Ethology Ecology & Evolution 19: 27-50, 2007

Appearances deceive: female "resistance" behaviour in a sepsid fly is not a test of male ability to hold on

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Received 22 February 2006, accepted 26 June 2006

Female rejections of males are crucial events in sexual selection by female choice and sexually antagonistic coevolution, but there are few detailed studies of the process of rejection. Female struggles when mounted by males are often assumed to function to dislodge the male. But this study, in which female receptivity was manipulated by using females of different ages, showed that this "dislodgement" hypothesis is incorrect in a group (sepsid flies) in which energetic female shaking behaviour was previously interpreted as female attempts to dislodge males. Mounts in *Archisepsis diversiformis* often failed, but males were nevertheless seldom thrown off; instead, they almost always dismounted while the female was quiet. Males also showed signs of being in control of dismounts, as they dismounted more quickly if the female had recently been mounted by another male. Predictions from two other hypotheses for the function of female resistance behaviour also either failed or were not consistently supported: (1) females resist in order to filter males with respect to their ability to hold on to the female or outlast her resistance, or to court while mounted ("male endurance/ female exhaustion" hypothesis); (2) females resist in order to sense the male's grip on her wings and thus filter males with respect to their species-specific clamps or to elicit other male courtship ("male screening" hypothesis). Several predictions of a further possibility, that (3) females resist in order to communicate their lack of receptivity to the male, and to induce him to leave ("communication" hypothesis), were confirmed. Although one type of data did not fit easily with the communication hypothesis, overall it was the most likely explanation for female shaking behaviour. Our results call into question conclusions from previous studies regarding male-female conflict in this and other groups, and suggest testable alternative hypotheses. A survey of behaviour in other flies (which are presumably indicative of other animals in this respect) indicates that female "resistance" behaviour probably has a variety of functions. In sum, facile interpretations of a forceful resistance function should not be accepted without careful analyses.

KEY WORDS: female resistance behaviour, sexual selection, female choice, sexually antagonistic coevolution, sepsid flies.

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INTRODUCTION

In many animals the female often reacts to a male by fleeing, or struggling when he attempts to grasp her and copulate. Such female behaviour is usually termed "resistance", and presumed to function to physically force the male to desist. Perhaps because of the linguistic trap laid by the word "resistance", other possible functions, such as communication with the male to induce him to leave, or screening among males, are much less often considered (but see PARKER 1974, THORNHILL & ALCOCK 1983, WEIGENSBERG & FAIRBAIRN 1994, RUTOWSKI 1997, BLANCKENHORN et al. 2000, PERETTI 2001, DING & BLANCKENHORN 2002, ZUK 2003). The distinction between resistance by physically overwhelming the male as opposed to resistance to communicate or screen can be difficult to document; but is important in attempts to evaluate the relative importance of traditional female choice (ANDERSSON 1994) as compared with new arms race models of sexual selection involving sexually antagonistic coevolution (HOLLAND & RICE 1998, CHAPMAN et al. 2003, ARNQVIST & ROWE 2005). If female resistance behaviour does not function to avoid males, it cannot be assumed to be a reliable indicator of sexually antagonistic coevolution (as in ROWE et al. 1994, ALLEN & SIMMONS 1996, ALEXANDER et al. 1997). Assuming, rather than testing possible functions of female behaviour is a common problem in current sexual selection literature (PIZARRI & SNOOK 2003).

Female resistance behaviour to mounted males has been studied in several animals, especially thoroughly in water striders (summarized by ARNQVIST 1997. On other groups, see LINLEY & ADAMS 1974; THORNHILL & SAUER 1991; CREAN & GILBURN 1998; BLANCKENHORN et al. 1998, 2000; JORMALAINEN et al. 2000; SPARKES et al. 2002; ARNQVIST & ROWE 2005). Several types of data have been used to support the hypothesis that the female's resistance is important in physically displacing mounted males: greater female resistance when the female's need for food increases

(Rowe 1992); reduced female resistance when males are more abundant and harass her more frequently (Rowe 1992); greater rates of predation on females when they were mounted by males (Fairbairn 1993, Rowe 1994); and more frequent rejection and greater female resistance when male energy reserves are exhausted (Sparkes et al. 2002).

In this study of the energetic female resistance behaviour in the sepsid fly, *Archisepsis diversiformis* (Ozerov), we follow the tradition of using the word "resistance" for female struggling behaviour, but we will be testing rather than assuming its functions. We will discriminate between direct physical consequences for the male of the female's struggles (our "dislodgement" and "male endurance/female exhaustion" hypotheses — see below) and other, more indirect effects. As in other sepsids (Parker 1972a, 1972b; Ward 1983), female *A. diversiformis* often shake energetically when mounted by males, which grasp the female's wings with their modified front legs (Eberhard 2001a). Previous authors have interpreted the female shaking behaviour in other sepsid species (Parker 1972a, Ward 1983, Ward et al. 1992, Allen & Simmons 1996, Ding & Blanckenhorn 2002, Hosken et al. 2003) as well as that in other flies (Otronen 1989, Crean & Gilburn 1998) as functioning to avoid or reject males. The behavioural details of female resistance that we report here indicate that the female's resistance behaviour does not function either to avoid the male by force, or to screen males on the basis of their abilities to forcefully overcome her resistance.

Hypotheses

We will test four general hypotheses to explain female shaking behavior:

Dislodgement. Resistance serves to physically dislodge the male. Female resistance behaviour, and in particular shaking behaviour, functions to forcefully throw off the mounted male.

Male endurance/female exhaustion. Resistance serves to test the endurance of the male (e.g., Crean et al. 2000). Female resistance wears down the male's ability to remain mounted, and only males able to maintain their hold and succeed in copulating. Seen from the female's perspective, there may also be a test of female endurance: female resistance to copulation may finally cease due to physical exhaustion. Female exhaustion is not a necessary prediction of a general version of the male endurance test hypothesis, however, as it is possible that the female could impose endurance tests of males that did not exhaust her. Female acceptance due to exhaustion is, however, implicit in versions of male-female conflict hypotheses that suppose that males physically impose acceptance on females after sustained struggles.

Male screening. Resistance serves either to enable the female to sense male stimulation of her wings with the clamping structures of his front legs, or to influence the male's ability to perform other aspects of courtship that she uses to screen males. By shaking, and thus causing the male's grip to stress her wings in different ways, the female can sense in a more detailed manner the form of the male's clamp. This hypothesis is inspired by the previous finding that a female's tendency to mate after a male has mounted her is strongly affected by details of the stimulation of her wings produced by his front legs (Eberhard 2001a, 2003a).

Communication. Resistance communicates the female's lack of receptivity to the male, inducing him to dismount. This hypothesis resembles the resistance and the endurance test hypotheses in proposing that resistance serves to cause the male to leave. It differs from these hypotheses in that the mechanism used by the female to rid herself of the male is not physical force that overcomes him, but rather transfer of information that increases the probability that the male, acting presumably in his own best interests, will dismount.

The first three hypotheses involve processes that may be directly related to sexual selection, as they could influence competitive advantages in male-male competition (to avoid dislodgement, to endure, or to stimulate the female). The communication hypothesis could also be linked to sexual selection, but less directly. Selection would favor male ability to judge female signals and to respond appropriately; leaving females whose signals indicate the mount will be fruitless, and thus avoiding loss of time that could be used to encounter other females; and remaining with and courting females whose signals indicate possible eventual acceptance. Female signals could be non-selective and independent of the traits of the male, or they could be modulated in response to stimuli received from the male during the course of the mount, thus exercising sexual selection on males. These hypotheses, their predictions that we tested, and the results of the tests are outlined in Fig. 1; logical bases of some predictions are explained further in the Results section.

