Springer

Dear Author:

Please find attached the final pdf file of your contribution, which can be viewed using the Acrobat Reader, version 3.0 or higher. We would kindly like to draw your attention to the fact that copyright law is also valid for electronic products. This means especially that:

- You may not alter the pdf file, as changes to the published contribution are prohibited by copyright law.

- You may print the file and distribute it amongst your colleagues in the scientific community for scientific and/or personal use.

- You may make an article published by Springer-Verlag available on your personal home page provided the source of the published article is cited and Springer-Verlag is mentioned as copyright holder. You are requested to create a link to the published article in LINK, Springer's internet service. The link must be accompanied by the following text: The original publication is available on LINK **http://link.springer.de.** Please use the appropriate URL and/or DOI for the article in LINK. Articles disseminated via LINK are indexed, abstracted and referenced by many abstracting and information services, bibliographic networks, subscription agencies, library networks and consortia.

- You are not allowed to make the pdf file accessible to the general public, e.g. your institute/your company is not allowed to place this file on its homepage.

- Please address any queries to the production editor of the journal in question, giving your name, the journal title, volume and first page number.

Yours sincerely,

Springer-Verlag Berlin Heidelberg

Behav Ecol Sociobiol (2001) 49:283–288
DOI 10.1007/s002650000292

ORIGINAL ARTICLE

Vikram K. Iyengar · Carmen Rossini
Thomas Eisner

Precopulatory assessment of male quality in an arctiid moth (*Utetheisa ornatrix*): hydroxydanaidal is the only criterion of choice

Received: 5 June 2000 / Revised: 10 September 2000 / Accepted: 16 October 2000 / Published online: 9 December 2000
© Springer-Verlag 2000

Abstract Females of the moth *Utetheisa ornatrix* (Lepidoptera: Arctiidae) mate preferentially with males that excel in three quantitatively correlated attributes: body mass, systemic content of defensive pyrrolizidine alkaloid (derived from the larval diet), and glandular content of the courtship pheromone hydroxydanaidal (derived from the alkaloid). By so choosing, the females obtain direct phenotypic benefits (alkaloid and nutrient received with the spermatophore), and indirect genetic benefits (genes for large size, a heritable trait). We asked whether the female appraises the courting male on the basis of all three attributes, or whether, as had been postulated, she does so on the basis of the intensity of the pheromonal scent alone. We present data indicating that male possession of hydroxydanaidal is indeed the sole criterion of choice. Females fail to differentiate between males that differ in body mass or alkaloid content if the males lack hydroxydanaidal, but choose between males that are size-matched and alkaloid-free if one of the males has been experimentally endowed with hydroxydanaidal. We show moreover that females are able to differentiate between males that contain unequal quantities of hydroxydanaidal. Females abide by these criteria whether or not they themselves contain alkaloid. Their choice was also unaffected by whether they were confined singly with 2 males in small mating chambers, or were in groups of 10 with 20 males in large flight cages.

Keywords Sexual selection · Courtship · Pheromone · Pyrrolizidine alkaloid · Nuptial gift

Communicated by D. Gwynne

V.K. Iyengar · C. Rossini · T. Eisner (✉)
Department of Neurobiology and Behavior,
Cornell University, Ithaca, NY 14853, USA
e-mail: te14@cornell.edu
Tel.: +1-607-2554464, Fax: +1-607-255-6186

Present address:
C. Rossini, Facultad de Química, Universidad de la República,
General Flores 2124, Montevideo CC 1157, Uruguay

