

## Sexual selection in a water strider: the function, mechanism of selection and heritability of a male grasping apparatus

Göran Arnqvist

Arnqvist, G. 1989. Sexual selection in a water strider: the function, mechanism of selection and heritability of a male grasping apparatus. – *Oikos* 56: 344–350.

Males of the water strider *Gerris odontogaster* have two abdominal ventral processes (MAPs) that provide a posterior attachment to females during mating. Females were reluctant to mate, and the MAPs were important for males to succeed in copulations. Low male mating success and absence of second male take-over attempts during mating, suggested the functional significance of the processes to be intersexual rather than intrasexual. The length of MAPs varied considerably in the studied population (range 0.08–0.22 mm, CV = 15.4%). Laboratory experiments showed that males with longer MAPs had a greater ability to endure females' rejection behaviour than males with shorter MAPs. The mating and non-mating fractions of a natural population significantly differed in length of MAPs, thus indicating sexual selection in the field. The heritability of process length was high, contrary to what is predicted by classic quantitative genetic theory for important fitness traits.

G. Arnqvist, Dept of Animal Ecology, Univ. of Umeå, S-901 87 Umeå, Sweden.

### Introduction

Morphological traits in insect males which keep the sexes together during mating, i.e. different forms of grasping morphologies of the male tarsi, femora, antennae etc. are "traditionally" seen as adaptations to reduce intrasexual competition (i.e. sperm competition) by preventing take-overs (Parker 1970, 1984, but see Thornhill 1984, Eberhard 1985). By grasping a female efficiently, males avoid being displaced by other males which may inseminate the same female.

Natural selection may be defined as a process, involving three fundamental conditions (Cade 1984, Endler 1986). The trait under consideration must exhibit phenotypic variation, this variation must at least partially be heritable (cf. below) and there has to be a relationship between variation in the trait and fitness.

Classical theoretical population genetics models predict that traits closely related to fitness should have negligible or little heritable genetic variation due to intense selection (Fisher 1958, Falconer 1981). If so, the adaptive value of female choice for "good" male genetic

quality seems obscure, since female mating preferences should deplete male additive genetic variation through directional selection, leaving choosy females with no genetic advantages compared with females who mate at random (Thornhill 1980a, Cade 1984). Nevertheless, recent studies have shown that considerable heritable variation occurs in characters closely related to fitness (Cade 1984, Jones 1987, Simmons 1987, Hedrick 1988). This fact has generated several theories concerning the persistence of genetic variation in fitness traits in natural populations. These theories involve factors such as mutations, pleiotropic effects, migration, frequency-dependent selection and variations in direction and intensity of selection (Maynard Smith 1978, Lande 1982, Istock 1983, Cade 1984, Jones 1987, Loeschke 1987, Turelli 1988).

Males of the water strider *Gerris odontogaster* (Zett.) (Heteroptera; Gerridae) are provided with a grasping apparatus consisting of two abdominal ventral processes (Fig. 1). The current study evaluates the functional significance of the male abdominal processes (MAPs) in *G. odontogaster*. Further, the study demonstrates the

Accepted 5 June 1989

© OIKOS

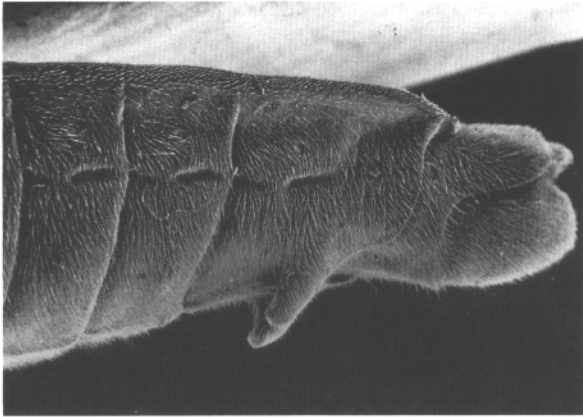


Fig. 1. Abdominal tip of a *G. odontogaster* male (lateroventral view) showing the general appearance of the male abdominal processes (MAPs) situated on the ventral surface of the seventh abdominal segment.

three fundamental conditions for natural selection to occur in *G. odontogaster* MAPs, and considers the mechanism of selection.