Hypotheses, major predictions, and tests

Hypothesis	Prediction	Confirmed?
1. Dislodgement	Males are dislodged during female resistance behaviour	No (almost never)
	Smaller males are more often "forced" to dismount	No
	Dismounts are not due to male "decisions"	No
2. Male endurance/female exhaustion		
A. Male hold onto wing	Copulation is more likely if male stays mounted longer	No (opposite trend)
	Very young females do not resist	No
	Larger males court more	Yes
B. Female exhaustion	Shaking intensity declines during mount	Yes
	Copulation more likely when mount is longer	No
	Smaller females offer less resistance	No
	Smaller females copulate more	No
3. Male screening	Larger males court more	Yes
	Very young females do not resist	No
4. Communication	Females that eventually mate resist less	Yes
	Resistance is shorter and less intense when the male is more attractive (larger)	Yes (both)
	Reduction in resistance just before cop. greater when male larger	Yes
	Mount duration is inversely correlated with intensity of resistance	Yes
	Younger females resist more	No (but see Discussion)

Fig. 1. — The hypotheses and their major predictions that are tested in this paper. See Results for explanations of the predictions, and tests of other, related predictions.

Sepsid flies

The sexual behaviour of sepsid flies is relatively uniform in several respects (Parker 1972a, Pont 1979, Schulz 1999), and the behaviour of *Archisepsis diversiformis* resembles that of the most often-studied species, *Sepsis cynipsea,* in several ways that are crucial to comparisons made in this study. Males usually encounter females at feeding and oviposition sites (dung, carrion, other rotting material), where males are usually present in larger numbers than females (W.G. Eberhard unpub.). Males of *A. diversiformis* mount females with little or no prior courtship, often as if taking them by surprise. Failed male mounting attempts (no copulation) end either before or after the male has grasped the female’s wings. The female often resists before her wings are grasped, but many quick dismounts without wing grasping also occur without overt female resistance (she is motionless or only briefly lifts her abdomen when the male mounts) (Eberhard 2002a; see Parker 1972a, 1972b on *S. cynipsea*). The present study concerns cases in which the male succeeded in grasping the female’s wings with his front legs.

The male grasps the bases of the female’s wings with specialized structures on his front femur and tibia whose species-specific bumps, grooves and spines mesh tightly with the wing veins of the female (Eberhard 2001a). A mounted male sometimes rides a female for many minutes as she oviposits, finally either copulating or dismounting (Eberhard & Pereira 1996; Eberhard 2001a, 2002a). Larvae feed on the substrate into which the egg was laid, and pupate nearby. Adults emerge with little or no reserves; new females are unreceptive (presumably sexually immature). In captivity they must feed within the first 12 hr of adult life or they die (W.G. Eberhard unpub.). Adults live for several weeks in captivity, and females lay several batches of eggs (Baena 2002). As in *S. cynipsea,* male-male battles over females virtually never occur in the field (no takeovers observed in several hundred encounters between solitary and mounted males in *A. diversiformis* — W.G. Eberhard unpub.). Females with mounted males walk about, feed and oviposit, apparently unhindered; they also fly, but may take off more slowly (W.G. Eberhard unpub.).

As in most other insects (Eberhard 2002a), intromission in *Archisepsis* cannot occur without active participation by the female. A female must flex her proctiger dorsally and expose her vulva for intromission to occur; the male’s genitalia often do not even touch the female just prior to intromission, and are in any case not mechanically capable of forcing her proctiger dorsally (Eberhard 2002a). Failed mounts are common in the field, and less than half of mounting attempts in which a male succeeds in grasping the female’s wings result in copulation (Eberhard 2001a).

Allen & Simmons (1996) found that males in copulating pairs of *S. cynipsea* in the field had more symmetrical foretibiae than those which were mounted but had not copulated, and argued that this correlation represented a cause-effect relationship involving physical force; symmetrical foretibiae were said to be favoured “because of their better competitive ability to grip the female’s wing bases and thereby remain on the dorsum of a struggling female ...”. This conclusion was weakened by failure to analyse alternatives such as differences in female receptivity or intensity of resistance, or the possibility that other male traits associated with foretibia asymmetry affect copulation success. In addition, the supposition that female struggles physically throw off mounted males was not documented.

Precise mechanical fit between the male clasping organ and the base of the female’s wing is not necessary to enable male *A. diversiformis* to remain mounted; neither substantial alteration of the male grasping organ or of the female wing led to reductions of mounting times, even though females resisted energetically (EBERHARD 2003a). Instead, these alterations strongly reduced the female's tendency to accept intromission (EBERHARD 2001a, 2003a). Female sense organs are not contacted directly by the male's front legs when he clamps her wings, but there are several campaniform sensilla nearby (EBERHARD 2001a). The male also courts the female both prior to and during copulation, using tactile, chemical and possibly also vibratory and visual stimuli (EBERHARD 2001b, 2001c, 2002b, 2005).

Both resistance and copulation are probably costly for female sepsids. Female resistance behaviour involves energy expenditure; it may also increase the female's susceptibility to predation, although the flies have defensive chemicals that discourage some predators (PARKER 1972b, EBERHARD 2002a). Predation does not seem to be common, however, at least in anthropogenic habitats such as pastures in Costa Rica (EBERHARD 2001a). It is possible that, as has been thought to occur in *S. cynipsea* (MÜHLHÄUSER & BLANCKENHORN 2002), female resistance increases the risk of wing injuries inflicted by the male's front legs. The data on this point are not entirely convincing, however, because damage was apparently evaluated at distal sites on the wing that are not grasped by the male's front legs (EBERHARD 2001a), and the damage may have resulted instead from wing wear in the small containers in which the flies were kept. Copulation may also appreciably increase the female's risk of predation, because it lasts many minutes (EBERHARD & HUBER 1998), and apparently makes them slower to take off flying. Copulation may also result in lesions in the female's reproductive tract from teeth on the male's genitalia, as in *S. cynipsea* (BLANCKENHORN et al. 2002). In sum, both resistance behaviour and copulation probably entail costs for female sepsids (see also HOSKEN et al. 2003), although some proposed costs are as yet uncertain.

METHODS

Flies were the offspring of females collected in pastures near San José, Costa Rica. They were placed in a cubical screen cage 43 cm on a side, provided with honey, water in vials with cotton stoppers, and previously frozen fresh cow dung in 6.3 cm dia. petri dishes for feeding and oviposition. Large and small adults were produced by varying the amount of dung/dish (approximately 62 g for large flies, 30 g for small). The flies emerged as adults between 07:00 and 10:00, and males and females were aspirated into separate containers containing honey, water and fresh dung. All mating trials involved virgin males and females. Trials with newly emerged "0 day-old" females were performed from 10:00 to 17:00 on the day they emerged. Trials with "1 day-old" females were performed the next day between 09:00 and 18:00, and those with "2 day-old" females the following day (09:00-18:00). Thus adult ages were approximately 1-10 hr for "0 day-old" females, 24-34 hr for "1 day-old" females, and 48-58 hr for "2 day-old" females. Flies were used only once, and were preserved in 80% alcohol after being observed. The length of the hind tibia was measured as an indicator of body size (WARD 1983).

