

# Mating behavior and sexual selection in a polygamous beetle

Wen LU<sup>1</sup>, Qiao WANG<sup>2\*</sup>, Mingyi TIAN<sup>3</sup>, Jin XU<sup>4</sup>, Jian LV<sup>5</sup>, Aizhi QIN<sup>1</sup>

<sup>1</sup> College of Agriculture, Guangxi University, Nanning 530005, China

<sup>2</sup> Institute of Natural Resources, Massey University, Private Bag 11222, Palmerston North, New Zealand

<sup>3</sup> College of Natural Resources and Environment, South China Agricultural University, Guangzhou 510642, China

<sup>4</sup> College of Agriculture, Yunnan University, Kunming 650091, China

<sup>5</sup> Library, Guangxi University, Nanning 530005, China

**Abstract** Mating behavior and sexual selection in relation to morphometric traits in a polygamous beetle, *Glenea cantor* (F.) (Coleoptera: Cerambycidae), were investigated. Upon encounter, a male approached a female, mounted her, grasped her terminal abdomen with his hind tarsi, and attempted to mate. Successful mating lasted about 3.5 h. Although all traits measured in females and half of traits in males were significantly correlated with mating success, the primary selection on virgin females was the genital trait, the bursa copulatrix length, and that on males was the body length and hind tarsal length. Longer bursa copulatrix accommodated a larger ejaculate, suggesting that this female trait benefits the male that first mates with the female in terms of increasing ejaculate size to beat subsequent males in sperm competition. Under a female-biased sex ratio, more than 20% of matings failed within 20s after the male genitalia had been inserted into hers, suggesting that males assess genital features of the female before insemination and undertake cryptic male mate choice. Larger males were more capable of grasping females and achieving mating. During the premating struggle the male almost always used his hind tarsi to lift the female terminal abdomen to the position for his genitalia to insert, and as a result, males with longer hind tarsi achieved higher mating success [*Current Zoology* 59 (2): 257–264, 2013].

**Keywords** Bursa, Body length, Mating behavior, Sexual selection, Tarsal length

Sexual selection has been used to explain the evolution of external morphological traits in different sexes that give a mating advantage for their bearers (Darwin, 1871). In this paper, premating sexual selection is defined as sexual selection before insemination occurs. Many external morphological traits in males (e.g., Danielsson, 2001; Wang, 2002; Jimenez-Perez and Wang, 2004; Wang and Zeng, 2004; Yang and Wang, 2004; Willemart et al., 2009) and females (e.g., Wang, 2002; Wang and Zeng, 2004; Yang and Wang, 2004; Stuart-Smith et al., 2007; Bussiere et al., 2008; Xu and Wang, 2010) are reported to be sexually selected in the premating process. Several studies show that genital traits are also subject to sexual selection (e.g., Hosken and Stockley, 2004; Yang and Wang, 2004; Xu and Wang, 2010) although genital features are often assumed to be under postmating rather than premating sexual selection (reviewed in Eberhard, 1996; Arnqvist and Danielsson, 1999; Kahn et al., 2010).

Variance in fitness among individuals within a sex is a prerequisite for sexual selection to occur (Clutton-Brock, 2007, 2009). However, as various studies (e.g.,

Clutton-Brock, 1983; Sutherland, 1985; Hubbell and Johnson, 1987; Gowaty and Hubbell, 2005; Tang-Martinez and Ryder, 2005; Pischedda and Chippindale, 2006) have suggested, these variances may not result in sexual selection because a substantial proportion of fitness variance within sexes may be caused by age, by random processes that do not contribute to selection, or by phenotypic differences that have no heritable basis. Therefore, it is not always easy to determine traits that are directionally selected and honestly reflect reproductive fitness when a number of traits are positively associated with mating success (Partridge and Halliday, 1984; Møller, 1994; Xu and Wang, 2010).

*Glenea cantor* (F.) (Coleoptera: Cerambycidae: Lamiinae) is a polygamous beetle with five generations a year in southern China (Lu et al., 2011a). Adults are diurnally active, and both tactile and visual cues play roles in short-range sex location and recognition (Lu et al., 2007). Premating interactions between sexes typically involve frequent contacts between antennae, legs, abdomens, and genitalia (Lu et al., 2007; this study). Successful mating lasts several hours and insemination

starts  $\approx 20$  min after their genitalia are connected (WL unpubl. data). Here we postulate that the traits of those body parts that are in frequent contact between sexes before insemination occurs may be involved in mutual assessment and may be subject to premating sexual selection in *G. cantor*.