Introduction

Utetheisa ornatrix (henceforth called *Utetheisa*) is an aposematic moth in which both sexes sequester pyrrolizidine alkaloids [henceforth called alkaloid(s)] from their larval foodplants, legumes of the genus *Crotalaria* (family Fabaceae). The alkaloid is stored systemically and retained through metamorphosis, and protects both larvae and adults from predators (Eisner and Meinwald 1987, 1995). At mating, the male bestows a sperm package (spermatophore) upon the female, amounting on average to 11% of his body mass (LaMunyon and Eisner 1994). The spermatophore contains sperm and nutrient, plus a quantity of alkaloid proportional to the amount of alkaloid stored systemically by the male (Dussourd et al. 1991). The alkaloid received by the female, which may contribute to her defense (González et al. 1999), is allocated in part by her, together with alkaloid of her own, to the eggs for their protection (Dussourd et al. 1988; Hare and Eisner 1993; Eisner et al. 2000). The nutrient received with the spermatophore enables the female to increase her egg production by 15% per mating on average (LaMunyon 1997). Females mate on average with four to five males during their lifespan (Pease 1968), but use sperm selectively from larger males, which produce larger spermatophores (LaMunyon and Eisner 1993, 1994). Body size is heritable in *Utetheisa* (Iyengar and Eisner 1999a).

Utetheisa males proclaim their fitness to females during courtship through a chemical signal. This signal, hydroxydanaidal (HD), aired by the male from two eversible brushes (coremata), is derived from the alkaloid and is produced by the male in quantities proportional to his alkaloid content (Dussourd et al. 1991). HD can therefore provide the female with a measure of the male's alkaloidal load and, by inference, his alkaloid-giving capacity. Both variables, the HD titer and the alkaloid content, correlate positively with male body size (and therefore with spermatophore size) (Conner et al. 1990; Dussourd et al. 1991; LaMunyon and Eisner 1994). These relationships are of consequence to the fe-

male, because by selecting an HD-rich male, she ensures receipt of a large alkaloid gift (phenotypic benefit) and genes that encode for large size (genetic benefit) (Iyengar and Eisner 1999a, 1999b).

Existing evidence indicates that the female selects the male on the basis of his HD content. Males with HD (raised on an alkaloid-containing diet) were favored by females over males lacking HD (raised on an alkaloid-free diet) (Conner et al. 1981). Missing from these experiments were data on the acceptability of males with quantities of HD intermediate between these extremes, leaving open the question whether the female can distinguish between incremental levels of HD. Also unsettled was whether the female might be able to assess males by their body size and/or alkaloid content, the two correlates of HD. Given that size plays a major role in mate assessment in insects and other organisms (see review by Andersson 1994), it seemed logical to investigate whether *Utetheisa* females can appraise males directly on the basis of size. By the same token, since resources are also often the object of selection in insects (Thornhill 1981; Steele 1986), it made sense to determine whether the alkaloid itself in the male could be the basis of quantitative appraisal.

We present data showing that HD is the sole parameter by which the female assesses the male in courtship. Specifically, we demonstrate that (1) females can indeed differentiate between males bearing high and intermediate levels of HD, and that they prefer the former; (2) females do not differentiate between males of different size if both males are HD free; (3) females can differentiate between alkaloid-free males if one male has been artificially endowed with HD, and they choose the male so endowed, and (4) females do not differentiate between males of different alkaloid content if the males have had their coremata removed (and are therefore unable to produce HD). Moreover, we present evidence that the coremata themselves do not have signal value (females do not differentiate between corematectomized and coremata-bearing males, if these males lack HD). Finally, we show that the female's choice of male is unaffected by whether or not she herself possesses alkaloid. All experiments were done in duplicate, in cramped (small chambers) and spacious (large cages) quarters, to determine whether mate selection is affected by the degree of confinement during courtship.

Methods

Alkaloid analyses

Whole bodies of *Utetheisa* were extracted with phosphate buffer and the extracts were analyzed by high-pressure liquid chromatography, as previously described (González et al. 1999).

Experimental moths: dietary categories

All *Utetheisa* were reared in the laboratory (from stock collected in Highlands County, Fla.), as previously described (Conner et al. 1981). Three dietary regimens were used:

