

DETERMINANTS OF REPRODUCTIVE SUCCESS OF MALE STICKLEBACKS IN THE FIELD AND IN THE LABORATORY

by

TIJS GOLDSCHMIDT^{1,*} & THEO C. M. BAKKER^{2,**}

⁽¹⁾*Ethology Research Group, Zoological Laboratory, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands*

⁽²⁾*Universität Bern, Zoologisches Institut, Abteilung Verhaltensökologie, Wohlenstrasse 50a, CH-3032 Hinterkappelen, Switzerland*

ABSTRACT

Several determinants of reproductive success of male three-spined sticklebacks, *Gasterosteus aculeatus* L., have been identified in the laboratory under semi-natural conditions. The impact of these determinants in natural populations is largely unknown. Here we analyse some determinants of reproductive success in natural Dutch stickleback populations and compare them with those obtained in a laboratory study of VAN DEN ASSEM (1967). Although we fail to affirm a positive correlation between territory size and aggression, the determinants of reproductive success revealed in VAN DEN ASSEM's study are shown also to be of importance under natural conditions. Superior reproductive success is associated with large territory size and males with large territories suffer less egg raiding. An enhanced likelihood of nest entering by ripe females occurs right after creeping through and this male behaviour is observed more frequently in males with relatively large territories. Further, ripe females are more apt to enter a nest that already contains eggs, and this is not a result of changes in the male's courtship through the presence of eggs in its nest. The functional significance of some behavioural patterns like creeping through, sneaking and egg-raiding is discussed.

KEY WORDS: *Gasterosteus aculeatus*, reproductive success, aggressiveness, territory size, courtship success, creeping through, sneaking, egg-raiding

INTRODUCTION

Polygyny inevitably involves a great variation in male reproductive success. There are many ways in which a male can increase his reproductive output. The array of possibilities may vary greatly among species and also between populations of one species as a result of the interplay of different forces of natural and sexual selection. The two alternative approaches to studying determinants of reproductive success, field and laboratory research, are not essentially different

* Present address: Ecological Morphology Research Group, Zoological Laboratory, University of Leiden, P.O. Box 9516, 2300 RA Leiden, The Netherlands.

** To whom offprint requests should be addressed.

from each other. The laboratory lends itself better to experimentation. On the other hand, in order to judge the impact of different determinants of reproductive success on fitness one is ultimately committed to the natural habitat.

One advantage of the three-spined stickleback, *Gasterosteus aculeatus* L., as an experimental animal in behavioural ecology is that it can easily be studied both in its natural habitat and in the laboratory under semi-natural conditions. Its ethology is well-known (e.g. WOOTTON, 1976) which facilitates both the planning and interpretation of experiments. In males, in the laboratory, superior reproductive success was found to be associated with large territories (VAN DEN ASSEM, 1967; BLACK, 1971; LI & OWINGS, 1978), concealment of nests (SARGENT & GEBLER, 1980; SARGENT, 1982), low levels of aggression (WARD & FITZGERALD, 1987), or the presence of eggs in the nest (RIDLEY & RECHTEN, 1981; JAMIESON & COLGAN, 1989). In female choice experiments, in the laboratory, females preferred red-throated males over non-red males (McPHAIL, 1969; SEMLER, 1971), larger over smaller males (ROWLAND, 1989), or males with more intensively red breeding coloration over less intensively coloured males (MILINSKI & BAKKER, 1990; McLENNAN & McPHAIL, 1990). Though feasible, studying male reproductive success and its determinants in the field is less easy and accordingly less field studies have been published. Those present seem to confirm the results of laboratory experiments with fish of corresponding populations and have led to the recognition of some additional determinants of reproductive success. A new element revealed in the field studies is the greater fitness of males nesting early in the reproductive season (KYNARD, 1978; MORI, 1990). Further, superior reproductive success was associated with nesting in sheltered habitats (MOODIE, 1972; KYNARD, 1978; MORI, 1990), nesting in deep water (KYNARD, 1978; since in this population, which was also studied by SEMLER, 1971, red-throated males nested in deeper water than non-red males, this association might be attributed to the female mating preference for red males), or small territory size which was paralleled by low levels of aggression (FITZGERALD, 1983; FITZGERALD & WHORISKEY, 1985). The latter correlation is in seemingly contrast with the reverse correlation found in some laboratory studies. However, it was established in a heterogeneous habitat with three stickleback species breeding sympatrically.

There is an obvious need for more field data. A detailed knowledge of stickleback behaviour in different natural populations may help to refute putative laboratory artefacts. Uncomprehended behaviour displays observed under laboratory conditions have recurrently been viewed as artefacts. Examples are diversionary displays (P.

SEVENSTER, personal communication) which are a common phenomenon in some stickleback populations (WHORISKEY & FITZGERALD, 1985; FOSTER, 1988; FOSTER, submitted) and aborted nest entries by seemingly ripe females (JAMIESON & COLGAN, 1989) which also frequently occur in nature (FOSTER *et al.*, in manuscript).

The present study was set up to verify, in a natural Dutch stickleback population, VAN DEN ASSEM's (1967) findings obtained in the laboratory. In short, some main results of his study relevant for the present study were: 1. that territory size was positively correlated with the number of attacks initiated by the owner; 2. that owners of large areas were more successful in courtship than their rivals in smaller territories. The probability of getting a female into the nest was correlated with absolute territory size; 3. that stealing of eggs was the major factor causing egg-losses. Nests in small territories suffered more from egg-stealing than nests in large areas. Stolen eggs were safe if a full clutch, obtained by courtship, was added later on.

To facilitate comparison, the collection and analysis of data was, whenever possible, focussed on similarities with VAN DEN ASSEM's study. The present paper reports some determinants of reproductive success in the natural situation. The functional significance of some behavioural patterns like creeping through, sneaking and egg-raiding is also discussed. Additional aspects will be treated in forthcoming papers (FOSTER *et al.*, in manuscript; GOLDSCHMIDT *et al.*, in preparation; GOLDSCHMIDT *et al.*, in manuscript).

MATERIAL AND METHODS

The sticklebacks used in this study belonged to freshwater populations that were monomorphic for the low plate morph (forma *leiura*, sensu BAKKER & SEVENSTER, 1988). Observations were made in two small ponds one at each of two trout cultivation stations some 15 km apart, one (dimensions: 40 × 50 m) located at "'t Smaller", Emst (near Vaassen) and the other (dimensions: 150 × 50 m) at "de Zwaanspreng", Apeldoorn, the Netherlands. The ponds were fed with water from brooks. The migration of sticklebacks between the ponds and brooks was limited. The two populations studied were probably not completely isolated from each other. In both ponds sticklebacks nested within and outside vegetation consisting of *Glyceria maxima*. To permit observation, the selected study sites had little or no vegetation. The bottom was sandy in both ponds. At "'t Smaller", observations began on 26 April 1978, less than two weeks after the onset of nesting, and continued until 20 July 1978 when only one nest remained. Observations were made at "de Zwaanspreng" from 20

July to 6 September 1978, from 26 July to 8 September 1981 and from 10 to 15 June and 17 to 21 July 1985. Observations were made from the shoreline. All selected nests were located in water one meter deep or less. Males in the sexual phase or at least still ready to court females were observed. Two observation methods were used. In the first, observations were usually made on only one courting male on a given day and the focal male was observed for 2-9 h. At "'t Smalvert" 144 h of such observations were made on 21 males, and at "de Zwaanspreng" approximately 130 h on 20 males. At "de Zwaanspreng", an additional 108 h of observations were made on 56 courting males. Only one courtship of each male was used for the analysis of this dataset. Details of aggressive interactions, sneaking behaviour and courtship were recorded.

Estimates of the territory size of nest owners were made by averaging the distances from the nest to the nests of the three nearest neighbours. When there were no rival males' nests within a radius of 150 cm, this value was used as the average nearest neighbour distance.