In the present study, we made observations on mating behavior to determine mating behavioural sequence and body parts involved in possible mate assessment in both sexes. We then attempted to infer sexually selected traits in each sex by carrying out mate choice experiments, recording short and successful matings, measuring those traits that were in frequent contact between sexes before insemination, and statistically analysing the data. Finally, we discussed the form and nature of premating sexual selection in both sexes of this beetle.

## 1 Materials and Methods

### 1.1 Rearing conditions and morphometrics

Insects were obtained from our laboratory colony mass-reared on freshly cut *Bombax ceiba* L. twigs at  $25\pm 2^\circ\text{C}$ ,  $75\%\pm 5\%\text{RH}$  and a photoperiod of 14:10 h (L:D) (Lu et al., 2011a), where all experiments were carried out.

To ensure virginity, we collected newly emerged adults from the colony daily and reared them individually in glass containers (10 cm diameter by 12 cm high), each with a freshly cut *B. ceiba* twig section (1.5 cm diameter by 2 cm long). Adults were reared for eight days before experiments because this species becomes sexually mature  $\approx$  six days after emergence (Lu et al., 2007).

All observations on mating behavior and mate choice experiments were conducted between 8 and 14 h into the photophase because most matings occur during this period (Lu et al., 2013).

Morphological traits were measured under a stereomicroscope (WILD M8, Switzerland), equipped with an ocular micrometer. All measurements of length and width reported here were greatest length and width. For example, body length was the length between the top of the head and the abdominal tip.

### 1.2 Observations of mating behavior

To observe the details of mating behavior, we set up 60 pairs, each in an above mentioned glass container with a freshly cut *B. ceiba* twig section (1.5 cm diameter by 2 cm long) as adult food. For each container we released one 8-day-old virgin male and one 8-day-old virgin female, and immediately started observing their behav-

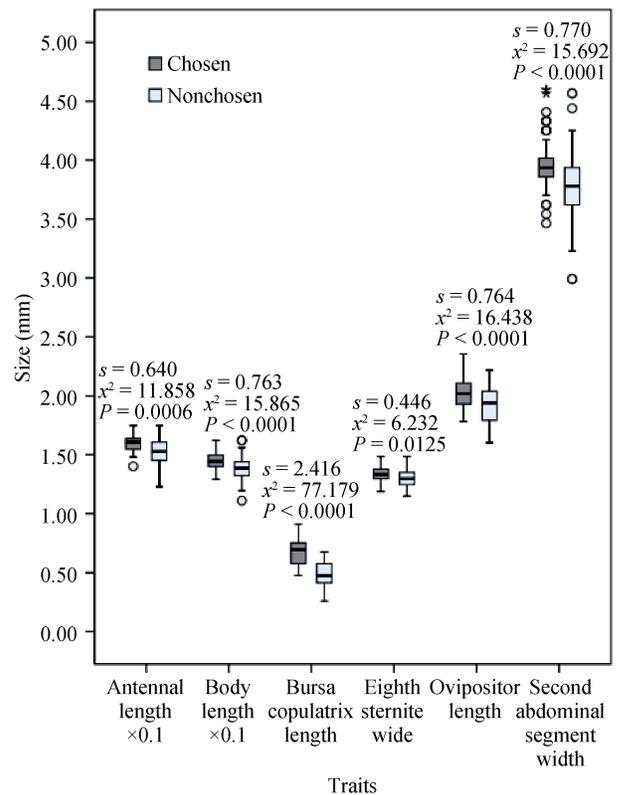
ior. We recorded all detailed activities from release to successful mating. Mating duration was also recorded.

In addition, we allowed ten 8-d-old pairs to mate, asphyxiated them in copula using  $\text{CO}_2$  and dissected them for examination of the position of male genitalia inside the female during mating.

### 1.3 Sexual selection on female traits

To determine female traits that were associated with mating success in female *G. cantor*, and to attempt to find traits that may be subject to directional sexual selection, we allowed mating to occur under a female-biased sex ratio. Sixty-seven replicates were set up. For each replicate, we released an 8-d-old virgin male and two 8-d-old virgin females to one of the above-mentioned glass containers and observed the mating events. Insects were placed in a freezer at  $-20^\circ\text{C}$  for 24 h immediately after successful mating for morphological measurement.

