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Mate choice and the supernormality effect in female sticklebacks (*Gasterosteus aculeatus*)

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Summary. Female threespine sticklebacks *Gasterosteus aculeatus* from a marine population were presented simultaneously with two dummy males that differed in size. When the dummies were moved with a carousel apparatus in a way that roughly simulated a male courtship activity (circling) females responded to the dummies with following behaviour normally directed to courting males. Female sexual response was elicited more effectively by the larger ("supernormal") dummy, even though it exceeded by 25% the length of the largest males in the study population. Females did not show complete preference for the larger dummy but allocated courtship effort in proportion to the sizes of the two dummies (Fig. 3). The relative projection areas of the two dummies provided the best predictor of how courtship was allocated between them, suggesting a perceptual basis on which females might select mates. This pattern of partial preference for the supernormal dummy occurred in females that exhibited either high or low amounts of following behaviour and is apparently independent of female responsiveness. Supernormality may therefore provide a mechanism whereby secondary sexual traits can be elaborated, even without evolutionary change in preference for those traits by the opposite sex.

Introduction

Female mate preference is known to occur in a diversity of taxa (e.g. Wilbur et al. 1978; Ryan 1980; Burley 1981; Cox 1981; Andersson 1982; Thornhill and Alcock 1983; Simmons 1986), including fishes (e.g. Haas 1976; Perrone 1978; Downhower and Brown 1980; Endler 1983; Bischoff et al. 1985; Hughes 1985). In the threespine stickleback *Gasterosteus aculeatus* females produce several clutches of eggs during the reproductive season and the total weight of these eggs may amount to 2–3 times the female's body weight (Wootton 1973). We would therefore expect female sticklebacks to exercise mate choice, and the results of several studies support this prediction. For example, choice experiments have revealed that female *G. aculeatus* preferentially mate with males of their own morph (Hay and McPhail 1975), males with red nuptial coloration (McPhail 1969; Semler 1971), males with eggs (Ridley and Rechten 1981), and males whose nests are located in shelter (Sargent and Gebler 1980).

Body size appears to be subject to selection in many species (Trivers 1985). For example, Moodie (1982) studied two populations of sticklebacks from the Queen Charlotte Islands. Individuals of a population that Moodie called "derived" were unusually large, with males averaging 80 mm standard length. Moodie found that females from this population preferred larger males over smaller males and concluded that heavy predation on the derived population probably selected for unusually large body size. Males from a parapatric population, which Moodie called "ancestral (?)", averaged 51 mm standard length. Ancestral (?) females, however, preferred the larger derived males over males of their own morph, leading Moodie to suggest that body size may also be subject to sexual selection, with derived males serving as a supernormal stimulus to ancestral (?) females.

In other studies *G. aculeatus* males from a marine population preferentially courted dummy females with excessive abdominal distention or body size (Rowland and Sevenster 1985; Rowland 1989b). The present study was therefore undertaken to determine whether or not females from this population showed a similar preference for supernormally large mates, and if so, whether the preference followed a pattern like that found in males. Results of this study are of interest because they may provide insight into common perceptual mechanisms that may influence or even drive mate choice in animals and ultimately influence evolution of body size and sexually selected traits in general. Study of how animals allocate limited resources among alternatives also contributes to our understanding of decision-making processes and optimization in animal behaviour.

Methods

Subjects

Threespine sticklebacks *G. aculeatus* were collected by seining brackish marsh pools on eastern Long Island, New York in March 1987 and 1988. The fish were transported to Bloomington, Indiana where they were held at high density (approximately 50 fish/80-l stock tank) in brackish water (15 g/l) at 70 °C on a light:dark cycle of 8:16 h. Such conditions appear to retard the development of ovarian activity and sexual behaviour in this species (van Iersel 1953; Baggerman 1957, 1985; Borg and van Veen 1982), thereby extending the availability of reproductive animals for study in the laboratory.

In preparation for the mate preference tests, females that had begun to show signs of gravidity were taken from the cold room and placed into laboratory holding tanks where they could gradually acclimate to the spring conditions simulated in the laboratory (18° C; light:dark cycle of 16:8 h). The acclimated females were then placed singly into test tanks. Each test tank measured 120 × 40 × 40 cm and contained brackish water, a layer of sand, filamentous algae, and a cluster of plastic plants at each end of the tank to simulate the habitat in which the fish were collected (Fig. 1). Females were fed several times daily on a diet of frozen *Artemia*. Under these conditions females became gravid within several days and were then tested for mating preferences.