#### Materials and methods

*Gerris odontogaster* overwinters on land as adult in a prereproductive state. The reproductive activities start in spring after a period of gonad maturation lasting approximately 1–2 wk (Vepsäläinen 1974). These activities, including copulation and egg laying, continue for 1–2 mo until the adults that overwintered die (Vepsäläinen 1974). The most widespread male mating behaviour of water striders is to mount and attempt to mate with a female, but females are generally reluctant to mate. Water striders may also exhibit a postcopulatory guarding behaviour, during which the male remains on the back of the female (Spence 1979, Wilcox 1979, Andersen 1982, Hayashi 1985, Vepsäläinen 1985, Wheelwright and Wilkinson 1985, Spence and Wilcox 1986, Arnqvist 1988, 1989).

The population of *G. odontogaster* investigated in the current study was monomorphic macropterous and inhabited the Gimonäs pond SE of Umeå in northern Sweden (63° 48' N, 20° 19' E). Unmated (immature) individuals for laboratory experiments were captured on 5–6 May, 1987, and 7–8 May, 1988, before the reproductive activities had begun. Female virginity was verified by the fact that these females laid only unfertilized eggs when isolated in the laboratory. Samplings of mating pairs and non-mating individuals were made with a hand net on 17–18 May, 1986. In the field, observations of mating behaviour and mating success were made with binoculars for approximately four hours every third day, from 17 May to 3 July, 1987. Water striders kept in the laboratory were fed with frozen fruit flies.

#### Functional significance of MAPs

To study the functional role of the MAPs, a number of mating pairs were frozen instantaneously in the laboratory in liquid nitrogen (–195°C). Each pair was glued to preserve relative position, dried and then photographed in a scanning electron microscope.

The importance of MAPs during mating was studied by comparing the mating success of two groups of males in the laboratory. The grasping apparatus of 15 males were made inoperative by anaesthetizing the males with ethylacetate, and applying a tiny drop of water-based glue anteriorly and proximal-medial to the MAPs. Fifteen control males were treated in exactly the same way, including anaesthetization, but a drop of water was used instead of glue. After recovery, each male was placed in a 30 cm diameter plastic container, and a female was introduced. Mating attempts were defined as when a male, making a pounce upon a female, attained the typical mating position on top of the female. Female reluctance rendered mating attempts either successful (genital joining and copulation) or unsuccessful (dislodgement). Over a 4-h period, all mating attempts were recorded.

In a second experiment, designed to compare the frequency of take-overs (male – male replacements in matings) in experimental and control groups, each of the males used in the first experiment was placed in a 30 cm diameter plastic container with a female. When copulation occurred, an additional unmanipulated male was introduced to each pair. The success of take-overs in subsequent encounters, when a single male pounded upon a pair in copula, was recorded.

#### Phenotypic variation and male mating success

Individuals from the mating and non-mating fractions of the population were measured with a micrometer eyepiece. All individuals were coded with a number, to avoid potential subjectivity in measuring. The characteristics that were measured (Tab. 1) were chosen to reflect aspects of variation in size and secondary sexual characteristics (MAPs). Total body length was measured from the anterior margin of the eye to the lateral tip of the seventh abdominal segment. Length of the MAPs was measured as the distance from the tip of the MAPs to the abdominal margin, when the individual was viewed laterally.