We measured external morphological traits of both mated and unmated females, and then dissected all females and measured their genitalia (Fig. 1). We selectively measured these traits because, based on the literature and our own observations (see Results), they



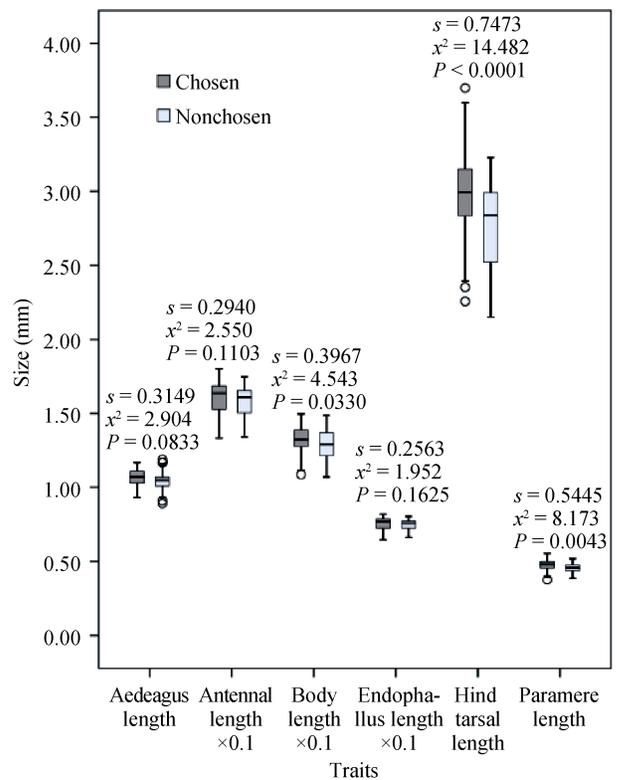
**Fig. 1 Comparison of morphological traits between females that succeeded in mating ( $n = 67$  for each trait) and those that failed ( $n = 67$  for each trait)**

may reflect female reproductive fitness and thus may be subject to sexual selection. Female body size is reported to be a function of reproductive potential in many insects (e.g., Kraak and Bakker, 1998; Stuart-Smith et al., 2007; WL unpubl data). Antennae are involved in the initial and subsequent contact with males in both pre-copulatory and copulatory *G. cantor* (this study), and their length could thus be a signal of female fitness. Abdominal size appears to be an honest signal of the number of mature eggs that females carry in several insect species (e.g., Funk and Tallamy, 2000; Yang and Wang, 2004; Li et al., 2005; Bussiere et al., 2008; Xu and Wang, 2010). The size of the reproductive opening in female cerambycids depends on the width of the eighth sternite, which may determine the efficiency of the male genitalia insertion. The ovipositor is an important organ in insects that helps ensure the maximal survival of offspring (e.g., Mousseau and Roff, 1995; Sivinski et al., 2001; Yang and Wang 2004; Lu et al., 2011b). The bursa copulatrix is a structure for ejaculate deposition in many species across insect orders including beetles (e.g., Dtingelhope and Schmitt 2006; this study), and the length of this structure is the function of its volume (see Results), which determines the amount of ejaculate a female can accommodate.

#### 1.4 Sexual selection on male traits

To determine male traits that were associated with mating success in male *G. cantor* and to attempt to find traits that may be subject to directional sexual selection, we set up mating trials and made measurements as above, but here we released one virgin female and two virgin males in each replicate. Sixty-one replicates were performed for this experiment.

We measured external morphological traits of both mated and unmated males, and then dissected all males and measured their genitalia (Fig. 2). We selectively measured these traits because, based on the literature and our own observations (see Results), they may reflect male reproductive fitness and thus may be subject to sexual selection. Many authors (e.g., Partridge et al., 1987; Danielsson, 2001; Jimenez-Perez and Wang, 2004) report that male insect body size is a determinant of his reproductive fitness. Males with longer antennae have better ability to detect females in several insect species (e.g., Jimenez-Perez and Wang, 2004; Yang and Wang, 2004). During the premating process in *G. cantor* male antennae frequently contact females on their antennae and abdomens (see Results) and their length could thus be a signal of male fitness. Although all six legs are involved in holding females in the premating process, the



**Fig. 2 Comparison of morphological traits between males that succeeded in mating ( $n = 61$  for each trait) and those that failed ( $n = 61$  for each trait)**

male hind tarsi play a major role in mating success (see Results). Therefore, male hind tarsal length may be subject to sexual selection. Parameres, aedeagus and endophallus appear to work together to achieve successful insertion of the male genitalia into the female reproductive tract, and may thus be under sexual selection.