Estimates of the number of aggressive encounters in which a nest owner was involved included the number of attacks (including biting and pursuit), intention attacks and threat movements directed at rival males and those directed by rivals at the focal male. The analysis of the relationship between aggression and territory size was based on the number of (intention) attacks per hour initiated by the focal male on rivals as well as those initiated by rivals on this male. Interactions for which it was unclear which male had initiated the interaction, were excluded from the counts. Interactions with non-conspecific fishes other than juvenile perch were extremely rare. Interactions with invertebrates (snails, leeches) and tadpoles have not been analysed.

In the analysis of courtship, the following stages were distinguished; 0 = no courtship activity, 1 = courtship initiated, 2 = female reaches the nest entrance, 3 = female enters nest, 4 = female spawns. We estimated the following transition probabilities: (1) the likelihood of initiating courtship given the appearance of a female with an extended belly, viz. a ripe female ($P_{01} = 1 - P_{00}$), (2) the likelihood that a female with whom courtship had been initiated reached the nest entrance (P_{12}), (3) the likelihood that a female at the nest entrance entered the nest (P_{23}) and, finally, (4) the likelihood that a female in the nest spawned (P_{34}). Thus $P_{01} \times P_{12} \times P_{23} \times P_{34}$ gives the likelihood of courtship success, if $P_{04} = 0$, $P_{14} = 0$, $P_{24} = 0$. Indeed, the latter three transitions did not occur.

Details on the analysis of sneaking behaviour and mate choice by females will be published in forthcoming papers (GOLDSCHMIDT *et al.*, in preparation; GOLDSCHMIDT *et al.*, in manuscript).

RESULTS AND COMPARISONS WITH DATA OBTAINED
IN THE LABORATORY

Aggressive Interactions

A preliminary analysis was made of the aggressive interactions between focal nest owners and other sticklebacks as well as juvenile perches. Three categories of interactions were distinguished: (A) interactions between two rival males not immediately preceded by an interaction between one of these males and another stickleback or juvenile perch, (B) interactions between a nest owner and an intruder (possibly a juvenile perch) not being a nesting neighbour, (C) interactions between two rivals immediately preceded by an interaction of one of these rivals with a third stickleback or a juvenile perch. The total number of aggressive interactions per hour at " 't Smallerlert" (13.5) was much smaller than at "de Zwaanspreng" (76.2). At " 't Smallerlert" A- and B-interactions both formed a large fraction of the total number of aggressive interactions, while C-interactions occurred less frequently (Table I). At "de Zwaanspreng" B-interactions were predominant over A- and C-interactions (Table I). The observations at "de Zwaanspreng" were carried out later during the season, at a time when juvenile sticklebacks which had been born earlier that season were frequently intruding the territories.

TABLE I

Classification of aggressive (non-courtship) interactions of males in the sexual phase at " 't Smallerlert" (observations of 21 males during 26.04-19.07.1978) and "de Zwaanspreng" (observations of 6 males during 20.07-29.07.1978). For explanation of interaction types see text.

<i>Interaction type</i>	<i>" 't Smallerlert"</i>			<i>"de Zwaanspreng"</i>		
	<i>n</i>	<i>n/hour</i>	<i>%</i>	<i>n</i>	<i>n/hour</i>	<i>%</i>
A	977	6.8	50.1	287	9.1	12.0
B	789	5.5	40.5	2024	64.4	84.5
C	183	1.3	9.4	84	2.7	3.5
Total	1949	13.5	100.0	2395	76.2	100.0

A more detailed analysis of the A-, B- and C-interactions revealed that 97.7% of the B-interactions at "de Zwaanspreng" were encounters with juvenile sticklebacks (Table II). At " 't Smallerlert", interactions with settling males were a more frequent type of B-interactions, both in an absolute and relative sense. Also C-interactions at "de Zwaanspreng" were usually caused by a preceding

TABLE II

Subdivision of the in Table I classified A-, B-, and C-types of aggressive (non-courtship) interactions of males in the sexual phase at 't Smaller' (Sm) and 'de Zwaanspreng' (Zw). For explanation of interaction types see text.

		<i>A-interactions, i.e. aggression between rivals (a and b) in the following situations:</i>										
		Male a or male b sneaks				Male a and/or male b in borderline area			Male a attacks male b in centre of its territory			
	n	n/h	%	n	n/h	%	n	n/h	%	n	n/h	%
Sm	113	0.8	11.6	745	5.2	76.3	119	0.8	12.2			
Zw	11	0.4	3.8	257	8.3	89.5	19	0.6	6.6			

		<i>B-interactions, i.e. aggression against the following territorial intruders:</i>													
		ripe female that flees after first approach			settling male			juvenile stickleback			juvenile perch				
	n	n/h	%	n	n/h	%	n	n/h	%	n	n/h	%	n	n/h	%
Sm	96	0.7	12.2	586	4.1	74.3	33	0.2	4.2	74	0.5	9.4			
Zw	7	0.2	0.4	40	1.3	2.0	1977	63.8	97.7	0	0.0	0.0			

		<i>C-interactions, i.e. aggression between rivals after preceding aggression against:</i>														
		neighbouring male			ripe female that has been courted or not			settling male			juvenile stickleback			juvenile perch		
	n	n/h	%	n	n/h	%	n	n/h	%	n	n/h	%	n	n/h	%	
Sm	26	0.2	14.2	78	0.5	42.6	67	0.5	36.6	2	0.0	1.1	10	0.1	5.5	
Zw	5	0.2	6.0	9	0.3	10.7	5	0.2	6.0	65	2.1	77.4	0	0.0	0.0	

interaction with a juvenile, while at " 't Smaller", females and settling males were the most common cause of C-interactions between rivals.

Most A-interactions at both localities occurred when one of the two rivals dwelt in the borderline area between the neighbouring territories. Much less common were interactions between a nest owner and a sneaking rival. Attacks by a nest owner on a neighbour which remained in the centre of its own territory were relatively uncommon too. However, such interactions were frequently seen shortly after the former male had successfully courted a female. A sudden increase in the level of aggression after a male has acquired a clutch of eggs has also been documented in the laboratory (SEVENSTER-BOL, 1962).

Aggressiveness and Territory Size

In order to acquire a territory and maintain it, male sticklebacks have to behave aggressively towards rival males. In a stable rival situation in the laboratory, the number of aggressive interactions initiated by a nest owner and the size of his territory showed a significant positive correlation (VAN DEN ASSEM, 1967). In our field population " 't Smaller", however, a negative correlation was found between territory size and the frequency of attacks initiated by the owner (fig. 1). Also, the number of attacks initiated by rivals, directed towards the focal male, was negatively correlated with the territory size of the focal male (fig. 1). Males with small territories were therefore more often involved in aggressive interactions, initiated both by themselves and by their neighbours. VAN DEN ASSEM's (1967) laboratory study suggested also that males with small territories were often targets of aggression by neighbouring males.

