THE ROLE OF
MALE COMPETITION AND FEMALE CHOICE
IN THE MATING SUCCESS
OF A LEK-BREEDING
SOUTHERN AFRICAN CICHLID FISH
PSEUDOCRENILABRUS PHILANDER
(PISCES: CICHLIDAE)

THESIS

Submitted in Fulfilment of the
Requirements for the Degree of

MASTER OF SCIENCE

of Rhodes University

by

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December 1987

"----- Courage, pugnacity, perseverance, strength and size of the body, weapons of all kinds, musical organs, both vocal and instrumental, bright colours and ornamental appendages, have all been indirectly gained by the one sex or the other, through the exertion of choice, the influence of love and jealousy, and the appreciation of the beautiful in sound, colour or form; ------" (Darwin 1871 in "The Descent of Man, and Selection in Relation to Sex")

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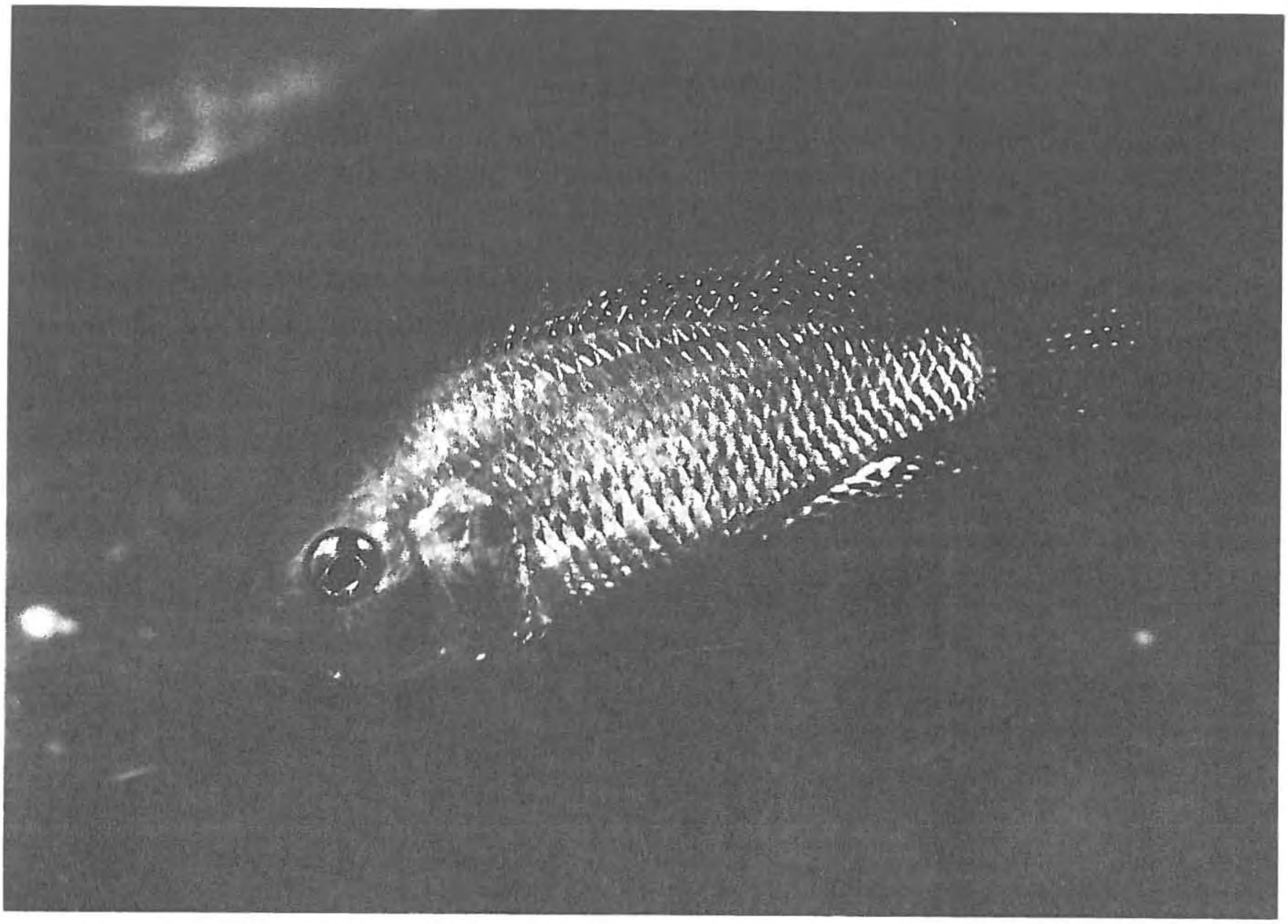
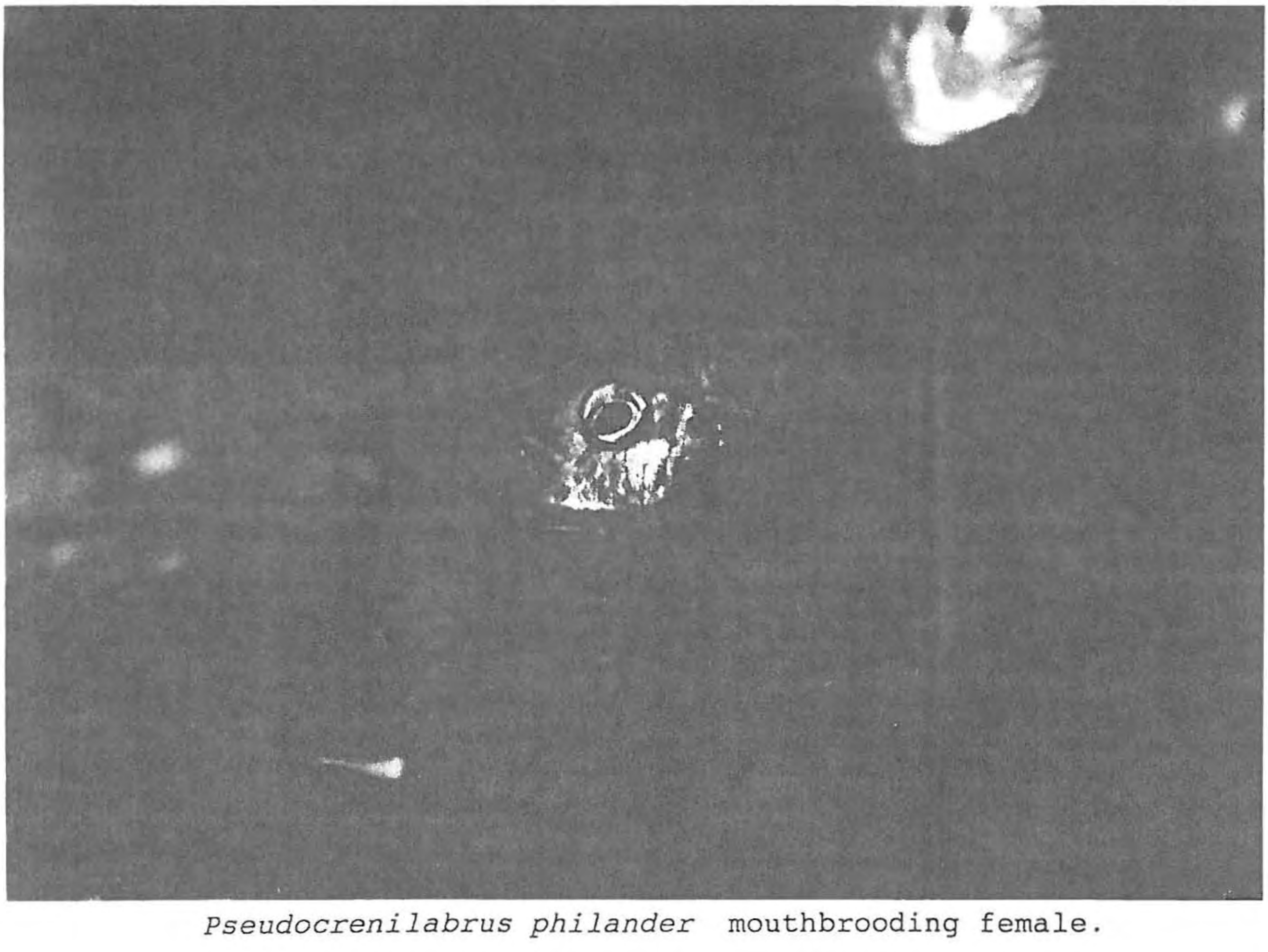


Pseudocrenilabrus philander territorial male in full nuptial colouration.



Pseudocrenilabrus philander mouthbrooding female.

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ACKNOWLEDGMENTS

I wish to thank the CSIR and Rhodes University for providing the opportunity and financial support for my study in South Africa. Grateful acknowledgments are extended to Prof. T. Hecht, Head of the Department of Ichthyology and Fisheries Science, Rhodes University for organizing my trip to South Africa, and Dr. A.J. Ribbink, Assistant Director, J.L.B. Smith Institute of Ichthyology, for supervision of the present study. Many thanks are also extended to the D-I-F-S and the J.L.B. Smith Institute of Ichthyology for offering various facilities, and to all staff for assistance of all sorts, particularly Ms. V. Twentyman-Jones and Mrs. A. Ribbink for their assistance in the preparation of this thesis by reviewing most of the English, D. Voorvelt for assistance with some of the illustrations. Finally, I would like to specially thank Mrs. S.E. Radloff of the Statistics Department, Rhodes University, for statistical counseling.

ABSTRACT

A lek-breeding cichlid fish *Pseudocrenilabrus philander* was studied experimentally. Females in choice-chamber experiments showed no active choice for male size and colour, or for other male attributes, but preferred males which courted most actively. In a laboratory lek, the significant determinants of the strongly skewed mating success in males were territory size, side-shake and female chasing frequency. Together these three variables explained 79% of the variation in male mating success, with territory size alone accounting for 75% of the variation and the other two variables each accounting for 2% of the remaining variation. As there was no difference in territory quality in the laboratory lek, territory size became the principal measure of the effect of male-male competition since it was directly related to dominance. Both side-shake and female chasing could be identified as the basic factors influencing female choice, as they had an immediate effect on the display-response mating system of females. Thus, the relative importance of these three variables indicated that sexual selection in this particular lek mating species operated chiefly through the agency of intrasexual competition for dominance. However, both female behaviour and their requirement for a prolonged pre-spawning courtship had the effect of promoting male rivalry and favouring mating with dominant males. Although the intense male competition excluded subordinate males from practising normal courtship behaviour, competitively inferior males might "make the best of a bad situation" by facultatively adopting an alternative sneaking tactic to gain access to females. Spawning intrusions by females to steal freshly-laid eggs also occurred frequently. However, territorial males appeared to be relatively more tolerant of female intruders than male sneakers. Interference during spawning could lead to a longer pre-spawning courtship and even multiple-mating by females. The results of the present study and the behavioural evidence shown by males and females did not support the "runaway selection model" of the mating pattern in terms of sexual selection in leks, but conformed to the rival "war propaganda model".

CHAPTER 1

INTRODUCTION

The luxuriant plumage of birds of paradise, the oversized antlers of irish elk and the magnificent colour in tropical fishes are just a few of the extravagant and, at least to the human eye, somewhat aesthetically pleasing features which have long fascinated, but also puzzled to zoologists who try to explain their evolution. Since females appear to choose to mate with males whose exaggerated adornments must be disadvantageous or useless for their survival, Darwin (1859, 1871) found himself having difficulty using his natural selection theory to explain the development of these extravagant sexual dimorphic characters and therefore proposed the theory of sexual selection to account for their evolution (but see Appendix). Sexual selection is the selection solely for obtaining more mates, or in monogamous species an earlier mating opportunity, through the action of male competition and female choice. Males of the same species drive away or kill their rivals for a mating opportunity, and compete with one another to attract females which select the more "agreeable" partners.

Similar to his natural selection theory, Darwin's theory of sexual selection also immediately received serious criticism (Wallace 1889; Richards 1927; Huxley 1938). The early opposition to this theory led, for various reasons (see Trivers 1972; Selander 1972; Mayr 1972, 1982; Ghiselin 1974; O'Donald 1977, 1980; Halliday 1978; Otte 1979; Thornhill 1979; Arnold 1983; West-Eberhard 1983), to sexual selection being largely ignored for nearly half a century. Recent advances in evolutionary theory with the emphasis on individual (eg. Williams 1966; Thornhill 1979; Emlen & Oring 1977; Thornhill & Alcock 1983), as well as gene selection (eg. Wilson 1975; Dawkins 1976, 1982) and the realization that social competition can decrease the optimum adaptation in ecological selection (eg. Lande 1976, 1980; Otte 1979; West-Eberhard 1979, 1983; Thornhill & Alcock 1983; Dawkins 1982; Heisler 1984; Barnard 1984) has led to a renewed awareness of the sexual selection theory. For this reason, sexual selection, especially that through female choice, is currently experiencing widespread popularity as a subject in evolutionary research (eg. Campbell 1972, Blum & Blum 1979; Mayr 1982; Bateson 1983; Dominey 1984b).

Evolutionary Effects of Sexual Selection:

Under the topic of sexual selection, there are two distinct types of phenomena, namely intersexual and intrasexual selection (after Huxley 1938).

Intrasexual Selection: Direct competition between members of one sex for mating opportunities (more precisely for syngamy).

Intersexual Selection: Preferential choice of mates.

As noted by Darwin (1871), there is a universal intra-masculine selection and females are traditionally coy, while the reverse is very uncommon. These phenomena of undiscriminating eagerness in males and discriminating passivity in females are now widely considered to be primarily caused by the difference in the size and number of gametes produced by males and females, and hence differential replacement costs, as a result of the fundamental physiology in sexual differentiation (eg. Bateman 1948; Williams 1966; Trivers 1972;; Mayr 1972; Thornhill 1979; Thornhill & Alcock 1983; Baylis 1978, 1981; Barnard 1984, but see Nakatsuru & Kramer 1982, Dewsbury 1982; Hieber & Cohen 1983; Arak 1984). Consequently, intrasexual selection is usually in the form of male-male competition and intersexual selection is through the action of female choice. Female choice can be further separated into adaptive female choice and arbitrary female choice, or pure sexual selection (*sensu* Arnold 1983). In adaptive female choice, the choice exercised by a female is directed at characters which reflect the male's general fitness. Arbitrary female choice is when the female chooses the male merely because he is attractive to her, like the appreciation of beauty by humans. The most controversial subject in sexual selection is on the effects of female choice, especially for the aesthetic choice of male adornments (Mayr 1972; Halliday 1978, 1983; Lambert *et al.* 1982; Thornhill & Alcock 1983; Bradbury & Gibson 1983; Heisler 1984, 1985; Boake 1985; Burley 1986; Partridge *et al.* 1987).

Arbitrary Female Choice and Runaway Selection:

Darwin rather emphasized the effect of female aesthetic sexual preference in the the evolution of the extraordinary sexual dimorphic characters in males (Wynne-Edwards 1966; Crook 1972; Lill 1974a; Majerus *et al.* 1982; Burley 1986; Borgia *et al.* 1987, but see Selander 1972). This idea is elaborated upon by Fisher (1930), and recent mathematical geneticists, as the "Runaway Selection Hypothesis" (O'Donald 1967; 1977; 1980; Lande 1980; 1981, 1982; Kirkpatrick 1982; Heisler 1984; 1985; Wu 1985; Seger 1985) or the "Sexy Son Hypothesis" (Weatherhead & Robertson 1979), because the only benefit the female can get from the male is having sons more "sexy" than other females can have.

The principal idea of the runaway hypothesis is that once female sexual preferences have developed, either by their initial relations to other selectively important traits (Fisher 1930; Mayr 1972; O'Donald 1967, 1977, 1980; Heisler 1984, 1985) or even merely by genetic drift (Lande 1981, 1982; Kirkpatrick 1982; Harvey & Arnold 1982; Arnold 1983; Wu 1985), they can then evolve solely through their association with male attractiveness and become negatively correlated or not related to viability selection (self and/or offspring survival). No matter how small the beginnings might be, the potential of the runaway process is that it will spread through the population. The further development of a preferred male physical character is pushed at an ever increasing speed by mutual reinforcement between both the sexual character in males and sexual preference in females, until it is checked by the severe counter-selection of inviability. Thus, proponents of the runaway selection hypothesis believe that this kind of selection can have a special evolutionary self-reinforcing potential to amplify the development of male sexual characters and this may represent a distinct evolutionary force which can result in rapid speciation and extinction (Lande 1980, 1981, 1982; Kirkpatrick 1982; Harvey & Arnold 1982; Arnold 1983; Dominey 1984b; Wu 1985), as well as the possibility of parapatric and sympatric speciation (Fisher 1930; Lande 1981, 1982; Kirkpatrick 1982, Arnold 1983; Wu 1985).

Adaptive Female Choice and Male Competition:

Opponents of the runaway hypothesis argue that adaptive female choice, and male-male competition, is more realistic in evolutionary process and that those extravagant sexual characters can be explained without the action of aesthetic sexual preference (eg. Wallace 1889; Huxley 1938; Williams 1966; Trivers 1972, 1976; Zahavi 1975; Borgia 1979; West-Eberhard 1979; Lambert *et al.* 1982; Thornhill & Alcock 1983). Following Wallace (1889), many different "good-genes" models (*sensu* Heisler 1984) of adaptive female choice have been put forward to replace the runaway model; such as the epigamic selection (Huxley 1938), parental investment hypothesis (Trivers 1972), handicap principle (Zahavi 1975), resource accrual theory (Trivers 1976), war propaganda model (Borgia 1979) and parasite load hypothesis (Hamilton & Zuk 1982). However, all of these "good-genes" models, as well as the effect of male-male competition, are criticized by runaway hypothesis proponents in that they cannot offer a good explanation of how characters become unusually exaggerated. They also lack the support of mathematical models based on population genetics (see Davis & O'Donald 1976; Dawkins 1976; Bells 1978; Halliday 1978, 1983; Borgia 1979; West-Eberhard 1979; O'Donald 1980; Harvey & Arnold 1982; Arnold 1983; Parker 1983).

Although theoretical genetic models largely support the runaway hypothesis (but see O'Donald 1983; Parker 1983; Cohen 1984), experimental and field investigations mostly favour the conservative "adaptive" hypothesis (see Halliday 1978, 1983; Thornhill 1979; Thornhill & Alcock 1983; Endler 1983; Borgia *et al.* 1987, but see Andersson 1982; Boake 1985; Burley 1986; Houde 1987). Lambert *et al.* (1982) even considered that almost all mate choice studies could be alternatively interpreted as the results of stabilizing selection, chance, male-male competition, ability to recognize high quality environment and/or adequacy of reproductive structures and behaviours instead of attractiveness to mates (also see Arak 1983; Wilkinson 1987).

Lek and Sexual Selection:

The classical model of the effect of sexual selection by female choice, is the true lek-breeding species (Darwin 1871; Borgia 1979; Diamond 1981; Harvey & Arnold 1982; Arnold 1983; Bateson 1983; Bradbury & Gibson 1983; Arak 1984). Lek is a Scandinavian word meaning play, which implies a place where males gather together only for breeding purpose and females come to visit exclusively for the purpose of mating (Emlen & Oring 1977; Borgia 1979; Bradbury 1981; Bradbury & Gibson 1983). Both males and females of lek species are polygamous. However, other than a mating site, males do not provide any resource for females and they do not participate in parental care. Nevertheless, females appear to have the options of exercising a choice both between existing leks and between males on a given lek (Bradbury & Gibson 1983). Lek-breeding has been reported in a variety of animal taxa (see Emlen & Oring 1977; Davies 1978; Bradbury 1981).

Supporters of the runaway selection hypothesis argue that since females will get "nothing" from males except gametes, and hence no selection is effected on females because every female will eventually be inseminated. Thus, female sexual preference in lekking species will be selectively neutral. However, by choosing an entirely arbitrary male trait, females can have "attractive sons", and hence runaway selection will be easily triggered and will be at its maximum potential (Lande 1981, 1982; Kirkpatrick 1982; Arnold 1983; Dominey 1984b; Heisler 1985; Wu 1985). In the "adaptive" approach, since the only benefit females can obtain from a lek mating system is male gametes, females in leks should go "shopping" amongst males and choose the fittest male available in order to obtain better "genes" (Selander 1972; Trivers, 1972, 1976; Zahavi 1975; Halliday 1978; Borgia 1979; Hamilton & Zuk 1982; Heisler 1984; Arak 1984) or other immediate benefit such as to mate more safely (Trivers 1972; Halliday 1983). Despite the large amount of controversy on the lek mating system, it has been suggested as a promising area for testing sexual selection theory ideas (Lill 1974a; Lambert *et al.* 1982; Bradbury & Gibson 1983; Wittenberger 1983).

Study of Sexual Selection in Fish:

Sexual selection has been studied in many fishes. However, most of them are emphasized on female choice and the majority of the studies are on monogamous species (eg. Perrone 1978; Noonan 1983; Keenleyside *et al.* 1985; Schwanck 1987) or polygamous substrate spawners (eg. Semler 1971; Downhower & Brown 1980; Brown 1981; Schmale 1981; Thresher & Moyer 1983; Downhower *et al.* 1983; Thompson 1986; Noltie & Keenleyside 1986; Ward & FitzGerald 1987, etc.) in which males participate in parental care. This is probably due to the fact that paternal care is prevalent in fish (Dawkins & Carlisle 1976; Loiselle 1978; Ridley 1978; Blumer 1979, 1982; Baylis 1981; Balon 1984; Gross & Sargent 1985). Non-guarding group spawners (eg. Warner *et al.* 1975; Kodric-Brown 1977, 1978, 1983; Warner 1984; Nakatsuru & Kramer 1982) should be referred to as resource-defense polygyny (Emlen & Oring 1977; Thornhill & Alcock 1983) instead of true lekking species (Thresher 1984, also see Kodric-Brown 1977). True lekking species are not common in fish (Thresher 1984) and are restricted to species where males do not participate in parental care and show internal fertilization or are external bearers, eg. livebearing Gila topminnow (Constantz 1975) and mouthbrooding cichlids (Ribbink 1975; McKaye 1983, 1984). Since in both cases the fertilized eggs are retained by females after spawning, the paternity of the males will not be as obvious as those of other fishes in which fertilized eggs remain in the male's territory. Therefore, the requirement of continuous and detailed underwater surveillance to estimate the mating success of males in these fishes further restricts the study of sexual selection in true lekking fish. Consequently, virtually no research of this kind has been undertaken.

Since in most of the fish studied the males provide parental care and/or control oviposit sites as part of their reproductive tactic, the female choice demonstrated was mostly "adaptive" by choosing males which are: larger (Perrone 1978; Downhower & Brown 1980; Brown 1981; Downhower *et al.* 1983; Noonan 1983; Keenleyside *et al.* 1985; Thompson 1986; Noltie & Keenleyside

1986; Schwanck 1987), of higher fertility (Nakatsuru & Kramer 1982), with complementary behaviour (Schwanck 1987), possessing better territory (Kodric-Brown 1978, 1983; Thompson 1986; Noltie & Keenleyside 1986), and with dominant or aggressive attribute signaling (Semler 1971; Schmale 1981; Thresher & Moyer 1983; Kodric-Brown 1983), so that females can obtain immediate benefit to increase their brood survival. Furthermore, many studies on sexual selection have been done on guppies, in which females choose males with novel or conspicuous colour (eg. Farr 1977, 1980; Endler 1983; Houde 1987). Nevertheless, although guppies have internal fertilization, their mating system is not that of a true lek because males do not show aggression nor do they defend territories.

Pseudocrenilabrus philander:

Pseudocrenilabrus philander (Weber 1897) is a small riverine cichlid endemic to southern Africa (Ribbink 1975). Remarkable sexual dimorphism in physical features and behaviour are characteristic of this fish. It may breed all year round in leks on open sandy substrata (Ribbink 1971, 1975). Territorial males are brightly coloured but females and juveniles are rather plainly coloured (Frontispiece). Males are promiscuous and compete aggressively with each other for territories. Although males will dig a small sand pit as a nest, they do not provide any resources other than a spawning site for females, nor do they participate in parental care. Females aggregate in schools and start visiting nests when they become receptive. Males enthusiastically court females near their territories and attempt to lead them to their nests. However, most of the leading attempts are unsuccessful and females generally visit several males, during which time they court but do not spawn. Actual spawning in females only occurs after several visits and after a period of courtship. Immediately after the fresh-laid eggs are passed over by the male, presumably to fertilize them, the female collects all the eggs into her mouth. After spawning is completed, the female leaves the lek. Mouthbrooding takes place in a refuge distant from leks and continues until the offspring become free-swimming.

The lek breeding of *P. philander* follows the "classical" pattern and makes this species ideal for a study of sexual selection in fish. To overcome the difficulties in the requirement of prolonged underwater observations for a detailed study of sexual selection in mouthbrooding fishes, the experiments recorded here were conducted in a laboratory lek and in choice chambers. The small size and readiness with which *P. philander* acclimatize, as well as the ease with which animals can be obtained in their natural habitats in South African waters, further suggested that it was a prime candidate for the present study.

Objectives:

The principle aim of the present study was to elucidate the roles of male competition and female choice in producing the presumably strong difference of mating success amongst males of this lekking fish, so that the dynamics of sexual selection in fish leks could be examined more carefully. It has been suggested that a knowledge of sexual selection in lekking fish is crucial to the understanding of their speciation (McKaye 1984, and references cited therein).

The main objectives of the experiments were to answer the following questions:

1. Do females really choose males, and if so which cue(s) do they use for their choice?
2. Which characters of the male significantly affect the success of the males in obtaining females, and what are their relative contributions to the variation in male mating success?
3. Is the affect of male competition or female choice more important in influencing male mating success?

Besides trying to understand the evolution of the highly aggressive and territorial nature, as well as the bright colour, of male *P. philander*, the results were also used to explain the mating behaviour in this fish and to evaluate the hypotheses for the evolution of male characters in lek species in general.