#### 1.5 Statistical analysis

To determine whether those morphological traits measured in each sex were correlated with each other, we performed Pearson analysis and generated Pearson correlation matrices.

To estimate the net sexual selection on traits and to identify the direct and indirect effect of selection, we used standardized bivariate and multivariate selection analyses (Lande and Arnold, 1983; Arnold and Wade, 1984), where morphological traits were used as independent variables and mating success as a dependent variable. Individuals that succeeded in mating were coded as 1, and those that failed as 0. All included independent variables were standardized to mean zero and unit variance prior to analyses. Standardization removes the effect of differential scaling and therefore allows for a comparison (in standard deviation units) of the relative importance of each variable (Gibson, 1987).

Directional selection differentials ( $s$ ) estimate the net selection acting on a trait by measuring the relative strength of bivariate relationships (bivariate analysis) between relative mating success and each trait (Pryke et al., 2001; Møller et al., 2009). A bivariate logistic regression was performed to calculate the correlation of mating success with each trait, where  $s$  was estimated by the coefficient of the regression. Directional selection gradients ( $\beta'$ ) quantify the strength of the selection acting on the trait independent of variation in other traits included in the regression model (Lande and Arnold, 1983).  $\beta'$  values were calculated as partial linear regression coefficients from multiple regressions (multivariate analysis) of relative mating success to the standardized value of the traits (Pryke et al., 2001; Møller et al., 2009). A multiple logistic regression was then applied to the multivariate analysis.

In the multivariate regressions strong correlations among the independent variables (multicollinearity) can lead to an overestimation of the standard errors of the regression coefficients, reducing the power of the analysis (Mitchell-Olds and Shaw, 1987). To assess the influence of multicollinearity on the results, we examined the PCA (principal component analysis) correlation matrix of the standardized variables in each regression. Condition numbers (square root of the ratio of the largest eigenvalue to the smallest) below 10 are considered acceptable (Fry, 1993). In the present study, the condition numbers from all selection gradients were less than 6, indicating that the correlations among the variables were not sufficiently high to adversely affect the significance tests.

Rejection level was set when  $\alpha < 0.05$  in all analyses. All analyses were made using SAS9.1 (SAS, 2006).

## 2 Results

### 2.1 Mating behavior

Released insects often walked for  $< 5$  min after released to glass containers, after which time sexual behavior occurred. When sexes were  $\approx 3$  cm apart, the

male approached the female, and upon contact with her body by his antennae, he mounted her and held her elytra with his front and mid tarsi and her terminal abdomen with his hind tarsi, and attempted to mate. During this process the male and female frequently contacted each other on their antennae, and the male frequently touched the female abdomen with his antennae.

Upon mounting, the male grasped the female terminal abdomen with his hind tarsi, stretched his parameres and aedeagus which were in contact with the female abdominal terminal and remained outside the female genital chamber, and then inserted his reversed endophallus. Male hind tarsi and stretched parameres and aedeagus appeared to play the major role in ensuring the successful insertion of his endophallus. Dissection shows that the male inserted his endophallus all the way to the end of the vagina where he reversed his flagellum and inserted it into the duct leading to the bursa copulatrix; the tip of the flagellum stopped at the opening of the bursa copulatrix where sperm were transferred ( $n = 10$ ). Successful mating lasted  $3.29 \pm 0.97$  h (mean  $\pm$  SE,  $n = 60$ ).

### 2.2 Sexual selection on female traits

Successful matings occurred in all 67 replicates. However, before the male eventually mated with one of the two females successfully, in 14 replicates the male performed short mating with one or both females, i.e. withdrawing his genitalia  $\approx 20$  s after genitalia insertion.

Pearson correlation analysis shows that all six traits measured were significantly correlated with each other (Table 1).

The initial bivariate analysis indicates that all six traits measured in females were significantly correlated with female mating success, with the bursa copulatrix length having the greatest selection differential value ( $s$ ) (Fig. 1). The multivariate analysis reveals that only the bursa copulatrix length was significantly directionally selected (Table 2).