Courtship Success and Territory Size

The transition probabilities of the successive courtship stages were analysed in relation to territory size (fig. 2). The likelihood of initiating courtship (P_{01}) was not correlated with territory size (fig. 2a). In the laboratory, the P_{01} has not been estimated quantitatively, but presumably approached 1.0, since females were selected on readiness to court. In contrast to this, in the field a fairly large fraction of females with extended bellies seemed not to be able to withstand the male's attack and fled or swam away (P_{01} combined for the 17 focal males: 0.58). The likelihood that a female reached the nest entrance given courtship initiation (P_{12}) was significantly positively correlated

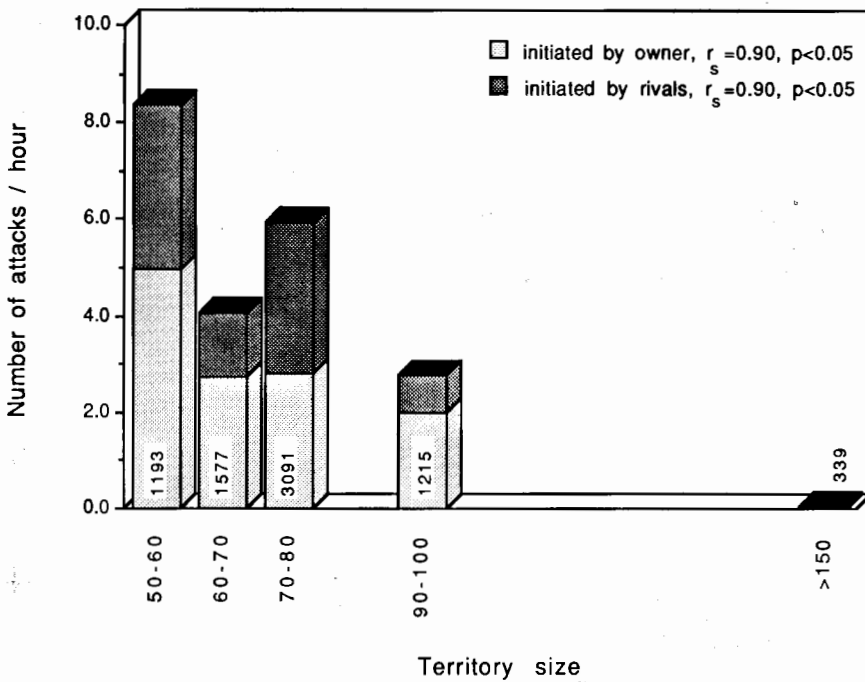


Fig. 1. The mean frequency of aggressive interactions, expressed as the number of (intention) attacks per hour, between focal males ($n = 17$) and rival males as a function of the territory size of the focal males at "t Smallest". A distinction is made between attacks initiated by focal males and those initiated by rivals. Indicated per territory size class is the duration of the observation period in minutes. Focal males in the respective size classes: 3, 3, 8, 2, 1. r_s is the Spearman rank correlation coefficient.

with territory size (fig. 2b). This seems in accordance with the findings of VAN DEN ASSEM (1967), who found that the average time between the introduction of a female and her first arrival at the nest entrance was significantly longer in the small territories. Furthermore, territory size showed a significant, positive correlation with the likelihood that a female at the nest entrance entered the nest (P_{23} ; fig. 2c), which agrees with VAN DEN ASSEM's (1967) findings. The likelihood that a female spawned, once she had entered the nest (P_{34}) did not differ significantly among territories of different size (fig. 2d). Combining the transition probabilities of the successive courtship stages reveals a highly significant positive correlation between territory size and courtship success (fig. 2e); thus, females preferred to spawn in nests of males with large territories.

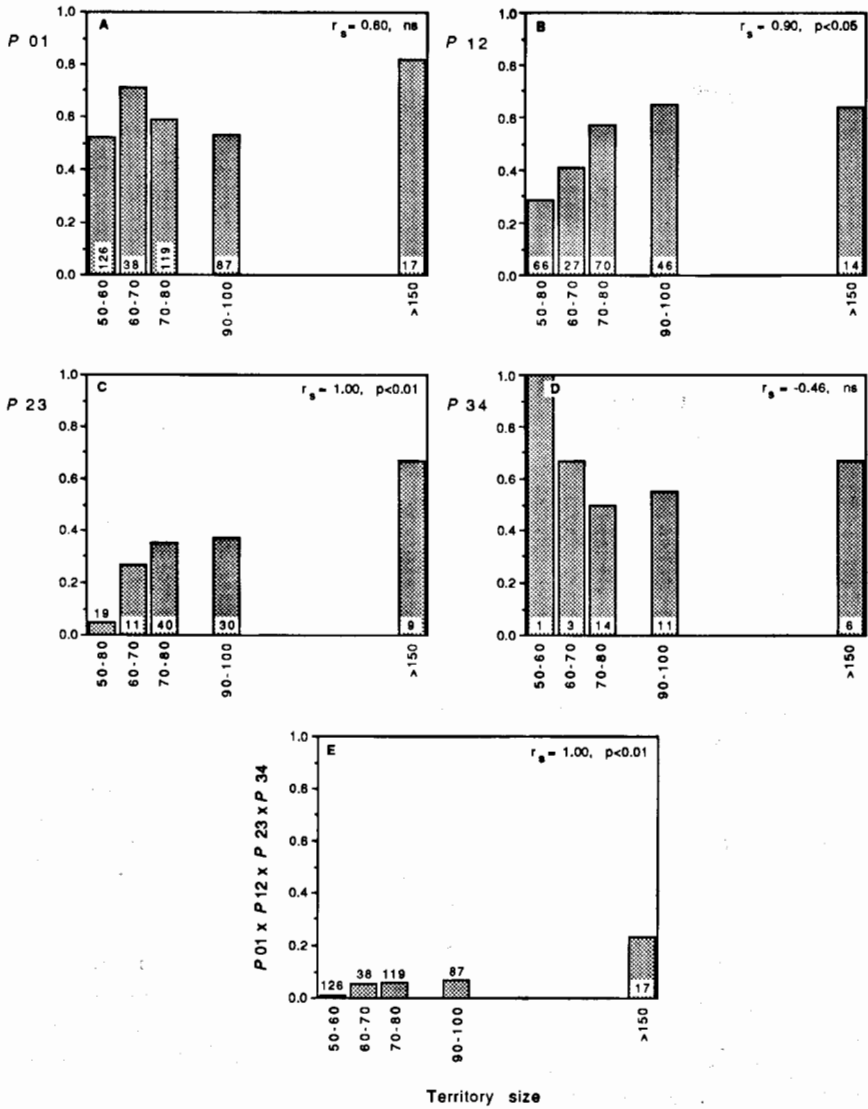


Fig. 2. Transition probabilities (P) in courtship of focal males ($n=17$) at "t Smaller" as a function of territory size. Courtship is divided into the following successive stages: 0, no courtship activity while female present; 1, courtship initiated; 2, females reaches the nest entrance; 3, female enters nest; 4, female spawns. Indicated are the number of cases in the initial stage of the transition. The multiplication of transition probabilities (graph e) is an estimation of the likelihood of courtship success given the appearance of a ripe female. r_s is the Spearman rank correlation coefficient.

Functional Aspects of the Creeping-through Cycle in Relation to Courtship

The first time that a male creeps through (CT) the nest marks the transition between the nest building phase and the sexual phase. From that moment onwards, the male is ready to court a female. The behaviour pattern is a common element in male courtship; directly after CT the male has a relatively high tendency to zigzag and a relatively low level of aggression (SEVENSTER, 1961; NELSON, 1965; 't HART, 1978). Under standard conditions in a tank (stimulation by a ripe female confined in a glass tube), a male in the sexual phase creeps through the nest with intervals of strikingly constant duration (NELSON, 1965; 't HART, 1978). But, if a ripe female is presented to a male until he has crept through and is subsequently removed, the male will creep through in such a way that the duration of the subsequent inter-creeping through intervals (ICTI) increases geometrically.