A trial began when one female and two males (one large, one small, both 2 days old) were aspirated into a petri dish; their behaviour was taped at 30 fps during the following hour using a Sony Hi8 video camera with +4 closeup lenses. This combination of flies was used because females often encounter multiple males in nature. Each time a male mounted the female, the camera was zoomed in so that the length of the female's body was approximately 1/4 the width of the visible field. Many details of the flies' behaviour could thus be distinguished in frame-by-frame analyses. Most pairs were taped in dorsal view, except when the female walked onto the side of the petri dish. The frequencies of pushing with the legs and bending abdomen behaviour by the female are probably underestimated because these movements may have sometimes been missed in dorsal view. The durations of different types of behaviour were recorded to the nearest 0.03 sec.

The intensity of female shaking behaviour was quantified in two ways: frequency (number of movements/sec); and relative duration (duration of the activity/duration of the mount); a third possible measure of intensity — the rapidity with which the female leaned from one side to the other, varied little in different treatments, and was used in only a few tests. The duration of a successful mount was the time elapsed from mounting until copulation began, while that of an unsuccessful mount (no copulation) was the time until the pair separated. Because the intensity of female shaking usually decreased gradually during longer mounts, and because most mounts lasted > 20 sec, some comparisons of intensities were made on the basis of behaviour during the first 20 sec of each mount. A male’s first mount was usually much longer than subsequent mounts (see “copulation and other behaviour” below), so only first mount for each female was analysed unless noted otherwise.

The distributions of frequencies and durations were generally not normal, and graphs present median values and quartiles rather than means and standard deviations. Because some important conclusions of this study derive from *lack* of significant differences, we employed sensitive parameteric rather than non-parametric statistical procedures in tests related to these conclusions, using data that was transformed on the basis of Box-Cox Tests to determine the most appropriate transformations for each variable (CRAWLEY 2002). In most cases a negative exponential transformation was most appropriate, and except where noted otherwise, this was used in all parametric tests. In some other tests, in which our conclusions derived from the presence of statistically significant differences, we employed non-parametric tests, or utilized parametric tests on rank-transformed data (CONOVER & IMAN 1981).

RESULTS

Behaviour patterns and general trends

The behaviour of 90 females and 180 males was analysed; 28 of the females were newly emerged (mounted by 40 males), 28 were 1 day old (mounted by 46 males), and 34 were 2 days old (mounted by 42 males). All females were mounted at least once, while 52 males failed to mount.

Female behaviour

In 92% of 224 unsuccessful mounts by 103 males, the female performed at least one type of resistance behaviour (below); in the rest the male eventually dismounted without copulating even though the female did not resist. The female resisted in all of the 25 successful mounts. Female resistance behaviour included:

(a) *Shaking* — The female shook from side to side. In high intensity shakes she leaned > 45° toward each side in the space of 0.03-0.06 sec; leaning her body from one side to the other was counted as a single shake; (b) *Rocking* — The female rocked rapidly forward, in high intensity up to > 60°, and then back. A single rocking movement consisted of rocking forward and back again; (c) *Bend abdomen* — The female bent her abdomen ventrally so that its tip was beyond the reach of the male’s genitalia when he lowered his abdomen; (d) *Onto back* — The female fell briefly onto her back, in an apparent attempt to dislodge the male; (e) *Walk* — The female walked; and (f) *Push with legs* — The female pushed posteriorly or dorsally on the male's legs or abdomen with her hind legs.

Shaking was by far the most common female resistance behaviour (Table 1), and in the discussions that follow, "female resistance" refers to shaking unless otherwise specified.

Male behaviour

The male held the bases of the female's wings with his front legs, and also performed two types of apparent courtship behaviour with his middle legs. A male initiated a bout of courtship by striking the female's antenna or their general vicinity one or more times with his middle tibiae or tarsi, followed immediately by briefly rubbing them rapidly on the anterior margins of the female's wings. These movements were taken to be courtship because they were stereotyped, were repeated many times both within and between mounts, were mechanically appropriate to stimulate the female, and were irrelevant with respect to other possible functions (see EBERHARD 1994). In addition, the male also made periodic genitalic contact that may have constituted courtship (see PARKER 1972a, EBERHARD 2005). He eased posteriorly on the female, and bent his abdomen ventrally so that his genitalia contacted her at or near the tip of her abdomen for up to several seconds. Most genitalic contacts did not lead to intromission.

Copulation and other behaviour

Younger females were less likely to copulate, and very young females were apparently not sexually mature (0% of 0 day-old copulated, 14.2% for 1 day-old, 61.8% for 2 days-old; $\chi^2 = 29.1$, df = 2, $P < 0.001$). Large males (mean hind tibia length 1.29 ± 0.12 mm) were more likely to copulate than small males (mean 1.10 ± 0.10): 21.1% of large and 6.7% of small males copulated ($\chi^2 = 8.1$, df = 1, $P < 0.01$).

In unsuccessful mounts, the median duration of a male's first mount (306 sec) was nearly 6 times longer than that of his second mount of the same female (53 sec), and about 13 times longer than that of his third (24 sec) ($F_{2,106} = 217.0$, $P < 0.0001$, N = 54 with one way-ANOVA for repeated measures, using positive exponential transformations for the first mount and natural log transformations for the other two). Durations of unsuccessful first mounts did not differ with female age ($F_{2,121} = 1.98$, $P = 0.14$ with one-way ANOVA).

Tests of hypotheses

Dislodgement hypothesis

The hypothesis that the female physically throws the male off predicts that males usually dismounted while females were shaking. Frame-by-frame analysis of video recordings showed, however, that males were rarely thrown off, and that dismounts only rarely occurred during shaking. Of 224 dismounts (all unsuccessful mounts included), 92% occurred while the female was immobile. The male generally dismounted in these cases by moving rearward and turning to climb off the female. Only 5.4% of the dismounts occurred while the female was shaking, and in only 1.4% did the male appear to be struggling to hold on while he came off as the female was shaking. Also arguing against forceful displacement (if one assumes that larger males are can hold on more effectively) was the fact that small males were not more likely to dismount during female shaking than were large males ($\chi^2 = 0.62$, df = 1, $P > 0.5$).

Male endurance/female exhaustion hypothesis

Two crucial predictions of the male endurance test hypothesis were not confirmed. Most importantly, the duration of successful mounts was not longer than that of unsuccessful mounts. There was, in fact a strong trend in the opposite direction (Fig. 2): successful mounts were much shorter than unsuccessful mounts (median durations were 34.6 and 305.5 sec). More than half of the unsuccessful males succeeded in remaining mounted longer (> 300 sec) than the time needed by > 90% of the successful males to achieve intromission.