- (–) *Utetheisa*. These were reared on a pinto bean-based diet lacking alkaloid [(–) diet] and the moths were therefore alkaloid free (Conner et al. 1981).
- (+) *Utetheisa*. These were reared on the same pinto bean-based diet as the (–) *Utetheisa*, but the diet was supplemented with seeds of *Crotalaria spectabilis*, a major foodplant of *Utetheisa*. *Utetheisa* reared on this supplemented diet [(+) diet] contain the principal alkaloid in *C. spectabilis*, monocrotaline, at a level [628±48 (SE) µg per adult; Bogner and Eisner 1992] commensurate with that of alkaloid in *Utetheisa* reared on *C. spectabilis* plants (701±59 µg per adult; Conner et al. 1990).
- (±) *Utetheisa*. These were reared on (+) diet for the first 11 days following hatching and were then shifted to (–) diet for the remainder of their larval life (approximately 14 days). We analyzed a sample of such individuals and found them to contain monocrotaline in an amount (217±35 µg, n=42 adults) equivalent to about 35% of that in (+) *Utetheisa*.

Experimental moths: other categories

- (– HD) *Utetheisa*. These were reared on (–) diet and received a supplement of HD (15 µg in 1 µl of methylene chloride) added directly to their coremata. Control individuals were treated by addition of l µl methylene chloride only. Treatment was effected by squeezing the moth's abdomen gently to evert the coremata, and then trickling the liquid sample directly onto the coremata from a micropipette.
- (C) *Utetheisa*. These were treated by surgical excision of the coremata. Depending on whether they were reared on (+) or (–) diet, they were designated (+ C) and (– C) *Utetheisa*, respectively. Corematectomy was effected by gently compressing the abdomen to evert the coremata, and then pulling out the primary corematal scales with forceps (Conner et al. 1981). Control individuals were similarly manipulated, but were treated by removal of some of the body scales adjacent to the coremata.

Body size criteria

Adults were judged to be "size matched" if they differed by less than 5 mg in body mass. They were judged to be "different-sized" if they differed by at least 20 mg (about 10%) in body mass. In males, a difference of 20 mg ensured that the individuals were discernibly different to the female (Iyengar and Eisner 1999b).

Mating protocol

Matings were carried out in two enclosure types, designated chambers and cages, differing greatly in size. The chambers were small cylindrical containers (0.35 l) with screened lids. The cages were screened cubical enclosures, 2 m to the side.

The experiments in the chambers and cages were of parallel design, in that the females were offered the same choice of males in each series. The two sets of experiments are therefore designated by the same letters A–G, with the subscript "c" being appended to denote those done in cages.

In the chambers, all experiments were carried out in duplicate, using (+) and (–) females. In the more spacious cages, where vastly greater numbers of individuals were required per trial, the experiments were done with (+) females only [or, in experiment B_c, with (–) females only].

Matings in chambers: experiments A–G

For a given trial, one female and two males, all 3-day-old virgins of known mass, were placed simultaneously in a chamber and checked visually (under red light) at 6-h intervals for the occurrence of mating (copulation lasts 10–12 h in *Utetheisa*; LaMunyon

and Eisner 1994). During the first hour, events were monitored more or less continuously to confirm that both males engaged in precopulatory behavior, that is, that they both undertook the sort of fluttering advances toward the female that are an integral part of the courtship ritual (Conner et al. 1981). A record was kept of which of the two males mated (the males were wing marked for recognition purposes). Trials were replicated 40–60 times per experiment. The data for each experiment (female mate choice, expressed as males that mated vs those that did not) were analyzed by conventional statistics (χ^2-test; Snedecor and Cochran 1989). Differences in mate choice of (+) and (–) females were also analyzed (*G*-test; Snedecor and Cochran 1989).

Matings in cages: experiments A_c–G_c

For a given trial, 10 females and 20 males, all 3-day-old virgins of known mass, were placed together for 24 h in a cage and checked visually (under red light) at 6-h intervals for matings (males were distinguished by wing marks). Ten replicate trials were done per experiment. For experiments C_c and D_c, males were randomly selected from the laboratory cultures without consideration of size; the data (mean body mass of mated vs mean body mass of unmated males) were analyzed using a paired *t*-test (Snedecor and Cochran 1989). For all other experiments in cages, the males consisted of 10 pairs, selected so the members of each pair were size matched but from opposite treatment groups; the mating success of males of the two treatment groups was compared using a Wilcoxon signed-rank test (Snedecor and Cochran 1989).