CT was frequently seen in the field. The duration of the ICTI's was much less predictable than it was under standard conditions in a tank. This is not surprising since interactions with sticklebacks other than ripe females (and non-conspecifics) continuously disturbed the male. Moreover, the availability of ripe females fluctuated through time. In the seven smallest territories, 23 CT's were observed during 2422 min of observation (0.57/h). In the seven largest territories, the frequency of CT was 1.6 times as high, viz. 0.92/h (45 CT's were observed during 2924 min). This difference is in accordance with VAN DEN ASSEM's findings (1967). He found that the probability of CT related to the total duration of courtship was 2.3 times higher in the large territories than in the small ones. Since in the present study both courtship success and the frequency of CT were higher in the relatively large territories, CT (or a correlate of CT) might lead to courtship success. An analysis of the relationship between courtship success and the time since the last CT, revealed that the likelihood of observing a female that enters and spawns was highest in the first five min after CT and then declined (fig. 3a: $r_s = -0.83$, $p < 0.01$, 1-tailed). The same trend is found if replicate observations (of different CT cycles on single males) are included (fig. 3a: $r_s = -0.84$, $p < 0.01$, 1-tailed). By far the most courtship successes occurred right (within one min) after the act of CT (fig. 3b: $r_s = -0.82$, $p < 0.06$, 1-tailed). If courtships in which a female entered but did not spawn are also taken into account, the enhanced likelihood of entering just after CT is even more pronounced (fig. 3a: $r_s = -0.86$, $p < 0.01$, 1-tailed; fig. 3b: $r_s = -0.98$, $p < 0.03$, 1-tailed). Thus CT (or a correlate of CT) increases the likelihood of courtship success, although it is unclear how this result is achieved (more vigorous courting, less aggression, more attractive

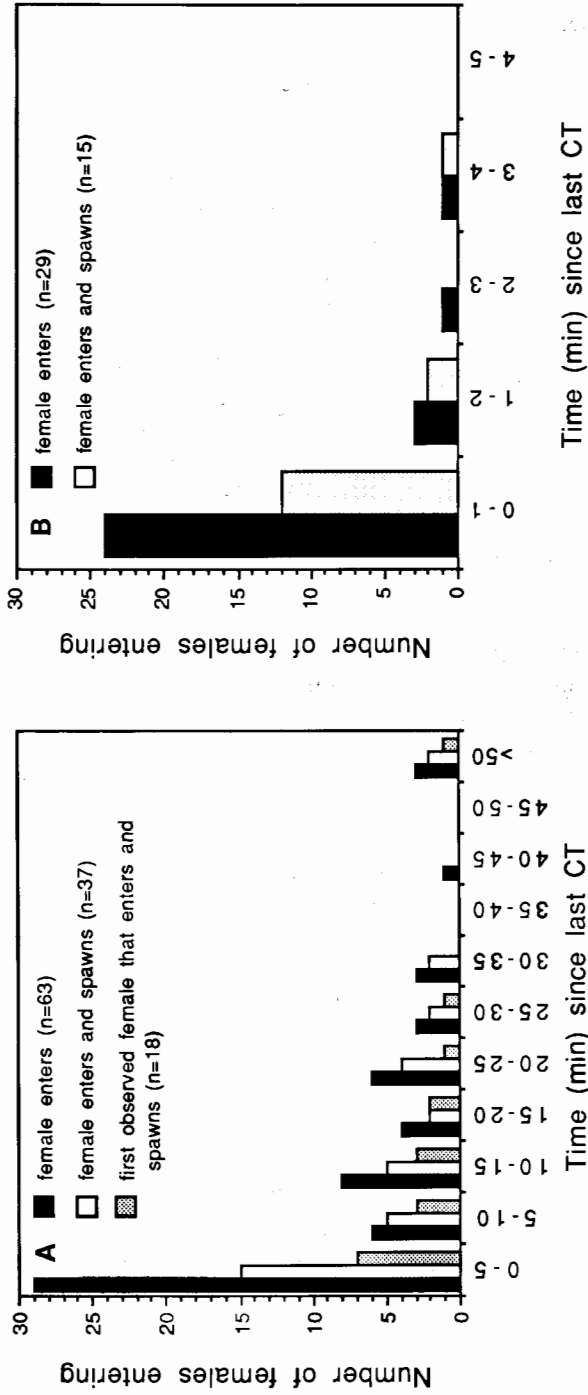


Fig. 3. (a) Timing of successful courtships after creeping through (CT). Data of 18 males collected at "t Smaller" and "de Zwaanspreng". (b) Idem for the first five minutes after CT.

coloration, open nest-tunnel, female better informed about the location of the nest-tunnel, etc.). One would therefore expect that sexually active males will creep through the nest as soon as a ripe female appears or has been found. Within the limitations of the CT cycle, this is precisely what happens. The appearance of a ripe female increases the likelihood of CT, or, shortens the ICTI. However, after CT there is a refractory period during which CT does not occur again, even if a female passes the territory. Exceptional in this respect is the small fraction of males that creeps through the nest for a second time and sometimes even more often than that directly after a CT. After this sort of multiple CT event, a refractory period follows. It had originally been presumed that these so-called 'maniacs' do not occur in nature. In the laboratory, maniacs were not observed in fishes that had been kept under winter conditions (SEVENSTER & 't HART, 1974). However, at "'t Smaller" and "de Zwaanspreng", maniacs did occur (from 28 males of which at least one CT was observed, four males showed one or more double CTs. In total, 13 CTs of maniacs were observed of which five were double). The phenomenon deserves some attention since there is tentative evidence that this Mendelian-inherited trait (SEVENSTER & 't HART, 1974) correlates with reproductive success; six out of 30 females (20%) with which courtship had been initiated by maniacs spawned in their nests, while in males of which no double CT was seen, only 26 out of 432 (6%) courted females spawned ($\chi^2 = 6.48$, $df = 1$, $p < 0.02$, 2-tailed).

Sneaking and Egg Raiding in Relation to Territory Size

In several fish species a separate category of smaller and/or non-territorial males attempt to gain access to females by sneaking and thus try to steal fertilizations from males which had claimed females through male-male competition. Apparently, these individuals apply an alternative reproductive strategy (e.g. GROSS, 1982, 1985; KODRICK-BROWN, 1986). In contrast to this, three-spined sticklebacks apply a mixed strategy. Each individual nest owner is at the same time a potential sneaker. Sneaking in three-spined sticklebacks was first described by VAN DEN ASSEM (1967). Near the border of its territory, a male may suddenly freeze and then slowly sink to the bottom while losing to a great extent the breeding coloration he had. His body coloration changes into a cryptic pattern. Then he creeps virtually millimeter by millimeter towards a neighbouring male. In the vicinity of the neighbour's nest, the male may then suddenly dash forward. Courtship is especially likely to elicit a sneaking attempt and, if a ripe female has just spawned in a rival's nest, a sneaker may attempt to fer-

tilize eggs either before the nest owner has had the chance to release sperm, or after him. After such a fertilization attempt, the sneaker almost always tries to steal eggs which he brings back to his own nest. Usually, the sneaker returns several times to rob a mouthful of eggs (VAN DEN ASSEM, 1967). Often these eggs are eaten (VAN DEN ASSEM, 1967; BLACK, 1971; WOOTTON, 1971; KYNARD, 1978). In some populations, males do not steal fertilizations, although eggs are frequently stolen by sneakers and then eaten (KYNARD, 1978). Finally, there are New World-populations in which sneaking has never been observed during several field-seasons (GOLDSCHMIDT *et al.*, in manuscript).

At "t Smallest" sneaking was frequently observed. These data will be treated more extensively elsewhere (GOLDSCHMIDT *et al.*, in manuscript). In the seven smallest territories, a total of six successful courtships were observed on four males (one male had three successes). During five of these six courtships (three different males), sneakers were active and raided eggs. In the seven largest territories, 14 successful courtships were observed on five males. Three of these 14 courtships (two males) were followed by egg raiding. Thus males with small territories were more likely to become the victim of sneaking attempts and egg raiding than males with relatively large territories (Fisher exact probability test, $p = 0.017$, 1-tailed). This result is in accordance with VAN DEN ASSEM's (1967) findings. Except in one case (1 out of eight cases) egg raids by sneakers were preceded by attempts to fertilize the clutch. In one of seven cases, the sneaker managed to pass through the nest before the nest owner, but usually the sneaker came second (GOLDSCHMIDT *et al.*, in manuscript). In the laboratory, sneakers fertilized a clutch much more frequently before the legitimate owner went through the nest, viz. in approximately half of the cases (VAN DEN ASSEM, 1967).