During the experimental periods, it was noted that some of the competitively inferior males sneaked up to and joined spawning pairs, apparently fertilizing eggs. Sneaking is directly related to male competition (West-Eberhard 1979; Dominey 1984b; Arak 1984). Furthermore, alternative reproductive behaviours such as sneaking, have become a popular topic in evolutionary theory due to its relation to Maynard Smith's (1974) theory of an Evolutionarily Stable Strategy (ESS) (see Gross 1982, 1984; Arak 1984). Therefore, the study of this phenomena in *P. philander* merited a separate chapter. Other than sneaking, various other forms of courtship interference also occurred. Another chapter was devoted to the description of these behavioural forms because they also related to male competition and female choice (Arnold 1976; Halliday 1978; Diamond 1981; Foster 1983; Bradbury & Gibson 1983; Arak 1984), as well as to the structure of leks (Lill 1974b; Foster 1983; Arak 1983, 1984).

CHAPTER 2

MATERIALS AND METHODS

Laboratory Lek Experiment:

Materials:

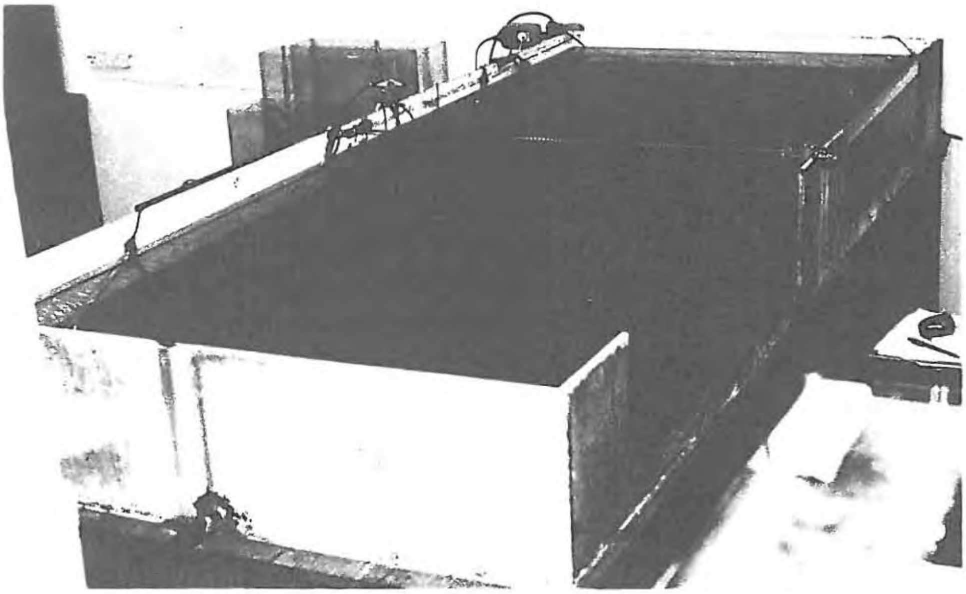
P. philander from Phongolo, Kwazulu were used. The lek arena was an asbestos tank 3m X 1.2m X 0.3m with one glass side (Pl. 1). The bottom of the tank was covered with a layer of river sand to a depth of 3cm. With the exception of necessary aquarium equipment, such as air stones, air pipes and heaters, no shelter was provided for the fish. Four rows of small rocks were embedded in the sand and used as reference points for mapping territories and also served as landmarks for the fish (see Constantz 1975; Kodric-Brown 1978). Water temperature was maintained at 26°C±2°C. The laboratory was lit for approximately 14 hours a day, by natural and artificial light. For most of the experiments, 30 gravid females of approximately 45 to 73mm Standard Length (SL), were randomly chosen from a stock population and kept in the arena. Different numbers and sizes of males were introduced to the arena during experimental manipulations. Fish were fed at a fixed point near the middle of the tank with a commercial flake food, and sometimes supplemented with live *Daphnia sp.*.

Identification of Individuals:

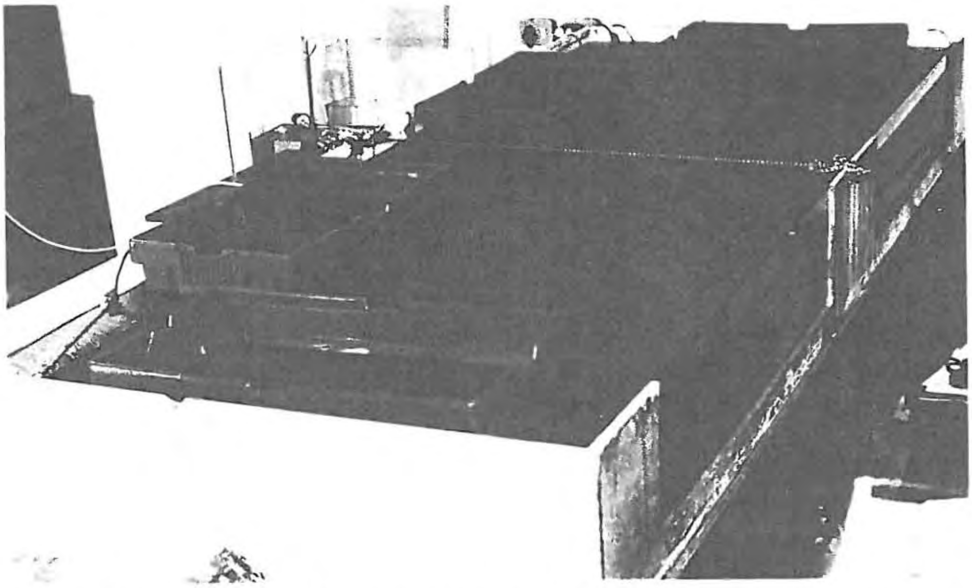
All males used in these experiments were marked by a single or several cuts made in the membranes between the spines or rays of the unpaired fins (Fig. 1). Their standard length was also measured at the beginning of each treatment. Such fin cutting is virtually harmless to fish and is similar to natural fin damage arising from intraspecific fights and other encounters in the environment (Ribbink 1971, 1975). Fin cuts were easily recognizable for 7-10 days, after which they were repeated if necessary.

Scheduled recordings:

Six behaviour patterns were monitored for each male based on the following criteria (for detailed behavioural descriptions of



Pl. 1. The experimental lek tank. Dimension of 3m X 1.2m X 0.3m.



Pl. 2. The arrangement of choice chambers (60cm X 30cm X 30cm) in the laboratory lek for female choice tests.

Pl. 3. Frontal view of the settings within a choice chamber.

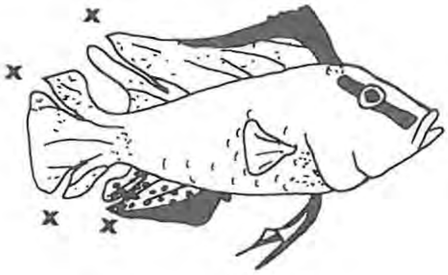


Fig. 1. Individual identification by a single or a combination of cuts at positions indicated by *.

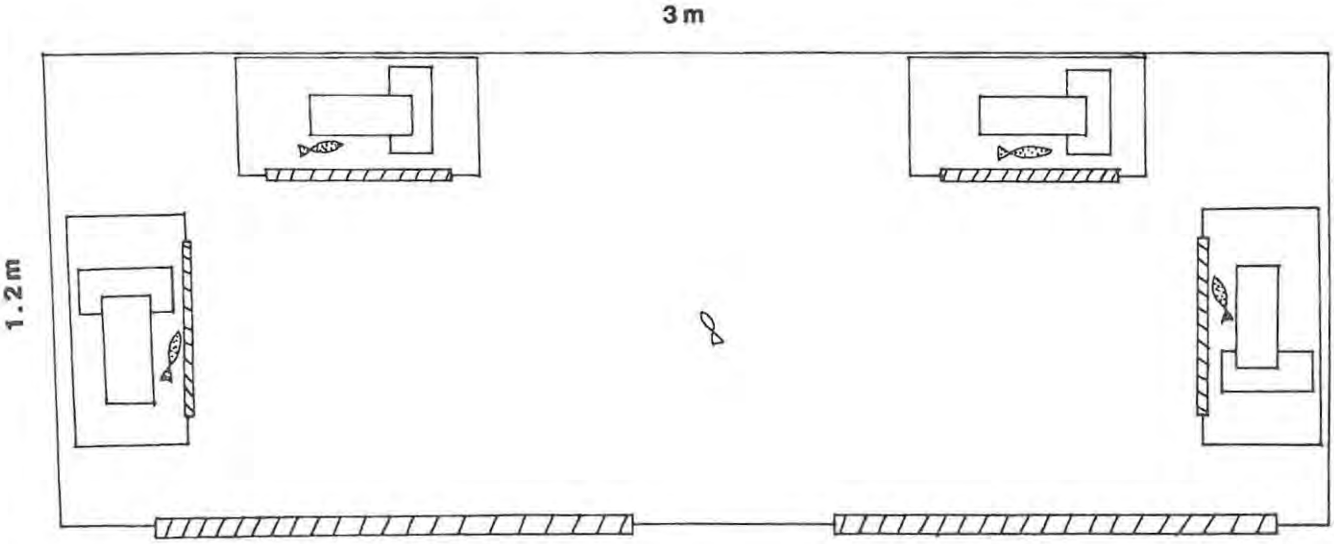


Fig. 2. The arrangement of choice chambers in the lek tank for the choice experiment. Depicted here is the single-female treatment. Shaded fish are males and the unshaded fish is a female. 25 females are placed in the lek tank in the multiple-female treatment.

P. philander see Ribbink 1971, 1975):

Side-Shake: The initial invitation to court, which was performed by the male before females started responding to him.

Nest Courtship: This referred to the entire courtship stimulus-response chain after side-shake and includes spawning sequences. Courtship ended when the female finally left the nest. Since the performance of this sequence was dependent the upon females' receptiveness, these data can also be alternatively interpreted as the positive response of females to the male.

Female Chasing: The chase of females.

Male Chasing: The chase of males.

Being Chased: When the male was chased by other fishes.

Agonistic Behaviour: Agonistic behaviour was considered to have started when the male expanded his branchiostegal membranes during threatening display, which included those which developed into fights, and ended when the branchiostegal membranes were retracted.

During the most active period of territorial and sexual activities, from 09h30 to 14h30 (Ribbink 1975), the above behaviour patterns of each male was recorded five times daily during initial experiments, but was reduced to three recordings when it was established that this was adequate to represent the behavioural trend. In each recording, each male was observed, in random order, for a consecutive 5min duration, during which the behaviour patterns listed above were recorded using a stopwatch at 0.1sec resolution. The number of various courtship interferences sustained and performed by the male within this 5-min period were also recorded. The territorial status of the males was assigned and the distribution of territories in the lek was mapped at each observation period.

Unscheduled Recordings:

Spawning and courtship interferences were recorded whenever they were observed. The preliminary visiting period was defined as the period between a female entering a nest and the initiation of nest-shake activity (see Ribbink 1971, 1975). Some females entered nests and then left before commencing with spawning behaviour, these were not counted and only those which subsequently laid eggs on that particular day were used in the analyses. The period of pre-spawning nest activity for females was taken from her first observed nest-shake to the point when the first egg was laid. The spawning period of females was measured from the initiation of egg laying to the completion of all spawning activities. Since the spawning activity of *P. philander* is normally longer than half an hour (Ribbink 1971), the tank was usually observed for about 1min in every half hour, between 09h00 and 16h00, to ensure that spawnings were not missed. A male was considered to have successfully elicited spawning if females laid eggs in his nest. He was then given a unit spawning score. However, if females laid eggs with more than one male, then the unit was divided. The elicitation of spawning was scored positively whether sneaking occurred or not. Sneakers did not elicit spawning but took advantage of the successful courtship of other males, so sneaking could not be given a positive score for spawning. Territorial displacement was recorded only when a territorial male, which had held a territory for more than one day, became a semi- or non-territorial male.

Duration of Experiments:

To avoid artificial stability within the laboratory lek, the number of males in the lek was changed after every seven consecutive days of data collection. A total of 11 combinations of males ranging from 3 to 18 individuals was used. It was likely that this procedure emulated trends which probably occurs in the natural environment.

Choice-Chamber Experiment:

Materials:

Four blue PVC tanks (60cm X 30cm X 30cm), with one side of glass, were placed in the lek tank as choice chambers. A single male was introduced into each of these chambers. The arrangement of the choice-chamber experiment is illustrated in Plates 2 and 3. In the multiple-female treatment, about 25 females were placed in the lek tank. Only one gravid female was used in the single-female treatment (Fig. 2). The size of females used in both treatments was approximately 45 to 65mm (SL) and that of the males was from 47 to 82mm (SL).

Methods:

Five physical and behavioural characteristics were monitored for each male based on the following criteria:

Size: The standard length of the male.

Colour: The colouration of the male was ranked on a scale of 0 to 5 with increasing colour intensity; plain body colour with deep stress bars was designated as 0, while deep, bright nuptial colour was ranked 5. Intermediate ranks were arbitrary assigned.

Appetitive Behaviour: This referred to the duration of glass-touching performed by the male, excluding those involved in mutual swimming with females on opposite sides of the glass partition.

Courtship Display: The duration of side-shake display and glass-touching performed by the male during mutual swimming with females on opposite sides of the glass partition.

Activity: The cumulative duration of "Appetitive" and "Courtship Display" behaviour.

The body length of the males was measured at the beginning of the test. Behaviour was recorded three times daily following the same procedure described in the laboratory lek experiment. Colour rank was assigned at the beginning of observations, even though males were always changing their colour during and between courtship. During the 5-min recording periods, the following female behaviour directed at that particular chamber was also monitored:

In the multiple-female treatment:

Female Courtship: When a female performed nest-shake and glass-touching during mutual swimming with the male on opposite sides of the glass partition.

Interruption: The number of interruptions by other females, when a female was performing courtship at the chamber.

In the single-female treatment:

Female Proximity: When the female was within an area which was

10cm in front of the glass side of the chamber.

The trial ended when a female "chose" a male(s) by spawning with him. The spawning score of males and different courtship periods of females were determined on the same basis as that described in the laboratory lek experiment. The female in the single-female treatment was replaced by a new gravid female randomly from the stock population after it had spawned, or after 3 to 5 days if it failed to spawn. Females which spawned in the multiple-female treatment were also replaced by new gravid females randomly from stock. The males in the choice chambers were rearranged or changed at night after a female spawned (sometimes two females spawned at the same day in the multiple-female treatment). Repeat-choice test was carried out to determine whether females chose the same male, whereby, the same set of males was rearranged into different chambers. Before proceeding to the next trial the males were replaced by a new set of males.

Two sets of controls were used for the choice-chamber experiment. In one control set, males of four different species of cichlid (*Aulonocara sp.* from Malawi, *Tilapia rendalli*, *T. ruweti* and *P. philander*) were placed separately in the four chambers. The other control set had one chamber which remained empty, while the other three contained *P. philander* males.

Treatment of Data:

Choice Test Data:

This experiment tested which of the male characters which had been monitored had a significant effect on male spawning scores. In each trial, the means of the data collected for each variable was ranked against each other (total of 4 ranks as only 4 chambers were present in each treatment). For all the trials in the multiple- or single-female treatments, a Kolmogorov-Smirnov one sample *D* test (Siegel 1956) was applied to the total spawning scores at each of the four ranks to determine if females were not spawning at random amongst different ranking males.

Laboratory Lek Data:

All the behavioural recordings obtained in each weekly trial were converted to a 5-min mean duration for each male. Territory size of males was represented by the mean of the relative territory size measured from each male (14 units for total area of lek tank). The number of spawnings secured by each male was a measure of its mating success. For comparative purpose the spawning scores of each male over a period of a week were used as workable assessment of mating success. weekly spawning scores. Sneaking events were ignored in evaluating spawning scores since fertilization success by sneaking was negligible (see Chapter 3). In parametric regression and correlation analyses, all the variables were transformed by using a log $(X+1)$ conversion to stabilize the variance and bring about additivity of effects, as well as to correct for any non-normality of the data (Snedecor & Cochran 1980, Sokal & Rohlf 1969). In these analyses, data obtained from 65 males in 8 treatments were used.

Other statistical tests used in data analysis are described in the relevant sections. The percentage of occurrence provided in describing various behaviour is based on clear observations (ie. n). Many of the behaviours observed were unexpected so that careful observations were only initiated at later in the experiments, thus the sample size (n) is different for each behaviour. Significance level was based on two-tailed 0.05. Statistical symbols mainly follow Zar (1974).

Terminology:

P. philander males described as "semi-T male" behave in essentially the same way as the "satellites" defined by Taborsky *et al.* (in press). However, the former term is preferred for *P. philander*. The term "satellites" is confusing, especially when there are "satellites" and "sneakers" present in the same species (see Wirtz 1982; Taborsky *et al.* in press). The term satellites was initially used for males which would never become T males (Hogan-Warburg 1966). This term also implies that these males were either tolerated by T males within their defended range (van Rhijn 1973; Kodric-Brown 1977, 1986; Wirtz 1982; Ross 1983; Taborsky *et al.* in press) or were ignored (Wirtz 1978;

Gross 1982). However, *P philander* semi-T males are rather aggressive and are not tolerated by T males (see Chapter 3). To avoid such confusion, therefore, males of *P. philander* are described in a hierarchy of territorial status.

The term "sneakers" is used to refer to any male which employs sneaking behaviour. Sneaking is a spawning intrusion behaviour with the intruder (ie. sneaker) showing submissive behaviour and loss of male colouration. This is different from "disruptive" behaviour (*sensu* Foster 1983), in which the intruder is pugnacious and with colouration brightly developed.

Since the aggressive relationship between *P. philander* territorial males is not a linear dominance (see Chapter 6), their social position is then described as successful or less successful. The term "subordinate" only refers to males without territories.

CHAPTER 3

ALTERNATIVE REPRODUCTIVE BEHAVIOURS

Introduction:

Alternative reproductive behaviours (ARBs) in males occur when recourse to normal reproductive behaviour is restricted to a segment of sexually mature individuals in the population. Such alternative reproductive behaviours are reminiscent of Maynard Smith's (1974, 1979, 1982) theory of an Evolutionarily Stable Strategy (ESS) as such by Gross (1982, 1984) and Arak (1984). Insects, fishes, amphibians, birds and mammals all have alternative reproductive behaviours (see proceedings of a symposium on Alternative Mating Tactics 1984, Am. Zool. 24:306-418, Weldon & Burghardt 1984) which are so widespread that it has been suggested that most males have the potential for employing ARBs (described as alternative mating tactics (AMTs) by Waltz & Wolf 1984, Taborsky *et al.* in press). In at least 64 species of fishes, the male may have more than one reproductive mode (Wirtz unpublished review cited in Taborsky *et al.* in press). Typically, normal reproductive behaviour is practised by territorial individuals, while those individuals which have been unable to acquire a territory are also unable to embark upon the typical courtship which culminates in the fertilization of females. Nevertheless, subordinate males may adopt ARBs such as sneaking and thereby steal fertilization. However, little is known about the ARBs of cichlids (eg. Fraley & Fernald 1982; McKaye 1983).

Spawning intrusions of *P. philander* had been noted in the field, but were considered to be merely for the purpose of egg-stealing (Ribbink 1975). However, in the laboratory lek, it was noted that submissive male intruders joined spawning pairs and did not steal eggs but went through the motion of fertilization. Although the release of sperm is invisible in most fishes, similar spawning intrusions have been documented as attempted fertilization by sneakers (Keenleyside 1972; Ross & Reed 1978; Wirtz 1978; Dominey 1980, 1981; Gross 1982; McKaye 1983; Taborsky *et al.* in press). In some fishes different discrete morphs practise normal reproductive behaviour and sneaking behaviour such as bluegill sunfish (Dominey 1980, 1981; Gross 1982, 1984) and salmon (Gross 1984, 1985). However, in *P. philander* the behavioural tactic followed depends on the social status of the individual and can be manipulated experimentally to switch between alternatives (see below). This suggests that sneaking is an opportunistic alternative to the typical mating tactic. This chapter describes the different categories of male and their behavioural tactics in the laboratory lek, and provides a quantitative assessment of their associated costs and benefits.

Results:

Figure 3 is a schematic description of the mating activity in the laboratory lek.

Categories of Male in the Laboratory Lek:

Three categories of male were recognized in terms of their territorial status:

Territorial Males (T Males) were brightly coloured individuals that successfully defended a territory against other males (Frontispiece).

Semi-Territorial Males (Semi-T Males) attempted to defend a small area, which normally had an abandoned nest, in-between (86%, *n*=28) or within the outer fringe (14%) of established territories. Semi-T males were always subordinate and less colourful than T males (Pl. 4).

Non-Territorial Males (Non-T Males) did not defend an area, spent most of their time schooling with females and had the same plain colouration as females (Pl. 5). Nevertheless, some non-T males showed mild aggression towards nearby non-T males and females, thus maintaining "individual distances", but they avoided semi-T and T males.

Figure 4 is the cumulative size range of different categories of male used in the laboratory, and shows that there was no significant difference between them ($F_{2,123}=2.13$, $P>0.05$). Figure 5 portrays the behaviour of different categories of male and indicates highly significant differences between them (ANOVA *F*, $P<0.001$). T males were always aggressively territorial and

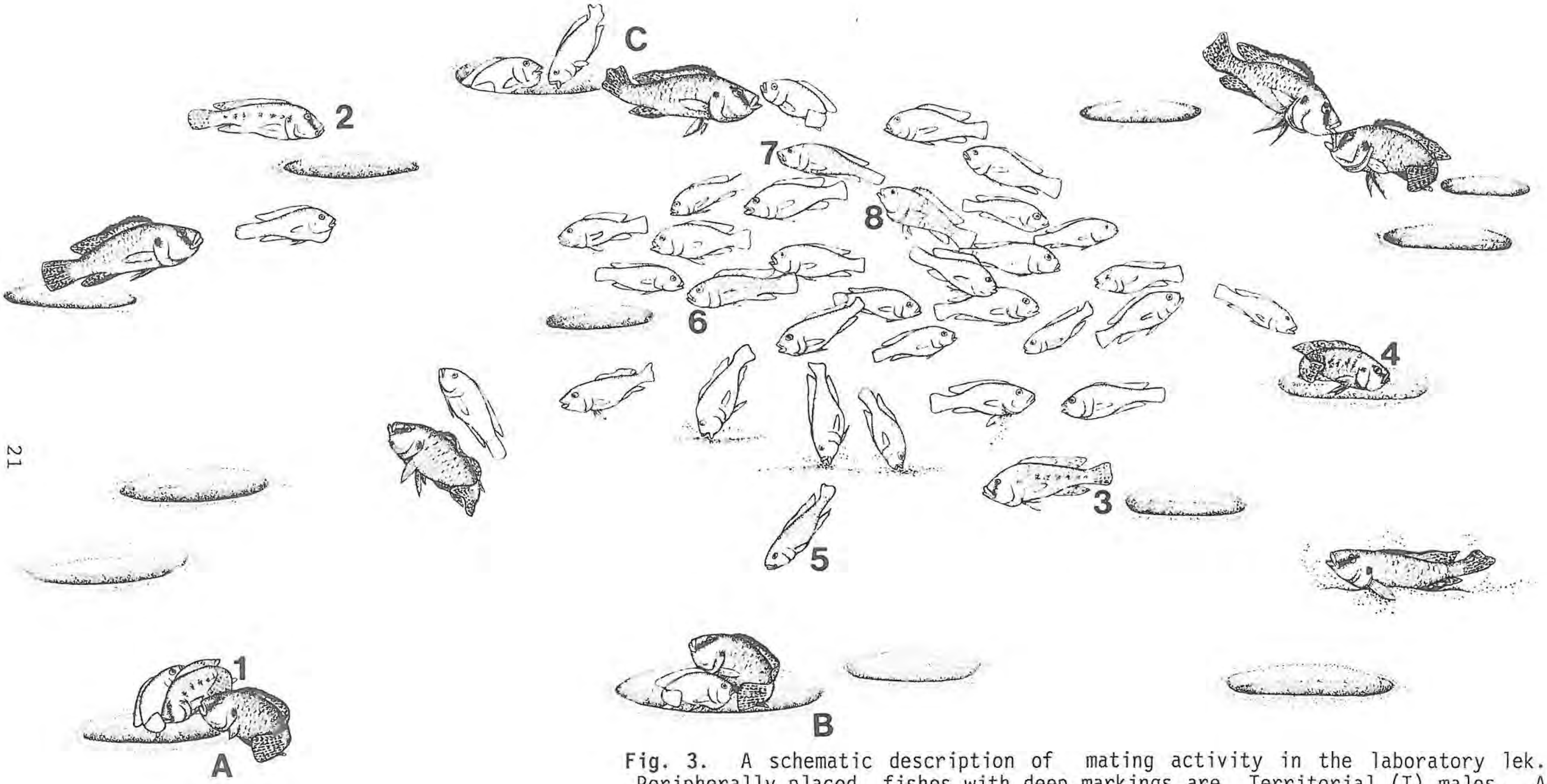
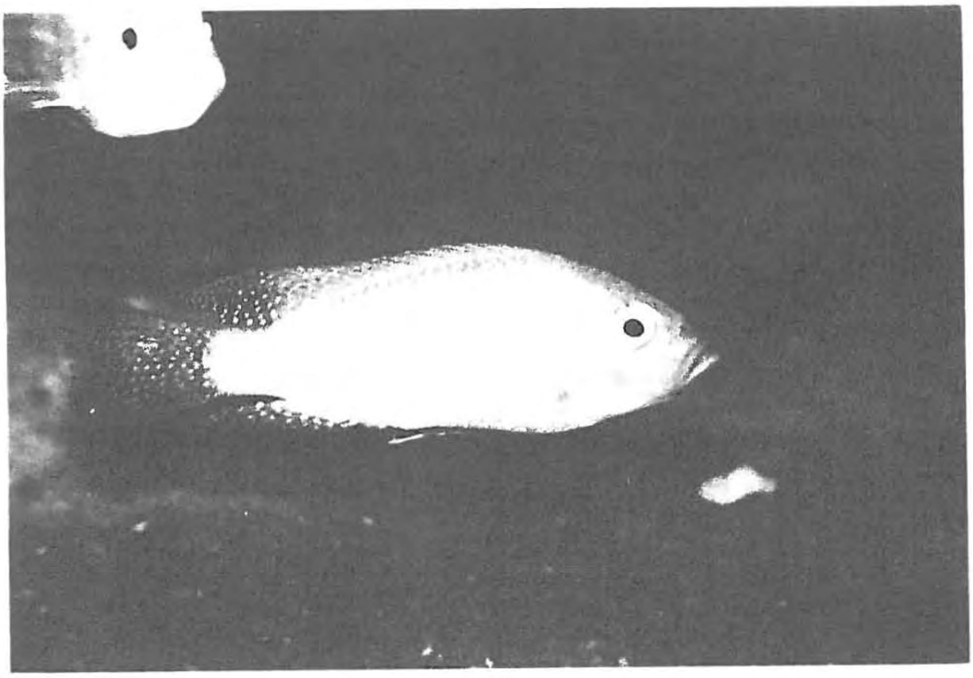
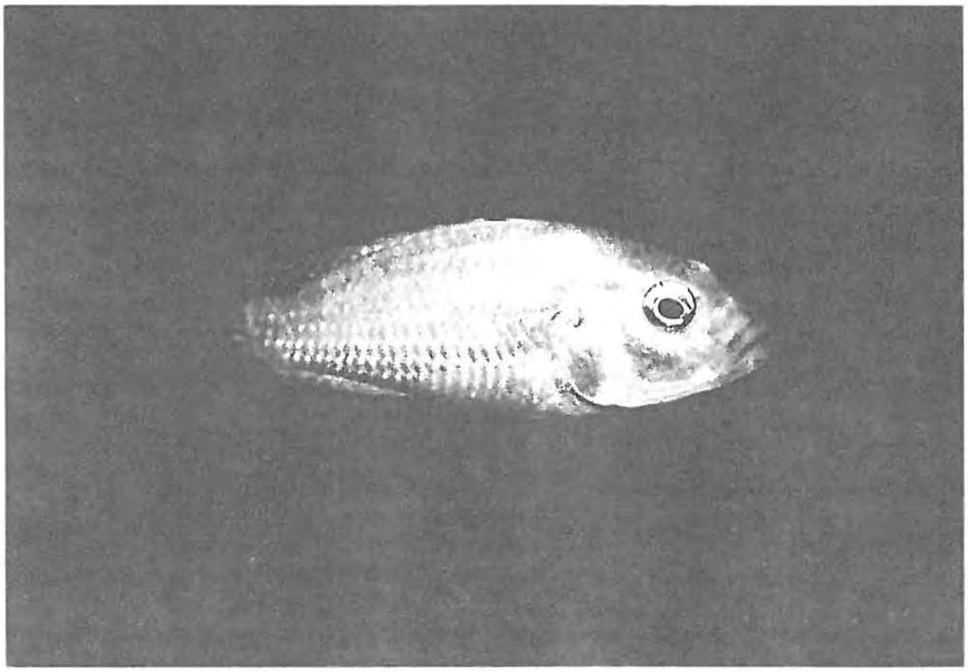


Fig. 3. A schematic description of mating activity in the laboratory lek. Peripherally placed fishes with deep markings are Territorial (T) males. A group of females occupies the central region. Fishes 1 to 4 are semi-territorial (Semi-T) males, while 5 to 8 are non-territorial (Non-T) males. Semi-T male 1 has sneaked into nest A. Semi-T male 4 is brightly coloured as it is opportunistically courting while the nearby T males (upper right corner) are fighting. Non-T male 5 is approaching the spawning pair at nest B and is about to intrude. Non-T males 6, 7 and 8 are schooling with females, with 8 being aggressive towards 7. The spawning in nest C is interrupted by the intrusion of an egg-stealing female and the mating T male is guarding against further intrusions from outside the nest.