To evaluate the importance of the length of the MAPs in mating success, a number of males were taken to the laboratory, anaesthetized, and the length of their processes were measured. Males were classified into three groups, according to the length of the MAPs. Group I had short (< 0.16mm), Group II intermediate (0.16–0.18 mm) and Group III long (> 0.18 mm) MAPs. Twenty-four males from each group were placed individually in 30 cm diameter containers. After 24 h, two females were introduced to each male and the beha-

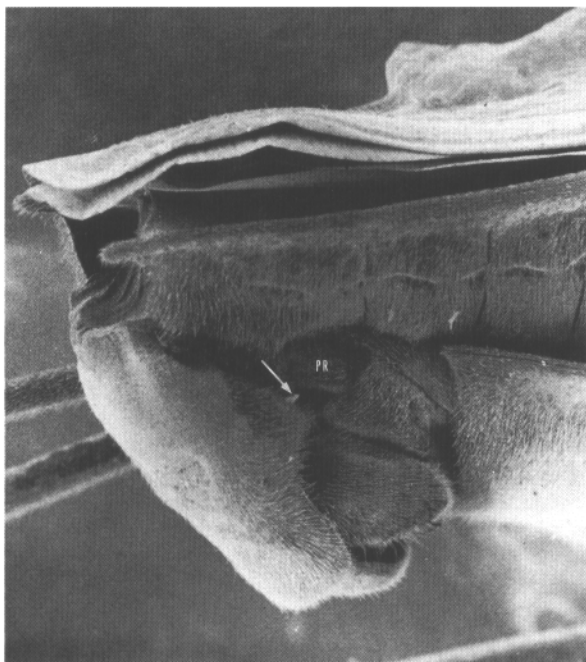


Fig. 2. The abdominal tips of a copulating pair of *G. odontogaster*. The male's genital segments is bent ventrally underneath the female's genital segments. Note that the female abdominal tip, or the proctiger (Pr), is wedged between the male's processes and the ventral surface of male's abdomen. The arrow indicates the tip of the process.

viour of the water striders was observed for 30 min. Two variables were registered, (1) number of mating attempts and (2) number of endured female "somersaults" (see results below) before dislodgement or copulation, in each mating attempt.

#### Heritability

To estimate the heritability of MAP length, a number of males were anaesthetized, and the lengths of their processes were measured. Twenty-five of these males were selected for a breeding experiment. Males were selected on the basis of the preliminary (cf. below) length of their MAPs, to produce a maximum range of variation in length of MAPs within the paternal group (cf. Falconer 1981: 169). Each male was isolated with a randomly chosen unmated female, and the eggs from each pair were subsequently hatched in the laboratory. Offspring were reared in 30 cm diameter plastic containers under identical conditions in the laboratory and fed daily with three fruit flies each. All offspring reaching adult stage were preserved in 70% ethanol. All individuals were subsequently coded, and the lengths of the paternal and male offspring MAPs were measured with a micrometer eyepiece. The heritability of length of MAPs was estimated using a regression of midoffspring

on parents (Falconer 1981). Since a character only occurring in males is considered, the regression is based on data from fathers and the mean value of their sons.

#### Results

Mating was initiated by males, who appeared to locate potential mates by surface waves. Males adjusted their orientation in relation to the wave-emitting object, after which they made a sudden pounce towards the potential mate often from distances exceeding 10 cm. Males also pounced towards, and tried to mount, conspecific as well as heterospecific males. When being pounced upon, the female's first response was to raise the abdomen and/or make a sudden vertical jump that prevented males from achieving copula position in 43–68% of the observed pounces.

When a male successfully grasped a female, he tried to remain in mating position by clasping the female's thorax with his forelegs and by hooking the female's proctiger with his MAPs. Females were reluctant to mate in all observed mating attempts (N = 442). They tried to dislodge males by raising the midlegs and thereby the body, causing the couple to tip over backwards. During these "backward somersaults" the tips of the couple's abdomens were pressed against the water surface film and drifted apart in approximately 10% of the somersaults, dislodging the male as a result. During the somersaults, which were performed 1–30 times in each mating attempt, the female tried to loosen the male's forelegs from her thorax with her own forelegs. If males were not dislodged, the reluctant behaviour of the females ceased after 10.7 (SD = 8.9, N = 24) somersaults and copulation followed.