### 2.3 Sexual selection on male traits

All 61 females successfully mated. No short mating

**Table 1** Pearson correlation matrix of morphological traits in females ( $*P < 0.05$ ;  $**P < 0.0001$ )

Traits	Body length	Antennal length	Eighth sternite width	Ovipositor length	Bursa copulatrix length	Second abdominal segment width
Body length	1					
Antennal length	0.86**	1				
Eighth sternite width	0.664**	0.711**	1			
Ovipositor length	0.578**	0.658**	0.709**	1		
Bursa copulatrix length	0.296**	0.308**	0.242*	0.381**	1	
Second abdominal segment width	0.866**	0.864**	0.766**	0.693**	0.323**	1

**Table 2 Multiple regressions of female morphological traits in relation to mating success**

Traits	$\beta'$	$\chi^2$	$P$
Body length (mm)	0.619	1.089	0.2967
Antennal length (mm)	-0.459	0.621	0.4305
Second abdominal segment width (mm)	0.691	0.957	0.3278
Eighth sternite width (mm)	-0.229	0.274	0.6004
Ovipositor length (mm)	0.219	0.288	0.5917
Bursa copulatrix length (mm)	2.449	27.939	<0.0001

**Table 3 Pearson correlation matrix of morphological traits in males (\* $P < 0.05$ ; \*\* $P < 0.0001$ )**

Traits	Body length	Antennal length	Hind tarsal length	Paramere length	Aedeagus length	Endophallus length
Body length	1					
Antennal length	0.893**	1				
Hind tarsal length	0.866**	0.861**	1			
Paramere length	0.53**	0.448**	0.546**	1		
Aedeagus length	0.557**	0.563**	0.571**	0.375**	1	
Endophallus length	0.475**	0.483**	0.517**	0.224*	0.382**	1

was observed in this trial. Pearson correlation analysis shows that all six traits measured were significantly correlated with each other (Table 3).

Analysis shows that of six male traits measured, three were significantly correlated with male mating success, with the hind tarsal length having the greatest selection differential value ( $s$ ) (Fig. 2). Further analysis of the three traits for directional selection gradients ( $\beta'$ ) indicates that only the hind tarsal length and body length were significantly directionally selected in males (Table 4).

**Table 4 Multiple regressions of male morphological traits in relation to mating success**

Traits	$\beta'$	$\chi^2$	$P$
Body length (mm)	1.055	6.060	0.0138
Hind tarsal length (mm)	1.538	11.181	0.0008
Paramere length (mm)	-0.328	1.825	0.1767

### 3 Discussion

In the present study, all insects used were of the same age and bred under the same nutritional and environmental conditions, minimizing the effect of age and environmentally-induced reproductive variance. We show that the genital trait, the bursa copulatrix length, in females (Table 2) and non-genital traits, the hind tarsal length and body length, in males were significantly directionally selected in *G. cantor* (Table 4).

Our study also shows that those traits not directionally

selected in sexual selection in *G. cantor* were also significantly correlated with mating success (Figs. 1 & 2). This may be because that they were significantly correlated with the directionally selected bursa copulatrix length in females (Table 1) and body length and hind tarsal length in males (Table 3).

In several insect species, female abdominal size appears to be sexually selected because a larger abdomen is positively correlated with fecundity (e.g. Li et al., 2005; Bussiere et al., 2008; Xu and Wang, 2010). Adult females of these insects are usually short-lived and probably pro-ovigenic. However, *G. cantor* adult females are long-lived and synovigenic with egg production and maturation continuing throughout their lifetime (Lu et al., 2011a, 2013). Therefore, the fact that the female abdominal size in this species is not directionally selected by males (Table 2) may be attributed to this trait not being a reliable signal of lifetime reproductive fitness in females.

In *G. cantor* the bursa copulatrix is an elongate blind sac open to the duct leading to the vagina at one end and to the spermatheca at the other end. Our measurement shows that the length of this structure is the function of its volume, and thus a longer bursa copulatrix can accommodate a larger ejaculate. Many studies have suggested that paternity is determined by the relative number of competing sperm in females from different males (e.g., Parker, 1990 1998; Gage and Morrow, 2003). Consequently, males should transfer larger ejaculates to

females to succeed in sperm competition (Cook and Gage, 1995; Simmons, 2001). Our previous study shows that *G. cantor* females mate multiply (Lu et al., 2013). Therefore, in the present study where virgin females are used, larger bursa copulatrix should benefit males in terms of allowing larger ejaculates to be transferred and thus better chance to outcompete subsequent males in sperm competition. This may account for the directional selection of the bursa copulatrix length in *G. cantor* females.