Dummy presentation technique

The dummy presentation technique was adopted in this study to avoid any confounding effects that might result from the behaviour of live stimulus males and to permit direct comparison with a study already conducted on males (Rowland 1989b). Mate preferences of sexually receptive females were tested by introducing two dummies simultaneously into the female's tank. This procedure provides a sensitive method for comparing the effectiveness of two stimuli and has been used before to measure male mate choice in *G. aculeatus* (Rowland 1982; Rowland and Sevenster 1985; Rowland 1989b). In past studies the dummies presented to the males were stationary, not unlike real females that are being courted, and these dummies were readily courted by males. The movement of the courting male, however, appears to be an important stimulus for eliciting sexual responses in female sticklebacks (ter Pelkwijk and Tinbergen 1937; Sevenster 1961; Sevenster-Bol 1962). I therefore devised a method by which I could present females with two dummies that simulated certain courtship movements of males closely enough to elicit a clear courtship response from females.

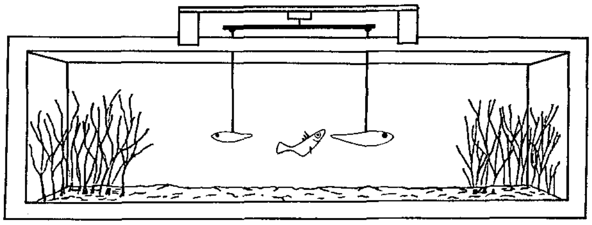

Fig. 1. Carousel apparatus used to test female courtship response to dummy males. The dummies and female have been drawn larger than scale for clarity

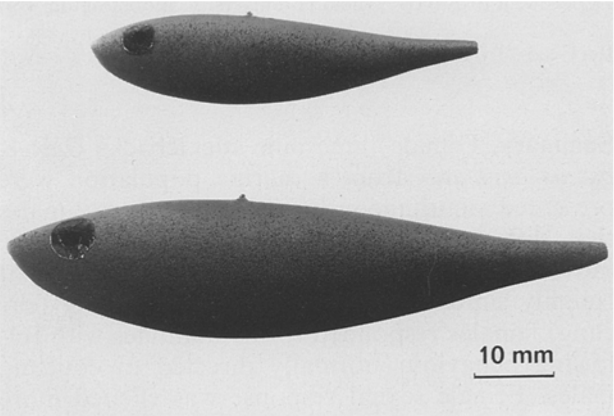

Fig. 2. Normal (top) and supernormal (bottom) dummy males similar to those used in the mate choice tests. Detailed description and dimensions of the dummies are given in the text and in Table 1

Carousel apparatus

To simulate male courtship movements I constructed a motorized carousel apparatus that could be placed on the top of each test tank (Fig. 1). The carousel incorporated a 30 cm metal beam, the middle of which served as a pivot point from which it was attached onto the shaft of a 4 rpm electric motor. The dummies were suspended head-to-tail and parallel to each other at opposite ends of the beam, facing the direction of movement. When the motor rotated, the diametrically opposed dummies moved at 6.3 cm/s in a circular path (30 cm diameter) in the horizontal plane, 5 cm from the bottom. The movement of the dummies thus resembled the circular swimming movements that courting *G. aculeatus* males commonly perform in the presence of gravid females. The yoked arrangement of the two dummies assured that their movements were identical, thus ruling out behaviour as a possibly confounding factor for female choice in the present study.

Dummies presented

The dummies used in this experiment consisted of epoxy castings that simulated reproductive *G. aculeatus* males of normal and supernormal sizes. The normal dummy was modelled from a preserved male of 50 mm standard length (Rowland 1979), within the size range of males from the Long Island population (Rowland 1983). The larger dummy was sculpted to the same shape and relative proportions as the normal dummy but was 1.5 times longer (see Fig. 2 and Table 1). Both dummies were

Table 1. Physical dimensions of dummy males

	Normal dummy	Supernormal dummy	Size ratio
Length (mm)	50	75	1.50
Volume (cc)	1.7	5.7	3.35
Maximum height (mm)	11.5	16.5	1.43
Frontal projection area (mm^2)	64	136	2.13
Lateral projection area (mm^2)	372	788	2.12

devoid of fins and had a pinkish-red coloured ventral region (Revell Color # 332) over a light olive-tan background body colour (Revell Color # 26). Eyes were constructed of small circles cut from a sheet of metallic blue aluminium foil. These were glued onto the dummies and pupils were drawn in with a black waterproof marking pen. Each dummy was mounted horizontally on a 32 cm staff of green florists wire by which it was attached to the carousel apparatus. When suspended in a tank alongside nuptially coloured males the dummies appeared to a human observer, at least, to match the colour pattern of the real males reasonably well.