#### Functional significance of MAPs

The male abdominal processes point downwards and forwards, thus forming an acute angle with the abdominal margin (Fig. 1). The SEM studies of pairs in copula showed that the tip of the female's abdomen was wedged between the male's processes and abdomen during mating. The female proctiger (tenth abdominal segment) was located in front of and between the processes (Fig. 2).

Out of 158 male mating attempts observed in the field, 28 were successful (18%). This frequency was not significantly different from the mating success of the control group in the laboratory ( $\chi^2 = 0.52$ , NS), in which there were 18 successful matings out of 124 attempts (15%). In the experimental group of males, with inoperative grasping apparatus, only 3 matings were successful out of a total of 110 attempts (3%). The experimental group had a significantly lower mating success than the control group ( $\chi^2 = 9.92$ ,  $P < 0.01$ ).

No take-over attempts were observed either in the field or in the laboratory experiments. Single males occasionally pounced upon mating pairs and apparently

Tab. 1. Morphological comparisons between the mating and non-mating fractions (N = 54 for both) of a natural population of *G. odontogaster*. All measurements are given in mm, levels of significance are calculated with t-test.

Character	Mating		Non-mating		t-value (d.f. = 106)	P
	$\bar{x}$	(SD)	$\bar{x}$	(SD)		
Females:						
Body length	7.58	(0.23)	7.52	(0.22)	1.31	NS
Males:						
Body length	6.50	(0.19)	6.48	(0.23)	0.48	NS
Width of anterior lobe of pronotum	1.082	(0.037)	1.076	(0.031)	0.85	NS
Width of fore femur	0.283	(0.010)	0.283	(0.012)	0.17	NS
Length of fore femur	2.045	(0.055)	2.040	(0.069)	0.37	NS
Distance between tips of abdominal processes	0.301	(0.039)	0.305	(0.039)	0.55	NS
Length of abdominal processes	0.177	(0.017)	0.162	(0.017)	4.54	P<0.001

tried to copulate (protruded the genital segments) with the mating male on top of the female. However, these events were terminated by the intruding male himself after 1–5 s, in the same manner as in mating attempts with single males.

#### Phenotypic variation and male mating success

Considerable phenotypic variation in the length of MAPs was found in the population, with lengths ranging from 0.08 to 0.22 mm (CV = 15.4%, N = 209). No male character was significantly correlated with the length of the MAPs, although body length approached significance ( $r = 0.184$ , N = 108, P = 0.064). Thus, no satisfactory morphological predictor for length of MAPs could be distinguished.

In the field population, mating males had significantly longer MAPs than non mating males (t-test, P < 0.001). No other measurements differed significantly between the two fractions (Tab. 1). There was no size assortative mating (Fig. 3), and the length of MAPs did not significantly correlate with female body length in mating pairs ( $r = -0.145$ , N = 54, NS).

The number of female somersaults endured before dislodgement in unsuccessful mating attempts (Fig. 4)

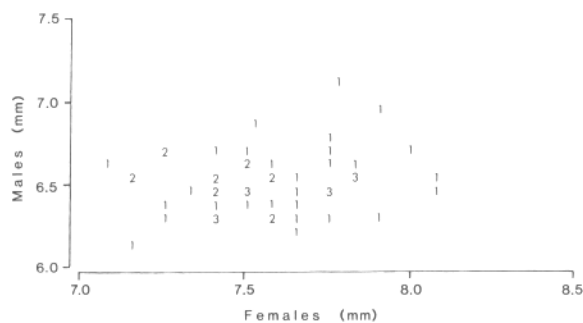


Fig. 3. The relationship between the body lengths of males and females in mating pairs (N = 54,  $r = 0.178$ , NS). Numbers represent the number of pairs at each point.

differed significantly between males with short, intermediate and long MAPs (Kruskal-Wallis test, H = 19.22, P < 0.01). Males with short MAPs had a significantly lower endurance than males with intermediate or long MAPs (Mann-Whitney U test, P < 0.01 in both cases), whereas there was no significant difference in endurance between males with intermediate and long MAPs (Mann-Whitney U test, P > 0.05).