Functional Aspects of Sneaking Behaviour, Stealing Fertilizations and Egg Raiding

The function of stealing fertilizations from a rival's nest seems obvious. In this way, a male can increase his fitness without more parental investment than that required by sneaking plus fertilization. Unfortunately, in the case of the stickleback, it has not been investigated whether and to what extent sperm competition occurs between successive ejaculations of different males. It does seem plausible to assume that the male which succeeds first in releasing sperm has (by far?) the greater share in fertilizations of freshly laid eggs. It would therefore pay for a sneaker to try and fertilize the clutch before the

nest-owner can do so. But even if he fails there, it may pay for a sneaker to release sperm immediately after the nest-owner, because he either may get some (minor?) share in fertilization of the current clutch or a possible share of fertilization of the next clutch collected by the nest-owner. It is not very likely that males are able to distinguish between clutches that have been fertilized by themselves or others and thus the legitimate owner of the clutch would take care even if all eggs have been fathered by the sneaker. On these assumptions it is surprising that sneakers always steal and transport eggs to their own nest, even if they have fertilized a clutch before the legitimate owner has done so. The number of raided eggs is usually too small to prime proper parental behaviour. In the laboratory, 74% (26/35) of the males with only stolen eggs in their nests had empty nests on day five of their cycle (VAN DEN ASSEM, 1967). At " 't Smaller", males who had nearly completed a parental cycle had at least a hundred eggs in their nest and usually many more (fig. 4a). Inspection of the nests of males who had not yet definitely entered a parental cycle showed that a fraction of nests contained from a few up to 37 eggs which at this locality is likely to be less than a full clutch (fig. 4b). We suspect that these eggs had been collected by raiding. In addition, there was a fraction of empty nests and there were nests which contained at least one full clutch. In populations where sneakers attempt to steal fertilizations, this behaviour and the subsequent raiding attempts at least diminish in frequency and often even stop completely in a male that has obtained a clutch by courting a female (VAN DEN ASSEM, 1967; confirmed at " 't Smaller"). These observations suggest a functional relationship between egg raiding and the acquisition of eggs through courting females. In recent years, it has been shown that, in several species of fish in which the male bestows parental care, females prefer males whose nests contain eggs. These studies were carried out partially on sticklebacks (RIDLEY & RECHTEN, 1981; JAMIESON & COLGAN, 1989), and partially on other fish species (CONSTANZ, 1985; MARCONATO & BISAZZA, 1986; UNGER & SARGENT, 1988; GRONELL, 1989; KNAPP & SARGENT, 1989; SIKKEL, 1989). RIDLEY & RECHTEN (1981) carried out sequential choice experiments in which females were confronted with single males in isolation. In these experiments, the likelihood of a female entering the nest, after 'nosing' into it, was higher if the nest already contained eggs. RIDLEY & RECHTEN (1981) concluded that females prefer to spawn with males whose nests contain eggs. However, these authors did not satisfactorily rule out the possibility that this preference might be partly caused by an effect of the presence of eggs on the male's courtship. JAMIESON & COLGAN (1989) extended the experiments of RIDLEY & RECHTEN (1981) by

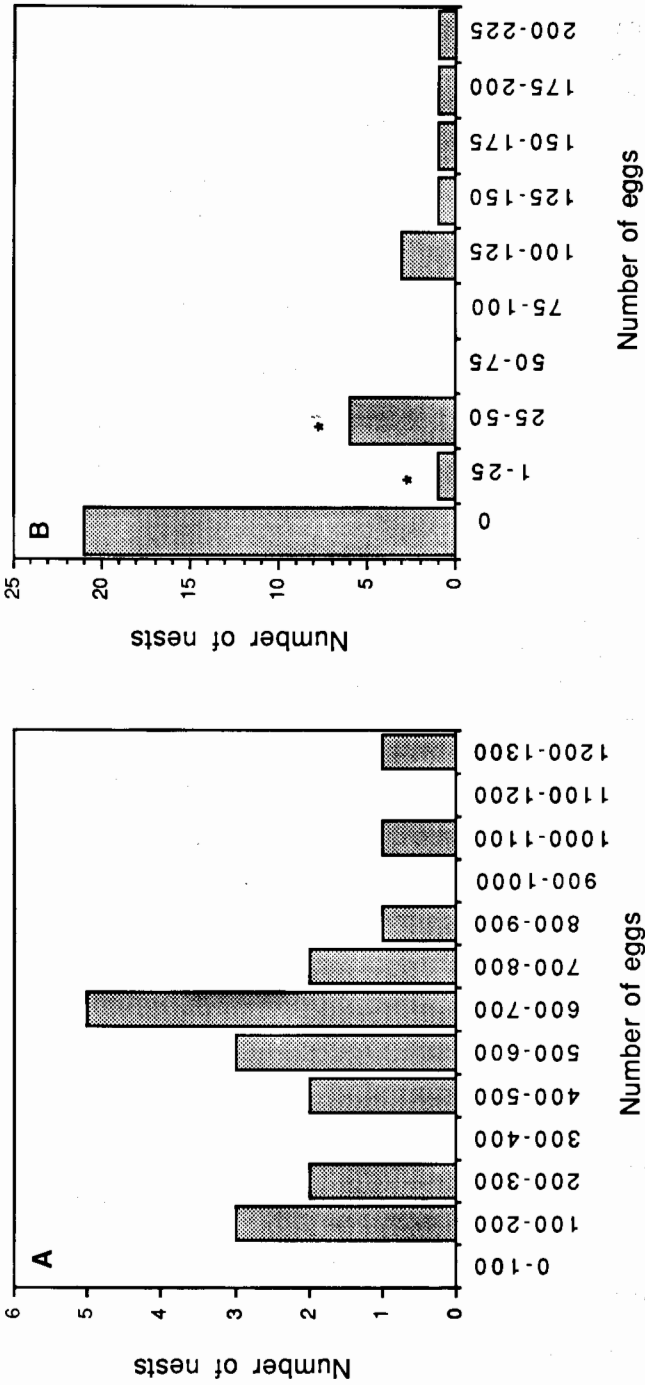


Fig. 4. Frequency distribution of the number of eggs in the nests at "t Smallerst" of (a) 20 males at the end of the parental phase, and (b) 35 males, males in the sexual phase or in the beginning of the parental phase. An asterisk indicates nests in which the eggs were probably obtained by raiding.

testing female choice in rival situations (which are more likely to reflect the natural situation). Like RIDLEY & RECHTEN, JAMIESON & COLGAN found that male sticklebacks which had recently courted successfully and had eggs in their nests, were preferred by females over males with empty nests. However, in contrast to RIDLEY & RECHTEN, these authors claim that female preference should more readily be attributed to differences in male courtship (more intensely courting and brighter coloration when the nest contains eggs) than to a direct effect of eggs on female choice.

In our field studies, courting females which nosed into the nest entrance of males with nests containing eggs were indeed more likely to enter a nest with eggs. Ten out of 27 females entered a nest with eggs, while only two out of 31 females entered a nest without eggs ($\chi^2 = 6.47$, $df = 1$, $p < 0.01$, 1-tailed). This result is in accordance with the hypothesis that females prefer males whose nests contain eggs, but again no control was made for possible differences in male quality (details in GOLDSCHMIDT *et al.*, in preparation). Therefore, a series of female choice experiments in the laboratory was done in which carefully selected ripe females could choose between pairs of males visible behind a transparent wall. On the day preceding the experiment, one randomly assigned male of each pair had been given the opportunity to spawn with a female, while the other male had been given courtship experience. In our experimental set-up, females did not show a preference for males of either category, viz. with a clutch of eggs or with an empty nest. This suggests that the preference of females for males whose nests contained eggs can be attributed to a direct effect of the eggs on the female. This is in accordance with the conclusions reached by RIDLEY & RECHTEN (1981), but seems to contradict JAMIESON & COLGAN's (1989) results.

With regard to our conclusion, it is worthwhile to mention that, in the field, courtships were frequently aborted when the female had nosed into the nest-entrance (FOSTER *et al.*, in manuscript). At "de Zwaanspreng" and "'t Smaller" the respective fractions of females which nosed into the nest entrance and subsequently fled were 66.3% (59/89) and 67.9% (74/109). It is possible that females 'sample' males' nests before making a definite choice.