A second prediction was that very young females, which are not sexually receptive and thus were not screening males, would not shake. Very young females did resist, however, and the relative durations of their possible resistance behaviour patterns were very similar to those of older females, differing during the first mount in only in two minor behaviour patterns: “walk” was more common in very young females, and “kick” was more common in the oldest females (F = 6.01 and 3.97, $P = 0.004$ and 0.024 respectively with MANOVA; Wilk’s Lambda $F_{10,108} = 2.33$, $P = 0.015$; frequency of shaking log transformed). With respect to frequencies, none of the female behaviour patterns differed with female age. During the first 20 sec of

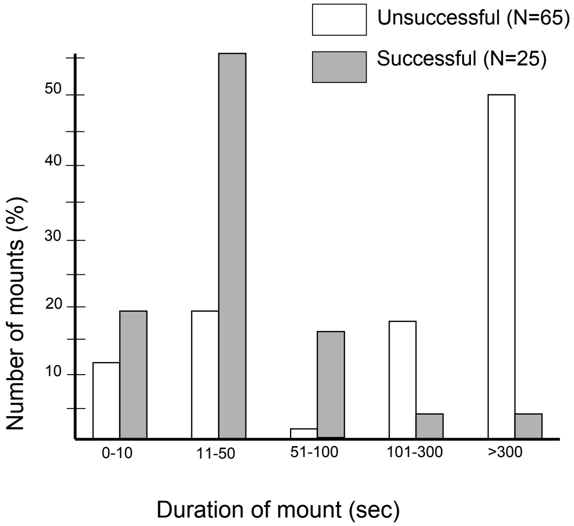

Fig. 2. — The distributions of the durations of successful and failed first mounts differed (Chi² test: $\chi^2 = 17.28$, df = 2, $P < 0.0001$) in a pattern not predicted by the endurance test hypothesis: most copulations occurred early (during the first 100 sec), and most failed mounts lasted longer (> 100 sec).

the first mount, shaking intensity was not significantly reduced in younger females (1-way ANOVA $F_{2,64} = 2.13$, $P = 0.13$ using log transformation). Shaking differed marginally in relative duration (1-way ANOVA $F_{2,64} = 3.14$, $P = 0.049$, using positive exponential transformation), but one day old females shook more than younger and older females ($P < 0.05$ with Tukey test). A third measure of intensity, the rapidity of female shaking (number of shakes/duration during a bout of shaking behaviour during the first 20 sec), also showed no differences with female age (1-way ANOVA of rank-transformed values: $F_{2,137} = 0.47$, $P = 0.62$**)**.

A related hypothesis, that also concerns a possible test of the male's ability to hold on, is that female shaking tested the male's ability to court her, and to make genitalic contact while he held on to her wings. If one assumes that larger males could hold on more securely, this idea was supported by the fact that larger males courted more often (median = 0.19 bouts/s, range 0-1.16, N = 91) than did small males (median = 0.12 movements/s, range 0-0.57, N = 108) in failed mounts (first and subsequent mounts combined) (Mann-Whitney U test: $P = 0.00003$). When only first mounts (both successful and unsuccessful) were analyzed, there was a similar trend for both courtship and genitalic contacts to last longer when the male was larger: in two-way-ANOVAs that included mount success (also significantly related to these male behaviour patterns, though not in this analysis — see below), $F_{1,87} = 14.9$, $P = 0.0002$ for courtship, $F_{1,87} = 4.94$, $P = 0.029$ for genitalic contact ($P < 0.05$ with Tukey tests; neither interaction with mount success was significant). Similar, though statistically non-significant trends occurred for relative numbers ($F_{1,113} = 3.18$, $P = 0.077$ for courtship, $F_{1,85} = 3.48$, $P = 0.065$ for genitalic contacts). The associated idea that more genitalic contact by the male during the first 20 sec positively influenced his chances of copulating was also supported in this two way-ANOVA for relative duration ($F_{1,87} = 12.45$, $P = 0.00006$; $P < 0.05$ with Tukey test); a similar analysis of relative duration of courtship showed no direct effect ($F_{1,87} = 0.13$, $P = 0.72$), but did show significant interaction with male size in relation to copulation chances ($F_{1,87} = 5.84$, $P = 0.018$).

However, several other trends contradicted the hypothesis that shaking tested the male's ability to court. If female shaking makes it more difficult for the male to perform courtship and genitalic contact behaviour, then one would expect less courtship when the female shook more. Instead, the only significant relations with male courtship and genitalic contact were positive rather than negative during the first 20 sec of first mounts (successful and unsuccessful mounts combined). For relative numbers (using positive exponential transformations), $r_s = 0.24$ ($P = 0.032$) for courtship, and $r_s = 0.17$ ($P = 0.13$) for genitalic contact. Corresponding figures for relative durations (using natural log transformations) were $r_s = 0.10$ ($P = 0.39$) for courtship and $r_s = -0.21$ ($P = 0.058$) for genitalic contact. The positive relationship between courtship frequency and female shaking was especially strong for successful mounts ($r_s = 0.59$, $P = 0.0021$). Positive correlations could result from male attempts to use courtship and genitalic contact to reduce female shaking, or from female attempts to use shaking to interrupt male behaviour. The second alternative is more likely in the case of genitalic contact, because contact usually preceded rather than followed shaking.

One prediction of the female exhaustion version of the male endurance test hypothesis was confirmed: the intensity of female shaking declined sharply during both unsuccessful (Fig. 3), and successful first mounts (Fig. 4), and in subsequent mounts (Fig. 5). Some further predictions, however, were not confirmed. Most importantly, long mounts, when females were presumably more likely to become exhausted, were associated failure to copulate, rather than with success (above). In addition, female size did not show the expected positive relation (assuming larger females have more endurance) with the intensity of shaking during either the entire mount ($r_s = 0.14$, $P = 0.25$ for frequency, $r_s = 0.14$, $P = 0.26$ for relative duration, N = 68), or the first 20 sec ($r_s = 0.047$, $P = 0.73$, N = 61 for frequency, $r_s = 0.16$, P

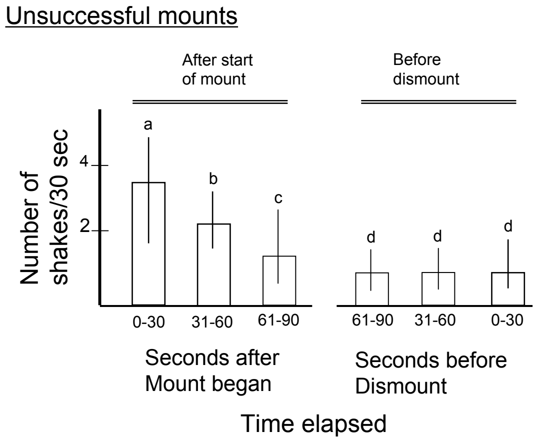

Fig. 3. — The frequency of shaking declined during the first 90 sec of an unsuccessful first mount (as predicted by the female exhaustion version of the endurance test hypothesis), and did not change during the last 90 sec prior to the male’s dismount from these same 38 females (1-way ANOVA for repeated measures: $F_{2,226} = 1017.8$, $P = 0.000001$). Values with the same letter did not differ significantly with Tukey tests ($P > 0.05$).