Number of mating attempts per male did not differ significantly among the three groups of males (Kruskal-

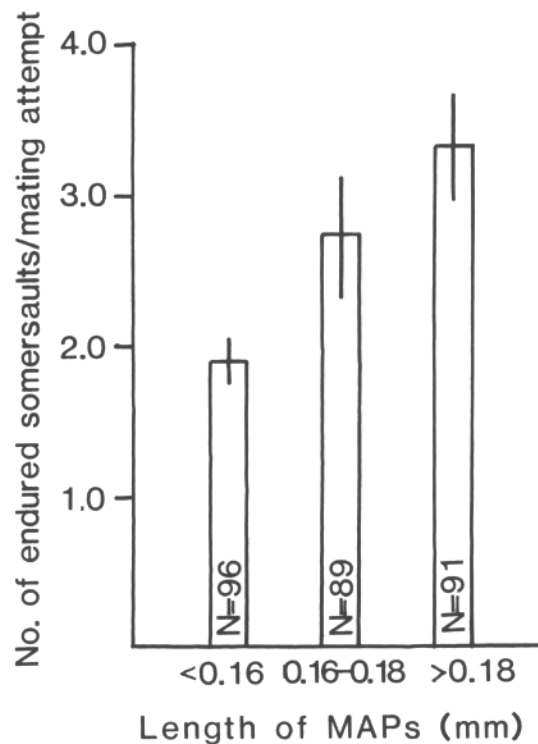


Fig. 4. Mean ( $\pm$ SE) number of female somersaults endured before dislodgement in unsuccessful mating attempts by males with short, intermediate and long abdominal processes.

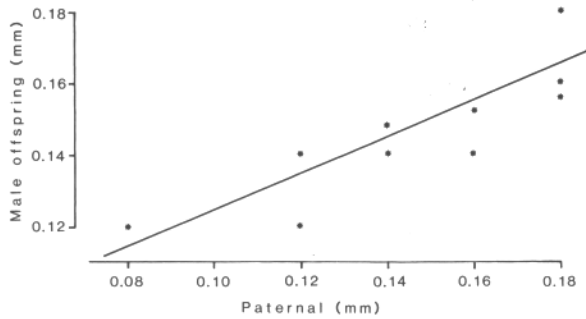


Fig. 5. Regression of the length of the MAPs of fathers and the mean value of their male offspring ( $y = 0.371 + 0.505x$ ,  $\sigma_b = 0.141$ ,  $r = 0.766$ ,  $P < 0.01$ ). Each point represents  $\bar{x} = 1.82$  male offspring.

Wallis test,  $H = 0.3054$ ,  $P > 0.5$ ). The pooled mean was 3.89 (SD = 3.12,  $N = 72$ ) mating attempts per male during the experiment.

#### Heritability

Eleven males fathered male offspring that reached the adult stage ( $N = 20$ ). The regression of mean MAP length for male siblings on paternal MAP length was (Fig. 5):  $b_{op} \pm \sigma_b = 0.505 \pm 0.141$ . The heritability of MAP length was estimated as (Falconer 1981: 151):  $h^2 = 2b_{op} \pm 2\sigma_b = 1.01 \pm 0.28$ .

#### Discussion

##### Functional significance of MAPs

Males of *G. odontogaster* used the abdominal processes to hook the females at the abdominal tip, and were thus able to grasp females both anteriorly with the forelegs and posteriorly with the MAPs. This additional attachment obviously increases male ability to grasp the female efficiently.