Mating test procedure

Prior to each mating test, the carousel apparatus was placed above the centre of the female's test thank so that the dummies hung in the water column 5 cm from the bottom. Each female was given 2–3 min to recover from any disturbance caused by the introduction of the dummies, and then the motor was turned on. If a female failed to approach either moving dummy within 10 min she was presumed nonreceptive and retested at a later date. If the female approached within a body length of either dummy during this period the test trial was begun immediately and continued for 10 min. A duration of 10 min was chosen for the test trial because this was within the time range males were observed to court live females in the laboratory. During each trial the observer sat behind a screen 1 m from the tank and recorded via a keyboard-activated event recorder the female's activities and the dummy toward which each was directed.

Results

Twenty-seven females approached the dummies at least once during the test trial and were therefore used as subjects for the present study. When the dummies were introduced into a test tank the female retreated to the end of the tank, hovered in the vegetation, and oriented to the stationary dummies. Some females occasionally approached the dummies, but interest soon waned. When the motor was turned on, however, interest increased. After several seconds of watching the dummies from behind vegetation, receptive females swam swiftly and directly towards one of the moving dummies, assumed a head-up posture beneath or beside the dummy, and followed it from a distance of one body length or less. The more responsive females maintained a concave back posture characteristic of intensely courting females (cf. Fig. 3 from ter Pelkwijk and Tinbergen 1937) as they followed the dummy and attempted to maintain contact. Females sometimes nipped the dummy while courting but this behaviour occurred too infrequently to permit statistical analysis. Following behaviour was therefore the dominant activity that receptive females directed to the moving dummies and this behaviour was virtually indistinguishable from the following behaviour females directed to courting males in the laboratory (ter Pelkwijk and Tinbergen 1937; Sevenster 1961).

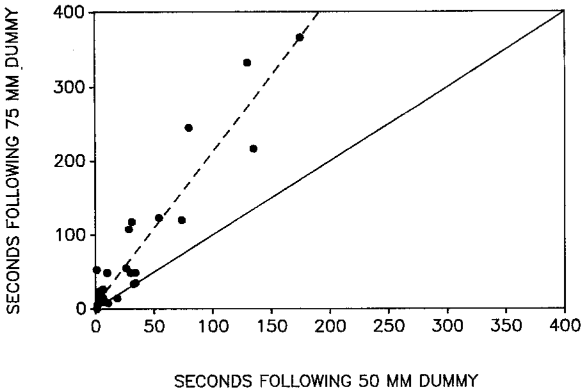

Fig. 3. Female responses to dummy males in the mate choice tests. The solid line represents the regression that would be expected if females responded equally to the two dummies. The dashed line represents the regression calculated from the data, showing that females spent approximately twice as much time on average following the larger dummy as they did the smaller one ($y = 2.06\,x + 5.74$, $r^2 = 0.89$, $P < 0.001$, $n = 27$)

Despite the wide variation in the amount of time females followed the dummies, they spent more time on average following the larger one. This is because bouts of following the large dummy were generally longer and slightly more frequent than bouts of following the normal size dummy (Table 2). Moreover, correlation analysis revealed that the total time a female followed one dummy was highly correlated with the total time she followed the other (Fig. 3); a nonparametric test for correlation confirmed this ($r_s = 0.81$, $n = 27$, $P < 0.001$). Therefore, the amount of time a female follows the normal size dummy predicts how much time she will follow the larger one.