Pl. 4. *P. philander* semi-territorial male.



Pl. 5. *P. philander* non-territorial male.

the most active in courtship while non-T males were the least active. Semi-T males showed territorial aggression, attempted courtship, sneaked most often and were chased most frequently.

Changes in territorial residency occurred when a resident male was defeated by an intruder after lengthy fights. Such displacement was recorded 21 times, 15 of which were larger males displacing smaller males ($X^2=3.86$, $P<0.05$). In those instances when smaller males displaced larger individuals, the size difference between them was small as it ranged from 0.5 to 2mm ($\overline{X}\pm SD=1.3\pm0.5$mm, $n=6$). The tendency, therefore, was for larger fish to displace those which were smaller. The displacement of territorial males occurred principally when other T males fought for and won a territory (52%) but also occurred when new large males were introduced to the lek (29%) and less frequently when a semi- (14%) or a non-T male (5%) challenged successfully. The ability to win and hold a territory was largely affected by status. Non-T males usually became semi-T males first and then became T males. Semi-T males became T males before further displacing other T males (Fig. 6).

Territorial Mating Pattern:

The typical mating pattern in *P. philander* was described by Ribbink (1971, 1975) and is illustrated in Figure 7. The average time of a preliminary visiting period for females in the laboratory lek was 67min (SD=56min, $n=44$, range=13-237min), followed by an average pre-spawning nest activity of 35min (SD=22min, $n=41$, range=7-101min) and a mean spawning period of 48min (SD=48min, $n=60$, range=9-237min); which corroborates the 48min reported by Ribbink (1971).

More than 78% of all the typical courtship recorded was performed by T males (Fig. 5). Subordinate males also opportunistically used the typical mating pattern to court females when nearby T males were otherwise involved in courtship or fights (95% by semi-T males and 5% by non-T males). Although subordinate males often still have stress bars on plainly coloured bodies when they initiated courtship, they rapidly became brighter as courtship progressed. Usually, however, such opportunistic courtship was disturbed quickly by males from any

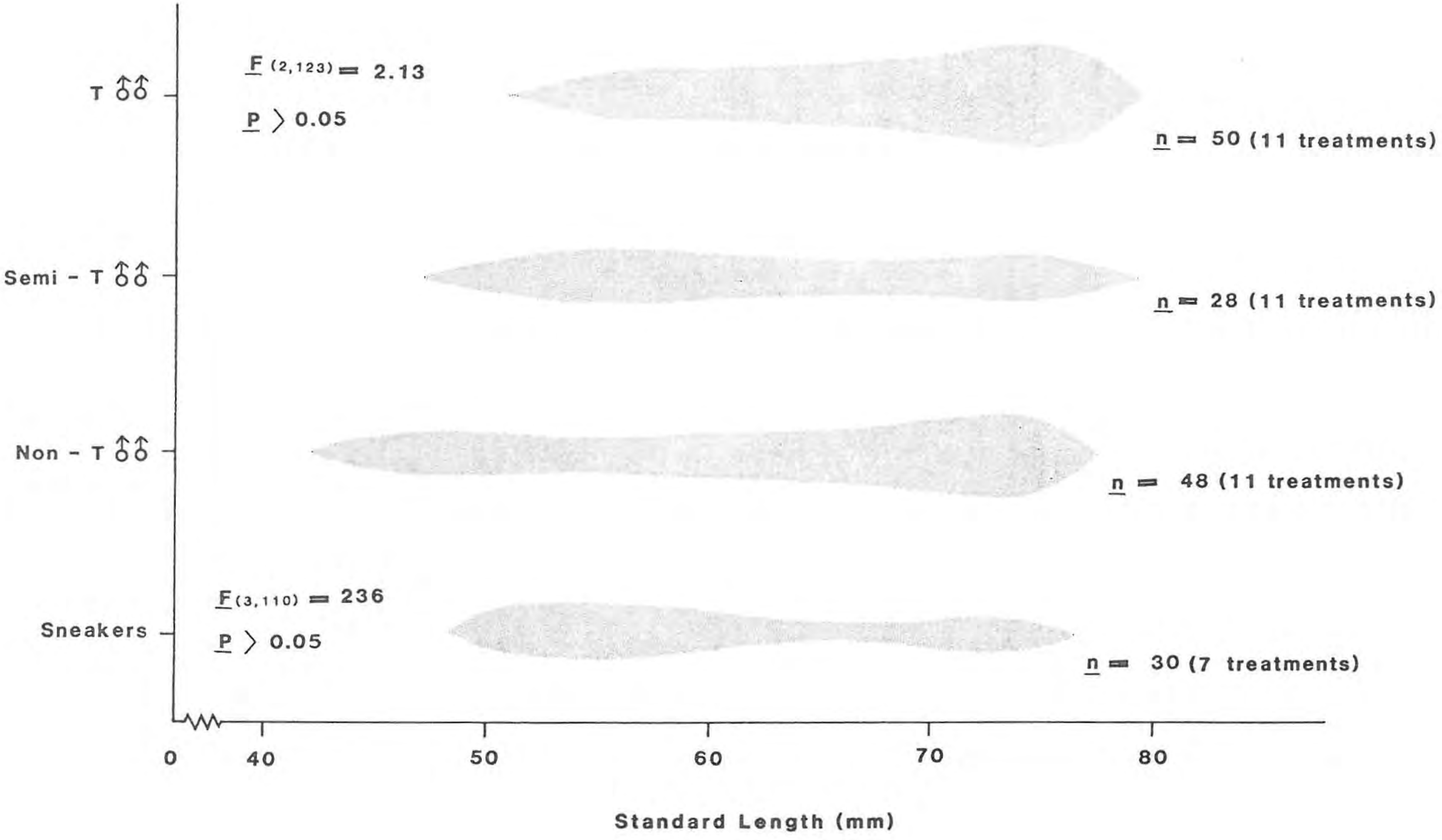


Fig. 4. The cumulative size range of different categories of male in the laboratory lek. ANOVA on sneakers and other categories of male was only calculated for those 7 treatments.

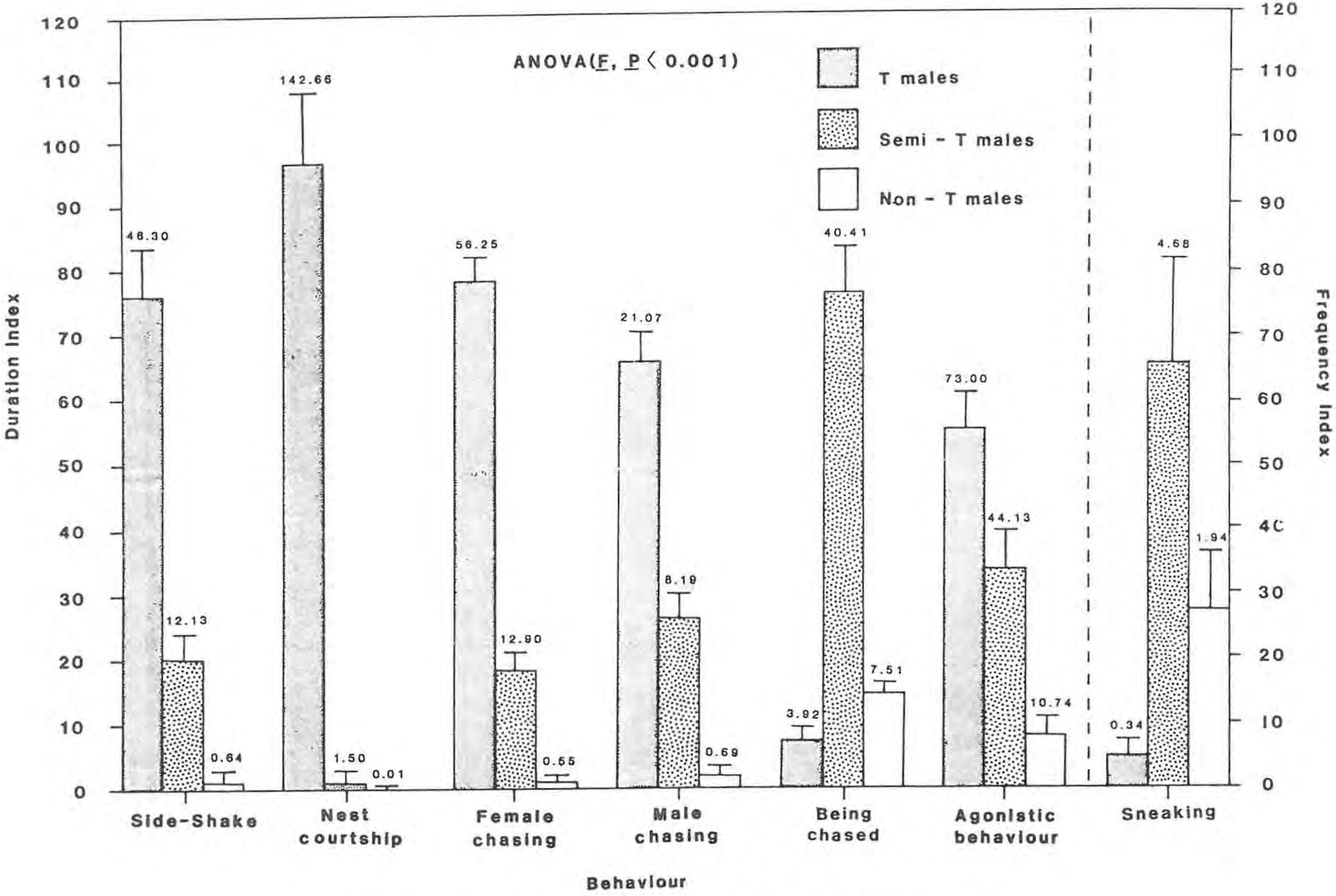


Fig. 5. The behaviour of different categories of male in the laboratory lek. Data were from 690 5-min observations on 37 T males, 212 on 23 semi-T males and 598 on 36 non-T males in 8 treatments. Data on "Sneaking" were from 32 T males, 19 semi-T males and 33 non-T males in 7 treatments. Bars represent standard error. Values on top of bars are means in units of 0.1sec/5min from "Side-Shake" to "Agonistic Behaviour", and in number/male at "Sneaking". Index = 100 X Mean in that particular category of male/Sum of all means in

of the three categories. Figure 8 demonstrates the advantages conferred upon T males relative to subordinate males in avoiding courtship interference (also see Fig. 17 in Chapter 4). Although the shortest recorded time from a female entering into the nest to the laying of the first egg was about 10sec, not once did a subordinate male successfully elicit egg laying in the laboratory. As a result, all of the 97 spawnings recorded were initiated by T males (Fig. 9).

<u>Frequency of Nest Intrusion by Sneakers</u>:

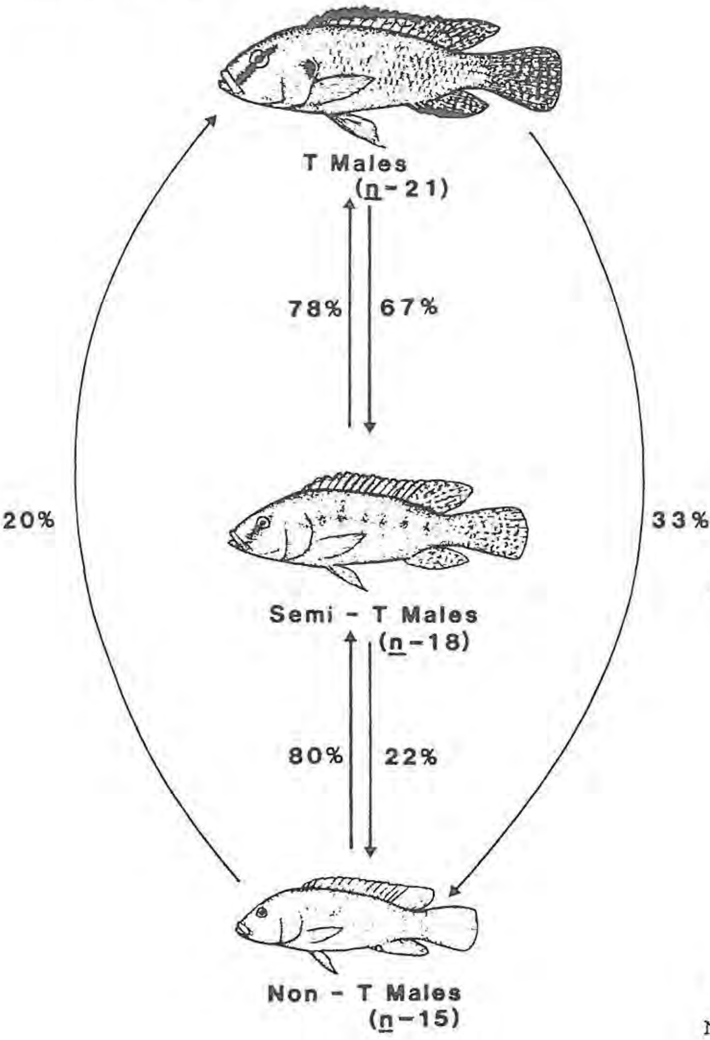
During the laboratory lek experiment a total of 164 instances of sneaking (including attempted sneaking) were observed. These were executed by 30 individuals at an overall rate of 1.5 sneaks per 5min of nest courtship (n=9255sec of nest courtship). If the object of sneaking is to fertilize eggs then the potential success of sneakers was not great. Only 40.3% (29 of 72) of spawnings in the laboratory lek were subjected to intrusion by sneakers, but very few of these (9.7%, 7 of 72) actually had sneaking occur when eggs were being laid (Fig. 10). Furthermore, as females lay several batches of eggs during a spawning, of those spawnings when sneaking did coincide with egg-laying, the sneakers were present in the nest for only 51% (SD=33%, range=13-100%) of the egg batches laid.

<u>Sneaking Behaviour</u>:

Sneakers cumulatively ranged in size from 48 to 76.5mm (Fig. 4), which overlapped almost entirely the size range of males belonging to all the three territorial categories ($F_{3,110}=2.36$, $P>0.05$). Eight males were observed switching between the territorial tactic and the sneaking tactic after their territorial status had changed. The frequency of sneaking employed by different categories of male is given in Figure 5, which showed significant differences between them ($F_{2,81}=10.32$, $P<0.001$), with semi- and non-T males accounting for 93.3% of all sneaking instances. There was no significant difference between the cumulative size of T male sneakers and subordinate male sneakers ($t_{28}=1.99$, $P>0.05$), and the sneaking behaviour by different categories of male was essentially the same.

The sneaking behaviour of *P. philander* is illustrated in

Fig. 6. The change of territorial status in different categories of male, indicated by the arrows.



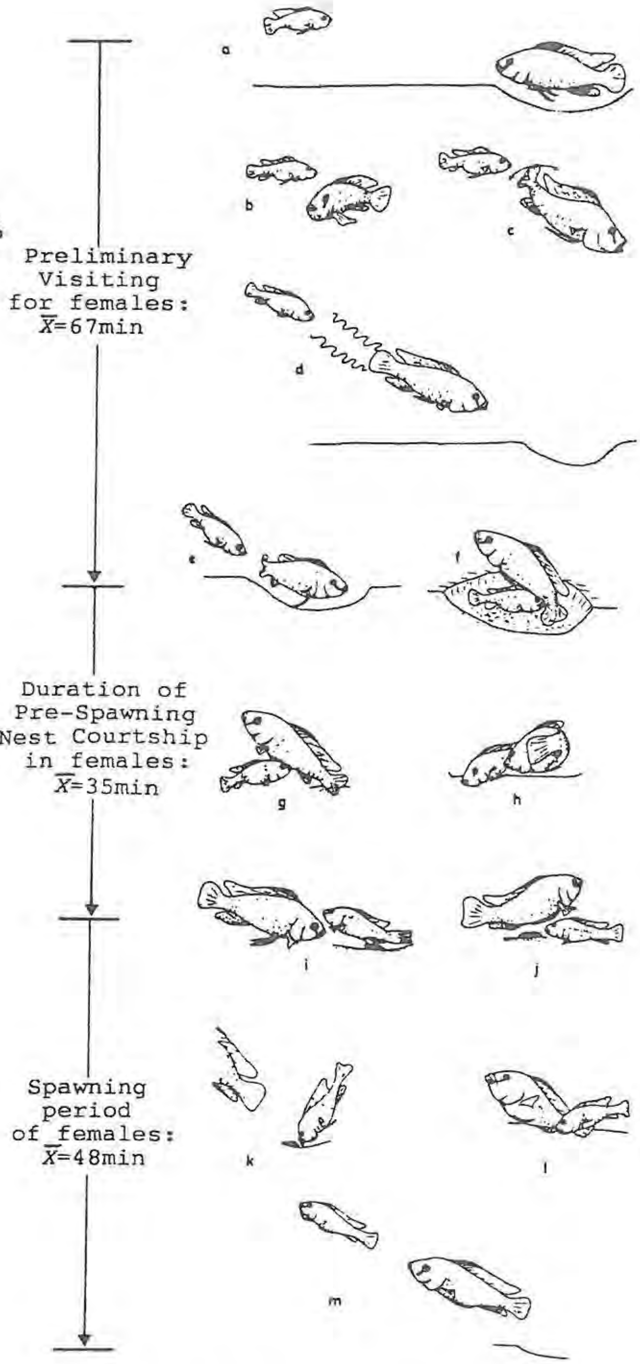


Fig. 7. The typical mating behaviour in *P. philander*. (a) a female near a male's nest; (b) side- shake; (c) follow-shake; (d) lead swim; (e) nest-shake; (f) vertical nest-shake; (g) the female prods the male; (h) the male prods the female; (i) the male observing oviposition; (j) the female observing fertilization; (k) the female gathers the eggs while the male chases potential intruders; (l) the female collects milt from the male; (m) the female carrying her eggs is chased off by the male. Figure modified from Ribbink (1971).

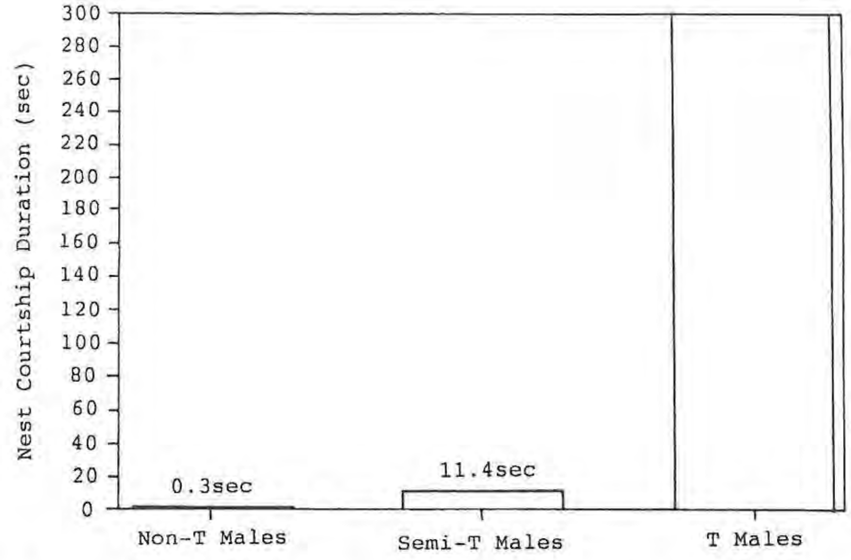


Fig. 8. The maximum duration of uninterrupted nest courtship in 5min for the different categories of male in the laboratory lek. *n*=690 5-min observations on 37 T males, 212 on 23 semi-T males and 598 on 36 non-T males.

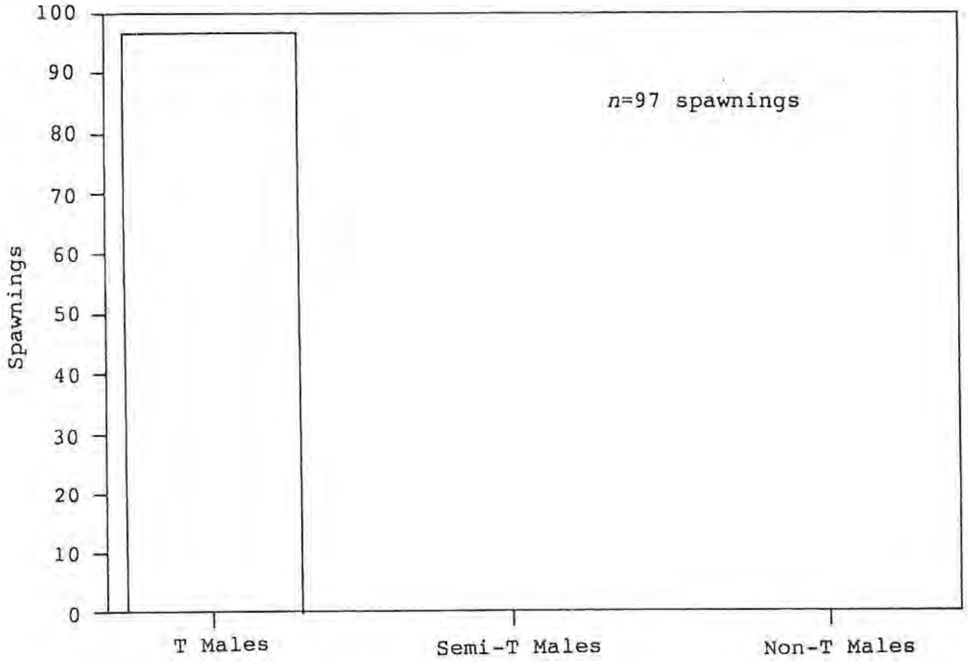


Fig. 9. The number of spawnings elicited by different categories of male in the laboratory lek.

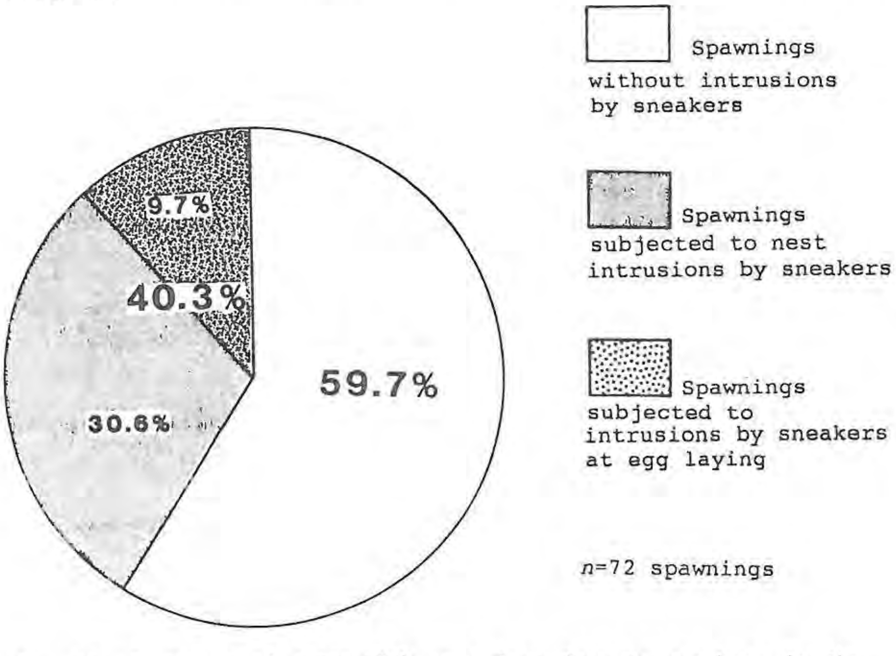


Fig. 10. The frequency of successful nest intrusions by sneakers in the laboratory lek.