The fact that no take-overs were observed either in field or in laboratory implies that take-over avoidance is not likely an important function of the MAPs. However, the laboratory studies showed that functional MAPs is an important component in males' ability to endure the females' rejection behaviour, and thus in copulation success. Hence, the functional significance of the grasping apparatus seems to be intersexual rather than intrasexual.

The MAPs in *G. odontogaster* represent a parallel to the dorsal clamps of *Panorpa* scorpionflies, which are believed to be intersexually selected (Thornhill 1984). As for MAPs, the dorsal clamps are essential in forced copulations (Thornhill 1980b, 1984). The frequent ea-

gerness of males and the low percentage of successful mating trials in many other insect species (reviewed by Thornhill and Alcock 1983) suggest that male grasping morphologies may be intersexually selected more often than previously thought (Thornhill 1984, Eberhard 1985).

##### Length of MAPs and fitness

The length of the MAPs obviously affected the male's ability to endure female rejection behaviour. Since females are reluctant to mate, males with shorter MAPs should be less likely to succeed in mating than males with longer MAPs. This conclusion is supported by the fact that mating males had longer MAPs on average than non-mating males in the field sample. The result indicates that the length of the MAPs affects male mating success and that sexual selection operates in the field (cf. Mason 1980, Johnson 1982, Manly 1985, Endler 1986). Hence, length of MAPs should be correlated to male mating success and thus constitute an important male fitness trait in *G. odontogaster*.

"Female choice" may seem an inappropriate term for the reluctant behaviour of *G. odontogaster* females. However, since females tend to bias matings towards males with long MAPs, this is a case of sexual selection by female choice (Kirkpatrick 1987). There are two major hypotheses which may explain the observed reluctance of females to mate. First, females may increase their fitness by choosing vigorous males with "good genes" as mates (see Kirkpatrick 1987). For example, females may benefit from choosing males with long MAPs, since length of MAPs is highly heritable and thus should be inherited by their male offspring ("sexy sons hypothesis"; e.g. Weatherhead and Robertson 1979). Second, reluctance may be beneficial simply to avoid superfluous matings. This may be the case since matings in *G. odontogaster* involve costs and risks to females such as increased vulnerability to predators and decreased mobility which should interfere with foraging (Arnqvist 1989). However, the two hypotheses are not mutually exclusive and though their relative importance is very difficult to assess, females might benefit in both ways.

##### Phenotypic variation and heritability of MAPs

An analysis of the variation and evolution of a morphological character also requires consideration of the genetic basis of the character (Arthur 1984, Christiansen 1984, Loeschke 1987). Genes contributing to a character may have pleiotropic effects (e.g. give rise to phenotypic correlations) which may also be subjected to selection. In *G. odontogaster* the length of the MAPs varied considerably in the studied population, but did not significantly correlate with any other measured morphological character, suggesting that MAPs may be subjected to selection as a separate trait.

The heritability estimated for length of MAPs in this study ( $h^2 = 1.01 \pm 0.28$ ) is very high even for a purely morphological character, which generally have the highest heritabilities (Falconer 1981, Arthur 1984, Cade 1984). Thus, length of MAPs in the studied population does have a potential for microevolution.