A functional explanation for stealing eggs from a rival's nest, irrespective of whether the sneaker has fertilized these eggs or not, may thus be that the presence of eggs in the nest increases the likelihood of further successes. Indeed, in the field, males often started courting females, but when they were not successful they would start sneaking at a certain moment. We had the qualitative impression that males which had been sneaking and managed to steal eggs often

courted successfully the next day. The question of whether males which stole their first eggs had, on average, a lower fitness than males which courted successfully without previous egg stealing is unanswered. If so, females might discriminate against egg raiders.

GENERAL DISCUSSION

In the natural stickleback population studied here, superior reproductive success was associated with a large territory size. This association resulted from a significant positive correlation between territory size and the likelihood that ripe females reached the nest entrance once they were courted by the territory owner and a significant positive correlation between territory size and the likelihood that ripe females entered the nest once they had reached the entrance. Further, the probability of egg-raiding by sneakers after successful courtships was significantly lower in the relatively large territories.

All the above results are in agreement with the results of VAN DEN ASSEM's (1967) laboratory study on territoriality of Dutch male sticklebacks in a semi-natural environment. This shows the suitability of this species for experimental behavioural research in the laboratory. The observed selective force in favour of large territories may not be the only sexual selection process operational (see Introduction). By selecting study sites with little vegetation we may have boosted similarity to VAN DEN ASSEM's situations, but it may be said that a significant proportion of males nested in open, non-vegetated sites. We also did not measure some other male traits that could potentially influence reproductive success. The most obvious ones are body size and intensity of red breeding coloration. However, the present study was not aimed at analysing how males get large territories. Laboratory experiments showed that brighter red males from this population had better chances in claiming unoccupied sites than duller males (BAKKER & SEVENSTER, 1983; BAKKER, 1985, 1986). Size differences between the males were not very important for this dominance ability (BAKKER, 1986). Successful artificial bidirectional selection for dominance ability showed the genetic involvement in variation of this male trait (BAKKER, 1985, 1986). These selection experiments revealed two further interesting things. First, artificial selection was only successful in a downward direction, i.e. for decreased dominance ability, suggesting sustained selection for high dominance abilities in the natural situation (BAKKER, 1985, 1986). Second, artificial selection resulted in a clear, correlated response of brightness of red coloration (BAKKER, 1985, 1986). Females in other populations showed a preference for red (McPHAIL, 1969; SEMLER, 1971) or more intensely coloured red males

(MILINSKI & BAKKER, 1990; McLENNAN & McPHAIL 1990) and it is possible that such a female mating preference also exists in the present population. The reproductive advantage of males with large territories may therefore be primarily based on a female mating preference for males with intense red breeding coloration. Intense red males may have an advantage in male-male competition for territories and may thus gain larger territories. In this way, intra- and intersexual selection may supplement each other, because males with relatively large territories experience superior success both in courtship and in hatching (VAN DEN ASSEM, 1967; this study). Unfortunately, neither we nor VAN DEN ASSEM quantified the intensity of the male's red breeding coloration.

In addition, it was shown that the likelihood that ripe females entered the nest once they had reached the entrance was influenced by the presence of eggs in the nest (in the laboratory, VAN DEN ASSEM could avoid this complication). This was a direct effect of the eggs on the female and not an indirect effect mediated by changes in the male's courtship behaviour when he has collected eggs in his nest (see also GOLDSCHMIDT *et al.*, in preparation). This is in agreement with the conclusion of RIDLEY & RECHTEN (1981), which has been criticized by JAMIESON & COLGAN (1989), but not with that of JAMIESON & COLGAN (1989). They claimed that males that had recently spawned courted more intensely. They seem to attach more importance to this non-significant ($p = 0.063$, 1-tailed) difference in courtship behaviour than to the more significant difference in brightness of coloration ($p = 0.03$). In addition, courtship intensity and brightness of coloration were measured while both males (one without and the other with eggs in his nest collected 4-24 h before the test) were courting a ripe female in a container at the border of their territories before the female was released. The differences found in this way may not reflect actual differences in sexual motivation and brightness of coloration between the males, but may be influenced by the choice behaviour of the female in the container. Unfortunately, JAMIESON & COLGAN (1989) did not quantify female behaviour in this stage.

In the stickleback population studied here, territory size appeared to be significantly negatively correlated with the level of aggression between rivals initiated both by the territory owner and rival males. This sharply contrasts with VAN DEN ASSEM's (1967) finding of a positive correlation between territory size and the number of attacks initiated by the owner. The discrepancy between VAN DEN ASSEM's and the present study with respect to the relation between territory size and level of aggression might be explained by population differences. The fish used by VAN DEN ASSEM originated from an anadromous

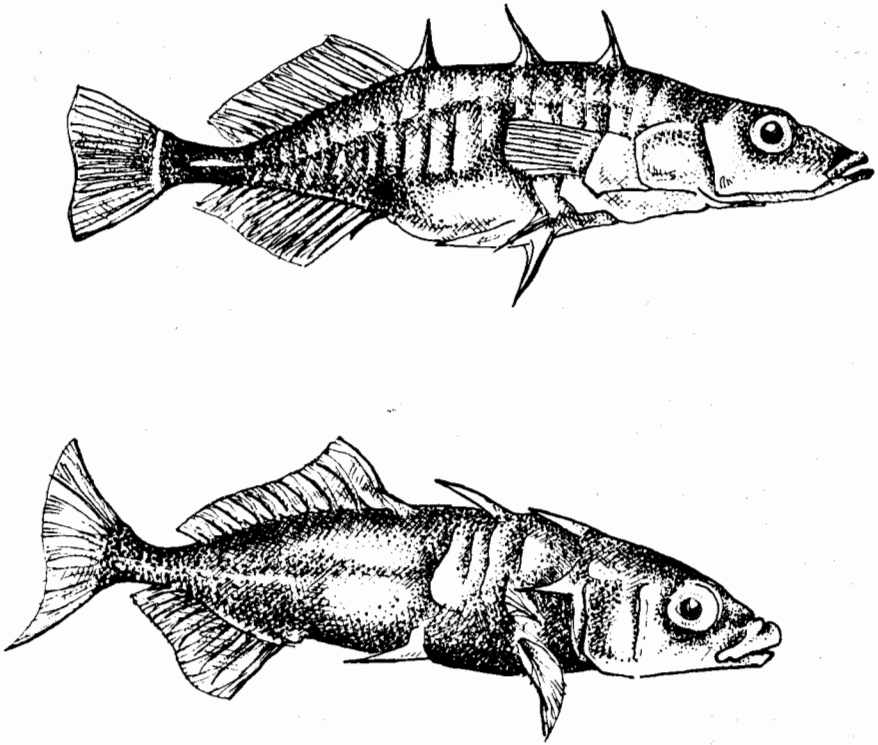


Fig. 5. Three-spined stickleback complete (top) and low (bottom) plate morphs (*Gasterosteus aculeatus* L. forma *trachura* and forma *leiura*, respectively). Drawings by G. W. POTTS.