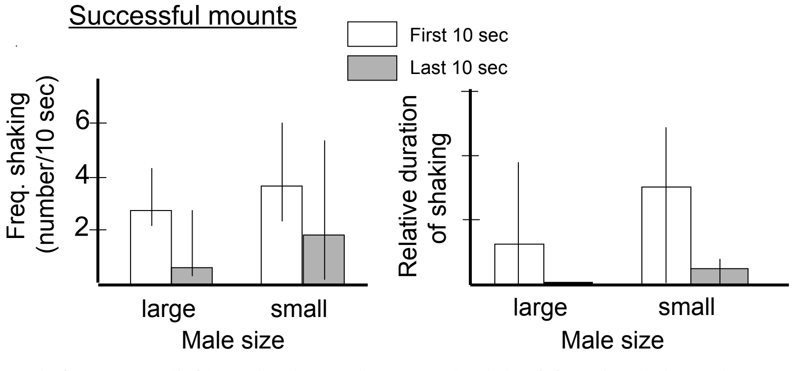

Fig. 4. — Both frequency (left) and relative duration (right) of female shaking during successful mounts was greater during the first 10 sec of the mount than during the 10 sec preceding copulation (1-way ANOVAs: $F_{1,5} = 19.5$, $P = 0.0069$; $F_{1,5} = 11.8$, $P = 0.018$ respectively. The relative duration of shaking just prior to copulation was shorter with large males (Mann-Whitney U test: $P = 0.018$). Neither the relative change in frequency nor the relative change in relative duration were affected by male size (two way-ANOVA for repeated measures, $F_{1,5} = 0.74$, $P = 0.43$, and $F_{1,5} = 0.25$, $P = 0.64$ respectively). There was no significant interaction between male size and the relations between first and last 10 sec for either measure of intensity ($F_{1,5} = 1.2$, $P = 0.32$, and $F_{1,5} = 0.068$, $P = 0.80$ respectively). Nor was there a significant interaction between the effects of male size and the first and last 10 sec period on female shaking (1-way ANOVA: $F_{1,3} = 0.084$, $P = 0.78$).

= 0.14, N = 86 for relative duration). Smaller females did not show the expected greater reduction in shaking intensity when the first 20 sec were compared with the next 20 sec (r_s = – 0.054, *P* = 0.71, N = 86 for frequency using a positive exponential transformation, r_s = 0.21, *P* = 0.15, N = 86 for relative duration using a positive exponential transformation). This reduction was also not greater when the male was larger (r_s = – 0.037, *P* = 0.80, N = 47 for frequency; r_s = – 0.056, *P* = 0.70, N = 47 for relative duration for all females; both using positive exponential transformations). Smaller females were not more likely to accept copulation than larger females (mean size of the 25 females which did copulate did not differ from that of the 65 that did not copulate (1.23 ± 0.12 mm vs 1.28 ± 0.15 mm; *t* test: *P* = 0.31).

An additional possibility was that male endurance with respect to persistence in remounting per se was important; larger males might have been more successful because they were more persistent in mounting females repeatedly and thus exhausting them. This hypothesis can be confidently rejected: 24 of 25 copulations occurred on the male's first mount.

In sum, two general points are clear. The intensity of female shaking decreased in the later stages of long mounts and in subsequent mounts, suggesting that resistance may decline due to female exhaustion. But female acceptance of copulation was clearly not due to exhaustion, because copulation generally occurred early in the first mount. Several additional differences predicted by different versions of the endurance test hypothesis between large and small males and females were not confirmed.

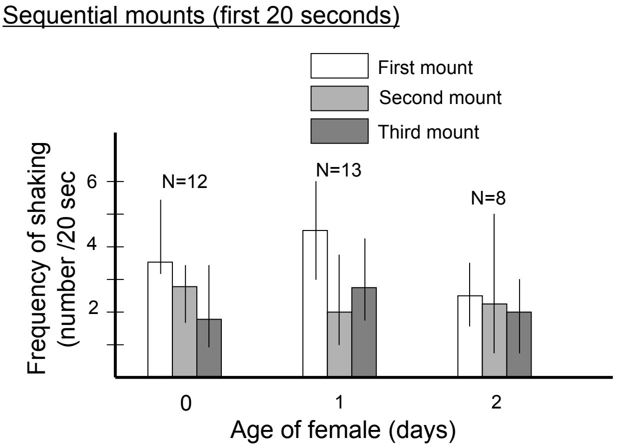

Fig. 5. — The rate of shaking declined during the first 20 sec of first, second, and third mounts of the same female (ANOVA for repeated measures using natural log transformations for second mount, positive exponential transformation for third): $F_{2,93}$ = 4.17, *P* = 0.011) (the first had a significantly higher rate than the others, *P* = 0.020, while the second and third were only marginally different, *P* = 0.050 with Tukey tests). The female's age had no effect on the rate of shaking ($F_{1,93}$ = 0.32, *P* = 0.57), and there was no significant interaction between female age and successive mounts ($F_{1,93}$ = 0.24, *P* = 0.79).

Male screening hypothesis

As in the endurance test hypothesis, the male screening hypothesis proposes that female resistance functions to filter males. The positive effects noted above of more genitalic contact and more courtship behaviour (in interactions with male size), and the apparent induction of shaking by male genitalic contact are in accord with this hypothesis. This support is weakened by the fact that cause-effect relations between male courtship behaviour other than genitalic contact and female behaviour were not determined. Most importantly, the screening hypothesis is strongly contradicted by the fact that female shaking behaviour was not less common in newly emerged, non-receptive females, which were not screening males. If females are screening males, and if shaking is costly in terms of energy and possibly also survival (as seems likely), then very young females should not shake.

Communication hypothesis

The intensity of shaking is predicted by the communication hypothesis to be negatively correlated with female receptivity in two ways: (a) those females which eventually mated should shake less intensely; and (b) those females which were mounted by more attractive, larger males (see "Copulation and other behaviour" above) should shake less intensely. Both predictions were fulfilled: (a) females that eventually mated shook less intensely, both during the first 20 sec of mounts (Fig. 6a-b) and during the entire mount (Fig. 6c-d); (b) the frequency of shaking was lower during the first 20 sec of a mount with larger males (Fig. 6a), and the relative duration showed a similar, marginally non-significant trend (Fig. 6b). The differences for different-sized males were even more pronounced during the first 10 sec of successful mounts (1-way ANOVAs: $F_{1,5} = 51.5$, $P = 0.00082$) for frequency, $F_{1,5} = 96.78$, $P = 0.00018$ for relative duration). Differences associated with male size disappeared, however, when female behaviour after 20 sec was included (Fig. 6c-d). Several other resistance behaviour patterns were also less intense when the female eventually copulated (Table 1).

Several other predictions were also confirmed. Females were expected to cease resisting and accede more rapidly when mounted by larger males: median durations for large (N = 19) and small (N = 6) males were, respectively 29.4 and 108.2 sec; Mann-Whitney U test: $P = 0.013$). And female shaking was expected to be less intense in the 10 sec just before copulation (when she had presumably become receptive) than before, as demonstrated above (Fig. 4). In addition, the crucial prediction that the male would "heed" the female's signal and dismount more quickly when female resistance was more intense, was also confirmed (natural selection can only be expected to favour female signalling if males sometimes respond to their signals). When female resistance during the initial 20 sec of an unsuccessful mount was more intense, the duration of the mount tended to be shorter (Fig. 7). As also might be expected, the intensity of male courtship was somewhat greater when females resisted more intensely (above).

However, one further important prediction was not confirmed. Very young, non-receptive females were expected to shake more intensely, but female age had no effect during the first 20 sec on either the rate or the relative duration (see also Fig. 5). The non-significant trends were in the opposite direction: very young females shook slightly less (Fig. 5).