To determine if there was a single parameter females might use to apportion following responses between two prospective mates, I compared size ratios for several physical dimensions of the dummies (Table 1) with the results of a regression analysis of female response to the dummies (Fig. 3). The ratio between frontal (2.13) or lateral (2.12) projection areas of the two dummies most closely approximated the ratio of following responses to

Table 2. Following responses of females to dummy males. Females followed the supernormal (75 mm) dummy significantly more than they followed the normal (50 mm) dummy, using a two-tailed paired-sample *t*-test

Female	Bouts per trial (number)		Median bout duration (s)		Total time per trial (s)	
	50 mm	75 mm	50 mm	75 mm	50 mm	75 mm
1	6	6	3.5	2.5	10.7	8.0
2	30	33	1.5	3.0	54.4	123.1
3	4	6	7.0	11.5	6.4	14.8
4	1	3	6.0	4.0	3.0	7.5
5	6	7	3.5	4.3	30.0	48.8
6	2	6	2.0	2.5	6.1	9.3
7	8	2	1.7	1.7	18.6	14.4
8	1	1	1.5	5.5	1.5	5.5
9	3	6	1.3	3.8	3.3	14.5
10	27	31	3.3	8.3	175.0	366.0
11	3	7	4.0	3.8	3.6	23.6
12	4	7	1.0	2.0	5.0	17.5
13	23	24	1.0	3.5	73.8	120.0
14	3	5	3.0	3.5	6.3	26.3
15	3	6	2.0	1.8	5.0	11.3
16	7	15	1.5	2.8	10.0	48.8
17	13	18	3.0	2.8	34.0	49.0
18	1	6	1.5	11.8	1.0	53.0
19	1	0	2.0	0.0	1.3	0.0
20	11	21	3.0	5.8	28.8	107.5
21	14	19	2.6	4.0	32.5	33.8
22	13	14	2.6	3.1	34.0	35.0
23	24	24	6.0	8.0	135.0	216.3
24	13	17	2.5	4.5	31.3	117.5
25	23	30	3.2	7.9	80.0	245.0
26	12	19	2.7	2.3	26.3	55.0
27	22	26	4.0	9.0	130.0	332.5
$\bar{X}$	10.30	13.30	2.85	4.58	35.07	77.93
±SD	9.02	10.01	1.53	2.98	45.94	100.04
P	<0.001		<0.005		<0.001	

them (2.06). The 95% confidence intervals for the *x* coefficient (1.77–2.35) included the ratios for lateral and frontal projection areas between the two dummies but excluded their ratios of length, volume, and height. The ratio of projection areas therefore best predicted how female sticklebacks apportioned the time spent following each dummy, suggesting that females use this parameter or one closely correlated with it to estimate the size of prospective mates.

Discussion

These results suggest that female sticklebacks prefer larger males to smaller ones, even if male size exceeds that in the natural population. This size preference in sticklebacks appears to be driven by a perception-response mechanism in which oversize males represent supernormal stimuli for the females.

Mating with larger males could provide several advantages for female sticklebacks. If larger fish are less vulnerable to predation than smaller ones (McPhail 1977), the offspring of larger males are less likely to be denied paternal care before they become independent. Larger males might also fan or defend eggs more effectively (Downhower and Brown 1980), although there are presently no conclusive data on this point for *G. aculeatus*. The offspring of large fathers should therefore enjoy higher survival rates. Larger male sticklebacks also compete more successfully for breeding territories in the laboratory, if size differences between opponents are large enough (Rowland 1989a). If body size in *G. aculeatus* has a heritable component (McPhail 1977) then males could transmit the tendency to attain large size and its advantages to their offspring.

Fisher (1958) proposed a "runaway process" whereby sexual selection might lead to the elaboration of a particular trait in a population, even if the trait did not confer an immediate advantage to the individual preferring it. Recognizing that females mating selectively with males bearing the trait would tend to produce sons with the trait and daughters expressing a preference for it, Fisher argued that the intensity of sexual selection should increase. This would lead to increased incidence of males with the trait and of females preferring it. Genetical models have since been formulated that confirm the basic operation of this process under a variety of conditions (O'Donald 1980; Lande 1981; Kirkpatrick 1985).

O'Donald (1977, 1980) recognized that supernormal stimuli (Tinbergen 1951) could play an important role in sexual selection. O'Donald pointed out that if female preferences are expressed relative to the average development of a male trait then more extreme development of the trait would result. The present study illustrates how supernormality could lead to the elaboration of male traits, even without further evolutionary change in female preference. Psychophysical properties of the perception-response mechanism in sticklebacks may predispose females to prefer supernormal males, not only of larger size, but with brighter nuptial colours, more vigourous courtship, etc. The striking effect of supernormal females on courting male sticklebacks (Rowland 1989b) as well as the distribution of supernormality across a diversity of behaviours and taxa (Lorenz 1943; Tinbergen 1951, 1965; Schmidt 1957; Gardner and Wallach

1965; Wickler 1968; Baerends and Drent 1982; Bielert and Anderson 1985), suggest that the effect is a conservative design feature of many nervous systems.