Figures 11, 12 and Plate 6. Other than the behaviour described in Figure 12-1, sneakers sometimes used shelters, such as a heater or filters, to reach the nest (Fig. 11-b). They also gained access to the nest by following a gravid female which was being led by a T male or by joining other intruders, in rapid succession or simultaneously. Sneakers which entered the nest (Fig. 11-d) tried to position themselves between the mating pair. They then performed courtship with the female and if eggs were present they moved over these, probably to release sperm. Reacting to the intrusion (Fig. 11-e), T males usually moved out of the nest as if to chase and remained there for a few seconds, but occasionally for more than half a minute, before returning to the nest to ram the sneaker. Once back in the nest, T males would squeeze between the sneaker and the female to isolate the sneaker and act aggressively towards it by tail-beating. The T male would chase any fish which went outside the nest during this time. Responding to the aggressive T male, sneakers fled or indulged in female-like behaviour by trying to butt the belly of the T male as would a spawning female. Spawning females usually responded to the sneaker by continuing the courtship with the intruder but 12% (3 of 25) left immediately after an intrusion had occurred (Fig. 11-f), though this was usually a consequence of repetitive intrusions. After the sneaker had been chased off, the female normally resumed spawning with the T male. T males generally chased away the intruding sneaker a few seconds (max. 30sec) later, but in 9.5% (2 of 21) of chasing instances the spawning females were mistakenly chased off by the T male instead of the sneaker. Females in the early stages of courtship were very sensitive to interference and often left the nest immediately an intrusion occurred (Fig. 11-f), and sometimes they left even before the oncoming sneaker had reached the nest during repetitive intrusions.

In 10% of sneakings (n=10) in which the female had left the nest, the T male and the sneaker continued the courtship with each other for a few seconds (Fig. 11-h), during which the sneaker emulated female behaviour. Mating females also showed aggression towards other fishes and on 16% of chasings (n=32)

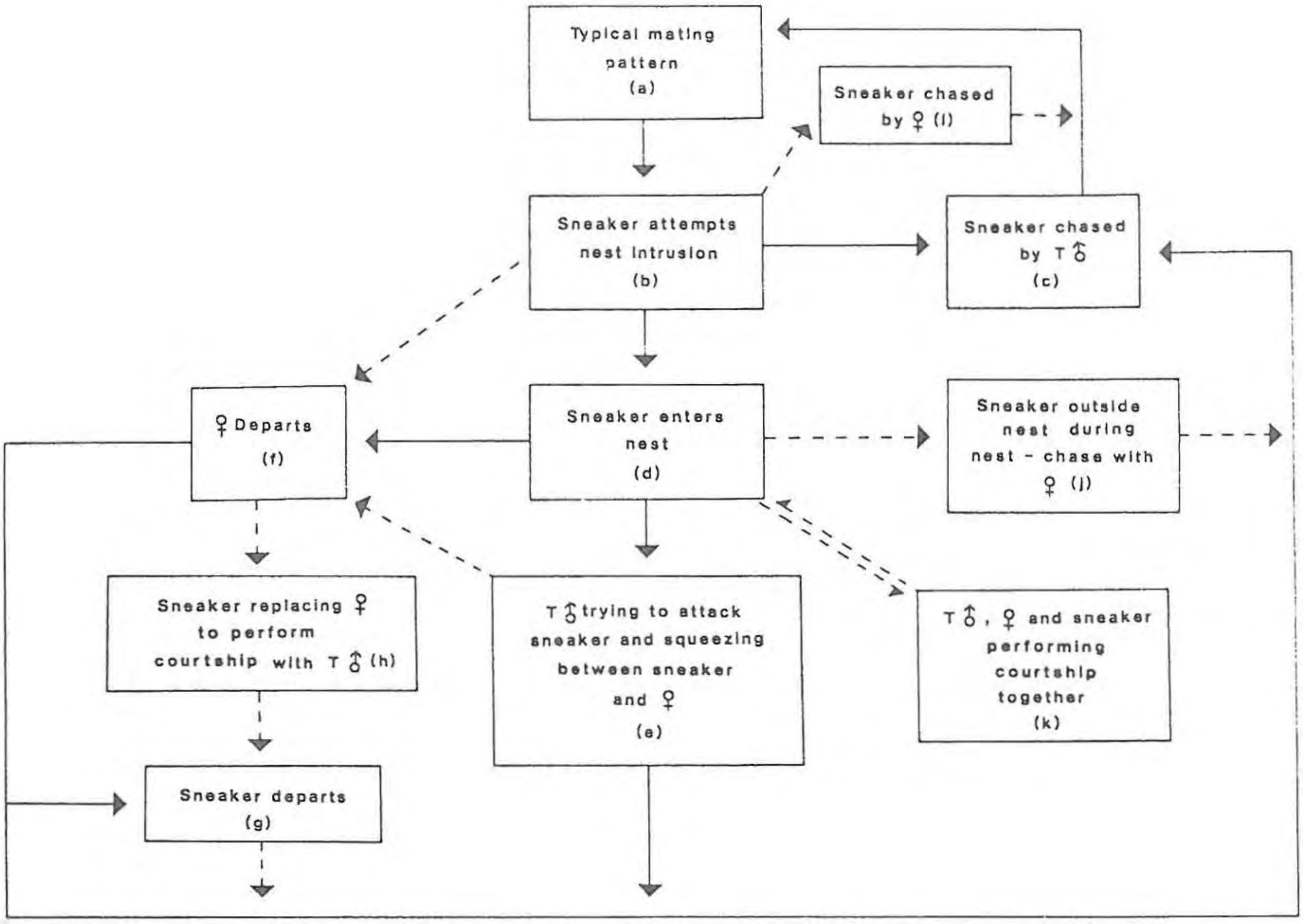
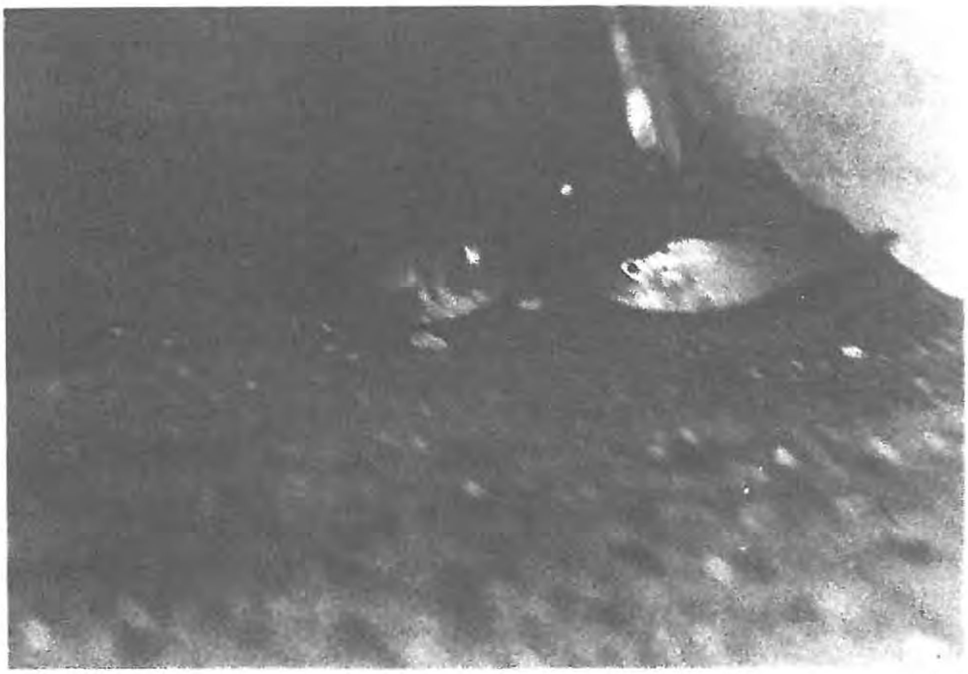


Fig. 11. The behavioural flow chart of the sneaker and the mating pair during sneaking. Solid arrows indicate the most common sequences. See text for details.



Pl. 6. Sneaking in action. The fish at the left is a sneaker and the spawning female is on the right is about to butt the belly of the sneaker. The territorial male (at the back) is about to squeeze in-between and isolate the two.

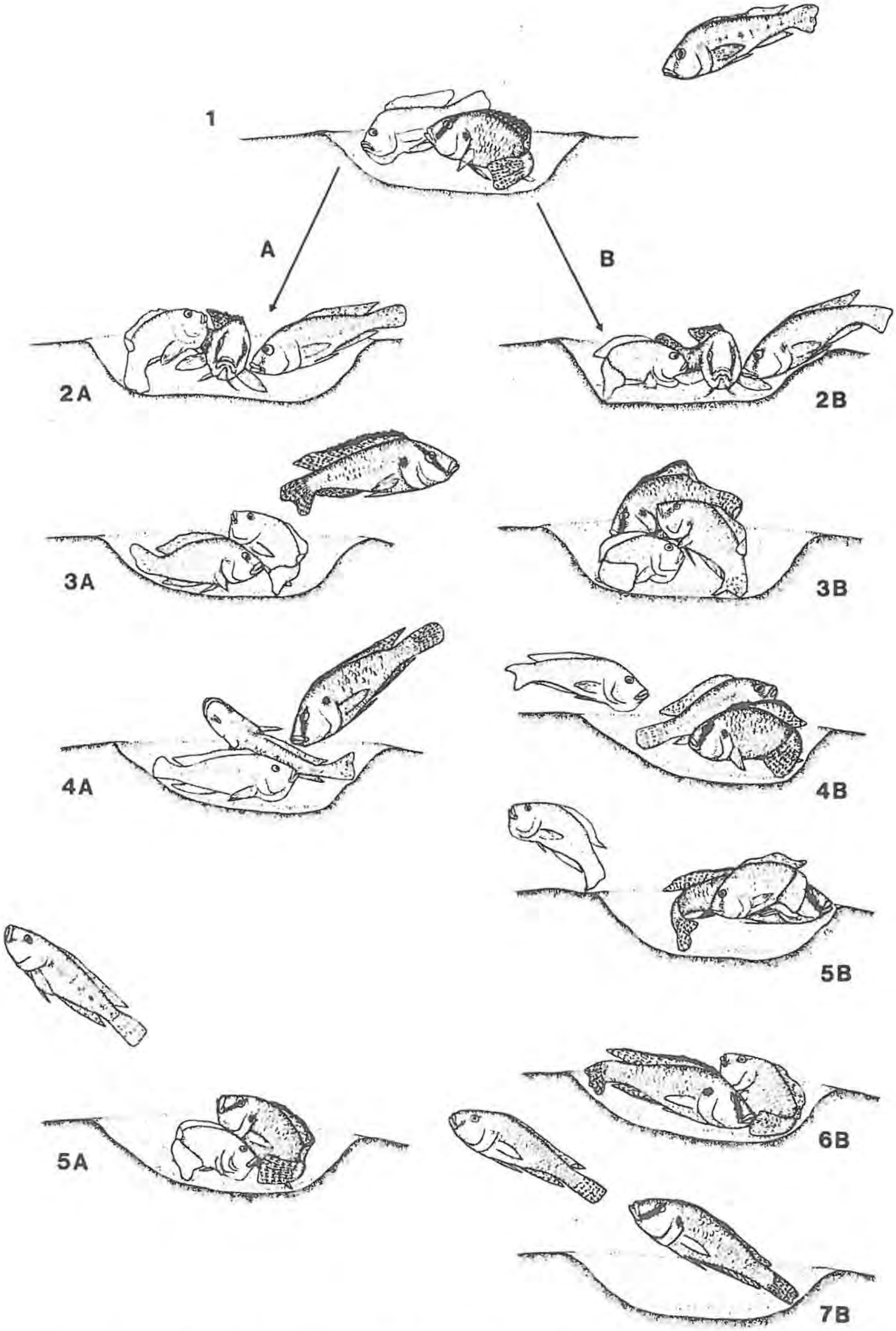


Fig. 12. A schematic description of the sneaking behaviour in *P. philander*. A is the common sequence. 1) The sneaker swims towards the nest in a yawing motion. 2A) The sneaker suddenly rushes into the nest at an appropriate opportunity and the mating of the spawning pair is interrupted. 3A) The T male then goes outside and guards the nest before taking further action. 4A) After a few seconds the T male returns to the nest and rams the sneaker. 5A) After chasing away the sneaker, the T male mates with the female again. 2B) The spawning pair appears not to notice the intruder and continues mating. 3B) The three fishes perform courtship together. 4B) The spawning female detects the presence of the sneaker and stops mating. 5B) The T male is still courting the sneaker even though the female has left. 6B) The sneaker mimics the female and continues the courtship with the T male. 7B) After some courtship with the T male, the sneaker leaves the nest.

they chased the approaching sneaker even before the mating male had taken action (Fig. 11-i). In 4% of sneakings (*n*=25), the aggressiveness of mating females during circular nest-chase resulted in the sneaker being pushed out of the nest and subsequently chased off by the T male (Fig. 11-j). Nevertheless, if the female was trying to ram, but missed the sneaker and went outside the nest before the sneaker, the T male would chase it away without hesitation. On 4% of intrusions (*n*=25) the mating pair appeared to ignore the sneaker and continued to mate for up to 30sec (Fig. 11-k). During this time the sneaker participated in butting associated with mating.

Table 1 summarizes the physical and behavioural characteristics of the different categories of male.

Discussion:

Generally larger males tend to be territory owners, but the different categories of male and sneakers do have overlapping cumulative size ranges (Fig. 4). This is because experimental manipulations in the laboratory lek alter male position on the social hierarchy so that T males are sometimes down graded to subordinate males. Alternatively, subordinate males may become T males if those higher on the hierarchy are removed. Thus, during its life a male *P. philander* may act in a reversible manner as a sneaker or as a T male and adopt the different mating tactics as circumstances demand. Less competitive males can be said to be forced into the subordinate AMTs (West-Eberhard 1979; Waltz & Wolf 1984). This is in contrast to sunfishes (Dominey 1980, 1981; Gross 1982, 1984) and salmon (Gross 1984, 1985) which have morphs which practise either one or other behavioural pattern throughout their sexually active life.

As in other fish species (eg. Fernald 1977; Fernald & Hirata 1977; Wirtz 1978; Dominey 1980, 1981; Gross 1982; Fraley & Fernald 1982; McKaye 1983; Taborsky *et al.* in press), *P. philander* sneakers appear to mimic females in nests. It is assumed that such behaviour reduces T male aggression, and enables sneakers to remain in the nest for longer. There is a neutral colouration and a neutral courtship behaviour in *P.*

TABLE 1. The physical and behavioural characteristics of different categories of male.

	T Males	Semi-T Males	Non-T Males
a. Body Size	Tend to be larger	Tend to be only slightly smaller than T Males	Tend to be smaller
b. Colour	Full nuptial colour	Change accordingly	Neutral colour
c. Aggressive interactions	Very aggressive	Aggressive	Submissive
d. Territory	Stable	Unstable	None
e. Being chased	Seldom	Frequently	Occasionally
f. Side-shake display	Unlimited	Limited	Virtually none
g. Nest courtship	Prolonged	Restricted	None
h. Attracting females	Successful	Usually unsuccessful	No success
i. Frequency of sneaking	Very low	Very High	High
j. Mating tactic	Typical territorial pattern	Sneaking and Opportunistic courtship	Sneaking

philander. The juvenile colouration can be referred to as the neutral colouration. Mature female and subordinate males retain the juvenile colouration, and only T males manifest the bright nuptial colour. The horizontal nest-shake and the corresponding belly-butting (Ribbink 1971, 1975) in the courtship behaviour of *P. philander* are essentially the same for males and females, with both sexes performing the same behaviour alternately. Therefore, it appears that *P. philander* sneakers mimic females simply by retaining the neutral colouration and by performing the neutral courtship behaviour in nests. Such low costs in developing mechanisms of deception probably favour the evolution of sneaking in *P. philander*.

There are two hypotheses to account for the limitation on the evolution of nest defence by T males to counter sneaking (see Dominey 1981; Gross 1982; Wirtz 1982; Barnard 1984; Arak 1984). The net benefit hypothesis supposes that the occurrence of sneaking has advantages as well as disadvantages to the T male, but there can be a net benefit for the T male. The other hypothesis is the parasite hypothesis, which presumes that the cost of preventing sneaking could exceed the cost of the sneaking itself. The presence of satellites in the territories of T males is also always interpreted in terms of "mutualist" and "parasite" hypotheses (Ross 1977, 1983; Kodric-Brown 1977, 1986; Ross & Reed 1978; Wirtz 1982). Nevertheless, the relationship between semi-T males and T males in *P. philander* appears to be also an agonistic relationship (ie. challenging T males), like that of the "type 3 males" in longear sunfish (Keenleyside 1972).

When approaching mating pairs, sneakers usually employed normal submissive male behaviour (the stress colour and yawing motion), and not female colouration. A possible explanation for this is that mating T males are also aware of possible female egg-stealing, and will actively chase nearby females as well as males. In longear sunfish (Keenleyside 1972) and Malawi lek-breeding cichlids (McKaye 1983, 1984), sneakers may eat the fresh-laid eggs in the nest, as well as fertilize them. In *P. philander*, sneakers have not yet been observed eating eggs nor performing the head down "nose-pushing" behaviour inside nests, although egg-stealing by female intruders is common (see Chapter 4). The reason why spawning females sometimes attack sneakers very aggressively, could be the result of their being mistaken for egg-stealing females.

In contrast to other fishes (Wirtz 1978; Dominey 1980, 1981; Gross 1982), the *P. philander* T males usually stay outside guarding the nest immediately after the intrusion, and for a period they leave the sneaker to court the female before "striking" back. This temporary stay-away may enable the T male to distinguish between the sneaker and the spawning female, while guarding the nest from further intrusions.

T males have been found to court plain coloured subordinate males. On eight occasions sneakers responded to and courted with T males in the absence of females ($\bar{X}\pm$SD=2.8$\pm$1.7sec). Dominey (1981) argued that by performing "courtship" with certain males, particular sneakers in sunfishes might be more tolerated by them. However, since such homosexual interactions in *P. philander* are very rare, attaching any adaptive function to this behaviour may be unwarranted (Jamieson & Craig 1987). Alternatively, this male-male "courtship" behaviour can also be explained by a selection process favouring sneakers to become more responsive to stimulation so that they can steal more fertilizations, and hence sometimes they become misdirected in such a stimulus-response chain. This idea is further supported as subordinate males sometimes attempted to sneak even when T males were only building nests.

Similarly T males occasionally sneak up to spawnings. In *P. philander*, such behaviour is rare and mainly occurred when the male was a new T male or its courtship was displaced by superdominant males (infrequently (3 of 11 treatments) one T male in the laboratory lek assumed superdominant status for a period and it might go beyond its territory to disrupt the matings of other T males, though most of the time it remained in its own territory), and therefore may have been due to an incomplete switch between different tactics. In general, established neighboring T males will not disturb each another's mating behaviour.

The opportunistic courtship behaviour in subordinate males is similar to the "cheating" behaviour of *Haplochromis burtoni* (Fraley & Fernald 1982) and the "nest-watching" behaviour of creek chub (Ross 1977). However, opportunistic courtship is fundamentally different from the nest-intrusion sneaking, but can be perceived as an incomplete form of the typical mating behaviour. By courting responsive females opportunistically, subordinate males may be able to successfully bypass the process of prolonged courtship required by the females (see Arak 1984). However, although such behaviour accounts for most of the spawning stolen by "satellites" in pupfish (Kodric-Brown 1986), no successful opportunistic courtship has been observed for *P. philander* semi-T males in the laboratory.

The possession of a territory is essential to successful mating for *P. philander* males because females need protracted periods of stimulation to prepare them for spawning (Fig. 9). The aggressive behaviour of territory owners also unrelentingly prevents subordinate males from settling. Although semi- and non-T males cannot provide undisturbed courtship (Fig. 8), they may employ sneaking to gain accesses to females. However, in less than 10% of the spawnings do sneakers enter nests at the same time as eggs (Fig. 10) and even then their presence is restricted to about half of the egg batches laid. A further inhibition to sneaker success is that it is likely that freshly-laid eggs are passed over by the mating T males before they are picked up by spawning females and the majority may be fertilized in this manner prior to intrabuccal fertilization (Ribbink 1971, 1975). This suggests that T males have an advantage even if sperm competition does occur for the unfertilized eggs in the spawning female's mouth when she is collecting sperm during sneaking. Undoubtedly, fertilization success will be related to the time spent in courtship with females, as this provides an enhanced opportunity to fertilize the eggs. Once again, T males are at an advantage as they are responsible for 99% of all nest courtship (see Fig. 5). Similar arguments can be applied also to the fertilization success of opportunistic courtship by subordinate males. An estimate of the proportion of the population's eggs which may be fertilized by sneakers is:

9.7% X 51% (physical contact with eggs) + 40.3% X 1% (nest intrusion) + 1% (opportunistic courtship) = 6.35%

As semi-T males sneaked more often (t_{50}=2.29, $P<0.05$) and performed more opportunistic courtship (t_{808}=3.35, $P<0.001$) (see Fig. 5), they probably steal more fertilizations than non-T males. Table 2 provides the possible costs and benefits of the alternative mating tactics derived from the data.

Since the reproductive success of sneaking (including opportunistic courtship) in *P. philander* is only about 6.8% of that of the territorial tactic, sneaking appears to be what Maynard Smith (1979) refers to as "merely making the best of a bad situation". Many authors have strongly linked ARBs with the ESS theory, although their relationship is unclear (see Austad 1984; Dominey 1984a; Waltz & Wolf 1984; Caro & Bateson 1986). The ARBs of *P. philander* should be phenotypically reversible and allogignous (*sensu* Austad 1984), if it is classified without ESS connotation. However, it is a conditional strategy in the ESS sense (see Maynard Smith 1979, 1982; Gross 1984; Dominey 1984a). Furthermore, the different submissive AMTs (semi- and non-T tactics) are not adopted stochastically (ie. "mixed strategy" *sensu* Maynard Smith 1979, 1982) by subordinate males since they are also with unequal payoffs (see Rubenstein 1984).

It has been argued that if one AMT has a higher reproductive success than another, the "losing" tactic should eventually be lost, or the plasticity in using AMTs should be restricted (see Rubenstein 1984; Howard 1984; Fairchild 1984). Accordingly, young and smaller males should defer reproduction to reduce risk and energy expenditure while simultaneously enhancing growth (Warner 1984). However, under aquarium conditions, the smallest *P. philander* male which could perform the typical mating pattern and succeed in fertilizing the eggs after the removal of dominant males was 34.5mm. It seems that such uninfluenced early maturation in *P. philander* may be an adaptation to the unstable riverine environment in southern Africa, and in such a way "predispose" them to sneaking despite the low fertilization success. Furthermore, enhancing offspring condition and

TABLE 2. Possible costs and benefits of the alternative mating tactics in *P. philander*.

	Territorial tactic		Sneaking tactic	
	Cost	Benefit	Cost	Benefit
a. Body Size	Delays in obtaining territory	Higher competitive ability	Lower competitive ability	Able to obtain fertilization earlier
b. Body Colour	Provokes aggression; increases predation risk	Attracts females; warning signal to reduce fights and chases	Limited female response	Reduces aggression; less predation risk
c. Aggressive behaviour	Uses time and energy which could be used for mating; may result in serious injury	Maintains territory; prevent subordinate males from performing courtship	Behaviour restricted	Reserves energy for future competition
d. Territoriality	Costs many aggressive encounters to maintain	Territoriality is a prerequisite to successful mating; permits relatively undisturbed courtship	Not attractive to females; courtship often interrupted	Saves energy by avoiding aggressive encounters
e. Courtship	Depletion of energy; provokes aggression and vulnerable to predator	More courtship correlates with more female responses	Cannot attract females	Saves energy; without provoking aggression
f. Reproductive success	High energy and long time investment; risk of agonistic injury, predation and fertilization stealing	Substantially enhance fertilization probability	Unable to attract females and therefore obtains few fertilizations	Steals fertilization with little time and energy investment

increasing fecundity, as well as other factors unrelated to Resource Holding Power (RHP -- Maynard Smith 1979, 1982) discussed by some authors (Constantz 1975; Kodric-Brown 1977, 1986; Foster 1983; Waltz & Wolf 1984) may also favour males attempting to reproduce before reaching prime RHP, and hence the occurrence of AMTs used by subordinate individuals.

The three tactics seem to be in a sequence: non-T males may initially resemble females, then become semi-T males hoping to establish territories, and finally become T males when the opportunity arises. This sequence can be reversed as well (Fig. 6). It is clear from Tables 1 and 2, that being a T male provides a great reproductive advantage, but it is also extremely costly, and probably cannot be maintained for long (ie. a high benefit/high cost behavioural option). While being a non-T male is the least expensive energetically, and probably carries the lowest risk, it has the poorest chances of fertilization (ie. a low benefit/low cost option). Yet, this can be a resting stage to conserve energy for later male-male competition. Semi-territorial status is a transition between T males and non-T males. Semi-T males attempt to build up territories, but meanwhile they also try to court females as well as sneak, to obtain as many fertilization opportunities as possible. Therefore, being a semi-T male is also energetically expensive and risky, but with only a few more reproductive benefits than being a non-T male. The thresholds for switching between these tactics is probably dependent on the size of the male, his available energy and position in the social hierarchy of the lek (Fig. 13).