#### Maintenance of variation in length of MAPs

All three fundamental prerequisites for natural selection to occur seem to be present in the studied population of *G. odontogaster* (Endler 1986). These results may seem paradoxical, since additive genetic variance is often thought to be diminished through the process of natural selection (Fisher 1958, Cade 1984, Jones 1987). Since heritable variation in length of MAPs exists in this population, one must ask, how can heritable variation for length of MAPs be maintained? The problem of maintaining heritable variation in natural populations has received considerable attention (Lande 1982, Istock 1983, Cade 1984, Endler 1986, Jones 1987, Loeschcke 1987, Turelli 1988). For MAPs in *G. odontogaster*, I suggest five major conditions which have the potential of maintaining heritable variation. (1) Genes controlling length of MAPs may have negative pleiotropic effects on physiological, developmental or morphological characters which I did not measure (antagonistic pleiotropy). Such negative correlations may theoretically maintain additive variation in fitness traits (Lande 1982, Partridge 1983, Loeschcke 1987). (2) Spatial or temporal variations in the intensity or direction of selection may further maintenance of additive genetic variation. (3) There may be an input to genetic variance in length of MAPs due to recombination and polygenic mutations (Lande 1976, Maynard Smith 1978). (4) Selection may depend on the relative frequency of phenotypes with different lengths of MAPs (frequency dependent selection, e.g. Maynard-Smith 1978, Endler 1986). (5) *G. odontogaster* is a good flier during spring dispersal and frequently inhabits temporary habitats (e.g. Vepsäläinen 1974). Immigration from adjacent populations with different genetic compositions and selective regimes, as well as founder effects, may influence the genetic variation (Jones 1987).

Quantifying or estimating the heritability of traits closely related to fitness under natural conditions is difficult (Endler 1986, Jones 1987). Nevertheless, although fitness may have negligible additive genetic variation in accordance with quantitative genetic theory (Fisher 1958), this study supports the view that considerable heritable genetic variation may occur in fitness traits subjected to selection in natural populations.

*Acknowledgements* – I thank J. Alcock, H. J. Brockmann, J. Elmberg, T. Olsson, C. Otto, J. R. Spence, R. Thornhill, K. Vepsäläinen and R. S. Wilcox for their constructive criticism on earlier drafts of the manuscript. G. Marklund prepared the figures. Further, I wish to express my gratitude to M. Arnqvist-Bonta, G. Englund, H. Fångstam and F. Johansson for assisting me with the experiments. This study was supported by

grants from the Swedish Natural Science Research Council (to C. Otto), "J. C. Kempes Minnes Stipendiefond" and the Royal Swedish Academy of Sciences.

#### References

- Andersen, N. M. 1982. The semiaquatic bugs (Hemiptera, Gerromorpha): Phylogeny, adaptations, biogeography and classification. – Entomonograph vol. 3, Scand. Science Press, Klampenborg, Denmark.
- Arnqvist, G. 1988. Mate guarding and sperm displacement in the water strider *Gerris lateralis* Schumm. (Heteroptera: Gerridae). – Freshwat. Biol. 19: 269–274.
- 1989. Multiple mating in a water strider; mutual benefits or intersexual conflict? – Anim. Behav. (In press).
- Arthur, W. 1984. Mechanisms of morphological evolution. – Wiley, New York.
- Cade, W. H. 1984. Genetic variation underlying sexual behavior and reproduction. – Am. Zool. 24: 355–366.
- Christiansen, F. B. 1984. The definition and measurement of fitness. – In: Shorrocks, B. (ed.), Evolutionary ecology. Blackwell, London, pp. 65–79.
- Eberhard, W. G. 1985. Sexual selection and animal genitalia. – Harvard Univ. Press, Cambridge, MA.
- Endler, J. A. 1986. Natural selection in the wild. Princeton Univ. Press, Princeton, NJ.
- Falconer, D. S. 1981. Introduction to quantitative genetics. – 2nd ed. Longman, New York.
- Fisher, R. A. 1958. The genetical theory of natural selection. – Dover, New York.
- Hayashi, K. 1985. Alternative mating strategies in the water strider *Gerris elongatus* (Heteroptera, Gerridae). – Behav. Ecol. Sociobiol. 16: 301–306.
- Hedrick, A. V. 1988. Female choice and the heritability of attractive male traits: an empirical study. – Am. Nat. 132: 267–276.
- Istock, C. A. 1983. The extent and consequences of heritable variation for fitness characters. – In: King, C. E. and Dawson, P. S. (eds), Population biology: retrospect and prospect. Columbia Univ. Press, Columbia, pp. 61–96.
- Johnson, L. K. 1982. Sexual selection in a brentid weevil. – Evolution 36: 251–262.
- Jones, J. S. 1987. The heritability of fitness: bad news for "good genes"? – Trends Ecol. Evol. 2: 35–38.
- Kirkpatrick, M. 1987. Sexual selection by female choice in polygynous animals. – Ann. Rev. Ecol. Syst. 18: 43–70.
- Lande, R. 1976. The maintenance of genetic variability by mutations in a polygenic character with linked loci. – Genet. Res. 26: 221–235.
- 1982. A quantitative genetic theory of life history evolution. – Ecology 63: 607–615.
- Loeschcke, V. 1987. Genetic constraints on adaptive evolution. – Springer, Berlin.
- Manly, B. F. J. 1985. The statistics of natural selection on animal populations. – Chapman and Hall, London.
- Mason, L. G. 1980. Sexual selection and the evolution of pair-bonding in soldier beetles. – Evolution 34: 174–180.
- Maynard Smith, J. 1978. The evolution of sex. – Cambridge Univ. Press, Cambridge.
- Parker, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. – Biol. Rev. 45: 525–567.
- 1984. Sperm competition and the evolution of animal mating strategies. – In: Smith, R. L. (ed.), Sperm competition and the evolution of animal mating systems. Academic Press, London, pp. 1–60.
- Partridge, L. 1983. Non-random mating and offspring fitness. – In: Bateson, P. (ed.), Mate choice. Cambridge Univ. Press, Cambridge, pp. 227–255.
- Simmons, L. W. 1987. Heritability of a male character chosen by females of the field cricket, *Gryllus bimaculatus*. – Behav. Ecol. Sociobiol. 21: 129–133.
- Spence, J. R. 1979. Microhabitat selection and regional coexis-