If preference for supernormally large mates reduced viability of an individual or its offspring enough, selection against such response should modify the perception-response mechanism accordingly. In *G. aculeatus*, however, increased body size and preference for larger mates may provide direct and indirect benefits through natural and sexual selection, respectively, until other factors counteract this assymetrical selection. Larger fish species, which *G. aculeatus* might confuse with larger conspecifics, are virtually absent in the marsh pools (personal observation), providing little opportunity for selection against response to supernormally large mates. This may explain why supernormality is so marked in this population. The upper limit to body size is therefore likely to result more from metabolic or ecological constraints than from behavioural ones, except in the unlikely case where size increased enough to exceed the range of the prospective mate's perceptual system (e.g. Magnus 1958) or to induce avoidance (e.g. Rowland 1975; Baerends and Drent 1982).

Previous investigation of *G. aculeatus* (Rowland 1982; Sargent et al. 1986) showed that males expressed a nonexclusive preference for larger females and that males presented with two dummy females divided courtship effort in proportion to the projection areas of the dummies, even if the latter were of supernormal size or shape (Rowland 1989b). The correspondence between projection area ratios of the different size dummy males used in the present study and the courtship that females directed to them suggests that the same principle applies to female sticklebacks. Examples as diverse as courtship in butterflies (Rutowski 1982) and egg incubation in herring gulls (Baerends and Drent 1982) suggest that the decision-making processes of animals are often based on such relatively simple features. This could explain the widespread use of medial fin erection in fishes, dorsal crests in newts, and lateral displays in general in animal communication.

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References

Andersson M (1982) Female choice selects for extreme tail length in a widowbird. Nature 299:818–820

Baerends GP, Drent R (1982) The herring gull and its egg. Part II. Behaviour 82:1–416

Baggerman B (1957) An experimental study of the timing of breeding and migration in the three-spined stickleback (*Gasterosteus aculeatus* L.). Arch Neerl Zool 12:105–317

Baggerman B (1985) The roles of daily and annual biological rhythms in the photoperiodic regulation of the breeding season of the stickleback *Gasterosteus aculeatus* L. Behaviour 93:1–7

Bielert C, Anderson CM (1985) Baboon sexual swellings and male response: a possible operational mammalian supernormal stimulus and response interaction. Int J Primatol 6:377–393

Bischoff RJ, Gold JL, Rubenstein DI (1985) Tail size and female choice in the guppy (*Poecilia reticulata*). Behav Ecol Sociobiol 17:253–255

Borg B, van Veen Th (1982) Seasonal effects of photoperiod and temperature on the ovary of the three-spined stickleback *Gasterosteus aculeatus*. Can J Zool 60:3387–3393

Burley N (1981) Male choice by multiple criteria in a monogamous species. Am Nat 117:515–526

Cox CR (1981) Agonistic encounters among male elephant seals: frequency, context and the role of female preference. Am Zool 21:197–209

Downhower JF, Brown L (1980) Mate preferences of female mottled sculpins, *Cottus bairdi*. Anim Behav 28:728–734

Endler JA (1983) Natural and sexual selection on color patterns in poeciliid fishes. Environ Biol Fish 9:173–190

Fisher RA (1958) The genetical theory of natural selection, 2nd edn. Dover, New York

Gardner BT, Wallach L (1965) Shapes of figures identified as a baby's head. Percept Mot Skills 20:135–142

Haas R (1976) Sexual selection in *Nothobranchius guentheri* (Pisces: Cyprinodontidae). Evolution 30:614–622

Hay DE, McPhail JD (1975) Mate selection in three-spine sticklebacks (*Gasterosteus*). Can J Zool 53:441–450

Hughes AL (1985) Male size, mating success, and mating strategy in the mosquitofish *Gambusia affinis* (Poeciliidae). Behav Ecol Sociobiol 17:271–278

Iersel JJA van (1953) An analysis of the parental behaviour of the male three-spined stickleback (*Gasterosteus aculeatus* L.). Behaviour (Suppl) 3:1–159

Kirkpatrick M (1985) Evolution of female choice and male parental investment in polygynous species: the demise of the "sexy son". Am Nat 125:788–810

Lande R (1981) Models of speciation by sexual selection of polygenic traits. Proc Natl Acad Sci USA 78:3721–3725

Lorenz K (1943) Die angeborenen Formen möglicher Erfahrung. Z Tierpsychol 5:235–409