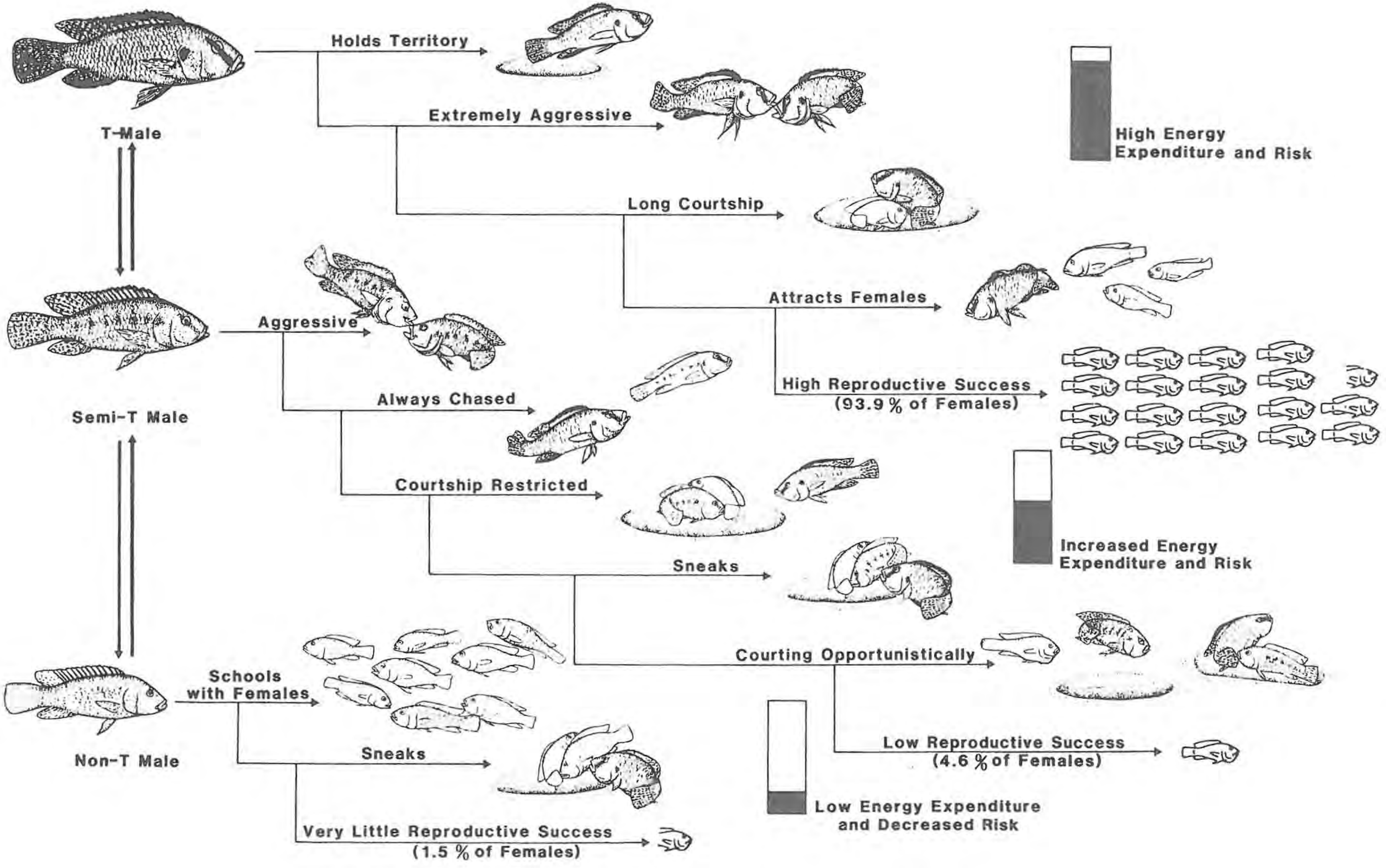


Fig. 13. A schematic summary of the characteristics and possible costs and benefits of different categories of male.

CHAPTER 4

COURTSHIP INTERFERENCES

Introduction:

Other than the alternative reproductive behaviour employed by subordinate males to intrude upon spawning pairs, many other courtship interferences were noted during the course of experiments and some of them were frequent. Although courtship interferences, excluding sneaking, are widespread in fish (eg. Semler 1971; McKaye 1983, Downhower *et al.* 1983; Kodric-Brown 1983; deMartini 1987; Ward & FitzGerald 1987), detailed reports are sparse (eg. Keenleyside 1972, Mrowka 1987b). Nevertheless, this behaviour has been suggested to be an important factor to affect the structure of leks (Lill 1974b; Arak 1983, 1984; Foster 1983) and can modify female choice (Diamond 1981; Bradbury & Gibson 1983; Arak 1984). This chapter, therefore, describes the various forms of courtship interferences observed in *P. philander* and their effect on spawning, but sneaking is omitted as it was described in the previous chapter.

Results:

Types of Courtship interferences:

Both males and females interfere with the courtship and spawning of others. Females intruded mainly to steal freshly-laid eggs or during spawning bouts. Male interferences can be separated into sneaking and disruption in terms of the behaviour of the interferer as described in Terminology (Chapter 2). Interferences in courtship can be further subdivided into side-shake disruption and nest intrusion. Most of the disruptive behaviour by males are side-shake disruption, while female interference and sneaking are nest intrusions.

Frequency of Spawning Interference:

A tentative calculated interference rate during spawning in the laboratory lek is provided in Figure 14. For individual spawnings, 29% (*n*=72 spawnings) were not disturbed (Fig. 15). Of the 71% disturbed spawnings, 40% were with intrusions by other

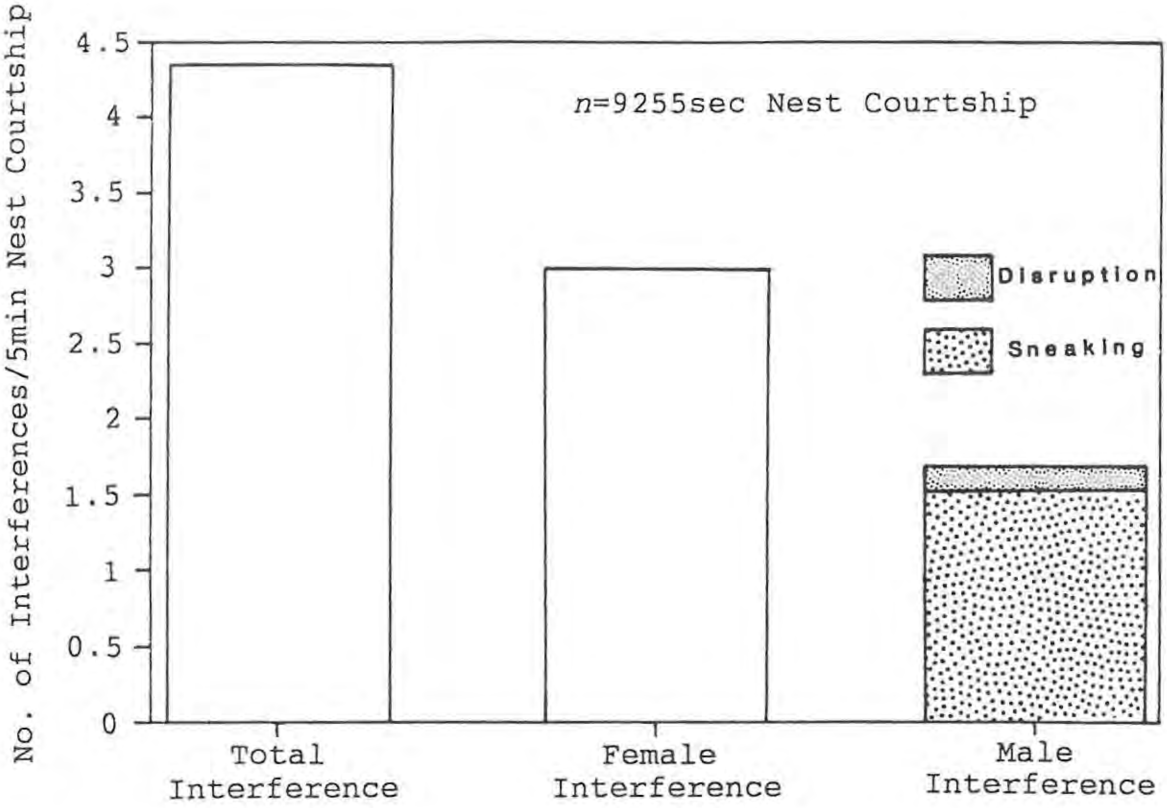


Fig. 14. An estimate of the rate of spawning interference in the laboratory lek. Rate was calculated by number of interferences/total duration of nest courtship.

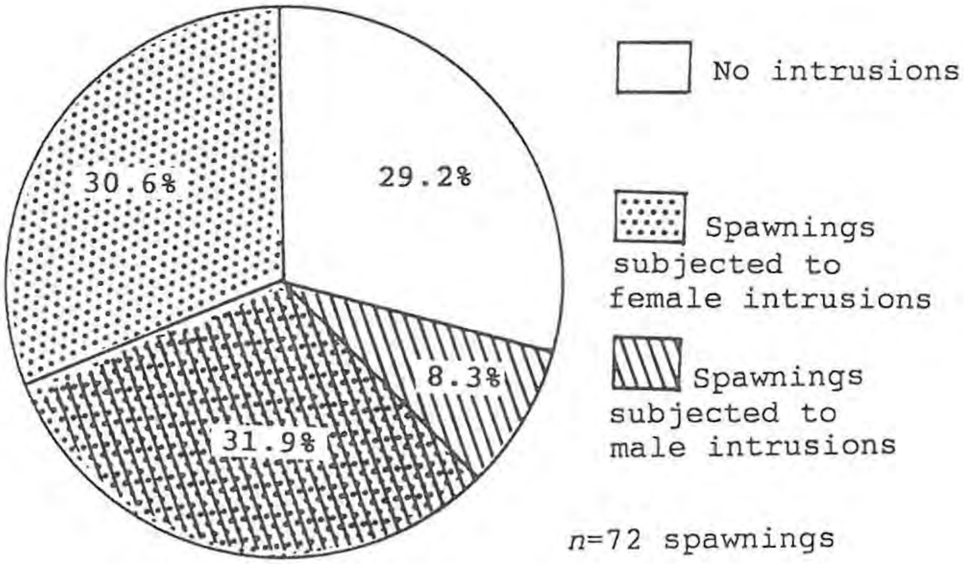


Fig. 15. The frequency of successful nest intrusions in the laboratory lek.

males and 63% were with intrusions by females (Test of differences between two proportions $z=3.64$, $P<0.001$).

Since females intruded spawning more often than males, it was of interest to find out whether T males chased females more often than males. Although Figure 4 shows that T males, as a whole, spent more time in chasing females than chasing males. However, the direct comparison of these two indices is misleading, since there were always more females than males present in the laboratory lek (data on spawning intrusion were based on successful intrusions and therefore no conversion is necessary). In order to examine the level of aggression of T males towards females and other males more correctly, a standardized chasing ratio was used for comparison instead. This ratio was obtained by dividing the male or female chasing durations by the total number of males or females present in the laboratory lek. The result of this conversion is provided in Figure 16. It shows that the female chasing ratio is smaller than the male chasing ratio, and that the difference between them is highly significant ($t_{1378}=4.23$, $P<0.001$).

Male Courtship Interferences:

Courtship interferences by males were at side-shake and spawning. The former being only in the form of disruption. Sneaking contributes to most of the spawning interferences by males (90.5%, Fig.14).

A tentative calculated side-shake disruption rate was 7.6 per 5min of side-shake (n=2543sec of side-shake in all males). However, such disruptive behaviour was performed mostly by T males interrupting the opportunistic courtship of subordinate males. Rates of side-shake and spawning disruption in T and in subordinate males are shown in Figure 17. The behaviour of a T male aggressively disrupting the opportunistic courtship of a subordinate male, is schematically described in Figure 18.

Female Spawning Intrusions and Egg-Stealing:

Of the 63% spawnings (n=72) in the laboratory lek where female intrusions occurred, 47% (29% for total spawnings) involved egg stealing (Fig. 19). Although in *P. philander* freshly-laid eggs are quickly picked up by the female, egg-

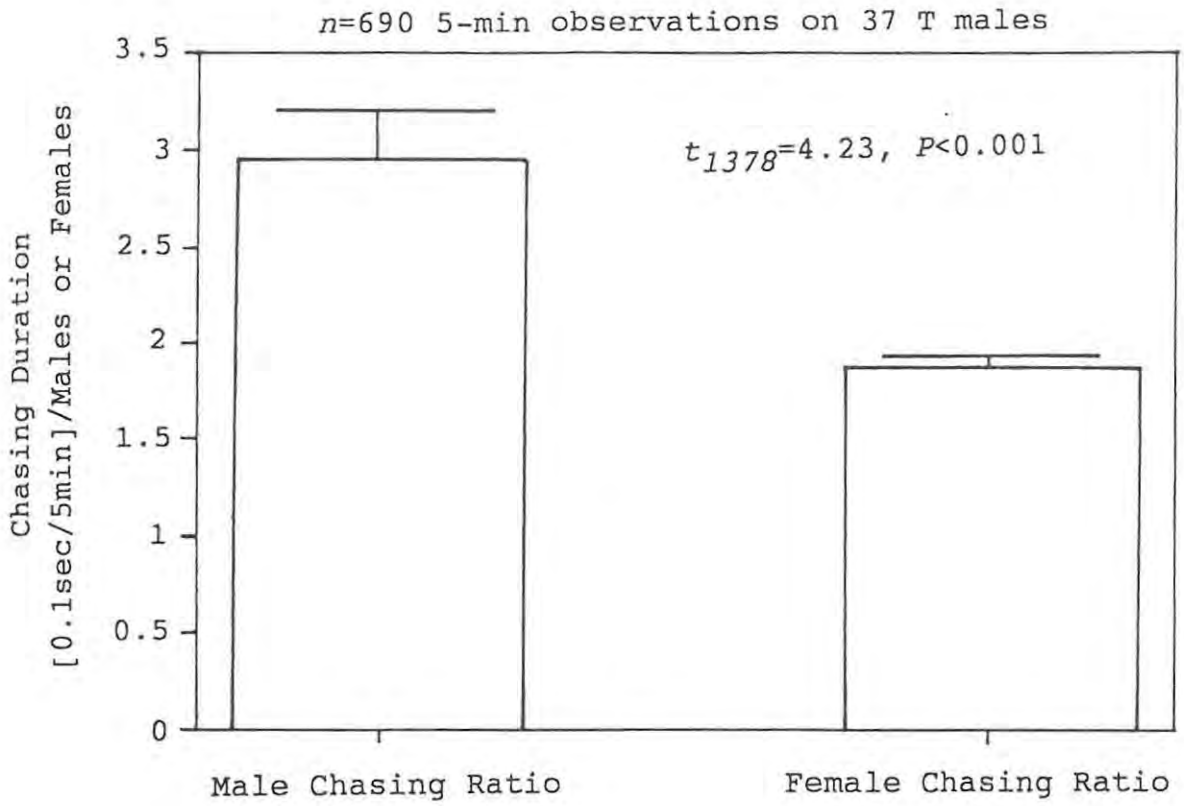


Fig. 16. Standardized chasing ratio of T males to other males and females. The ratio was calculated by duration of chasing/number of males or females in the lek tank. **Bars represent standard error.**

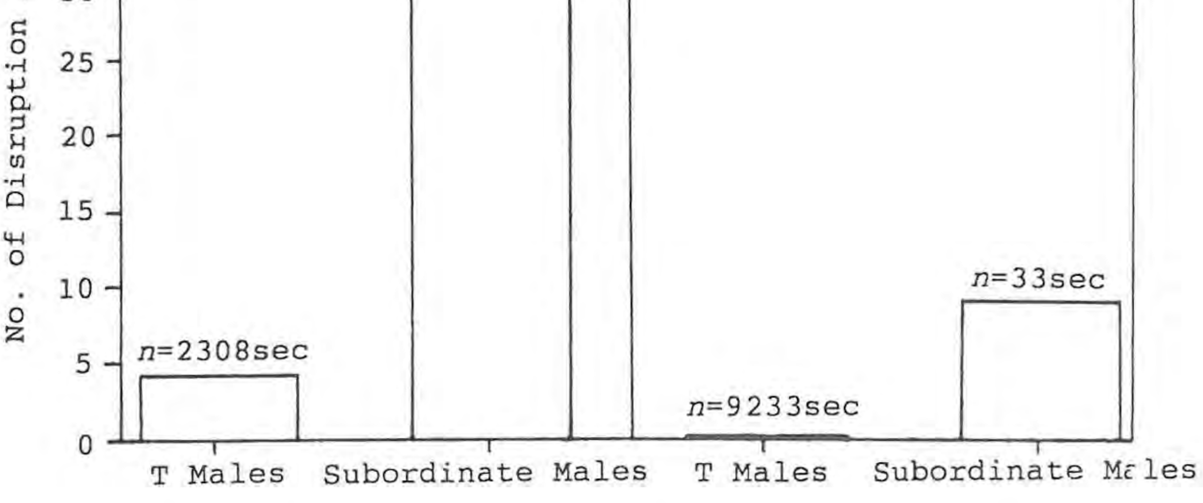


Fig. 17. An estimate of the disruption rate of T males and subordinate males in the laboratory lek. Rate was calculated by number of disruptions/total duration of side-shake or nest courtship.

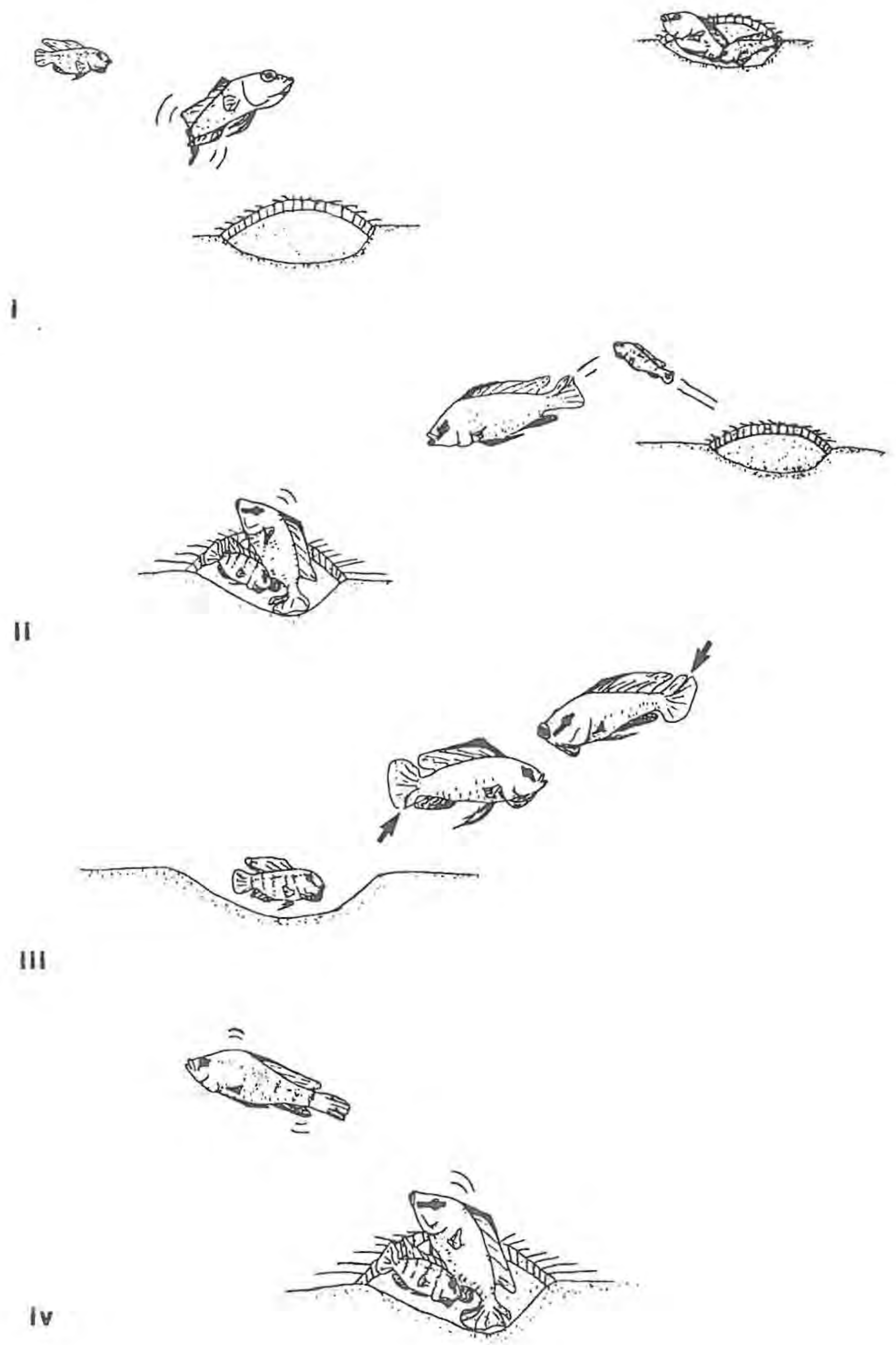


Fig. 18. A schematic description of disruption by a T male on an opportunistically courting semi-T male. Male with a cut at upper part of the caudal fin (indicated by an arrow) is a T male. The semi-T male has a cut on the lower part of the caudal fin. (i) The semi-T male opportunistically courting a spawning female while the nearby T male (upper right corner) is courting another female. The coloration of the semi-T male gradually becomes brighter during the course of courtship. (ii) After the spawning of the T male is completed, it detects the courtship of the semi-T male and moves towards the semi-T male in a highly aggressive manner. (iii) The semi-T male responds by producing a threat display and the intruder further exaggerates his nuptial coloration and threat posture. (iv) After some agnostic interaction, the semi-T male flees from the aggression of the intruder and becomes pale in colour. The T male takes over the courtship and mates with the female.

stealing by female intruders is possible during the few seconds ($\overline{X}\pm SD=9.2\pm 6.5$sec, $n=94$, range 1-34sec) during which the eggs are exposed. The frequency of egg-stealing is significantly higher than that of successful sneaking (see Fig. 10, Test of differences between two proportions $z=3.55$, $P<0.001$). A total of 322 instances of female intrusion, including attempted intrusions, were observed. Female intruders were not of any particular size, and could be foraging, gravid, or even mouthbrooding females. They might intruded alone (75% $n=222$) or in groups (25%; max. 11 females together). In 12% (27 of 233) of successful intrusions the female intruder(s) participated in spawning. Spawning with one or several females in this manner is referred to as a spawning bout.

The female nest intrusion behaviour is illustrated in Figures 20 and 21. Female intruders approached the mating pair either at a constant speed, or by punctuating their approach with pauses. They also reached the nest by following a female which was responding to the lead swim of males or by joining other intruders, but very seldom did they use shelters (Fig. 20-b). Upon arrived at the nest, female intruders immediately performed the head-down, nose-pushing behaviour and stole any freshly-laid eggs that were present (Pl. 7). Except for mouthbrooding intruders, egg-stealing females usually immediately ate the stolen eggs, but occasionally they kept them for a while before swallowing them, especially those who were involved in spawning bouts. In spawning bouts, the female intruder would also try to replace the nest female so as to mate with the male (Fig. 20-d). Similar to male sneaking, the mating male usually left and guarded outside the nest for a few seconds immediately after an intrusion occurred, then returned to the nest, squeezing in-between the females and courting both of them. Generally (88%, $n=76$) the nest female tried to ram the female intruder (Fig. 20-f), but in 12% of intrusions she immediately left the nest. Leaving the nest was mostly likely in the early and late stages of nest activity, namely before eggs were laid and after most batches of eggs had been laid (Fig. 20-e). Reacting to the aggression of the nest female, the female intruder might leave

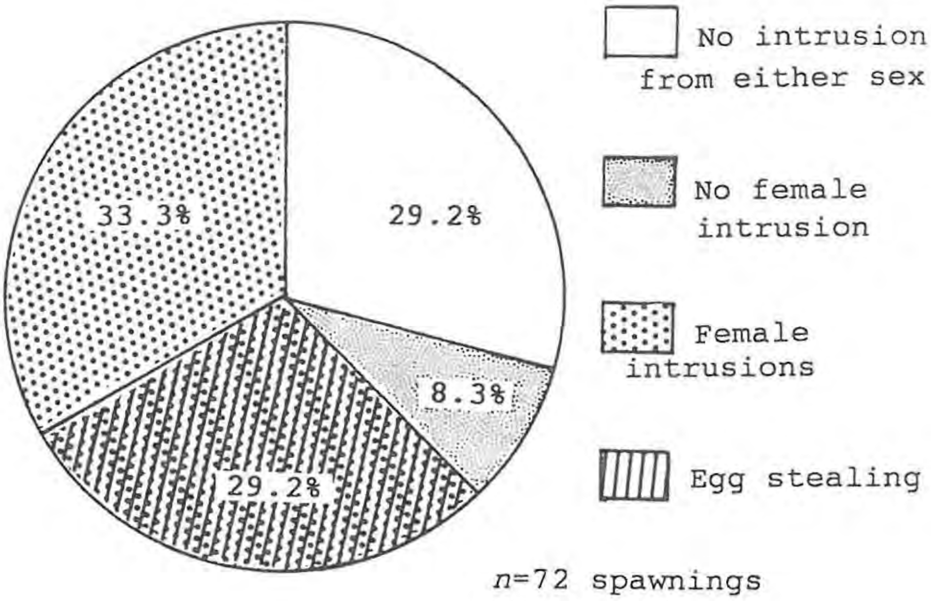


Fig. 19. The frequency of successful spawning intrusions and egg stealing by females in the laboratory lek.