population (polymorphic for the formae *trachura*, *semiarmata*, and *leiura*; fig. 5) sampled at Den Helder (Netherlands), while we studied Dutch freshwater populations (monomorphic for the forma *leiura*; fig. 5 bottom). These different modes of life are accompanied by differences in an array of life-history and behavioural characters (BAKKER & FEUTH-DE BRUIJN, 1988; BAKKER *et al.*, 1988; BAKKER & FEUTH-DE BRUIJN, unpublished results) some of which may be responsible for the discrepancy between the two studies. BAKKER and co-workers compared laboratory-bred and -reared offspring from wild-caught parents originating from VAN DEN ASSEM's population and from "t Smaller". In the freshwater population, brightness of male red breeding coloration was an important determinant of dominance ability, while this was not the case in the anadromous population. Territorial aggressiveness was significantly greater in males from the

freshwater population. There were indications for a larger territory size of males from the anadromous population. It is not clear how these population differences can cause the population difference in the direction of correlation between territory size and level of aggression, but it is likely that they have a bearing upon this correlation. In addition, in the present study, nest owners were observed at a later stage of their reproductive cycle than the males in the stable rival situation in VAN DEN ASSEM's study. At "'t Smallerst", males in the sexual phase or the beginning of the parental phase were selected. Their mean attack rate was about 30 times lower than that of the laboratory males; mean number of attacks initiated by the owner \pm S.D. in this study 3.1 ± 2.4 per hour ($n = 17$) and in VAN DEN ASSEM's (1967) study 23.0 ± 9.9 per 15 min ($n = 14$). This might have had an influence upon the correlation between territory size and number of attacks initiated by the owner. Waning of aggression towards rivals once the territory borders have been settled has been well documented (e.g. VAN DEN ASSEM & VAN DER MOLEN, 1969; PEEKE, 1969; PEEKE *et al.*, 1969; PEEKE & VENO, 1973; ROWLAND, 1988). Maybe, in general, no simple relationship exists between territory size and territorial aggressiveness. Dominance ability is a more likely determinant of territory size, but one has to realize that the way aggressiveness has been measured in VAN DEN ASSEM's and this study is not a standardized measure of aggressive motivation. As in VAN DEN ASSEM's study, the amount of space available to the males was limited by the dimensions of the tanks, the absolute territory sizes in his and our study cannot directly be compared. Nevertheless, the range of absolute territory sizes in the field fell within the experimental range used by VAN DEN ASSEM, although the latter was much larger in either direction.

While the rhythmicity of creeping through (CT) the nest of nest-owners during the sexual phase and correlated behaviour patterns have been extensively studied from a causal point of view (NELSON, 1965; 't HART, 1978, 1985; SEVENSTER, 1986), functional aspects have so far been greatly neglected. Such a functional analysis should attempt to reveal both the function of the act of CT itself and the rigid rhythmicity with which it is performed. CT marks the transition in the animal from a relatively aggressive to a relatively sexual state (SEVENSTER, 1961; NELSON, 1965; VAN DEN ASSEM, 1967; WILZ, 1975; 't HART, 1978). The act of creeping through has an effect on the pattern of moving about (SEVENSTER, 1961; VAN DEN ASSEM, 1967; 't HART, 1978; T.G.'s field observation). After CT, the male tends to dwell more frequently near the surface and explores a larger area than before. Probably the male is in search of females. During CT, the colour of the male changes, becoming almost translucent in some places

(SEVENSTER, 1961; SARGENT, 1982; McLENNAN & McPHAIL, 1989). This may also have an effect on courtship success, since colour cues play a major role in female mating preference (MILINSKI & BAKKER, 1990). In addition to the effect of CT on behaviour and coloration, CT may help to keep the nest tunnel in good shape; when it is made out of growing plant material (filamentous algae), CT may prevent the obstruction of the tunnel, and when it is made out of dead plant material, CT may prevent the accumulation in the tunnel of microorganisms and waste products that may affect the viability of future eggs. Furthermore, since CT is often a part of courtship, it may increase the likelihood that a female finds the nest entrance as soon as she has been led to the nest. Females rarely enter a male's nest without previous "leading" and "showing" by the male. Remarkably, most cases of nest-entering in the laboratory without the male's "showing" of the nest entrance were observed when he crept through the nest during courtship; at the moment he wriggled through the tunnel, the female dashed for the entrance and entered the nest (VAN DEN ASSEM, 1967; T.C.M.B.'s unpublished results). As CT resembles fertilization and both behaviours elicit nest-raids, CT may deceive undetected sneakers (SARGENT, 1982). In the present study, CT was observed more frequently in males with relatively large territories. Further, it was found, that right after CT the likelihood of nest entering by ripe females was enhanced.

The functional significance of the refractory period after CT, if there is any, is unclear. The importance of maintaining a favourable environment for embryo development and of keeping the nest-tunnel in good shape may set lower limits to the frequency of CT. For an event of low frequency, a regular occurrence might offer a better guarantee to avoid too long intervals than an irregular one (K. KORTMULDER, personal communication). Further, regularity might be easier to achieve (causally speaking) than irregularity (P. SEVENSTER, personal communication). No further suggestions have been made with regard to the possible functional significance of the rigid cyclicity of CT. Assuming that CT increases the likelihood that a male (1) finds a female by exploring the places where females dwell more intensively and/or (2) successfully courts females, the following hypothesis may be worthwhile investigating. CT with cyclicity guarantees that males regularly look for females. If there is a cyclicity in the availability of females and if the male's cycle can be attuned to this cyclical availability by a Zeitgeber, anticipation of males on the appearance of females seems possible. Such an anticipation may be crucial if there is male-male competition for ripe females. Males nesting in shallow tidal areas may be candidates to test this speculative idea.

ACKNOWLEDGEMENTS

We would like to dedicate this paper to Piet Sevenster on the occasion of his professional retirement. We acknowledge gratefully his suggestion to initiate this study and his critical attitude during the collection and analysis of the field-data. E. Feuth-de Bruijn is kindly thanked for carrying out the laboratory experiments and for her willingness to help in practical affairs. C. J. M. Elbers is gratefully acknowledged for stimulating discussions. J. Kroese is thanked for his assistance in the field. K. Kortmulder and J. van den Assem made valuable comments on the manuscript. G. W. Potts made the fine stickleback drawings.

REFERENCES

- ASSEM, J. VAN DEN, 1967. Territory in the three-spined stickleback, *Gasterosteus aculeatus* L. An experimental study in intra-specific competition. *Behaviour Suppl.* **16**: 1-164.
- ASSEM, J. VAN DEN & J. N. VAN DER MOLEN, 1969. Waning of the aggressive response in the three-spined stickleback upon constant exposure to a conspecific. I. A preliminary analysis of the phenomenon. *Behaviour* **36**: 286-324.
- BAKKER, TH. C. M., 1985. Two-way selection for aggression in juvenile, female and male sticklebacks (*Gasterosteus aculeatus* L.), with some notes on hormonal factors. *Behaviour* **93**: 69-81.
- BAKKER, TH. C. M., 1986. Aggressiveness in sticklebacks (*Gasterosteus aculeatus* L.): a behaviour-genetic study. *Behaviour* **98**: 1-144.
- BAKKER, TH. C. M. & E. FEUTH-DE BRUIJN, 1988. Juvenile territoriality in stickleback *Gasterosteus aculeatus* L. *Anim. Behav.* **36**: 1556-1558.
- BAKKER, TH. C. M., E. FEUTH-DE BRUIJN & P. SEVENSTER, 1988. Population differences in aggressiveness of sticklebacks (*Gasterosteus aculeatus* L.). *Behav. Genet.* **18**: 706.
- BAKKER, TH. C. M. & P. SEVENSTER, 1983. Determinants of dominance in male sticklebacks (*Gasterosteus aculeatus* L.). *Behaviour* **86**: 55-71.
- BAKKER, TH. C. M. & P. SEVENSTER, 1988. Plate morphs of *Gasterosteus aculeatus* Linnaeus (Pisces: Gasterosteidae): comments on terminology. *Copeia* **1988**: 659-662.
- BLACK, R., 1971. Hatching success in the three-spined stickleback (*Gasterosteus aculeatus*) in relation to changes in behaviour during the parental phase. *Anim. Behav.* **19**: 532-541.
- CONSTANTZ, G. D., 1985. Allopaternal care in the tessellated darter, *Etheostoma olmstedi* (Pisces: Percidae). *Env. Biol. Fish.* **14**: 175-183.
- FITZGERALD, G. J., 1983. The reproductive ecology and behaviour of three sympatric sticklebacks (Gasterosteidae) in a saltmarsh. *Biol. Behav.* **8**: 67-79.
- FITZGERALD, G. J. & F. G. WHORISKEY, 1985. The effects of interspecific interactions upon male reproductive success in two sympatric sticklebacks, *Gasterosteus aculeatus* and *G. wheatlandi*. *Behaviour* **93**: 112-126.
- FOSTER, S. A., 1988. Diversionary displays of paternal stickleback. Defenses against cannibalistic groups. *Behav. Ecol. Socobiol.* **22**: 335-340.
- GRONELL, A. M., 1989. Visiting behaviour by females of the sexually dichromatic damselfish, *Chrysiptera cyanea* (Teleostei: Pomacentridae): a probable method of assessing male quality. *Ethology* **81**: 89-122.