The female genital features are usually considered under postcopulatory rather than premating sexual selection (Eberhard, 1996; Arnqvist and Danielsson, 1999) probably because it is usually assumed that males cannot assess them before mating occurs. However, in *G. cantor* under a female-biased sex ratio, more than 20% of matings failed (no insemination) after the endophallus had been inserted into the vagina. It is suggested that during the process before successful mating, *G. cantor* males may well have the opportunity to assess female genital features and to decide whether or not to transfer sperm. This could be an empirical example of cryptic male mate choice (Bonduriansky, 2001).

Our observations show that to achieve successful mating, the male needs to firmly hold the female with his legs and push his genitalia in to prevent them from disconnecting with hers. As a result, longer males are more capable of grasping females in *G. cantor*. This may largely account for the fact that larger males are significantly more likely to achieve mating. Furthermore, various studies report that larger males are sexually selected by females because larger males have better genes and more ejaculate supply over smaller ones (Phelan and Barker, 1986; Kempnaers et al., 1992; Keller and Reeve, 1995; Bissoondath and Wiklund, 1996). Therefore, females that mate with larger males may have sons and daughters that can carry alleles for these beneficial characters.

Several studies have assessed the roles that male insect legs play in mating success. For example, all six tarsi are important for paternity success in a male beetle (Edvardsson and Arnqvist, 2005); male tarsal length (particularly the fore tarsi) is sexually selected by females in two beetle species (Trumbo and Sikes, 2000), and in an assassin bug sexual selection appears to act on the length of male hind tarsi (McLain and Boromisa, 1987). During the premating process in *G. cantor* the male almost always uses his hind tarsi to hold the terminal segments of the female abdomen and attempt to

lift them to the position for his endophallus to insert. If the female runs and attempts to dislodge the mounting male, he holds the substrate firmly with his hind tarsi to prevent her from running. As a result, males with longer hind tarsi have significantly better chance to achieve mating. Aedeagus and parameres also appeared to play roles in ensuring male genitalia insertion but why these male genital traits are not sexually selected is not clear.

We conclude that differences in the bursa copulatrix length in females and body length and hind tarsal length in males may reliably reflect variance in reproductive fitness of *G. cantor*, and that variance in these traits may have evolved under sexual selection. The form and nature of sexual selection of all species mentioned above reveal that sexual selection may act on different morphological traits in different species, probably due to the diverse mating systems.

**Acknowledgments** We thank L.Y. Qin, L.H. Qin, Q.Y. Qin, and Y.X. Zhong for technical assistance. We also thank three anonymous reviewers for their constructive comments on an earlier version of this paper. This research was supported by the National Natural Science Foundation of China (No. 31260432), Natural Science Foundation of Guangxi (GUIKEZI: 0447006 and GUIKEZI: 0991041), and Massey University Overseas Research Leave Fund.

## References

- Arnold SJ, Wade MJ, 1984. On the measurement of natural and sexual selection: Applications. *Evol.* 38: 720–734.
- Arnqvist G, Danielsson I, 1999. Copulatory behavior, genital morphology, and male fertilization success in water striders. *Evol.* 53: 147–156.
- Bissoondath CJ, Wiklund C, 1996. Effect of male mating history and body size on ejaculate size and quality in two polyandrous butterflies, *Pieris napi* and *Pieris rapae* (Lepidoptera: Pieridae). *Funct. Ecol.* 10: 457–464.
- Bonduriansky R, 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol. Rev.* 76: 305–339.
- Bussiere LF, Gwynne DT, Brooks R, 2008. Contrasting sexual selection on males and females in a role-reversed swarming dance fly *Rhamphomyia longicauda* Loew (Diptera: Empididae). *J. Evol. Biol.* 21: 1683–1691.
- Clutton-Brock TH, 1983. Selection in relation to sex. In: Bendall BJ ed. *Evolution from Molecules to Men*. Cambridge: Cambridge University Press, 457–481.
- Clutton-Brock TH, 2007. Sexual selection in males and females. *Science* 318: 1882–1885.
- Clutton-Brock TH, 2009. Sexual selection in females. *Anim. Behav.* 77: 3–11.
- Cook PA, Gage MJG, 1995. Effects of risks of sperm competition on the numbers of eupyrene and apyrene sperm ejaculated by the moth *Plodia interpunctella* (Lepidoptera, Pyralidae). *Behav.*