Results

The results of the experiments in chambers and cages are given in Tables 1 and 2, respectively.

Matings in chambers

In all experiments done in chambers (experiments A–G), there was no difference in the selectivity of (+) and (–) females (*G*-tests: experiment A: G=0.30, P=0.59; B: G=0.01, P=0.94; C: G=0.20, P=0.65; D: G=0.05, P=0.82; E: G=0.05, P=0.82; F: G=0.18, P=0.67; G: G=0.45, P=0.50).

Experiment A: size-matched males, one (+), one (–)

The males differed only in that one contained alkaloid and HD and the other contained neither compound; the females favored the male with these chemicals.

Experiment B: size-matched males, one (+), one (±)

The males differed only in the amounts of alkaloid and HD they contained; the females favored the more richly endowed male.

For the 42 trials with (–) females, we ascertained the actual alkaloid contents of the mated and unmated males. For the unmated males, we obtained the value by analyzing the male. For the mated males, we analyzed both the male and female after mating, and expressed the male content as the sum of the two values (the female was analyzed because she received a part of the male's alkaloid by seminal transfer). The mated males, on average, contained more alkaloid (505.35±33.79 µg) than the unmated males (274.07±45.15 µg; paired *t*-test, t=3.52, df=41, P<0.005).

Experiment C: different-sized males, both (+)

The males differed in size and could be expected to contain different amounts of alkaloid and HD; the females favored the larger male, that is, the one more richly endowed with the two chemicals.

Experiment D: different-sized males, both (–)

The males differed only in size and were both alkaloid and HD free; the females did not differentiate between the males.

Table 1 Mating incidence (number of males that mated per total number of trials) of 3-day-old virgin males presented as pairs to single females, in courtship trials in chambers

Experiment	Female	Male 1	Male 2	Number of trials	Mating Incidence (male 1/male 2)	χ^2 (df=1)	P-value
A	(+)	(+)	(–)	44	32/12	9.09	<0.001
	(–)	(+)	(–)	41	28/13	5.49	<0.05
B	(+)	(+)	(±)	43	30/13	6.72	<0.01
	(–)	(+)	(±)	42	32/10	11.52	<0.001
C	(+)	(+ large)	(+ small)	60	43/17	11.27	<0.001
	(–)	(+ large)	(+ small)	47	34/13	9.38	<0.005
D	(+)	(– large)	(– small)	42	23/19	0.38	0.51
	(–)	(– large)	(– small)	41	20/21	0.24	0.63
E	(+)	(– HD)	(–)	40	27/13	4.90	<0.05
	(–)	(– HD)	(–)	43	28/15	3.93	<0.05
F	(+)	(+ C)	(– C)	43	26/17	1.88	0.19
	(–)	(+ C)	(– C)	43	27/16	2.81	0.09
G	(+)	(–)	(– C)	42	24/18	0.86	0.35
	(–)	(–)	(– C)	40	21/19	0.10	0.75

Table 2 Mating incidence (mean number of males that mated per trial) of 3-day-old virgin males presented in groups of 20 to 10 females, in courtship trials in cages (n=10 trials per experiment, df=9 for all statistics). Values are given as mean±SE

Experiment	Female	Male 1	Male 2	Mean matings per trial	Mating incidence (male 1/male 2)	Statistical test	Statistic	P-value
A_c	(+)	(+)	(–)	9.10±0.35	6.30±0.42/2.80±0.25	Wilcoxon signed rank	Z=2.80	<0.005
B_c	(–)	(+)	(±)	8.20±0.23	5.70±0.45/2.50±0.37	Wilcoxon signed rank	Z=2.52	<0.05
C_c	(+)	(+), of various sizes		8.30±0.50	Larger males preferred[a]	Paired t	t=18.78	<0.001
D_c	(+)	(–), of various sizes		5.40±0.58	No size preference[a]	Paired t	t=–1.56	0.15
E_c	(+)	(– HD)	(–)	8.10±0.30	5.90±0.37/2.20±0.46	Wilcoxon signed rank	Z=2.67	<0.01
F_c	(+)	(+ C)	(– C)	7.40±0.54	4.20±0.44/3.20±0.33	Wilcoxon signed rank	Z=1.60	0.10
G_c	(+)	(–)	(– C)	7.80±0.51	4.10±0.35/3.70±0.30	Wilcoxon signed rank	Z=0.93	0.34

[a] See text for mean body mass values of mated and unmated males

Experiment E: size-matched males, one (– HD), one (–)

The males were equal-sized and free of both alkaloid and endogenous HD, but one had received an HD supplement; the females favored the supplemented male.