Other trends in subsequent mounts

We found two additional trends that support hypotheses that could help explain the sharply reduced durations of successive unsuccessful mounts ("Copulation and other behavior" above) without invoking forceful dislodgement or male endurance/female exhaustion hypotheses:

Female change

Evidence indicated that the female is somehow changed by having been mounted (perhaps due to a chemical mark left by the male?), and this change was

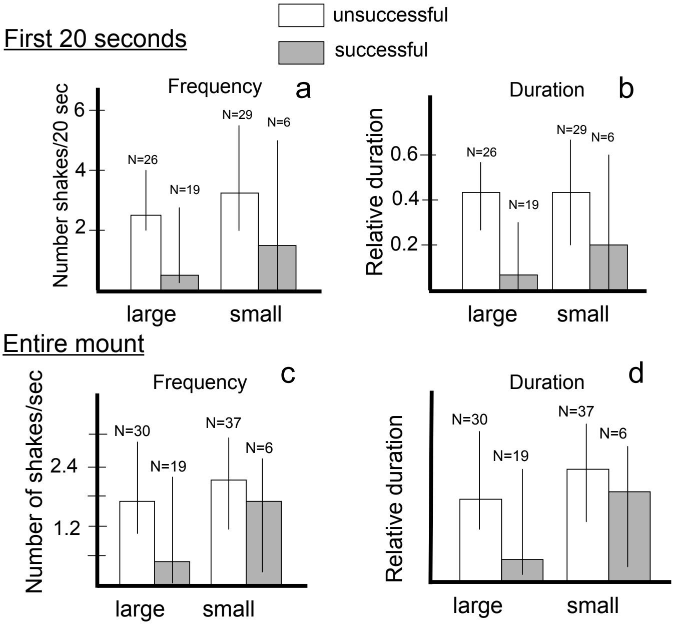

Fig. 6. — During the first 20 sec (a and b), the female shook more in unsuccessful mounts than in successful mounts, both with respect to frequency (a) and relative duration (b) (two-way ANOVASs: for frequency, $F_{1,75} = 13.3$, $P = 0.00049$, $P < 0.005$ with Tukey Test; for relative duration, $F_{1,75} = 13.4$, $P = 0.00046$, $P < 0.005$ with Tukey Test. Shaking was significantly less frequent, and of nearly significantly less relative duration when the male was large (for frequency, $F_{1,75}$, 6.55, $P = 0.012$, $P < 0.005$ with Tukey Test; for relative duration, $F_{1,75} = 3.47$, $P = 0.069$). The interaction between male size and mount success had no significant effect on either measure of shaking (for frequency, $F_{1,75} = 0.25$, $P = 0.62$; for relative duration, $F_{1,75} = 0.33$, $P = 0.57$). During the entire mount (c and d), the female shook more in unsuccessful mounts than in successful mounts, both with respect to frequency (c) and relative duration (d) (two-way ANOVAs using positive exponential transformations: for frequency, $F_{1,88} = 4.00$, $P = 0.049$, $P < 0.005$ with Tukey Test; for relative duration, $F_{1,88} = 4.35$, $P = 0.040$, $P < 0.005$ with Tukey Test). Male size did not affect either measure of shaking (for frequency $F_{1,88} = 2.66$, $P = 0.11$; for relative duration $F_{1,88} = 2.87$, $P = 0.094$). The interaction between male size and mount success had no significant effect on either measure of female shaking (for frequency $F_{1,88} = 0.22$, $P = 0.64$; for relative duration $F_{1,88} = 0.16$, $P = 0.69$).

Table 1.

Relative intensity of different types of female resistance behaviour (untransformed data) in successful and unsuccessful first mounts (Mann-Whitney U Tests).

	Failed mounts (N=65)			Successful mounts (N=25)			
Behaviour	Median	Min.	Max.	Median	Min.	Max.	*P*
Shake	1.43	0	12.12	0.53	0	4.75	0.060
Rock	0.30	0	2.73	0.12	0	1.12	0.20
Walk	0.04	0	0.26	0	0	0.067	0.0003
Push with legs	0.0	0	0.23	0	0	0.036	0.013
Onto back	0.0014	0	0.24	0	0	0	<0.0001
Relative duration[1]							
Shake	0.193	0	1.0	0.073	0	0.46	0.024
Rock	0.046	0	0.47	0.019	0	0.18	0.15
Walk	0.13	0	0.62	0	0	0.21	<0.0001
Push with legs	0	0	0.46	0	0	0.022	0.0020
Onto back	0.0007	0	0.33	0	0	0	<0.0001

[1] Duration/duration of mount.

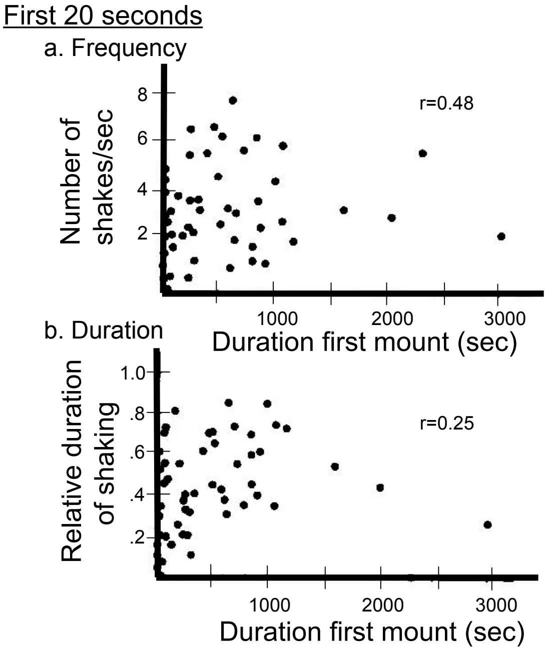

Fig. 7. — The duration of 65 unsuccessful mounts (using a positive exponential transformation) was negatively correlated with the intensity of female shaking during the first 20 sec for both frequency (using a natural log transformation) (a) (r_s = – 0.37, *P* = 0.0021) and relative duration (b) (r_s = – 0.41, *P* = 0.0007).

sensed by subsequent males and induced them to abandon her more quickly, possibly because the female's lack of receptivity was more obvious. Thus, a male's first mount was shorter if the female had already been mounted by the other male. In 47 females that were mounted by both males, the median durations of the first mount of the first male and second male were, respectively, 251.7 and 126.1 (Wilcoxon test: $P = 0.022$). There was no evidence of a cumulative effect of previous mounts, as a greater number of previous mounts by the first male was not associated with a reduction in the duration of the second male's mount (Spearman Correlation: $r_s = -0.049$, $N = 46$, $P = 0.74$).

An alternative possibility regarding "female changes" that could produce the observed shortening of successive mounts was also contradicted. Female resistance did not increase in successive mounts, and instead was lower (Fig. 5). Female exhaustion was also not responsible, as it would be expected to produce increased rather than the observed reduced durations of successive mounts.

Male change

Evidence also suggested that a male's experience of having recently failed to copulate after mounting (for instance, due to memory or to exhaustion) induced him to abandon future mounts more quickly. The amount of reduction in mount duration when the same male remounted the female was be greater than that when his mount followed one or more mounts by the other male (thus controlling for changes in the female induced by being mounted). The duration of the first mount of the second male to mount (effect of female change only) was longer (median = 135 sec, N = 46) than the duration of the second mount of the first male when the other male had also mounted (effect of female change plus effect of male change (median = 35 sec, N = 55; Mann-Whitney U test: $P = 0.0026$).