- GROSS, M. R., 1982. Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Z. Tierpsychol.* **60**: 1-26.
- GROSS, M. R., 1985. Disruptive selection for alternative life histories in salmon. *Nature* **313**: 47-48.
- HART, M. 't, 1978. A study of a short term behaviour cycle: creeping through in the three-spined stickleback. *Behaviour* **67**: 1-66.
- HART, M. 't, 1985. The influence of fertilization on the creeping through cycle of the three-spined stickleback. *Behaviour* **93**: 194-202.
- JAMIESON, I. G. & P. W. COLGAN, 1989. Eggs in the nests of males and their effect on mate choice in the three-spined stickleback. *Anim. Behav.* **38**: 859-865.
- KNAPP, R. A. & R. C. SARGENT, 1989. Egg-mimicry as a mating strategy in the fantail darter, *Etheostoma flabellare*: females prefer males with eggs. *Behav. Ecol. Sociobiol.* **25**: 321-326.
- KODRIC-BROWN, A., 1986. Satellites and sneakers: opportunistic male breeding tactics in pupfish (*Cyprinodon pecosensis*). *Behav. Ecol. Sociobiol.* **19**: 425-432.
- KYNARD, B. E., 1978. Breeding behavior of a lacustrine population of threespine sticklebacks (*Gasterosteus aculeatus* L.). *Behaviour* **67**: 178-207.
- LI, S. K. & D. H. OWINGS, 1978. Sexual selection in the three-spined stickleback. I. Normative observations. *Z. Tierpsychol.* **46**: 359-371.
- MARCONATO, A. & A. BISAZZA, 1986. Males whose nests contain eggs are preferred by female *Cottus gobio* L. (Pisces, Cottidae). *Anim. Behav.* **34**: 1580-1582.
- MCLENNAN, D. A. & J. D. MCPHAIL, 1989. Experimental investigations of the evolutionary significance of sexually dimorphic nuptial colouration in *Gasterosteus aculeatus* (L.): temporal changes in the structure of the male mosaic signal. *Can. J. Zool.* **67**: 1767-1777.
- MCLENNAN, D. A. & J. D. MCPHAIL, 1990. Experimental investigations of the evolutionary significance of sexually dimorphic nuptial colouration in *Gasterosteus aculeatus* (L.): the relationship between male colour and female behaviour. *Can. J. Zool.* **68**: 482-492.
- MCPHAIL, J. D., 1969. Predation and the evolution of a stickleback (*Gasterosteus*). *J. Fish. Res. Bd. Canada* **26**: 3183-3208.
- MILINSKI, M. & TH. C. M. BAKKER, 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* **344**: 330-333.
- MOODIE, G. E. E., 1972. Morphology, life history and ecology of an unusual stickleback (*Gasterosteus aculeatus*) in the Queen Charlotte Islands, Canada. *Can. J. Zool.* **50**: 721-732.
- MORI, S., 1990. The breeding system of the three-spined stickleback, *Gasterosteus aculeatus* (*leivurus* form), with reference to spatial and temporal pattern of nesting activity. Ph.D. Thesis, Kyoto University, Japan.
- NELSON, K., 1965. After-effects of courtship in the male three-spined stickleback. *Z. vergl. Physiol.* **50**: 569-597.
- PEEKE, H. V. S., 1969. Habituation of conspecific aggression in the three-spined stickleback (*Gasterosteus aculeatus* L.). *Behaviour* **35**: 137-156.
- PEEKE, H. V. S. & A. VENO, 1973. Stimulus specificity of habituated aggression in the stickleback (*Gasterosteus aculeatus*). *Behav. Biol.* **8**: 427-432.
- PEEKE, H. V. S., E. J. WYERS & M. J. HERZ, 1969. Waning of the aggressive response to male models in the three-spined stickleback (*Gasterosteus aculeatus* L.). *Anim. Behav.* **17**: 224-228.
- RIDLEY, M. & C. RECHTEN, 1981. Female sticklebacks prefer to spawn with males whose nests contain eggs. *Behaviour* **76**: 152-161.
- ROWLAND, W. J., 1988. Aggression versus courtship in threespine sticklebacks and the role of habituation to neighbours. *Anim. Behav.* **36**: 348-357.

- ROWLAND, W. J., 1989. Mate choice and the supernormality effect in female sticklebacks (*Gasterosteus aculeatus*). *Behav. Ecol. Sociobiol.* **24**: 433-438.
- SARGENT, R. C., 1982. Territory quality, male quality, courtship intrusions, and female nest-choice in the threespine stickleback, *Gasterosteus aculeatus*. *Anim. Behav.* **30**: 364-374.
- SARGENT, R. C. & J. B. GEBLER, 1980. Effects of nest site concealment on hatching success, reproductive success, and paternal behavior of the threespine stickleback, *Gasterosteus aculeatus*. *Behav. Ecol. Sociobiol.* **7**: 137-142.
- SEMLER, D. E., 1971. Some aspects of adaptation in a polymorphism for breeding colours in the Threespine stickleback (*Gasterosteus aculeatus*). *J. Zool., Lond.* **165**: 291-302.
- SEVENSTER, P., 1961. A causal analysis of a displacement activity (fanning in *Gasterosteus aculeatus* L.). *Behaviour Suppl.* **9**: 1-170.
- SEVENSTER, P., 1986. Eine innere Uhr: Motivationsanalyse einer kurzfristigen Periodizität im Verhalten des Stichlings. In: G. TEMBROCK, R. SIEGFRIED & M. NICHELMANN (Eds.): *Verhaltensbiologie. Internationales Symposium 1983*: 177-181. Wissenschaftliche Schriftenreihe der Humboldt-Universität zu Berlin, Berlin.
- SEVENSTER, P. & M. 't HART, 1974. A behavioural variant in the three-spined stickleback. In: J. H. F. VAN ABELEN (Ed): *The Genetics of Behaviour*: 141-165. North-Holland Publishing Company, Amsterdam.
- SEVENSTER-BOL, A. C. A., 1962. On the causation of drive reduction after a consummatory act (in *Gasterosteus aculeatus* L.). *Archs néerl. Zool.* **15**: 175-236.
- SIKKEL, P. C., 1989. Egg presence and developmental stage influence spawning-site choice by female garibaldi. *Anim. Behav.* **38**: 447-456.
- UNGER, L. M. & R. C. SARGENT, 1988. Allopaternal care in the fathead minnow, *Pimephales promelas*: females prefer males with eggs. *Behav. Ecol. Sociobiol.* **23**: 27-32.
- WARD, G. & G. J. FITZGERALD, 1987. Male aggression and female mate choice in the threespine stickleback, *Gasterosteus aculeatus* L. *J. Fish Biol.* **30**: 679-690.
- WHORISKEY, F. G. & G. J. FITZGERALD, 1985. Sex, cannibalism and sticklebacks. *Behav. Ecol. Sociobiol.* **18**: 15-18.
- WILZ, K. J., 1975. Cycles of aggression in the male three-spined stickleback (*Gasterosteus aculeatus*). *Z. Tierpsychol.* **39**: 1-7.
- WOOTTON, R. J., 1971. A note on the nest-raiding behaviour of male sticklebacks. *Can. J. Zool.* **49**: 960-962.
- WOOTTON, R. J., 1976. *The Biology of the Sticklebacks*. Academic Press, London.