Experiment F: size-matched males, one (+ C), one (– C)

The males were equal-sized, lacked coremata (and therefore HD), and differed only in that one contained alkaloid; the females failed to differentiate between the males.

Experiment G: size-matched males, one (–), one (– C)

The males were equal-sized, were both alkaloid and HD free, and differed only in that only one had intact coremata; the females failed to differentiate between the males.

Matings in cages

A comparison of Tables 1 and 2 shows clearly that the females exercised the same criteria of choice in the cages as in the chambers.

In experiment B_c, we ascertained the alkaloid content of all males (using the same procedure as with males in experiment B) and found that mated males, on average, contained significantly more alkaloid (349.57±23.60 µg) than unmated males (211.58±21.26 µg; t-test, t=4.28, df=198,P<0.001).

In experiment C_c, where (+) males of various sizes were offered, the mean mass of mated males was 99.28±1.73 mg (n=83) compared to 80.88±1.59 mg (n=117) for unmated males. In experiment D_c, where (–) males of various sizes were offered, the mean mass of mated males was 88.26±2.41 mg (n=54) compared to 91.58±1.51 mg (n=146) for unmated males.

Discussion

Both sets of experiments demonstrated that *Utetheisa* females are able to chose between males only if they differ in HD content. Neither male size alone nor male alkaloid content provides the female with an adequate criterion of choice. The three parameters – HD content, alkaloid content, and body size – are usually correlated in the male (Conner et al. 1990; Dussourd et al. 1991), so that the female, by favoring males rich in HD, does indeed secure partners that are alkaloid rich and large, but she appears unable to assess the male solely on the basis of alkaloid content or size. HD proved effective even as an experimental subsidy to males devoid of intrinsic HD. The compound evidently has compelling signal value, and may be the exclusive pheromonal factor that the female heeds as she assesses the male during precopulatory interplay. Indeed, while we were not surprised to find that the females exercised normal mate choice within the relatively spacious confines of the cages, we did not initially expect them to be comparably selective within the cramped quarters of the chambers. That they were provides evidence that females, in the presence of males and ready for courtship, are virtually oblivious to factors other than HD.

That the alkaloid itself is devoid of signal value in courtship is not unexpected. It is less volatile than HD and for that reason alone less suited for communicative purposes. But more important, by virtue of being present in both the female and the *Crotalaria* plants that form the backdrop of courtship in *Utetheisa* (Conner et al. 1980), the alkaloid is too much a component of the environmental noise to serve as an effective pheromonal signal. That male size should have no signal value is also not surprising. As a physical parameter, size might simply be too difficult for the female to gauge, given that he is actively fluttering rather than quiescent during courtship, when she makes her assessment. One wonders, in fact, how size is appraised by other organisms that select for this parameter in courtship. While size appraisal does indeed take place directly in some cases (Gwynne 1981; Møller 1988), that this is always the case is by no means

certain. The possibility that the criterion of selection is actually an indirect correlate of size, as in *Utetheisa*, cannot be ruled out in many instances. And does male pheromone production, which is widespread among moths (see review by Phelan 1997), serve as a quantitative indicator of male fitness in other species as well?.

A significant finding was that the females could discriminate between (+) and (±) males, i.e., between males of different alkaloid content. In previous papers on *Utetheisa*, we had assumed that females have this ability (Dussourd et al. 1991; Iyengar and Eisner 1999b) and showed that females have antennal receptors highly sensitive to HD (Grant et al. 1989), but we had only demonstrated that females can discriminate between alkaloid-possessing males and males lacking alkaloid altogether (Conner et al. 1981). The present finding provides support for the notion that HD is a chemical yardstick by which the female *Utetheisa* ascertains not merely possession, but her suitor's degree of alkaloid possession. The idea that males are put quantitatively to the test in courtship is, of course, not new, and has its counterparts in mating systems where the appraisal is on the basis of acoustic and visual cues (Ryan 1983; Hill 1990; Andersson 1994).