- Ecol. Sociobiol. 36: 261–268.
- Danielsson I, 2001. Antagonistic pre- and post-copulatory sexual selection on male body size in a water strider *Gerris lacustris*. Proc. R. Soc. Lond. B. Biol. Sci. 268: 77–81.
- Darwin C, 1871. The Descent of Man and Selection in Relation to Sex. London: John Murray.
- Düngelhopfe S, Schmitt M, 2006. Functional morphology of mating in Chrysomelidae-Criocerinae and Bruchidae (Insecta: Coleoptera). Bonner Zool. Beitr. 54: 201–208.
- Eberhard WG, 1996. Female control: Sexual selection by cryptic female choice. Princeton: Princeton University Press.
- Edvardsson M, Arnqvist G, 2005. The effects of copulatory courtship on differential allocation in the red flour beetle *Tribolium castaneum*. J. Insect Behav. 18: 313–322.
- Fry JC, 1993. Biological data analysis: A practical approach. New York: IRL Press.
- Funk DH, Tallamy DW, 2000. Courtship role reversal and deceptive signals in the long-tailed dance fly *Rhamphomyia longicuada*. Anim. Behav. 59: 411–421.
- Gage MJG, Morrow EH, 2003. Experimental evidence for the evolution of numerous, tiny sperm via sperm competition. Curr. Biol. 13: 754–757.
- Gibson RM, 1987. Bivariate versus multivariate analyses of sexual selection in red deer. Anim. Behav. 35: 292–293.
- Gowaty PA, Hubbell SP, 2005. Chance, time allocation, and the evolution of adaptively flexible sex role behavior. Integr. Comp. Biol. 45: 931–944.
- Hosken DJ, Stockley P, 2004. Sexual selection and genital evolution. Trends Ecol. Evol. 19: 87–93.
- Hubbell SP, Johnson LK, 1987. Environmental variance in lifetime mating success, mate choice, and sexual selection. Am. Nat. 130: 91–112.
- Jimenez-Perez A, Wang Q, 2004. Sexual selection in *Cnephasia jactatana* (Lepidoptera: Tortricidae) in relation to age, virginity, and body size. Ann. Entomol. Soc. Am. 97: 819–824.
- Kahn AT, Mautz B, Jennions MD, 2010. Females prefer to associate with males with longer intromittent organs in mosquitofish. Biol. Lett. 6: 55–58.
- Keller L, Reeve HK, 1995. Why do females mate with multiple males? The sexually selected sperm hypothesis. Adv. Stud. Behav. 24: 291–315.
- Kempnaers B, Verheyen GR, Vandenbroeck M, Burke T, Vandenbroeckhoven C et al., 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. Nature 357: 494–496.
- Kraak SBM, Bakker TCM, 1998. Mutual mate choice in sticklebacks: Attractive males choose big females, which lay big eggs. Anim. Behav. 56: 859–866.
- Lande R, Arnold SJ, 1983. The measurement of selection on correlated characters. Evol. Dev. 37: 1210–1226.
- Li Z, Li D, Xie B, Ji R, Cui J, 2005. Effect of body size and larval experience on mate preference in *Helicoverpa armigera* (Hübner) (Lepidoptera, Noctuidae). J. Appl. Entomol. 129: 574–579.
- Lu W, Wang Q, Tian MY, He XZ, Zeng XL et al., 2007. Sex location and recognition in *Glenea cantor* (Fabr.) (Coleoptera: Cerambycidae: Lamiinae): Roles of host plant health, female sex pheromone and vision. Environ. Entomol. 36: 864–870.
- Lu W, Wang Q, Tian MY, Xu J, Qin AZ, 2011a. Phenology and laboratory rearing procedures of an Asian longicorn beetle *Glenea cantor* (Coleoptera: Cerambycidae: Lamiinae). J. Econ. Entomol. 104: 509–516.
- Lu W, Wang Q, Tian MY, Xu J, Qin AZ et al., 2011b. Host selection and colonization strategies with evidence for a female-produced oviposition attractant in a longhorn beetle. Environ. Entomol. 40: 1487–1493.
- Lu W, Wang Q, Tian MY, Xu J, Lv J et al., 2013. Reproductive traits of *Glenea cantor* (F.) (Coleoptera: Cerambycidae: Lamiinae). J. Econ. Entomol. 106: in press.
- McLain DK, Boromisa RD, 1987. Stabilizing sexual selection and density-dependent correlates of copulatory success in the ambush bug *Phymata wolffii* (Hemiptera: Reduviidae). Am. Midl. Nat. 118: 94–102.
- Mitchell-Olds T, Shaw RG, 1987. Regression analysis of natural selection: Statistical inference and biological interpretation. Evol. Dev. 41: 1149–1161.
- Møller AP, 1994. Sexual Selection and the Barn Swallow. Oxford: Oxford University Press.
- Møller AP, Couderc G, Nielsen JT, 2009. Viability selection on prey morphology by a generalist predator. J. Evol. Biol. 22: 1234–1241.
- Mousseau TA, Roff DA, 1995. Genetic and environmental contributions to geographic variation in the ovipositor length of a cricket. Ecol. 76: 1473–1482.
- Norry FM, Calcagno G, Vera MT, Manso F, Vilardi JC, 1999. Sexual selection on male morphology independent of male-male competition in the Mediterranean fruit fly (Diptera: Tephritidae). Ann. Entomol. Soc. Am. 92: 571–577.
- Parker GA, 1990. Sperm competition games: Raffles and roles. Proc. R. Soc. Lond. B. Biol. Sci. 242: 120–126.
- Parker GA, 1998. Sperm competition and the evolution of ejaculates: Towards a theory base. In: Birkhead TR, Møller AP ed. Sperm Competition and Sexual Selection. London: Academic Press, 3–54.
- Partridge L, Halliday TR, 1984. Mating patterns and mate choice. In: Krebs JR, Davies NB ed. Behavioral Ecology: An Evolutionary Approach. Oxford: Blackwell Scientific Publications, 222–250.
- Partridge L, Hoffman A, Jones JS, 1987. Male size and mating success in *Drosophila melanogaster* and *Drosophila pseudoobscura* under field conditions. Anim. Behav. 35: 468–476.
- Phelan PL, Barker JC, 1986. Male size related to courtship success and intersexual selection on tobacco moth *Ephesia cautella*. Exp. 42: 1291–1293.
- Pischedda A, Chippindale AK, 2006. Intralocus sexual conflict diminishes the benefits of sexual selection. PLOS Biol. 4: 2099–2103.
- Pryke SR, Andersson S, Lawes MJ, 2001. Sexual selection of multiple handicaps in the red-collared widowbird: Female choice of tail length but not carotenoid display. Evol. 55: 1452–1463.
- SAS I, 2006. User's manual. Cary: SAS Institute Inc..
- Simmons LW, 2001. Sperm competition and its evolutionary consequences in the insects. Princeton: Princeton University Press.