- tence in Water-striders (Heteroptera: Gerridae). – Ph.D. Thesis, Univ. of British Columbia, Vancouver.
- and Wilcox, R. S. 1986. The mating system of two hybridizing species of water striders (Gerridae). II. Alternative tactics of males and females. – Behav. Ecol. Sociobiol. 19: 87–95.
- Thornhill, R. 1980 a. Competitive, charming males and choosy females: Was Darwin correct? – Fla. Ent. 63: 5–30.
- 1980 b. Rape in *Panorpa* scorpionflies and a general rape hypothesis. – Anim. Behav. 28: 52–59.
- 1984. Alternative hypotheses for traits believed to have evolved by sperm competition. – In: Smith, R. L. (ed.), Sperm competition and the evolution of animal mating systems. Academic Press, London, pp. 151–178.
- and Alcock, J. 1983. The evolution of insect mating systems. – Harvard Univ. Press, Cambridge, MA.
- Turelli, M. 1988. Phenotypic evolution, constant covariances, and the maintenance of additive variance. – Evolution 42: 1342–1347.
- Vepsäläinen, K. 1974. The life cycles and wing lengths of Finnish *Gerris* Fabr. species (Heteroptera, Gerridae). – Acta Zool. Fennica. 141: 1–73.
- 1985. Exclusive female vs. male territoriality in two water-strider (Gerridae) species: hypothesis of function. – Ann. Ent. Fennici. 51: 45–49.
- Wade, M. J. and Arnold, S. J. 1980. The intensity of sexual selection in relation to male sexual behaviour, female choice, and sperm precedence. – Anim. Behav. 28: 446–461.
- Weatherhead, P. J. and Robertson, R. J. 1979. Offspring quality and the polygyny threshold: “the sexy son hypothesis”. – Am. Nat. 113: 201–208.
- Wheelwright, N. T. and Wilkinson, G. S. 1985. Space use by a Neotropical water strider (Hemiptera: Gerridae): Sex and age-class differences. – Biotropica 17: 165–169.
- Wilcox, R. S. 1979. Sex discrimination in *Gerris remigis*: Role of a surface wave signal. – Science 206: 1325–1327.