.001$) and in males ($R = 0.57$, $P = 0.035$)

	Male wing length	Male leg length	Male balloon size
Female wing length	0.114	-0.509	0.081
Female leg length	-0.050	-0.332	0.320

$P = 0.456$), in wing length between dominant (mean = 5.798 ± 0.035 mm) and subordinate males (mean = 5.840 ± 0.026 mm; $t = -1.312$, $df = 84$, $P = 0.193$), or in balloon volume between dominant (mean = 67.617 ± 2.855 mm³) and subordinate males (mean = 66.727 ± 2.786 mm³; $t = 0.502$, $df = 66$, $P = 0.617$).

Male-female interactions

E. snoddyi males that obtained copulations and unsuccessful males that did not obtain copulations were analyzed to determine if male body size or male balloon size were important criteria for male mating success. The wing length of mated males (mean = 5.886 ± 0.052) was slightly longer than in unmated males (mean = 5.826 ± 0.016 mm). Femur length of mated males (mean = 3.098 ± 0.029 mm) was also only slightly longer than in unmated males (mean = 3.053 ± 0.010 mm). Male balloon size was smaller for mated males (mean = 57.213 ± 4.643 mm³) compared to unmated males (mean = 67.624 ± 1.446 mm³) and this difference was significant ($t = 2.046$, $df = 310$, $P = 0.042$). Results from the multiple regression showed that male balloon size significantly affected male mating success and selection associated with mating appears to favor smaller balloons (Table 3). However, male body size (measured as wing length) and balloon size were significantly correlated ($R = 0.25$, $P < 0.001$). Selection was primarily directional. There were no significant non-linear selection gradients or correlational selection gradients.

PCA of the male traits resulted in two interpretable factors (Table 4). Factor 1 described an overall increase in body measures (wing and leg length) and balloon size measures (explaining 55% of the variance) and factor 2 described an increase in body size measures (wing and leg length) with a decrease in balloon size (explaining 28% of the variance). A selection analysis of the PCA factors by performing a multiple regression of the two factors on relative male mating success showed that only factor 2 had a significant effect on male mating success ($P = 0.012$) (see Table 4). The results from the PCA selection analyses suggest that there is significant linear selection acting on increasing male body and decreasing male balloon size.

The selection measures calculated from the multiple regression were visualized using a non-parametric distance-weighted least-squares method (Fig. 1). Male body size was measured as wing length and balloon size was measured as balloon volume. A high peak of relative male mating success appeared for larger males with intermediate size balloons. (Fig. 1). Males with body size and balloon size measures corresponding to the peak had the highest male mating success of males in the population. Males with body and balloon size measures corresponding to the sides of the peak had somewhat lower success than males located at the middle of the peak.

Table 3 Results from multiple regression of male *E. snoddyi* body size and balloon size on relative male mating success. Only male balloon size significantly affects male *E. snoddyi* mating success, however, there is a non-significant trend towards positive selection on male body size

Character	P-value	Standardized selection gradient	Selection differential	Standardized selection intensity
Body size	0.132	0.450	0.056	0.192
Balloon size	0.022	-0.510	-9.998	-0.406

Table 4 PCA of body size and balloon size measurements based on 237 males. Selection gradients determined by regression of individual factor loadings on relative fitness (Brodie et al. 1995)

	Component loadings	
	Factor 1	Factor 2
Wing length	0.801	0.353
Leg length	0.829	0.217
Balloon volume	0.561	-0.825
Percent variance explained	54.79%	28.41%
Selection gradient (β)	0.003	0.588
P-value	0.987	0.012

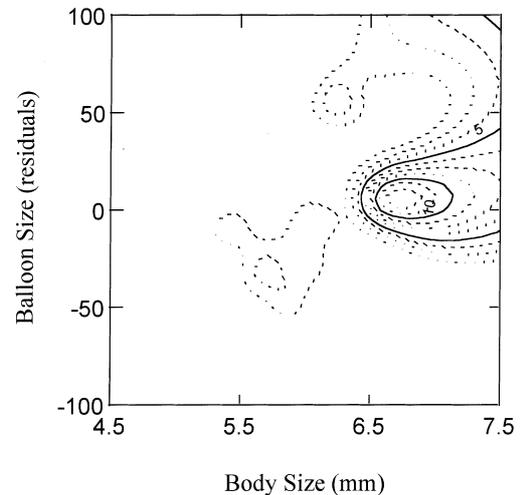


Fig. 1 Non-parametric (DWLS) visualization of selection of male balloon size (measured as balloon volume residuals), male body size (measured as wing length), and relative male mating success on the z-axis. The highest peak of male mating success appears for larger males with intermediate size balloons

Discussion

Sexual selection in *E. snoddyi*

As predicted, interactions within and between the sexes suggest an important role for sexual selection in this species. However, the outcome of pairwise male-male interactions does not appear to depend on body size or balloon size despite frequent and vigorous male-male interactions. Thus, based on analysis of contemporary

selection, it does not appear that empty balloons have evolved as a result of male-male competition. Nonetheless, these results do not completely exclude the effect of male-male competition on other factors that influence male mating success. If a dominance hierarchy is present within a swarm of males, females may base their mate preferences on each male's position; certain positions in the swarm may indicate higher male fitness or quality to females (Thornhill 1980).

Male balloon size does appear to affect male-female interactions, but not in the predicted manner. Our selection study showed that there was significant negative selection on male balloon volume and a trend towards positive selection on male body size. These results are surprising given the significant positive correlation between male body size and balloon size. Due to this positive correlation, the selection intensity on male balloon size was smaller than the standardized selection gradient due to indirect effects (Table 3). Results from the multiple regression of the two PCA factor scores showed significant positive linear selection acting on increasing male body size and decreasing male balloon size. These selection measures indicate that the biggest males with the smallest balloons should have the highest mating success. Visualizing the selection surface using non-parametric methods provided more detail about the most successful strategy for males to follow in this population of *E. snoddyi*. The selection surface suggested that in this population of *E. snoddyi*, bigger males with intermediate-size balloons have the highest mating success (Fig. 1).