- Sivinski J, Vulinec K, Aluja M, 2001. Ovipositor length in a guild of parasitoids (Hymenoptera: Braconidae) attacking *Anastrepha* spp. fruit flies (Diptera: Tephritidae) in southern Mexico. *Ann. Entomol. Soc. Am.* 94: 886–895.
- Stuart-Smith J, Swain R, Wapstra E, 2007. The role of body size in competition and mate choice in an agamid with female-biased size dimorphism. *Behav.* 144: 1087–1102.
- Sutherland WJ, 1985. Measures of sexual selection. *Oxf. Surv. Evol. Biol.* 2: 90–101.
- Tang-Martinez Z, Ryder TB, 2005. The problem with paradigms: Bateman's worldview as a case study. *Integr. Comp. Biol.* 45: 821–830.
- Trumbo ST, Sikes DS, 2000. Sexual selection and leg morphology in *Nicrophorus orbicollis* and *Ptomascopus morio*. *Entomol. Sci.* 4: 585–589.
- Wang Q, 2002. Sexual selection of *Zorion guttigerum* Westwood (Coleoptera: Cerambycidae: Cerambycinae) in relation to body size and color. *J. Insect Behav.* 15: 675–687.
- Wang Q, Zeng WY, 2004. Sexual selection and male aggression of *Nadezhdiella cantori* (Hope) (Coleoptera: Cerambycidae: Cerambycinae) in relation to body size. *Environ. Entomol.* 33: 657–661.
- Willemart RH, Osses F, Chelini MC, Macias-Ordonez R, Machado G, 2009. Sexually dimorphic legs in a neotropical harvestman (Arachnida, Opiliones): Ornament or weapon? *Behav. Proc.* 80: 51–59.
- Xu J, Wang Q, 2009. A polyandrous female moth discriminates against previous mates to gain genetic diversity. *Anim. Behav.* 78: 1309–1315.
- Xu J, Wang Q, 2010. Form and nature of premating sexual selection in both sexes of a moth. *Naturwis.* 97: 617–625.
- Yang LH, Wang Q, 2004. Premating sexual selection in *Nysius huttoni* White (Heteroptera: Lygaeidae) in relation to morphometric traits. *J. Insect Behav.* 17: 695–707.