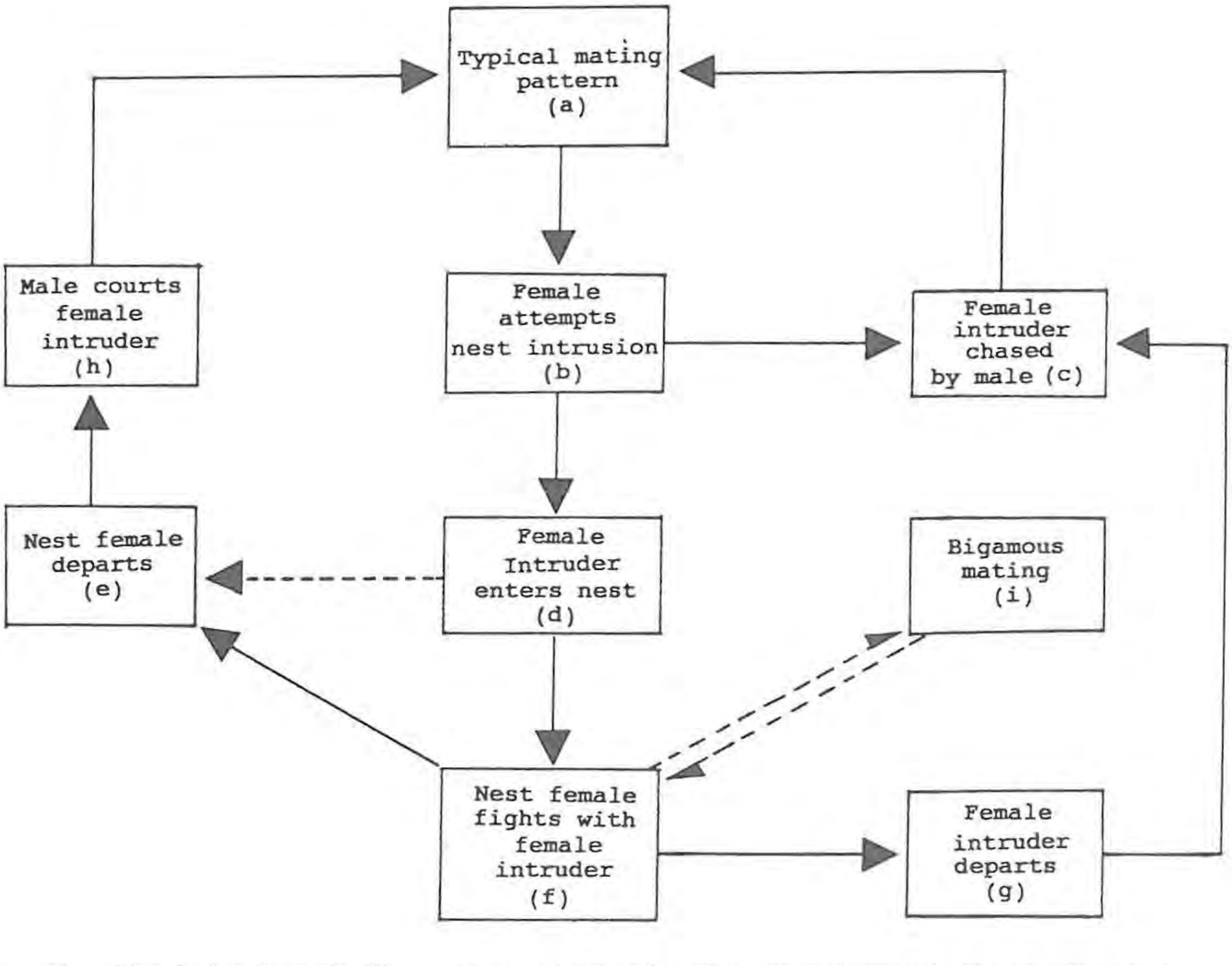


Fig. 20. The behavioural flow chart of the female intruder and the mating pair during spawning intrusion by females. Solid arrows indicate the most common sequences. See text for details.

the nest (Fig. 20-g), or butt the belly of the nest female. During the fight between females (max. 3min) the male waited at the periphery of the nest. The male would immediately chase the female which was out of the nest, regardless of whether that female was the partner or the intruder. If the spawning female had left before the female intruder (64%, 34 of 53), the mating male would continue courting the female intruder (Fig. 20-h). Even if the female intruder was not in a spawning bout, it might still stay in the nest for up to 2min, and in 12% (4 of 34) of the instances she did perform courtship with the male before leaving. In 18% (14 of 76) of intrusions, the spawning female changed from being aggressive, to performing courtship with the female intruder, after the intruder had butted its belly (Fig. 20-i). The mating male then joined the two females and bigamous mating took place (Pl. 8). Bigamous mating could last for more than 3min, but on only two occasions did one of the females lay eggs.

In 10 intrusions (4%, *n*=233), a total of 12 mouthbrooding females were involved and in 5 of these the mouthbrooding females were observed to steal and adopt the eggs. However, in 8 of these 10 intrusions the mouthbrooding intruders were actually in spawning bouts, which included all those 5 egg-stealing mouthbrooding females. Nevertheless, mixed broods consisting of undeveloped eggs and yolk-sac fry, were found in two mouthbrooding females.

Some female persistently followed spawning females and tried to intrude upon their spawnings, but they themselves had not spawned on that particular day. They were not necessarily gravid, but one of these intruders was found to keep the stolen eggs for a while before swallowing them. These female intruders visited males when spawning females were active, but would cease visiting soon after spawning females became inactive.

Effect of Spawning Interferences:

40% (*n*=72) of the spawnings observed in the laboratory lek involved the spawning female performing nest-shake with more than one male (max. with 3 males), while 55% of them (22% of all spawnings) actually spawned with more than one male (max. with 3

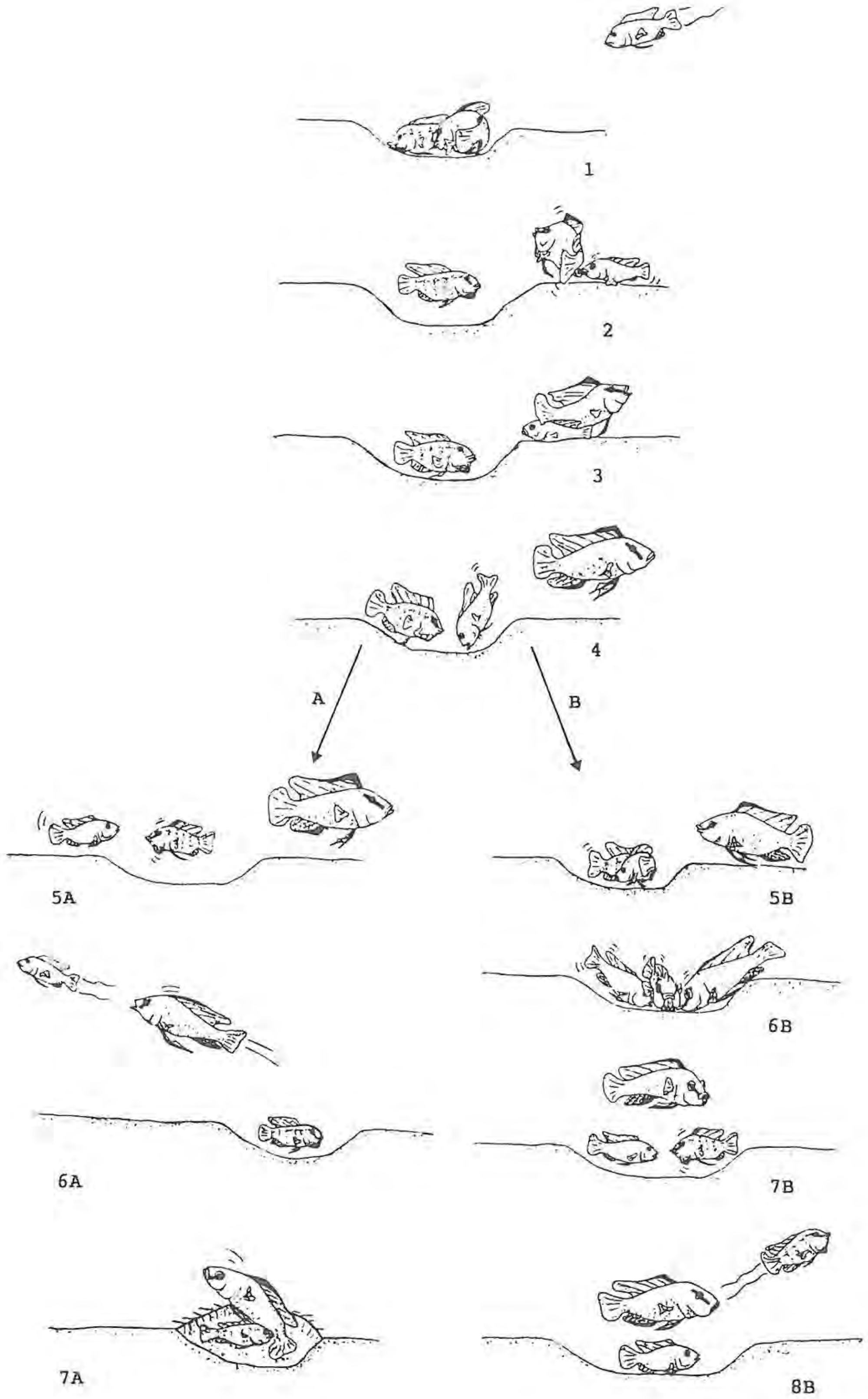
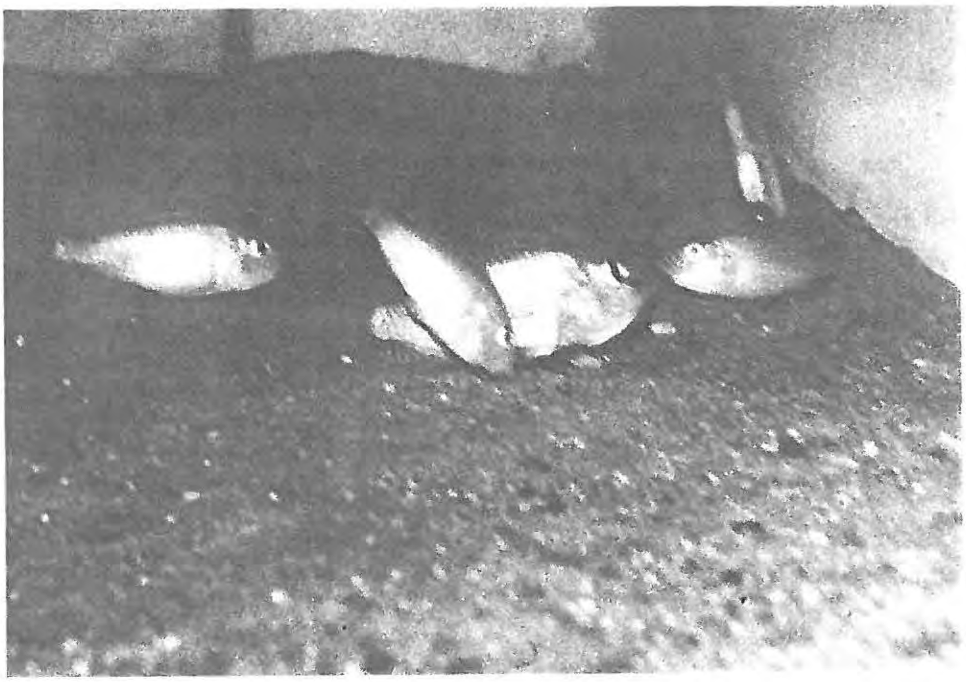
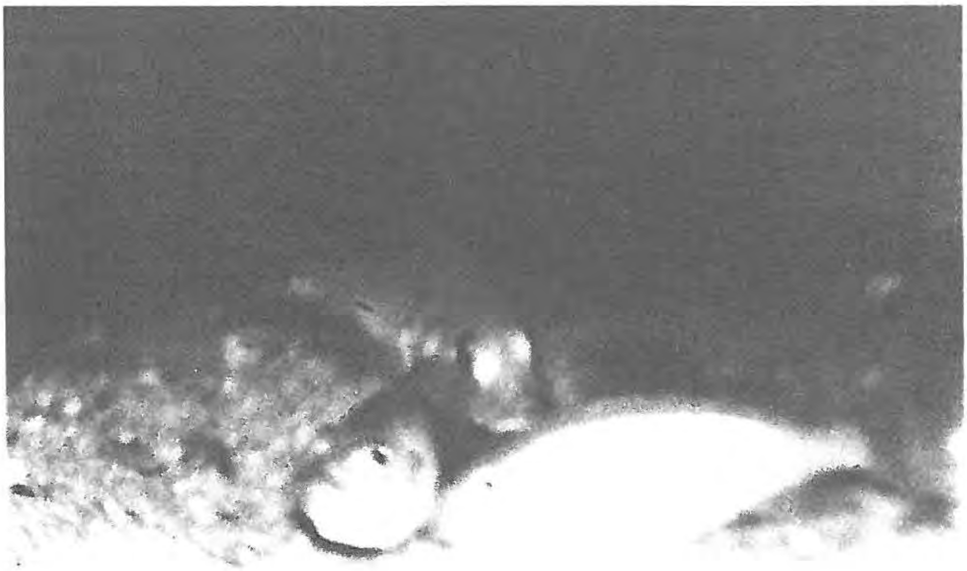


Fig. 21. A schematic description of female intrusion behaviour in *P. philander*. A is the common sequence. 1) A female intruder approaches the mating pair. 2) The mating male is only able to detect the intruder when she is already too close to the nest, and he then tail-beats her at the fringe of the nest. 3) The intruder butts the belly of the male and squeezes past him. 4) The female intruder immediately performs the head-down, nose-pushing behaviour when reaching the nest, while the spawning female shows aggression towards her. 5A) The spawning female tries to ram the intruder, while the male guards outside the nest. 6A) When the intruder gets pushed outside the nest by the spawning female, it is immediately chased by the male. 7A) After chasing away the intruder, the male mates with the spawning female again. 5B) The spawning female accepts and courts with the female intruder after the intruder butts her belly. 6B) The male returns to the nest and joins the courtship. 7B) After some courtship the spawning female stops mating and shows aggression towards the intruder again. 8B) The spawning female leaves the nest while the male and the female intruder remain there.



Pl. 7. Egg-stealing by two female intruders. The spawning female is pushed outside the nest in the far right. The first egg-stealing female is performing the head-down, nose-pushing behaviour to pick up eggs and is being tail-beaten by the mating male (largest and most colourful fish). The second egg-stealing female is fish arriving at the nest on the far left.



Pl. 8. Bigamous mating with two females. The female intruder (laterally positioned) is butting the nest female, with the male at the back just about to squeeze in-between them joining the mating.

males) (Fig. 22). 93% (27 of 29) of these multiple-mating by females experienced interferences ($X^2=21.6$, $P<0.01$).

Discussion:

In order to understand the evolution of courtship interference, it is necessary to distinguish between selfish and truly spiteful behaviour, as well as those that are just incidental (Arnold 1976; Foster 1983; Arak 1984). All of these behaviours cause harm to a rival. A selfish behaviour directly benefits the performer. In a spiteful behaviour the performer is also not benefited, and unavoidable harm is merely an unfortunate consequence of an incidental behaviour. Although theoretically a spiteful act can increase the "absolute" fitness (*sensu* Hamilton 1970) of the performer by causing a loss of absolute fitness in others. However, mathematical models indicated that truly spiteful behaviour is very unlikely to evolve (see Hamilton 1970; Rothstein 1979; Knowlton & Parker 1979), principally because the maintenance of such behaviour by selection will depend only upon the relative fitness of the disrupter versus its non-disrupting counterparts. This is well illustrated by the extremely low spawning disruptions between *P. philander* T males (Fig. 17). After a disruption, the female does not necessarily return with the disrupter to its territory and the chances of her going to a particular T male were nearly the same as for all the T males in the laboratory lek. If the female has started egg-laying, disruption even is not worth it since she is more likely to return the previous territory (see Chapter 5). Although the victim loses a spawning opportunity, the chance of the interrupter obtaining the spawning is not enhanced but energy is spent and risks are increased in the act of disruption. Therefore, it is not cost-effective to be a disrupter, but rather to be an observer which just waits for the chance to come.

The aggressive disruption of subordinate males, by T males, is actually a reassertion of rank (Foster 1983), and through this the exercise of "free choice" by females on all the males in the lek is also restricted (Diamond 1981; Arak 1984). It can also be perceived as a selfish behaviour. By disrupting the courtship

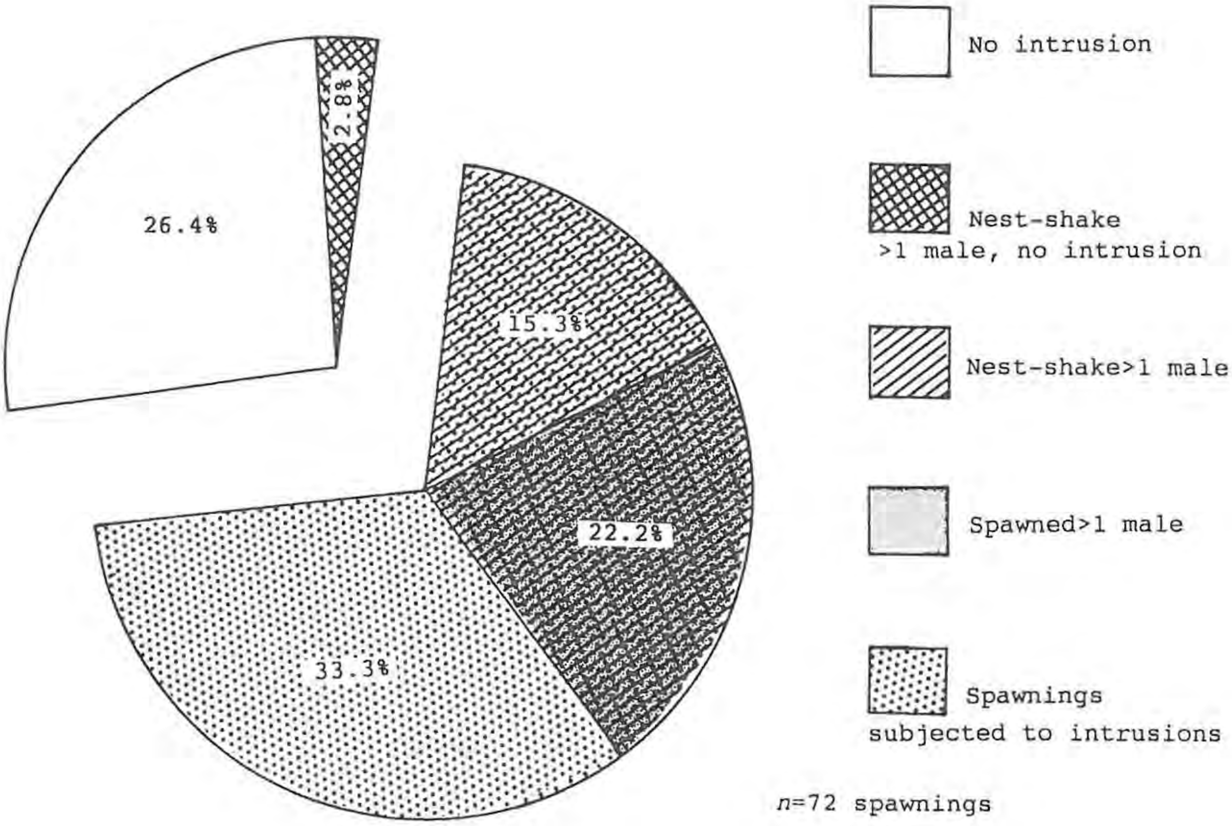


Fig. 22. The frequency of multiple-mating by females and its relation with spawning interference in the laboratory lek. Multiple-mating by females includes spawning females performing nest-shake with other males.

of subordinate males, T males can ensure that spawning will only be disturbed among the relatively small number of T males in the lek.

Although much lower than that of subordinate males, side-shake disruption is still rather high for T males. Since almost all of the side-shake disruptions between T males occurred at territorial boundaries, this form of disruption may well be a causal territory defense response due to the high level of aggression among T males at leks (see Foster 1983). In the laboratory lek, *P. philander* T males were intolerant of any other males, courting or fighting in and near their territories and would quickly disrupt them. Many fights between neighboring T males were triggered when a T male was courting females near a common boundary. In addition, it was observed that a T male left a female in his nest and joined the fight between two other T males when they shifted into his territory. Therefore, such disruptive behaviour is neither a selfish nor a spiteful behaviour, but rather an unavoidable consequence of the selection for high aggressiveness of males in leks (see Foster 1983).

The behaviour pattern of egg-stealing females is essentially the same as that of sneakers, and both are selfish, with the former mainly feeding on freshly-laid eggs while the latter fertilizes eggs. Apparently, it is disadvantageous for subordinate males to join a lek with the highly aggressive T males since they are unable to attract females. However, the scrounging behaviour of subordinate males and non-receptive females may partly explain their gathering in leks (Arak 1983, 1984). Although it is disadvantageous for both males and females to have their spawning interfered (see Foster 1983), the evolution of counter-adaptations, or sexual defense (*sensu* Arnold 1976; Halliday 1978; Arak 1984), will also be costly to the mating pair in terms of time and energy (see Barnard 1984). Further discrimination will stop evolving if the cost of making a mistake is balanced by the benefit obtained from preventing or distinguishing deceptors.

Egg predation by conspecifics is well documented (eg. Semler 1971; Keenleyside 1972; Downhower *et al.* 1983; Kodric-Brown 1983;

DeMartini 1987; Ward & FitzGerald 1987) and includes mouthbrooding cichlids (eg. McKaye 1983, 1984; Mrowka 1987b). In a closely related species *Pseudocrenilabrus multicolour*, Mrowka (1987b) argued that egg-stealing females, including mouthbrooding intruders, are "mimicking" males to stimulate spawning females to lay eggs. However, most of the successful egg-stealing in *P. philander* is by raiding the nest immediately after the spawning female had laid a batch of eggs (94%, 29 of 31). Although female intruders which were in spawning bouts behaved in exactly the same way as other female intruders, it would be very misleading to interpret these females as mimicking males since they also subsequently spawned. The apparent mutual courtship of spawning-bout females is interpreted as misdirected behaviour by both. This is due to the similarity of courtship activities of both sexes: the females respond to their motivations and release behaviour in one another as their activities resemble those of males.

Mrowka (1987b) considered that those mouthbrooding females *P. multicolour* which intruded upon spawning pairs and became involved in courtship were "sophisticated male-mimic" to steal eggs. It was postulated that such mimicry enabled these mouthbrooding intruders to induce the nest females to lay eggs so that they could steal the eggs. The observations of *P. philander* suggest, however, that mimicry is unlikely and that a continuation of previous courtship is more probable. This behaviour is rare (10 mouthbrooding female intrusions in 233 female intrusions; 4%) and all the five cases of mouthbrooding females stealing eggs occurred while they had been spawning elsewhere a short time previously. It seems that these mouthbrooding females responded to spawning activity and in so doing picked up eggs that were laid by the nest female, not as a specific adaptation (see Mrowka 1987b) but merely as a misdirected response because they were still involved in spawning. Furthermore, after spawning, mouthbrooding females in the field would move to brooding refuges distant from leks to mouthbrooding young (Ribbink 1975). But in the laboratory lek, mouthbrooding females were still confined in the tank and in close contact with courting males, and hence those misdirected behaviours would be more likely to be exaggerated. In small aquaria (30cm X 30cm X 30cm), the occurrence of mouthbrooding females, which spawned some days before, interfering spawning and stealing eggs is more frequent (per. obser.). Therefore, the spawning intrusion and egg-stealing of mouthbrooding females, as well as those females in spawning bouts, are probably misdirected incidental acts for reasons of high internal motivation for spawning (see Mrowka 1987a), rather than a selfish behaviour, although their behaviour are the same as that of other egg-stealing females.

Neither T males nor sneakers, have been observed to steal freshly-laid eggs. However, in two instances a spawning T male ate a few eggs which were washed outside the nest due to the shaking activity of the mating pair. The spawning female failed to notice these eggs for about half minute and only then did the mating male eat them. Normally, the mating males did not cannibalize their own eggs as reported in other lek-breeding cichlids (eg. McKaye 1983, 1984) and other fish species (eg. Kodric-Brown 1977, 1983; DeMartini 1987).

The frequency of female intrusion and egg-stealing is significantly higher than that of male intrusion and sneaking (Figs. 10, 19). This indicates that females have readier access to the nest and hence to freshly-laid eggs, than do sneakers. However, the standardized chasing ratio shows that T males direct less aggression towards individual females than towards individual males. This may suggest that T males are relatively more "tolerant" of female intruders than male intruders. Although the reproductive success of a male will be decreased by the occurrence of egg-stealing as well as by sneaking, generally there are more drawbacks for T males to actively chase females than to actively chase males (see Dominey 1981; Gross 1982; Foster 1983).

The difference in bigamous mating further supports the suggestion that T males are relatively more "tolerant" of the presence of another female than a male in the nest. Bigamous mating involving two females (female bigamy), occurs about 4 times more often than that involving male bigamy (18% versus 4%, Test of differences between two proportions $z=3.5$, $P<0.001$). For T males, female bigamy can increase reproductive output, since several females may become receptive at the same time. As it is advantageous not to lose receptive females, T males will be selectively favoured by being less discriminate against other females in the nest, even though some eggs may be lost due to egg-stealing by non-receptive females. It has been observed that males left a spawning female in the nest to invite other females to their nests. Furthermore, there is also the possibility that the male can attract more females by the increased mating activity in the nest (the net-benefit hypothesis, see Dominey 1981 and "female copying" in Bradbury & Gibson 1983). For sneaking or male bigamy, however, there are only disadvantages for T males. Even though it has been suggested that the occurrence of sneaking may also enhance the attractiveness of the T males to females (see Dominey 1981), the net-benefit from male bigamy would always be much less than that from female bigamy in the T male's view.

Although there are no apparent advantages, but only disadvantages, for spawning females in both male and female bigamy, spawning females also appear to be rather indiscriminate. They always readily performed courtship with sneakers, and female intruders, even or when another female was tail-beating them in the first few seconds (see Chapter 5). For this reason, the behaviour of T males becomes more important than that of spawning females in determining the mating pair's "tolerance" towards the presence of other fish in the nest, and hence the apparent greater "tolerance" of the mating pair towards female intruders than to male intruders.