Magnus D (1958) Experimentelle Untersuchungen zur Bionomie und Ethologie des Kaisermantels *Argynnis paphia* L. (Lep Nymph). Z Tierpsychol 15:397–426

McPhail JD (1969) Predation and the evolution of a stickleback (*Gasterosteus*). J Fish Res Board Can 26:3183–3208

McPhail JD (1977) Inherited interpopulation differences in size at first reproduction in threespine stickleback, *Gasterosteus aculeatus* L. Heredity 38:53–60

Moodie GEE (1982) Why asymmetric mating preferences may not show the direction of evolution. Evolution 36:1096–1097

O'Donald P (1977) Theoretical aspects of sexual selection. Theor Popul Biol 12:298–334

O'Donald P (1980) Genetical models of sexual selection. Cambridge University Press, Cambridge

Pelkwijk JJ ter, Tinbergen N (1937) Eine reizbiologische Analyse einiger Verhaltensweisen von *Gasterosteus aculeatus* L. Z Tierpsychol 1:193–200

Perrone M (1978) Mate size and breeding success in a monogamous cichlid fish. Environ Biol Fish 3:193–201

Ridley M, Rechten C (1981) Female sticklebacks prefer to spawn with males whose nests contain eggs. Behaviour 76:152–161

Rowland WJ (1975) The effects of dummy size and color on behavioral interaction in the jewel cichlid, *Hemichromis bimaculatus* Gill. Behaviour 53:109–125

Rowland WJ (1979) Some methods of making realistic fish dummies for ethological research. Behav Res Methods Instrum 11:564–566

Rowland WJ (1982) Mate choice by male sticklebacks, *Gasterosteus aculeatus*. Anim Behav 30:1093–1098

Rowland WJ (1983) Interspecific aggression and dominance in *Gasterosteus*. Environ Biol Fish 8:269–277

Rowland WJ (1989a) The effects of body size, aggression and nuptial coloration on competition for territories in male threespine sticklebacks *Gasterosteus aculeatus*. Anim Behav 37:282–289

Rowland WJ (1989b) The ethological basis of mate choice in male sticklebacks, *Gasterosteus aculeatus*. Anim Behav 37

Rowland WJ, Sevenster P (1985) Sign stimuli in the threespine stickleback (*Gasterosteus aculeatus*): a re-examination and extension of some classic experiments. Behaviour 93:241–257

Rutowski RL (1982) Epigamic selection by males as evidenced by courtship partner preferences in the checkered white butterfly (*Pieris protodice*). Anim Behav 30:108–112

Ryan MJ (1980) Female mate choice in a neotropical frog. Science 209:523–525

Sargent RC, Gebler JB (1980) Effects of nest site concealment on hatching success, reproductive success, and parental behaviour of the threespine stickleback, *Gasterosteus aculeatus*. Behav Ecol Sociobiol 7:137–142

Sargent RC, Gross MR, van den Berghe EP (1986) Male mate choice in fishes. Anim Behav 35:545–550

Schmidt W (1957) Attrappenversuche zur Analyse des Lachens. Psychol Beitr 3:223–264

Semler DE (1971) Some aspects of adaptation in a polymorphism for breeding colours in the threespine stickleback (*Gasterosteus aculeatus*). J Zool (London) 165:291–302

Sevenster P (1961) A causal analysis of a displacement activity (fanning in *Gasterosteus aculeatus*). Behaviour (Suppl) 9:1–170

Sevenster-Bol ACA (1962) On the causation of drive reduction after a consummatory act (in *Gasterosteus aculeatus* L.). Arch Neerl Zool 15:175–236

Simmons LW (1986) Female choice in the field cricket *Gryllus bimaculatus* (De Geer). Anim Behav 34:1463–1470

Thornhill R, Alcock J (1983) The evolution of insect mating systems. Harvard University Press, Cambridge

Tinbergen N (1951) The study of instinct. Oxford University Press, Oxford

Tinbergen N (1965) Animal behavior. Time, New York

Trivers RL (1985) Social evolution. Benjamin Cummings, Menlo Park

Wickler W (1968) Mimicry in plants and animals. McGraw-Hill, New York

Wilbur HM, Rubenstein DI, Fairchild L (1978) Sexual selection in toads: the roles of female choice and male body size. Evolution 32:264–270

Wootton RJ (1973) Fecundity of the three-spined stickleback, *Gasterosteus aculeatus* (L). J Fish Biol 5:683–688