The significant linear selection for increasing body size and decreasing balloon size combined with the success of larger males with medium-size balloons in this population cannot be explained simply. It is possible that this result reflects male-female courtship interactions within the mating swarm. Female *E. snoddyi* actively circle and often chase males some distance out of the swarm. Females may be evaluating a male's flying efficiency; therefore, a larger balloon may be more unwieldy and inhibit the male's flying speed or flying ability. If the female uses some aspect(s) of the male's flying ability to determine his quality, a larger balloon would be a hindrance. Also, flying is energetically costly and it is possible that males with smaller balloons are able to swarm for longer periods of time than males with larger balloons, thus increasing their probability of obtaining a mate. In either scenario, selection would act to decrease balloon size and increase body size; however, the interpretation from the visualization of the selection surface suggests that bigger males with intermediate-size balloons (not the smallest balloons) have the highest mating success in this population of *E. snoddyi*. This interpretation of the selection surface suggests a possible trade-off in display behaviors for males between long-range attraction of females (larger balloons are more visible) and close-range attraction (smaller balloons are less energetically costly and easier to manipulate in flight).

The evolution of empty balloons

The empty balloon produced by some species of empidine flies has been hypothesized to be a sexually selected trait (Cumming 1994). However, the roles of intersexual and intrasexual selection have not been examined for most empidine mating systems. Furthermore, where sexual selection has been examined in empidines, males provide nutritious gifts (e.g., *E. borealis*: Svensson and Petersson 1987, 1988); the male gift reflects parental investment through this nutritional offering. In *E. borealis*, the nuptial gift is so nutritionally valuable that sex role reversal occurs (i.e., female-female competition and male choice); however, females mate longer with males that have larger nuptial gifts (Svensson and Petersson 1987, 1988; Svensson et al. 1990). *Empis snoddyi*, in contrast, provides a balloon that is never eaten and therefore provides no direct nutritional benefits to females. Thus, sexual selection in this species could reflect phylogenetic history: preferences for large balloons may be ancestral if empty balloons are derived (Thornhill and Alcock 1983). This hypothesis suggests that balloon size should be positively correlated with female preferences, with larger balloons being maintained by sexual selection without current direct benefits to females.

An alternative hypothesis is that the empty balloon, as in the *E. snoddyi* mating system, evolved directly rather than as a phylogenetic holdover. This requires balloons to be an indicator of male quality. If balloons are ornaments that reflect male condition, females may use balloons directly to assess male quality resulting in direct selection on the balloon. The balloon then functions as an honest signal. Theory and observations suggest that many secondary sexual characteristics develop in proportion to the condition of the male (Andersson 1994). Male display performance is also likely to be condition dependent (Price et al. 1993). Indicator traits that are condition dependent will develop in proportion to the nutritional and health status of the male (Andersson 1994). However, for such signals "bigger" need not be "better": increasingly smaller signals as honest indicators of quality can evolve (Wolf et al. 1997). Under this hypothesis, females prefer balloons that correlate, positively or negatively, with male condition.

Finally, the balloon of *E. snoddyi* may function in species recognition. This hypothesis gains some support from the preference of females for average-size balloons. Stabilizing selection may be more common when signals function in species recognition rather than in sexual selection (Butlin et al. 1985). However, this hypothesis further suggests the presence of sympatric species with similar signals (Butlin et al. 1985). While there are other dance flies present at our study site, there appear to be no other sympatric empidine species that use any type of balloon in their courtship ritual.

While it appears that in the *E. snoddyi* mating system female preference is the most important type of sexual selection occurring, females appear to discriminate

among males and their empty balloons in an unexpected manner. Contrary to previous hypotheses that suggested that larger balloons indicate higher male fitness, and that larger male balloons should be preferred by females, we find that the opposite is true for *E. snoddyi*. In general, selection acts to increase male body size while decreasing male balloon size; specifically, in this population of *E. snoddyi*, the largest males with intermediate balloons are the most successful in obtaining matings. The empty balloon in the *E. snoddyi* mating system appears to be not only a stimulus that attracts potentially receptive females, it is also an important cue (and perhaps an honest signal of male quality) that influences females in their mating decisions. Future studies should examine how male quality and male balloon size are related in species that present gifts with some nutritional value, as well as species that provide empty balloons with no nutritional value.

Acknowledgements We would like to thank the staff of Great Smoky Mountains National Park. We are especially grateful to Chuck Parker of the National Biological Service whose assistance and expertise was invaluable to this project. We thank Norman Woodley, Department of Entomology, at the National Museum of Natural History for confirming the identification of our samples of *E. snoddyi*. We are grateful to the following individuals for assistance in the field: M. Sadowski, M. Alfieri, S. Greer, J. Rapp, and K. Jackson. M. Alfieri, C. Allen, L. Corley, R. Preziosi, C. Rauter, and A. Sih all provided valuable comments on this manuscript. Members of the Brodie and Moore laboratories provided support, encouragement, and enlightening discussions about this work. Darryl Gwynne, Jeff Cumming, and an anonymous reviewer provided comments that greatly improved this manuscript. This project was supported by grants from the Animal Behavior Society, Sigma Xi Grants-in-Aid, the University of Kentucky Graduate School, NSF/KY/EPSCoR EHR-91-08764 to J.A.S., and NSF grants DEB-9521821 and IBN-9616203, as well as State and Federal Hatch support to A.J.M.

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Communicated by D.T. Gwynne