It would be interesting to know how sensitive female *Utetheisa* are to differences in HD concentration and how accurately HD indicates the male's alkaloid content. Making the necessary chemical determinations should pose no problem, given the sensitivity of current analytical techniques. Particularly intriguing would be to determine whether the quantitative relationship of corematal HD to systemic alkaloid content holds even for males of low systemic alkaloid levels. If not, one would want to determine whether a male with little alkaloid "lies" to the female by emitting a disproportionately intense HD signal. A male could clearly gain by misrepresenting himself through an exaggerated corematal message when he is at a competitive disadvantage vis-à-vis other males (although there is obviously a limit to the frequency of lying that is possible before females would ignore the signal; Grafen 1990). One would also need to explain if alkaloid-underendowed males represent themselves honestly by way of uninflated HD signals. The data so far available on the proportionality of corematal HD to systemic alkaloid load (Dussourd et al. 1991), in male *Utetheisa* of low alkaloid content, are insufficient to resolve these issues.

Also of interest is the finding that, in exercising choice, the female is unaffected by her own alkaloid content. This would seem to indicate that the female discriminates against lesser males no matter what the circumstances, even if she herself is already well endowed with the two commodities, alkaloid and nutrient, that males can provide. Since the *Utetheisa* female constantly voids both alkaloid and nutrient into her eggs, and her capacity for egg production can be expected to increase as a function of nutrient received (LaMunyon 1997), she might indeed demand at all times that males be able to deliver alkaloid and nutrient in disproportionately high amounts. At any rate, by being thus selective, the female ensures receipt of enhanced genetic benefits (Iyengar and Eisner 1999b). Precisely how, over time, nutrient and alkaloid are allocated by the female to the eggs, and whether or not female preferences for partners change as they mate with male after male in the course of their lives remains to be determined. It seems certain, though, that females may at times mate with more males than had been previously assumed. In a Florida population of *Utetheisa* that we studied recently, the females (n=45) were found (by dissection of the bursa and tally of the colla) to have had on average 11, and up to a maximum of 22 male partners.

Acknowledgements J.B. Grant, E.V. Iyengar, H.K. Reeve, and P.W. Sherman provided helpful comments on earlier versions of the paper. We are indebted to Silvina García for providing us with hydroxydanaidal, and to J. Schlesinger for technical assistance. Research support was provided by National Institutes of Health Grant AI02908 (to T.E.), a predoctoral fellowship from the National Science Foundation (to V.I.), and a Johnson & Johnson fellowship (to C.R.). This study complies with all current US laws. This is paper number 172 in the series "Defense Mechanisms of Arthropods."

References

Andersson M (1994) Sexual selection. Princeton University Press, Princeton, NJ

Bogner F, Eisner T (1992) Chemical basis of pupal cannibalism in a caterpillar (*Utetheisa ornatrix*). Experientia 48:97–102

Conner WE, Eisner T, Vander Meer RK, Guerrero A, Ghiringelli D, Meinwald J (1980) Sex attractant of an arctiid moth (*Utetheisa ornatrix*): a pulsed chemical signal. Behav Ecol Sociobiol 7:55–63

Conner WE, Eisner T, Vander Meer RK, Guerrero A, Meinwald J (1981) Precopulatory sexual interaction in an arctiid moth (*Utetheisa ornatrix*): role of a pheromone derived from dietary alkaloids. Behav Ecol Sociobiol 9:227–235

Conner WE, Roach B, Benedict E, Meinwald J, Eisner T (1990) Courtship pheromone production and body size as correlates of larval diet in males of the arctiid moth, *Utetheisa ornatrix*. J Chem Ecol 16:543–552