DISCUSSION

Why do female A. diversiformis *shake?*

All of the hypotheses are contradicted by at least one type of evidence (Fig. 1). The strongest implications are those that contradict the two intuitively most "obvious" hypotheses — the dislodgement and the male endurance/female exhaustion hypotheses. These hypotheses are associated with assumptions made in previous studies of sepsids (Parker 1972a, 1972b; Ward 1983; Ward et al. 1992; Allen & Simmons 1996; Eberhard & Pereira 1996; Hosken et al. 2003) that physical coercion occurs. Despite the impression of physical male-female conflict, it is very likely that forceful resolution of male-female interactions in *A. diversiformis* is not an important function of the female shaking behaviour. The most important evidence leading to this conclusion is that males usually dismounted without having been dislodged by female shaking, and most copulations occurred after only relatively short mounts and on the first rather than on subsequent mounts. The male tendency to dismount during periods when the female was quiet may function to allow him to avoid possible physical damage. Males apparently decided to dismount rather than being forced off, as male dismounts were induced by changes in both the male (memory?) and the female (marks left by previous males?). The changes in mount duration were thus presumably due (at least in part) to decisions by the male rather than by forceful female coercion.

One could argue that the function of shaking is physical displacement, but that it is ineffective in accomplishing this end. However, given the very infrequent payoff in dislodgement (as low as 1.4%), the seeming irrelevance of female shaking in avoiding copulation (both simple ventral deflection of her abdomen, and lack of elevation of her proctiger from its resting position are sufficient to exclude the male), the lack of more shaking in young, non-receptive females, and the very frequent female investment in sustained and apparently energetically costly shaking (which probably also reduces her ability to avoid predators), sustained female use of such ineffective and costly behaviour seems paradoxical. Most importantly, this "usually failed dislodgement" hypothesis leaves unanswered the question of why males so often dismounted (> 92%) after having apparently succeeded in resisting the female's supposed attempts to dislodge him.

Further indications that simple physical force is not a critical factor in determining the outcome of a mount were the lack of effects of female size on either the intensity of shaking behaviour or the likelihood of copulation. The conclusion that physical force was not important in determining the success of a mount is also in accord with a previous study of the function of the male's modified front legs in *A. diversiformis* (EBERHARD 2003a), which showed that elimination of the fine mechanical fit between the male's clamping structures and the female's wing (thus probably weakening his hold on her) did not reduce the duration of mounts, despite the apparently more intense female resistance; instead the modifications resulted in a sharply reduced likelihood that the female would allow copulation (raise her abdomen and lift her protiger), presumably because she received inadequate stimulation from the male.

One consequence of rejecting the dislodgment and male endurance/female exhaustion hypotheses is that it is not possible to explain the greater mating success of larger males in *A. diversiformis* as being due to greater ability of larger males to resist female rejection responses (this is one of the two explanations proposed by WARD 1983) (see also W.U. BLANCKENHORN in prep.). Instead, as proposed by BLANCKENHORN et al. (2000) to explain a similar preference for larger males in *S. cynipsea*, females may sense male size when males mount and clasp their wings. Our results also call into doubt the explanation given by ALLEN & SIMMONS (1996) that the greater mating success of more symmetrical males of *S. cynipsea* was due to their greater staying power.

It is important to note that our data concern only female behaviour after a male has succeeded in clasping the female's wings with his front legs. We did not test the hypothesis that prior female shaking behaviour, at the moment when the male climbs onto her, functions to forcefully prevent him from clasping her (PARKER 1972a, 1972b). Frequent observations of males of *A. diversiformis* (and also *A. ecalcarata*) dismounting quickly without clamping the female's wings, even when she did not shake (EBERHARD 2001a, 2002a, in prep.), suggest that forcefully dislodging males may be unimportant in this context also; but they do not eliminate the possibility that it sometimes occurs.

Conclusions regarding the other two hypotheses — male screening, and communication — are less clear. Although the female apparently screens males on the basis of both their size (this study) and the stimuli she receives from their wing clamping structures (EBERHARD 2001a, 2003a), our results imply that shaking does not function to promote this screening. Our evaluation of the screening hypothesis has several limitations, however. The measurements of male courtship traits (which females might be using to screen males) were relatively simple (duration of courtship, number of genital contacts) may not reflect the criteria of females; and some variables did show correlations with mating success. Our assumption may be mistaken that 0 day-old females are not screening males (a larger sample might reveal that they do occasionally mate, in which case resistance by these young females would not necessarily contradict the male screening hypothesis). We have raised many hundreds of flies for other projects, however, without observing mating between male and female adults that are only a few hours old (but this could possibly be due to male immaturity).

One further consideration regarding data from 0 day-old females gives further reason to doubt the male screening hypothesis (and at the same time has positive implications for the communication hypothesis). Newly emerged adult flies have low energy reserves, so it may be relatively more costly for them to perform sustained shaking behaviour. This would mean that the observations of resistance by 0 day-old females constitute an even stronger contradiction of the male screening prediction. In contrast, this same consideration of female energy reserves weakens the reasons to reject the communication hypothesis: the more intense resistance that was predicted for very young females may have failed to occur due to energy limitations.

The communication hypothesis seems the strongest overall. Its predictions were supported by five trends in female behaviour: less intense early shaking when the female would eventually copulate; less intense early shaking when the male was large; greater reduction in shaking just before copulation when the male was large; more rapid acceptance when the male was large; and shorter duration of unsuccessful mounts following more intense early female shaking (Fig. 7). This last is especially important because females would gain no advantage from communicating if males did not at least sometimes heed their messages. As just noted, the strongest contradiction of this hypothesis, the lack of more intense shaking in very young females, may be explained by energy limitations in these females. The positive correlation between the intensity of male courtship behaviour and the intensity of female shaking is not convincing evidence against the communication hypothesis, as the correlation did not distinguish cause from effect. The fact that initiation of male genitalic contacts often preceded rather than followed shaking suggests that female resistance may be stimulated by male behaviour (and thus be communicative), rather than vice versa. Additional data from a related species, *Sepsis duplicata*, give a further reason to suspect a communication function for shaking: females of this species perform similar shaking immediately *after* a rejected male has dismounted, as an apparent visual display (W.G. EBERHARD unpub.).

The applicability of our results in the field is unclear. Both female and male behaviour near dung pats in the field, where both non-virgin females come to feed and oviposit (EBERHARD 1999), differs in several respects, and female shaking is less common (EBERHARD 2001a). These differences might be because most are females in the field non-virgins while those in this study were virgins. However, mounts of non-virgin females in the lab also often involve sustained bouts of shaking by the female (L. RODRIGUEZ pers. comm.) that are seldom seen in the field. Alternatively, females may be generally more receptive in the field than in petri dishes. This could explain why only 62% of the 2 day-old virgin female copulated in our study.