The significant relationship between multiple-mating by females and spawning interference indicates that interference can cause spawning females to move to other males where they resume courtship (Fig. 22). Multiple-mating by females including spawning female performed nest-shakes with more than one males because during which they would also collect sperm from other males. The implication from this is that if females were to make a choice among T males, spawning interference from other fishes could sufficiently modify, or curtailed, their choice. Similar findings have been made for other animals (Borgia 1981; Diamond 1981; Trail 1983; Arak 1984, but see Bradbury & Gibson 1983). Although almost all of the multiple-mating by females was as a result of interference, 43% of the disturbed spawnings were not accompanied with multiple-mating (Fig. 22). This suggests that females prefer not to be involved in multiple-mating, and such preference can sometimes override the effect of interference. This contradicts the argument that multiple-mating by females is an adaptation (Arak 1984). If males of the species are extremely promiscuous, as in lek species, they are likely to deplete sperm quality and quantity (Nakatsuru & Kramer 1982; Arak 1984). The frequent occurrence of spawning bouts and bigamous mating further negates the suggestion of Nakatsuru & Kramer (1982) that in promiscuous fish species females should prefer males that have not spawned recently. As *P. philander* is a mouthbrooder and females only lay relatively few large eggs (Fryer & Iles 1972; McKaye 1984), they probably require less sperm for successful fertilization of all her eggs. It is argued that promiscuity of one sex will be genetically correlated with promiscuity of the other sex (see Halliday & Arnold 1987), but this is also not necessarily the case with *P. philander*.

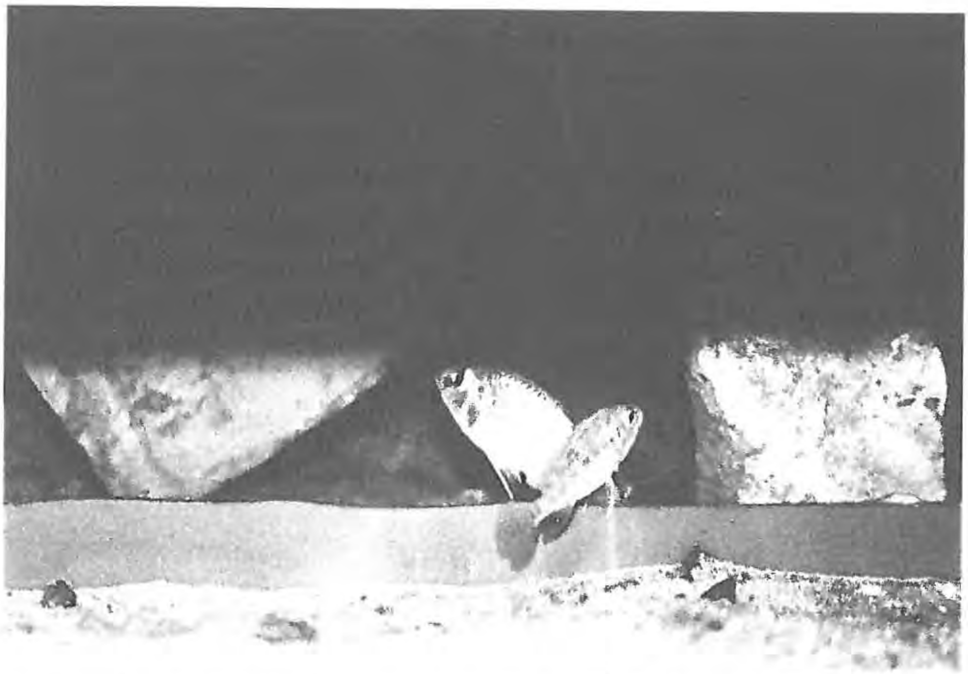
CHAPTER 5

FEMALE CHOICE

Introduction:

Female choice of mates is generally considered to be the principal mechanism of sexual selection, and therefore, the demonstration of this is popular (eg. Bateson 1983). The term "mate choice" does not necessarily imply that a female makes a conscious or rational choice between males, but simply describes any female behaviour which results in a female mating with some males but not others (*sensu* Halliday 1978; O'Donald 1983; Partridge *et al.* 1987; Ward & FitzGerald 1987). Although the immediate effect of female choice is the same, whether females have prior preference for certain males, or not, many authors point out that it is very important to distinguish between "active choice" and "passive choice" (eg. Lloyd 1979; Borgia 1981; Lambert *et al.* 1982; O'Donald 1983; Parker 1983; Halliday 1983; Partridge 1983; Arak 1983, 1984), as the two mechanisms of female choice can lead to very different evolutionary consequences (see Parker 1983; O'Donald 1983; Partridge 1983). Observing patterns of non-random mating alone is not sufficient to demonstrate female choice indirectly, mainly because the effect of male-male competition is usually not eliminated (Kingett *et al.* 1981; Lambert *et al.* 1982; Halliday 1983; Arak 1983; Partridge 1983; Parker 1983; Partridge *et al.* 1987; Sullivan 1987). Furthermore, there is relatively little direct documentation on female choice of particular male phenotypes in all animal taxa (Halliday 1983; Partridge 1983; Partridge *et al.* 1987), and in fish the data are largely on species in which females can benefit directly from choosing a male (eg. Semler 1971; Haas 1975; Nakatsuru & Kramer 1982; Noonan 1983; Endler 1983; Keenleyside *et al.* 1985; Ward & FitzGerald 1987; Schwanck 1987, but see Houde 1987).

In order to demonstrate positively, and to study the female choice in *P. philander*, choice-chambers were used to control the effect of male-male competition in this fighting fish (Pl. 9).



Pl. 9. A female visiting a choice-chamber and being courted by the male.

TABLE 3. The Kolmogorov-Smirnov one sample *D* test on the spawning scores at each of the 4 ranks (4 for 4 chambers) of the males' characteristics. Data exclude heterospecific-choice control. The only variable with significant effect on the spawning scores in different ranks is "Courtship Display" in the single-female treatment.

	Size	Colour	Appetitive Behaviour	Courtship Display	Activity
Single-Female Treatment:					
Rank#			Spawning Scores		
1:	3	3	3	6	4
2:	1	2	3	1	2
3:	2	1	1	0	1
4:	1	1	0	0	0
$D(n=7)$	0.18	0.21	0.36	0.61**	0.36
Multiple-Female Treatment:					
Rank#			Spawning Scores		
1:	1.7	3.8	2.8	4.8	2.8
2:	5.5	4.7	2	2.5	3
3:	2.8	0.8	3.5	2.7	2.5
4:	0	0.7	1.7	0	1.7
$D(n=10)$	0.25	0.35	0.08	0.25	0.08

#Data from each variable ranked within each trial (1: highest, 4: lowest).
** $P<0.01$.

Although choice-chambers have been used to study female choice in many fish species (eg. Semler 1971; Haas 1975; Noonan 1983; Nakatsuru & Kramer 1982; Schwanck 1987), very few used multiple chambers (eg. Keenleyside *et al.* 1985; Ward & FitzGerald 1987). In some of them, the female choice was judged by the relative time she spent near the chambers, but without actual occurrence of spawning (eg. Haas 1975; Nakatsuru & Kramer 1982; Ward & FitzGerald 1987). Therefore, the demonstration of female choice in these experiments is somewhat incomplete. For a more comprehensive study, four choice chambers were used simultaneously, and only when egg-laying occurred, was it regarded as choice of male by the female. Moreover, in order to further elucidate the effect of spawning interference on female choice, the choice-chamber experiment was divided into a single-female treatment (only one female in the lek tank and hence no interference) and a multiple-female treatment (about 25 females in the lek tank, resulting in many interactions between females).

Results:

There was no significant difference in the spawning scores at the four different chambers ($X^2=0.62$, $P>0.8$). In the heterospecific-choice control (see Chapter 2), females in both treatments only laid eggs at the chamber containing a conspecific male ($n=4$ trials). However, spawning females in the multiple-female treatment performed some courtship behaviour at other chambers containing males of different species (max. at 3 chambers). Nevertheless, no female spawned, nor performed any courtship behaviour, at the empty chamber ($n=2$ trials).

The result of the Kolmogorov-Smirnov one sample test on the spawning scores of the different ranks of the monitored male characteristics, is given in Table 3. In the multiple-female treatment, no particular male characteristics were associated with females spawning significantly at some ranks. In the single-spawning treatment, there were significant differences in females spawning with males ranked according to "Courtship Display", and most of the spawnings were at the highest ranked male (6 of 7). However, females did spawn with the same male in only 25% of the repeat-choice tests (*n*=4, with one repeated twice) in the single-female treatment. Females in the multiple-female treatment might spawn at different chambers because of interruptions by other females, and not always a particular male had the major share of the spawning(s) in the repeat-choice tests (*n*=4).

Although there was a positive correlation between "Female Proximity" and "Male Courtship Display" (r=0.7 on untransformed data, n=566, $P<0.001$), Figure 23 shows that considerable variations exist in male responses. An ANOVA on the courting rates (Male Courtship Display/Female Proximity) of different individual males indicates that there was a significant difference between them ($F_{10,77}$=3.13, $P<0.01$) (Fig. 24).

The preliminary visiting, pre-spawning nest-courtship and spawning periods of females in the three different experiments were compared and shown in Figure 25. There were significant differences in the duration of pre-spawning nest-courtship and spawning periods ($F_{2,56}$=20,$P<0.001$); $F_{2,75}$=9.2, $P<0.001$ respectively); with those in the laboratory lek the shortest and those in the multiple-female treatment the longest. However, a *posterior* Scheffe method revealed that the difference in the duration of spawning, between the multiple- and single-female treatments, was actually not significant. The duration of preliminary visits were not significantly different between the three experiments ($F_{2,54}$=0.63, $P>0.5$).

The different spawning situations in the two choice-chamber treatments is shown in Table 4. In the multiple-female treatment, all the spawnings were frequently interrupted by other females, with an estimated rate of 69 interruptions per 5min of female courtship behaviour (*n*=555sec), which is about 23 times higher than that in the laboratory lek (Fig. 26). This resulted in 63% (5 of 8) of the spawnings involving egg-stealing. Due to frequent interruptions, spawning females were often forced to visit different chambers during a single spawning. However, since the males were isolated from the females, the interrupting females just followed the spawning female, and continually interrupted the spawning female whenever it performed courtship

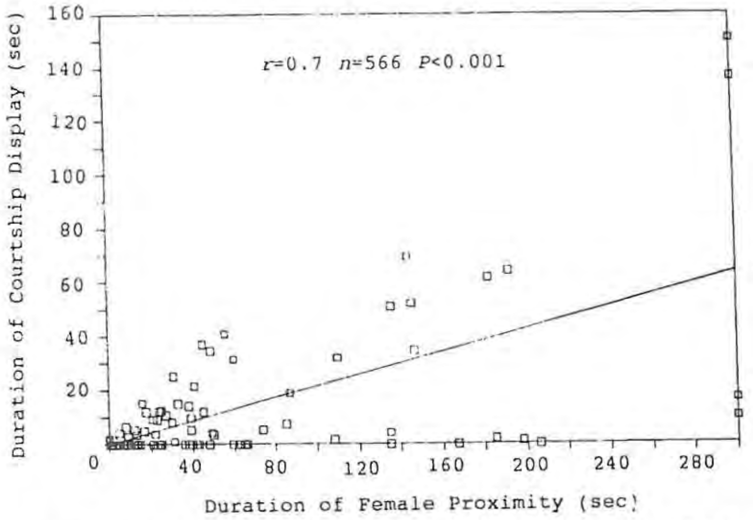


Fig. 23. Relationship between female proximity and male courtship display on untransformed data obtained from 566 5-min observations in the choice-chamber experiment. The linear regression line is highly significant. Showing a positive correlation between female proximity and male courtship display.

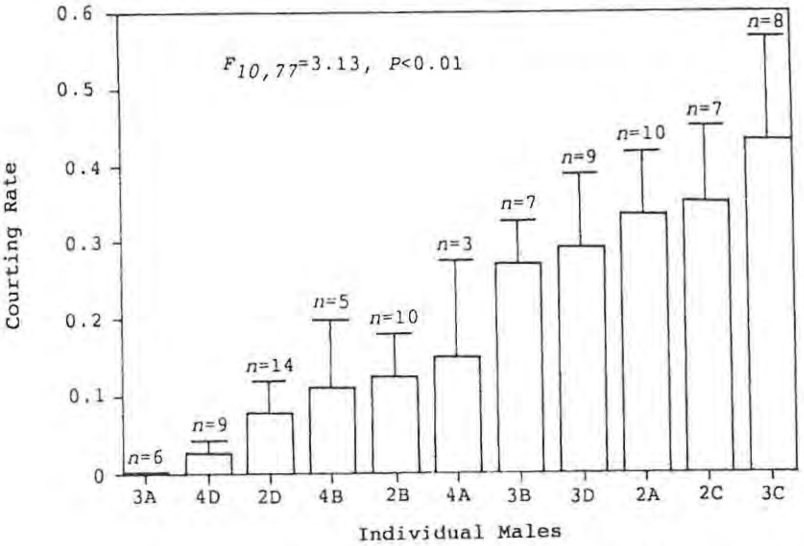


Fig. 24. The courting rate (male courtship display/female proximity) of 11 individual males tested in the choice-chamber experiment. Bars represent standard error. n given on top of the bars is the number of 5-min observations which involved such a relationship. There is a significant difference in their courting rates.

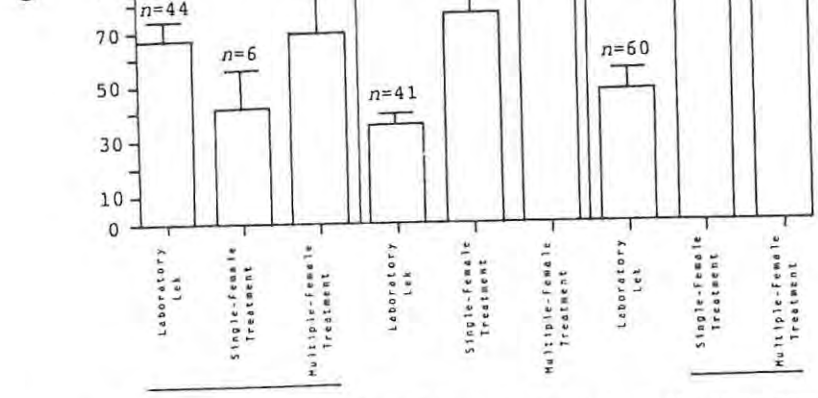


Fig. 25. The duration of different courtship periods in the three experiments. Bars represent standard error. The line underneath indicates no significant difference between the experiments as revealed by the 95% Scheffe method.

behaviour. For this reason, in 75% (9 of 12) of the spawnings, the spawning female performed courtship at more than one chamber (max. with 3 chambers) and in 50% (4 of 8), laid eggs at two different chambers. Interestingly, in four spawnings (33% of all spawnings), the spawning female made a nest (actually a small sand pit) hidden behind a choice chamber, and swam back and forth to visit and court with the male at the glass front of the chamber (not necessarily the one next to her hidden nest), but laid her eggs in the hidden nest. Two more females were recorded making such hidden nests, but they did not lay eggs successfully later.

In the single-female treatment, no spawnings occurred where the female laid eggs at more than one chamber, nor were any hidden nests recorded (*n*=9). Nevertheless, 71% (5 of 7) of the spawning females left the nest for a while to hide, later returning to the same chamber to continue courtship behaviour. On only one occasion (11%, *n*=9) did the spawning female perform courtship at another chamber, but this was at the late stage of the spawning (191min after the last batch of eggs had been laid). It hid first, and then came out to court at a different chamber. After spawning was complete, mouthbrooding females usually remained at the glass side of a choice chamber, until they were eventually disturbed by the observer, often which they went into hiding.

Discussion:

The choice-chamber experiment shows that females do not choose males of particular colour or size. The repeat-choice test further indicates that females do not choose any other physical features of the males which have not been monitored, nor do they show preference for certain males over others. 25% chose the same male, corresponding with the probability of a 1/4 chance of spawning at the same chamber again, as there were only 4 chambers present. Of all the variables monitored, only courtship display shows a significant effect on spawning scores. Although courting is largely induced by the presence of a receptive female, the ANOVA indicates that there are significant

TABLE 4. Different spawning situations, with different numbers of females, in the choice-chamber experiments. Illustrating the effect of interruptions on spawning is highly significant. Data include heterospecific-choice control.

	Multiple-Female Treatment	Single-Female Treatment	Test Statistic z#
Rate of interruptions	69/5min courtship	Nil	Nil
Egg Stealing	63%	Nil	Nil
Spawning female performed courtship at more than one chamber	75%	11%	4.7***
Spawning female laid eggs at more than one chamber	50%	0%	2.83**
Spawning female laid eggs at hidden nest	33%	0%	1.99*

#Test of Difference between Two Proportions.
*$P<0.05$ **$P<0.01$ ***$P<0.001$.

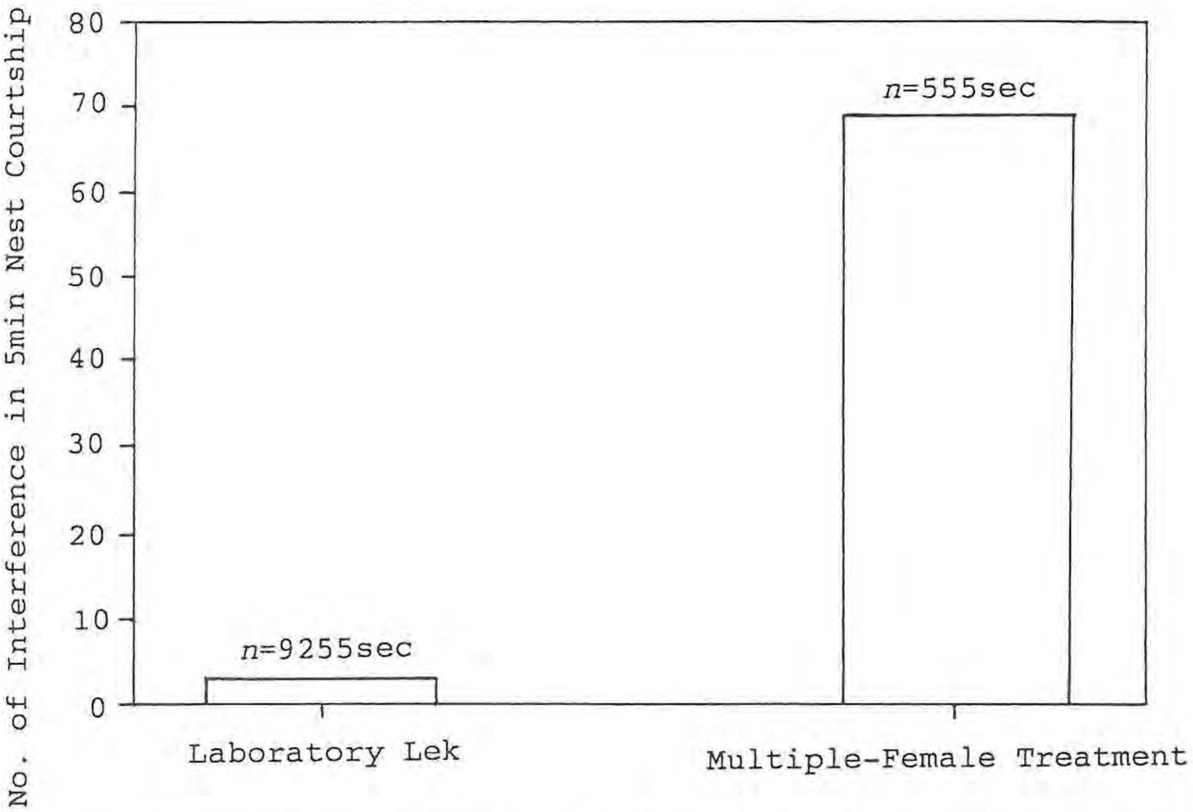


Fig. 26. A comparison between the female interference rate in the laboratory lek and the multiple-female treatment. *n* above bars is the total duration of observed nest courtship. Interference in the multiple-female treatment is 23 times greater than that in the laboratory lek.

differences in the extent of such responses between individual males. From Figure 24, it is obvious that males on the right of the figure show more persistence to court when there is a female nearby, while other males on the far left of the figure are indifferent; therefore this is partly a purely male effect. The result of the repeat-choice test also shows that an individual male's behaviour was not consistent; sometimes it courted more and sometimes less often. This could be due to the change in condition of the males under different environments in replicate trials. In mottled triplefin (Thompson 1986), there is no significant relationship between courting frequency and male mating success, similar to some lekking birds (Lill 1974a; Wiley 1978; Bradbury & Gibson 1983). Furthermore, male guppies (Farr 1980) and *Cichlasoma nigrofasciatum* (Keenleyside *et al.* 1985) also show significant differences in their courtship display rate. Therefore, it can be concluded that in *P. philander*, different persistence in courting amongst males can significantly affect the spawning scores; alternatively, females appear to prefer males which court more frequently.

However, females choosing males merely by responding more readily to those that perform more courtship display, is considered as passive choice (Parker 1983; Partridge 1983; Houde 1987, but see Farr 1980) and without prior preference (O'Donald 1983); although such an outcome still satisfies the criteria for female choice (see Introduction of this Chapter). In active choice, females should respond differently to the physical features of males, rejecting certain males in favour of others (Parker 1983, O'Donald 1983). The results of character-choice and repeat-choice tests strongly suggest that there is no active choice by *P. philander* females. This is different from other direct female choice studies in fish, where females actively choose more conspicuously coloured males (Semler 1971; Haas 1976; Endler 1983; Houde 1987), or larger males (Downhower & Browns 1980; Noonan 1983; Keenleyside *et al.* 1985; Schwanck 1987). The results obtained here are similar to those of the threespine stickleback, studied by Ward and FitzGerald (1987). They demonstrated that females do not actively choose less aggressive males, but that these males obtain more mates merely because the highly aggressive males court less by always prematurely terminating courtship.

Nevertheless, females may use courting frequency as an assessment cue to "choose" males. In monogamous species, persistence in courting may indicate a male's acceptance of females and commitment to parental care, and this becomes a cue for female choice (Schwanck 1987). The duration of courtship display in guppies (Farr 1980) and in damselfish (Schmale 1981; Thresher & Moyer 1983) is also thought to signal overall vigor or dominance and is chosen by females.

Although *P. philander* females do not actively choose between conspecific males, they show a definite choice of their own species in the heterospecific choice test. This is to be expected in terms of the Specific-Mate Recognition System (Paterson 1978, 1980, 1981). However, the small amount of courtship behaviour performed by spawning females at chambers containing different species in the multiple-female treatments, indicates that interruptions can substantially alter female choice. The effect of interruptions on female choice is further illustrated by the loss of effect of courtship display in determining male mating success in the multiple-female treatment (Table 3), and the complete opposite spawning situations which result between the two treatments (Table 4).

In the multiple-female treatment, females did not stop spawning even under continuous interruption and egg-stealing. This suggests that *P. philander* females do not have strict control over the spawning process after reaching a threshold of sexual stimulus from males. Nevertheless, Figure 26 reveals that normally about 96% of the interruptions would be prevented by the presence of a T male.

25% of females in the multiple-female treatment did not show multiple-mating, giving further support to the preference of females for not being involved in multiple-mating, thus overriding the effect of interruption. This persistence of females to remain at a particular chamber during spawning is demonstrated in the single-female treatment. Nevertheless, such strong persistence of females can be perceived as only an adaptation of the spawning process itself and irrelevant, or not directly related, to sexual selection, because the choice is only made after spawning has been initiated. Furthermore, it appears that such in-spawning persistence of females is not directed at particular males, but rather at particular nest sites, similar to that in other lek-breeding animals (eg. Buechner & Schloeth 1965; Lill 1974a; Wiley 1978; Trial 1985). In the laboratory lek, a spawning female might leave the nest after an interruption, but always returned directly to the same nest shortly afterwards on her own, to wait for the male if he was involved in fighting or chasing away intruders. However, the spawning female would readily court sneakers, and even female intruders, in the nest if the T male was temporarily unavailable. Furthermore, females in the multiple-female treatment readily courted interrupting females, especially when these females were tail-beating them. Even so, such in-spawning persistence for particular nest sites can also be altered, or modified, if interruptions are frequent.

The duration of pre-spawning nest-courtship and spawning in females, increased through the laboratory lek experiment, single-female treatment, to the multiple-female treatment (Fig. 25). The shorter periods in the laboratory lek experiment, compared to those in the choice-chamber treatments, may suggest that females receive additional stimuli from other physical and chemical cues, as well as from visual cues, and hence reach the spawning threshold more rapidly. As the egg size of *P. philander* is relatively large, the physical action of butting may facilitate females to lay the large eggs (Ribbink 1971, 1975). This is probably also the reason for there being no significant differences in the preliminary visiting times of females in the three treatments, as there was no physical contact involved in the process at this stage.

The significant difference in the pre-spawning nest-courtship period of females between multiple- and single-female treatments, indicates that interruption can delay the initiation of egg-laying in females. However, interruption does not appear to have a significant effect on spawning duration in females; females could be adapted to complete spawning as soon as possible. After a long pre-spawning period, involving assessment of males, a further delay in the spawning process would not help in re-assessing males. The advantages of saving time and decreasing vulnerability to predators (see Borgia 1981; Foster 1983), as well as reducing egg-stealing during the spawning process, would outweigh the gain from prolonging spawning for re-assessing males (see "cost of choice" in Parker 1983; Wittenberger 1983). Several females in the multiple-female treatment spawned at hidden nests, showing that spawning females try to avoid interruption. However, they are only able to delay the spawning process slightly, and are unable to halt the whole process entirely, if sexual stimuli is still persistent. Indeed, when the threshold for laying is reached females in captivity will lay eggs even in the absence of males (Ribbink 1971).

CHAPTER 6

DETERMINANTS OF MALE MATING SUCCESS

Introduction:

Two components of the sexual selection process, mating competition and female choice, usually operate together, and individuals strive to enhance both to increase their mating success (Halliday 1978, 1983; Wittenberger 1983). Thus, the effect of these two components is combined, so their relative contributions to variations in male mating success is difficult to distinguish (Darwin 1871; Mayr 1972; Halliday 1978, 1983; Sullivan 1987; Partridge *et al.* 1987).