Dussourd DE, Ubik K, Harvis C, Resch J, Meinwald J, Eisner T (1988) Biparental defensive endowment of eggs with acquired plant alkaloid in the moth *Utetheisa ornatrix*. Proc Natl Acad Sci USA 85:5992–5996

Dussourd DE, Harvis C, Resch J, Meinwald J, Eisner T (1991) Pheromonal advertisement of a nuptial gift by a male moth (*Utetheisa ornatrix*). Proc Natl Acad Sci USA 88:9224–9227

Eisner T, Meinwald J (1987) Alkaloid-derived pheromone and sexual selection in Lepidoptera. In: Prestwich GD, Blumquist GJ (eds) Pheromone biochemistry. Academic Press, Orlando, Fla, pp 251–269

Eisner T, Meinwald J (1995) The chemistry of sexual selection. Proc Natl Acad Sci USA 92:50–55

Eisner T, Eisner M, Rossini C, Iyengar VK, Roach BL, Benedikt E, Meinwald J (2000) Chemical defense against predation in an insect egg. Proc Natl Acad Sci USA 97:1634–1639

González A, Rossini C, Eisner M, Eisner T (1999) Sexually transmitted chemical defense in a moth (*Utetheisa ornatrix*). Proc Natl Acad Sci USA 96:5570–5574

Grafen A (1990) Biological signals as handicaps. J Theor Biol 144:473–516

Grant AJ, O'Connell RJ, Eisner T (1989) Pheromone-mediated sexual selection in the moth *Utetheisa ornatrix*: olfactory receptor neurons responsive to a male-produced pheromone. J Insect Behav 2:371–385

Gwynne DT (1981) Sexual difference theory: Mormon crickets show role reversal in mate choice. Science 213:779–780

Hare JF, Eisner T (1993) Pyrrolizidine alkaloid deters ant predators of *Utetheisa ornatrix* eggs: effects of alkaloid concentration, oxidation state, and prior exposure of ants to alkaloid-laden prey. Oecologia 96:9–18

Hill GE (1990) Female house finches prefer colourful males: sexual selection for a condition-dependent trait. Anim Behav 40: 563–572

Iyengar VK, Eisner T (1999a) Heritability of body mass, a sexually selected trait, in an arctiid moth (*Utetheisa ornatrix*). Proc Natl Acad Sci USA 96:9169–9171

Iyengar VK, Eisner T (1999b) Female choice increases offspring fitness in an arctiid moth (*Utetheisa ornatrix*). Proc Natl Acad Sci USA 96:15013–15016

LaMunyon CW (1997) Increased fecundity, as a function of multiple mating, in an arctiid moth, *Utetheisa ornatrix*. Ecol Entomol 22:69–73

LaMunyon CW, Eisner T (1993) Postcopulatory sexual selection in an arctiid moth (*Utetheisa ornatrix*). Proc Natl Acad Sci USA 90:4689–4692

LaMunyon CW, Eisner T (1994) Spermatophore size as determinant of paternity in an arctiid moth (*Utetheisa ornatrix*). Proc Natl Acad Sci USA 91:7081–7084

Møller AP (1988) Female choice selects for male sexual tail ornaments in the monogamous swallow. Nature 332:640–642

Pease RW Jr (1968) The evolutionary and biological significance of multiple pairing in Lepidoptera. J Lepid Soc 22:197–209

Phelan PL (1997) Evolution of mate-signaling in moths: phylogenetic considerations and prediction from the asymmetric tracking hypothesis. In: Choe JC, Crespi BJ (eds) The evolution of mating systems in insects and arachnids. Cambridge University Press, Cambridge, UK, pp 240–256

Ryan MJ (1983) Sexual selection and communication in a neotropical frog, *Physalaemus pustulosus*. Evolution 37:261–272

Snedecor GW, Cochran WG (1989) Statistical methods. Iowa University Press Ames

Steele RH (1986) Courtship feeding in *Drosophila subobscura*. II. Courtship feeding by males influences female mate choice. Anim Behav 34:1099–1108

Thornhill R (1981) *Panorpa* (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive efforts. Annu Rev Ecol Syst 12:355–386