Female behaviour in other sepsids

Several comparisons can be made between the behaviour of *A. diversiformis* and that of the well-studied sepsid, *S. cynipsea* in captivity. As in *A. diversiformis*, female *S. cynipsea* were also more likely to copulate with large than with small males (Blanckenhorn et al. 2000), and the duration of female shaking behaviour was much shorter in successful than in unsuccessful mounts (Blanckenhorn et al. 2000, Ding & Blanckenhorn 2002). These data argue strongly against the male endurance/female exhaustion hypothesis in *S. cynipsea*. It is not certain whether female *S. cynipsea* offer less resistance to larger males, although shaking duration in successful mounts in captivity showed a non-significant trend ($P > 0.2$) in this direction (Blanckenhorn et al. 2000). Ding & Blanckenhorn (2002) concluded that female shaking in *S. cynipsea* is a non-selective female attempt to avoid copulation (“shaking duration in *S. cynipsea* primarily reflects female resistance to mate with any male ...” p. 270). Indirect evidence from both behaviour (Parker 1972a; Ward et al. 1992; Ding & Blanckenhorn 2002; Eberhard 2003b, 2005) and genitalic morphology (Duda 1925, 1926; Pont 1979; Steyskal 1987; Eberhard 2005) suggests that males of other sepsids are also incapable of forcefully inserting their genitalia into the female without female cooperation, reinforcing the idea that females control whether intromission occurs. Given the female’s ability to easily prevent intromission, the dramatic female resistance, which includes energetic side-to-side shaking, seems surprising unless it also functions as a signal. Female shaking may be ancestral in sepsids, as it occurs in other related families (Crean et al. 2000, Ramirez 2004).

In the field, female *S. cynipsea* shook for a smaller proportion of the time in successful mounts (Ward et al. 1992), again contradicting the male endurance/female exhaustion hypothesis, and apparently supporting the communication hypothesis. Other field data regarding male size from *S. cynipsea* are somewhat contradictory. Blanckenhorn et al. (1999) and Kraushaar & Blanckenhorn (2002) confirmed the overall advantage for larger males originally documented by Ward (1983). But both Ward et al. (1992) and Allen & Simmons (1996) found no sign of significant effects of male size on the success of mounts once the female left the dung pat (this is the context in which differences in female shaking behaviour would presumably bias male success). Perhaps there are also substantial differences between field and laboratory matings in *S. cynipsea* as in *A. diversiformis*. Most of the shaking by virgin female *S. cynipsea* mating in captivity occurred before oviposition began (Blanckenhorn et al. 2000), while shaking in the field may occur mostly after oviposition is finished (Ward 1983, W.G. Eberhard unpub.) (see also Parker 1972a, who reported female resistance both prior to and during oviposition). Also, in accord with *A. diversiformis*, measures of the intensity of possible male courtship (abdomen strikes, and genital contacts) in *S. cynipsea* in the field were positively correlated with mating success (Ward et al. 1992).

Unfortunately, differences in data analysis preclude further comparisons with studies of *S. cynipsea*. Blanckenhorn et al. (2000) and Ding & Blanckenhorn (2002) used total durations of female shaking behaviour per mount to analyse female willingness to copulate. We did not use this variable because (as noted by Blanckenhorn et al. 2000) the duration of female shaking behaviour is directly determined by both the male and the female: by the female’s tendency to shake more or less, and by the male’s tendency to remain mounted for a longer or shorter time. Thus, for instance, the observation of lower duration of shaking with smaller males (Ding & Blanckenhorn 2002) could have been due to a lower female tendency to initiate and sustain shaking behaviour, to a lower tendency for small males to remain mounted, or both. Our results lead us to believe that these male and female factors are largely independent in *A. diversiformis*. An additional problem with summing up female shaking behaviour, at least in *A. diversiformis*, is that the changes in the frequency and duration of shaking during a mount can confound analyses: the sharp decrease that occurred in shaking rates by females after the first 30 sec of a mount (Fig. 3) could result in longer mounts being automatically judged to involve lower rates of shaking. The sharp difference in the duration of the first mount of a male *A. diversiformis* compared with his subsequent mounts could also make a female's shaking effort/mount seem to decrease when she was mounted more than once. If similar decreases occur during mounts in *S. cynipsea* (as is suggested by the field data in fig. 18 of PARKER 1972a), the correlation between mating success and lower overall rates of shaking that was found by WARD et al. (1992) may need further analysis (their finding that the total mount duration away from the dung was not associated with mating success suggests, however, that this may not have been a problem).

Female behaviour in other flies

A partial review of studies of other species in other families of flies indicates that great care must be used in interpreting the function of female "resistance" behaviour. The behaviour of sepsid females contrasts sharply with that of females of the seaweed fly *Coelopa ursina* (Coelopidae), in which female resistance behaviour (kicking, shaking and abdomen curling) gives several signs of functioning to physically reject the male (the dislodgement and male endurance/female exhaustion hypotheses of the present study). The resistance of female *C. ursina* to mounted males was longer in successful than in unsuccessful mounts, and mounts were longer when the male was larger (CREAN & GILBURN 1998). As predicted by the physical resistence hypotheses, small females of *C. ursina* were also more often mated than large females (CREAN et al. 2000) (this trend was absent in four other species of *Coelopa*). One critical observation that could help distinguish between the physical displacement and male endurance/female exhaustion hypotheses for these flies is still lacking: it is not clear whether male dismounts occur at moments when females are actively resisting.

The observations of LINLEY and colleagues of a more distantly related fly, the ceratopogonid *Culicoides melleus*, contrast with the coelopid data, and are more similar to ours on *A. diversiformis*. Female struggles in *C. melleus* do not bring about physical displacement of the male, and may function instead, at least at some stages of male-female interactions, as communication of female receptivity. Females routinely kicked at mounted males with their hind legs, both prior to and during copulation (LINLEY & ADAMS 1972, LINLEY & MOOK 1975). But males were generally not physically forced to dismount, and much of the relatively gentle and ineffectual female kicking during copulation was not sufficiently forceful to displace the male (LINLEY & ADAMS 1972, LINLEY & MOOK 1975). LINLEY concluded (1975) that kicking during copulation "acts as a stimulus causing the male to release his claspers" (LINLEY 1975), and argued (LINLEY & MOOK 1975) that it provides a "stimulus to which the male, depending on his sensitivity [which depends on previous mating experience], may or may not respond".

Female resistance behaviour probably has still further functions in other flies. Both female shaking and pushing at the male's head with her front legs during copulation in the micropezid *Ptilosphen variolatus* appear to function as solicitation behaviour, as they were positively correlated with the rate of male delivery of regurgitated liquid to the female (Ortiz 2002). Females of *Scathophaga stercoriaria* perform subtle, low amplitude shakes both before and during copulation that may communicate lack of receptivity (W.U. Blanckenhorn et al. in prep.). Females of the phorid fly *Phalacrotophora halictorum* perform cyclic bursts of shaking and dorso-ventral vibrations of the abdomen during copulation that do not dislodge the male (Wcislo 1990). Female *Drosophila willistoni* shake vigorously during about one quarter of the approximately 8 min copulation, but not when first mounted (Ramirez 2004); males of this species have an especially strong genitalic clamp (Eberhard & Ramirez 2004), and are not dislodged by female shaking. Various other female behaviour patterns resembling resistance also occur in other groups of insects in several different contexts during copulation (Rodriguez 1998, Bloch Qazi 2003).

In summary, female "resistance struggles" probably have quite different functions in different groups. Further studies, which steer clear of the simplistic assumption that all female resistance is designed to forcefully repel the male, promise to provide insights that increase understanding of male-female interactions. Avoiding this assumption will help eliminate problems that result from overly facile interpretations of apparent male-female conflict.

ACKNOWLEDGEMENTS

We thank Rogelio Macias-Ordoñez for extensive, helpful discussions of many points, Federico Escobar Sarria for important help of several kinds, and Wolf Blanckenhorn, David Hosken, Dan Papaj, Bill Wcislo, Mary Jane West-Eberhard for thoughtful comments on the manuscript. Financial support came from the Smithsonian Tropical Research Institute.

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