This chapter intends to formulate the relationship and disentangle the relative importance between male competition and female choice in influencing male mating success of *P. philander.* This is done by means of quantitative measurement of several physical and behavioural male characters which are potentially related to male mating success. A total of 8 variables of each male were considered: duration of side-shake display; nest courtship; chasing other males; chasing females; being chased; agonistic behaviour; territory size; size of the males. Multivariate analyses were used to evaluate the relative significance of the various male characters in contributing to variation in male mating success (Lande & Arnold 1983; Arnold & Wade 1984a, b; Gibson 1987; Sullivan 1987). The multivariate technique has been applied to some other fish species for similar purposes (eg. Schmale 1981; Kodric-Brown 1983). Colour variation was tested in the choice-chamber experiment. The variation in the basic colour pattern between males is not pronounced within a population (Ribbink 1975), although the manifestation of nuptial coloration in males is strictly determined by their social environment and can be changed instantly. Furthermore, ranking of colour intensity is unsuitable for quantitative multivariate methods (Siegel 1956; Sokal & Rohlf 1969), so it is not included in this analysis (but see Kodric-Brown 1983). Separate consideration was also given to the effect of interference and the sequence of introduction of males to the laboratory lek on male mating success.

Results:

The distribution of mating success of the males in the laboratory lek, is given in Figure 27. A *posterior* Scheffe test revealed that only the cumulative mating success of the first three most successful males, was significantly different ($F_{4,45}=86.77$, $P<0.001$). Together, they monopolized 95% of all the spawnings, with the most successful male obtaining about half of these. Such trends of strongly skewed mating success, amongst males, was generally consistent (Coefficient of Variation $V<18\%$) even though there was a great variation in the number of males in the lek (3 to 18 in 10 treatments). For this reason, the typical strongly skewed mating pattern characteristic of leks, was successfully duplicated in the laboratory. However, a Chi Square test on the spawning scores, for the four equal sized regions (divided by the longitudinal and transverse midlines of the tank), revealed no significant differences in territory quality in the laboratory lek ($X^2=5.83$, $P>0.1$).

Although the interference rate differed vastly between T males and subordinate males, and the last two chapters show that interference can modify female choice, a Friedman two-way analysis (Table 5a) failed to show that the disparity in spawning scores of the three most successful males (only their mating success was significantly different from each other) was significantly related to spawning interference ($Xr^2=2$, $P>0.45$).

The Pearson sample correlation (r_{ij}) matrix of the measured variables is provided in Table 6. There were strong positive correlations between mating success and side-shake, nest courtship, female chasing and territory size. Male chasing and agonistic behaviour were moderately correlated with mating success, while male size was only weakly correlated with mating success, and being chased was not significantly correlated with mating success. Figure 28 represents the scattergrams (in untransformed data) of the different variables plotted against male mating success.

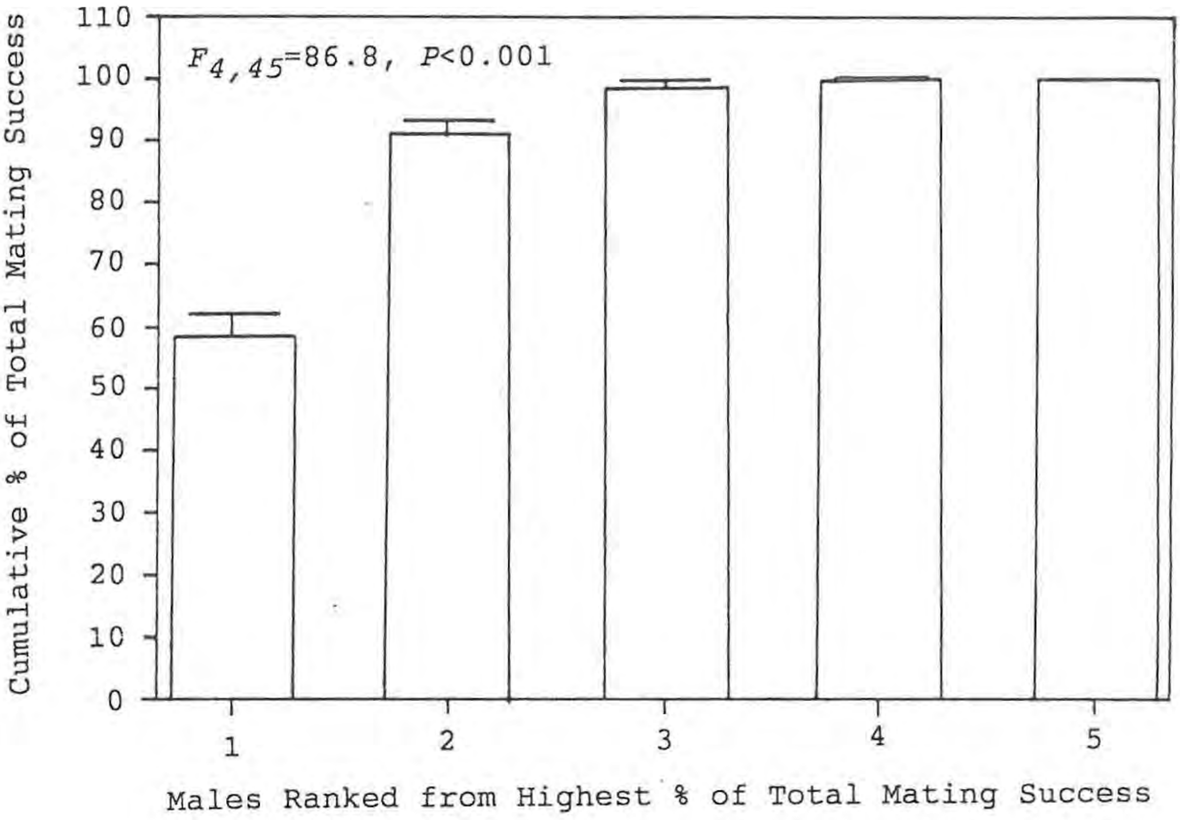


Fig. 27. The cumulative mating success of successful males in each of the 10 treatments in the laboratory lek experiment, with the number of males in the lek tank ranging from 3 to 18. Bars represent standard error. Only the cumulative mating success of the first three most successful males is significantly different, with the most successful male obtaining about half of all the spawnings.

Table 6 shows that all of the variables were strongly intercorrelated with each other, probably due to the natural association between these characters. In order to control the effect of intercorrelation between variables, partial correlation ($r_{ij...}$) analysis was employed, so that each variable's independent relationship with mating success, as well as with other variables, could be more carefully examined. Since the variable "Nest Courtship" was more an "effect" than a "cause" of a male's ability to obtain females, it was disregarded in the partial correlation analysis. For the same reason, mating success was excluded from the partial correlation matrix of the causal variables. The result of such a partial correlation analysis is provided in Table 7. This showed that only side-shake and territory size were still significantly and positively correlated with mating success. When other variables were held constant, female chasing become negatively correlated with mating success. Although weak, such a correlation was significant. Male chasing, agonistic behaviour and male size were revealed to actually have no independent effect on male mating success. Again, as in the sample correlation, being chased was not correlated with mating success.

Stepwise multiple regression analysis was used on the causal variables, so that the relative significance of their contribution to male mating success could be estimated. A method of stepwise backward elimination of variables was employed (Snedecor & Cochran 1980, Zar 1974). This involved a procedure whereby the least significant variable (the one with the lowest *F*-to-remove value) in the model would be removed first, followed by variables which became the least significant of the remaining variables. The result of a backward stepwise variable selection, is shown in Table 8. If the *F*-to-remove value was determined as being less than 4 (a criterion for withholding variables which had significant determination of male mating success), only territory size, female chasing and side-shake remained in the final model. Together, these three variables accounted for 79% of the variation in male mating success. Territory size alone, accounted for 75% of the variation, while female chasing and

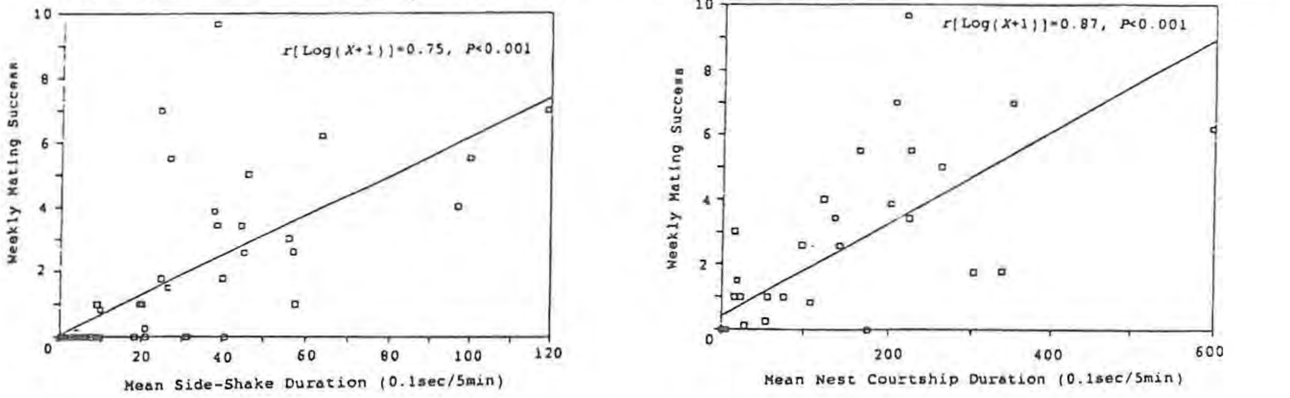
TABLE 5. Friedman two-way analysis by ranks on spawning interference rate to: a) mating success and b) territory size, for the three highest males. Interference rate was calculated from number of successful nest-courtship interferences/total nest courtship duration. Data were then ranked within each treatment (1: least, 3 most frequently interfered). Highest mating success and largest territory size were categorized as I. No significant different in spawning interference rate were found in both cases.

Treatments	a:Mating Success			b:Territory Size		
(*n*=7)	I	II	III	I	II	III
A	1	2	3	1	2	3
B	2	3	1	3	2	1
C	2	1	3	1	2	3
D	1	3	2	1	3	2
E	1	2	3	2	1	3
F	3	2	1	3	1	2
G	1	2	3	1	2	3
Average Rank:	1.6	2.1	2.3	1.7	1.9	2.4
Xr^2:		2, $P>0.45$			2, $P>0.45$	

TABLE 6. Pearson sample correlation (r_{ij}) matrix of major male variables obtained from the laboratory lek. Showing the variables are highly intercorrelated.

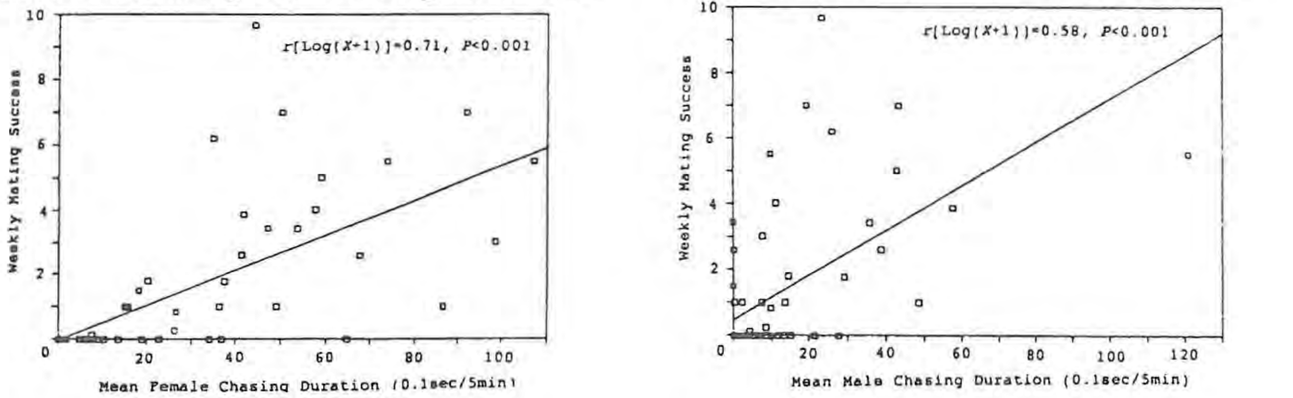
Variables# *n*=65 males.	Side-Shake	Nest Courtship	Female Chasing	Male Chasing	Being Chased	Agonistic Behaviour	Territory Size	Male Size
Mating Success	0.75***	0.87***	0.71***	0.58***	-0.17	0.46***	0.86***	0.25*
Side-Shake		0,80***	0.96***	0.70***	0.13	0.71***	0.88***	0.31*
Nest Courtship			0.78***	0.68***	-0.15	0.62***	0.92***	0.37**
Female Chasing				0.73***	0.13	0.75***	0.89***	0.30*
Male Chasing					0.16	0.62***	0.72***	0.17
Being Chased						0.05	-0.12	-0.48***
Agonistic Behaviour							0.66***	0.60***
Territory Size								0.35**

#Log(X+1) transformation applied.
*$P<0.05$ **$P<0.01$ ***$P<0.001$.



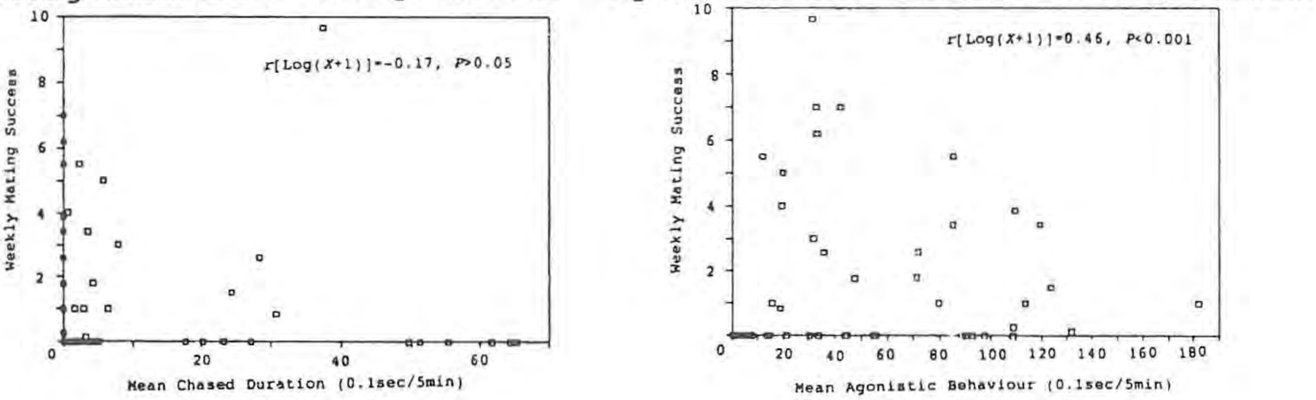
(a) Side-Shake vs Mating Success

(b) Nest Courtship vs Mating Success



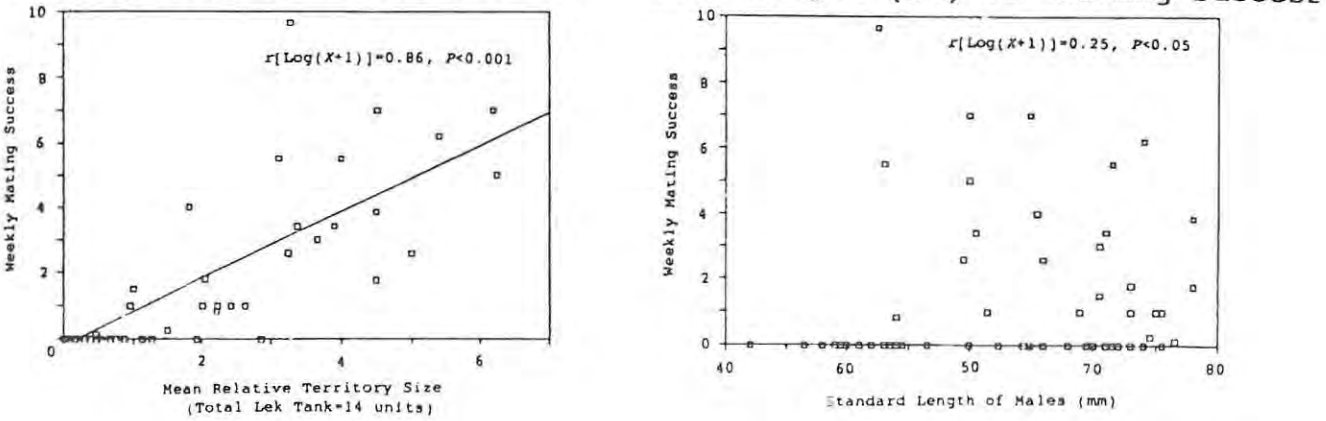
(c) Female Chasing vs Mating Success

(d) Male Chasing vs Mating Success



(e) Being Chased vs Mating Success

(f) Agonistic Behaviour vs Mating Success



(g) Territory Size vs Mating Success

(h) Male Length (SL) vs Mating Success

Fig. 28. Relationships of the eight causal variables with male mating success on untransformed data obtained from 65 males. A linear regression line is only provided when it is significant for the untransformed data.

side-shake each accounted for about 2% of the remaining variation. The other four variables only accounted for a further 1% of the remaining variation in male mating success.

Although territory size was the most important determinant of male mating success, a Friedman two-way test (Table 5b) also failed to show that the rate of spawning interference was significantly different between the three largest territorial males ($Xr^2=2$, $P>0.45$).

Discussion:

Figure 27 indicates that usually only three males in the laboratory lek monopolized almost all of the spawnings. Such high disparity of mating success amongst males, implies that there is a strong sexual selection on *P. philander* males.

Although the sample correlation analysis (Table 6) shows that all the variables monitored, except "Being Chased", are significantly correlated with male mating success, a stepwise multiple regression analysis (Table 8) reveals that the causal variables, which have a significant determination on male mating success, are only territory size, side-shake and female chasing duration. The direct effects of other variables on male mating success are actually insignificant. Their significant correlations with mating success in simple correlations, by referring from the matrix in Table 6, are merely due to their direct or indirect positive relationships with territory size and/or side-shake. A similar result is also shown in the partial correlation analysis (Table 7).

Territory size is the most important determinant of male mating success (Fig. 28g). Since there are no differences in territory quality in the laboratory lek, territory size can be regarded as a function of the social status of males, probably arising from intensive male-male competition (see Kodric-Brown 1978). The direct negative relationship between territory size and being chased, indicated in the partial correlation matrix, further suggests that territory size is associated with male dominance. The dominance relationship between *P. philander* T males in a tight lek is not a "true" dominance hierarchy, where

TABLE 7. A. Partial correlation coefficients ($r_{ij...}$) of the seven major variables to male mating success in the laboratory lek. Indicates only Side-Shake, Female Chasing and Territory Size remain significant correlated with mating success.

B. Partial correlation matrix for the seven causal variables.

Variables#	Side-Shake	Female Chasing	Male Chasing	Being Chased	Agonistic Behaviour	Territory Size	Male Size
A: *df*=57							
Mating Success	0.33*	-0.34**	0.03	-0.08	-0.09	0.63***	-0.08
B: *df*=58							
Side-Shake		0.74***	-0.09	0.17	-0.07	0.23	0.13
Female Chasing			0.08	0.13	0.29*	0.35**	-0.12
Male Chasing				0.13	0.27*	0.32*	-0.17
Being Chased					0.28*	-0.52***	-0.56***
Agonistic Behaviour						-0.07	0.67***
Territory Size							-0.06

*$P<0.05$ **$P<0.01$ ***$P<0.001$.
#Log(X+1) transformation applied.

TABLE 8. Backward stepwise variable selection for multiple regression on the seven major variables with male mating success in the laboratory lek. Indicates the significant determinants of male mating success are only Territory Size, Female Chasing and Side-Shake, in decreasing order of importance.

Variables# n=65 males	Order of Removal##	Variance(R^2) Accounted for	Cumulative Variance(R^2)	Partial Regression Coefficient(b_i) in Final Model**
Territory Size	7	0.7475*	0.7475	1.16
Female Chasing	6	0.0192*	0.7667	-0.35
Side-Shake	5	0.0234*	0.7901**	0.26
Agonistic Behaviour	4	0.0072	0.7973	Nil
Male Size	3	0.0006	0.7979	Nil
Being Chased	2	0.0013	0.7992	Nil
Male Chasing	1	0.0002	0.7994	Nil

*Remained when value for F-to-remove<4.00.
**Final model when value for F-to-remove<4.00.
#Log(X+1) transformation applied.
##Order of removal based on choice of least significant variable remaining in model.

individuals share a territory and form a single unit in leks but there is a linear hierarchy present and only the dominant male in the unit has the "right" to display and mate with females (see Foster 1983). As in most other lekking species, the aggressive behaviour associated with *P. philander* T males is territorial interaction (or "mutually-exclusive territoriality", Lill 1974b). This involves a social unit with an individual male occupying an exclusive space, and agonistic behaviour is manifested between independent social units. Although all males with territories are free to display to and court females in a tight lek, the dominance relationship is usually identified by the location and characteristics of the territories (see Lill 1974b; Wiley 1978; Foster 1983; Trail 1985). If dominance is the main factor in determining male mating success, other dominance-linked behaviours such as male aggression (ie. agonistic behaviour, male and female chasing), side-shake display and male size can be expected to be indirectly correlated with male mating success due to their direct relationship with dominance, or territory size in this case. Furthermore, form the data of territorial displacement (see Chapter 3), it appears that the sequence of arrival in leks is also not an important factor in terms of territory possession.

Other than the indirect effects caused by their relationship with territory size, side-shake and female chasing also have their own independent effects on male mating success. However, both the partial correlation and stepwise multiple regression analyses revealed that female chasing actually has a negative effect on male mating success. This negative relationship may provide an explanation for the relative "tolerance" of T males towards female intruders discussed in Chapter 4. Although the negative effect of female chasing on male mating success poses a dilemma for males with regard to territory defence, the stepwise multiple regression model indicates that this effect is not strong. It can be compensated for, by enhancing other variables such as more side-shake performance and/or defence of a larger territory. The strong positive relationship between female chasing and side-shake revealed in the partial correlation and there being no significant differences in interference rates between successful males of different territory size, probably reflect such a compromise. This may also partly explain why the disparity in mating success between successful males is not significantly related to spawning interference. Even though spawning females may lay eggs with more than one male due to interference, the more nest-courtship a male acquires can be strongly correlated with the number of egg batches it obtains (Fig. 28b). Thus, spawnings are still eventually distributed only among those successful males, even though female choice can be altered. This is similar to other "lek-like" fish (Keenleyside 1972) and lekking birds (reviewed by Foster 1983; Bradbury & Gibson 1983), where the interruption rate is not likely to be different between dominant males and less successful males. Nevertheless, such a spawning pattern of females may well be an adaptation to ensure that most, if not all, of their spawnings are with males which have the "right" to court (see Borgia 1981; Partridge *et al.* 1987).

The effect of side-shake is the same as that of "Courtship Display" measured in the choice-chamber experiment. When territory size is experimentally held constant by the equal size of the choice-chambers and the aggression of males is shielded by the clear partition, the independent effect of side-shake is well manifested. Side-shake is the most immediate sexual stimulation received by females, while chasing of female has the opposite effect, directly repulsing females. Thus, these two variables can be identified as being the characters which can directly affect female choice, with side-shake having a positive effect and female chasing a negative effect. The sign of the partial regression coefficient of these two variables in the multiple regression model agrees with this interpretation. In damselfish (Schmale 1981; Thresher & Moyer 1983) and guppies (Farr 1980), courtship display rate, which is equivalent to the side-shake duration in *P. philander*, is the most important variable in the determination of male mating success, and is considered to be promoted by female choice. In another cichlid, *Cichlasoma nigrofasciatum*, the relatively more intensive courtship behaviour of smaller males can sometimes even stimulate females to spawn with them instead of with larger males, which are otherwise strongly favoured by females (Keenleyside *et al.* 1985). Nevertheless, although the effects of these two variables are significant in *P. philander*, they are weak, and the order of their importance to male mating success, is subordinate to territory size. Together, their effect is only 5.3% (4% versus 75%) that of territory size.

Therefore, territory size is the variable which reflects the effect of male-male competition for the establishment of a dominance relationship, while both side-shake and female chasing account for female choice. The multiple regression analysis suggests that both male competition and female choice have a significant influence on male mating success in *P. philander*. However, the effect of male competition is much more important than that of female choice in determining male mating success.

CHAPTER 7

GENERAL DISCUSSION

As in other lekking animals (eg. Buechner & Schloeth 1965; Wiley 1978; Diamond 1981; Trail 1983, 1985; Halliday 1983; Arak 1983; Koenig & Albano 1987), the present study indicates that male competition for dominance is the major driving force of the intensive sexual selection in *P. philander*. Mate choice by *P. philander* females is made passively by favouring males which show more persistence in courting. The strong positive correlation between territory size and side-shake (Fig. 29) shows that males of higher rank display more. This is probably because their dominant status allows them to concentrate less on territory defense and hence advertise more (see optimal advertisement level, Parker 1983). It is further supported by the strong positive correlation between side-shake and aggressive behaviours (Table 6), as such a relationship is thought to be an important element in maintaining a clear "right of way" to execute courtship display in highly competitive environments (Schmale 1981; Thresher & Moyer 1983; Simmons 1986). Furthermore, as dominant males have larger territories, their chances of encountering females will also be higher (see Constantz 1975). Therefore, the strongly skewed mating success amongst males may well be due to the fact that females tend to be passively attracted to dominant males as a function of the relatively higher intensity of their signals. This passive attraction may be a consequence of a greater stimulus or facilitation effect hastening her arousal to a maximum, rather than a result of the female directly comparing and discriminating between males, although the final outcome of both is similar, (O'Donald 1983, Parker 1983; Arak 1983, 1984; Partridge *et al.* 1987).

Nevertheless, other than the stochastic advantages gained by dominant males, *P. philander* females possibly also indirectly use side-shake frequency as a cue to assess male status (see Farr 1980; Schmale 1981; Thresher & Moyer 1983; Thornhill & Alcock 1983). Females always visit many males and frequently leave the

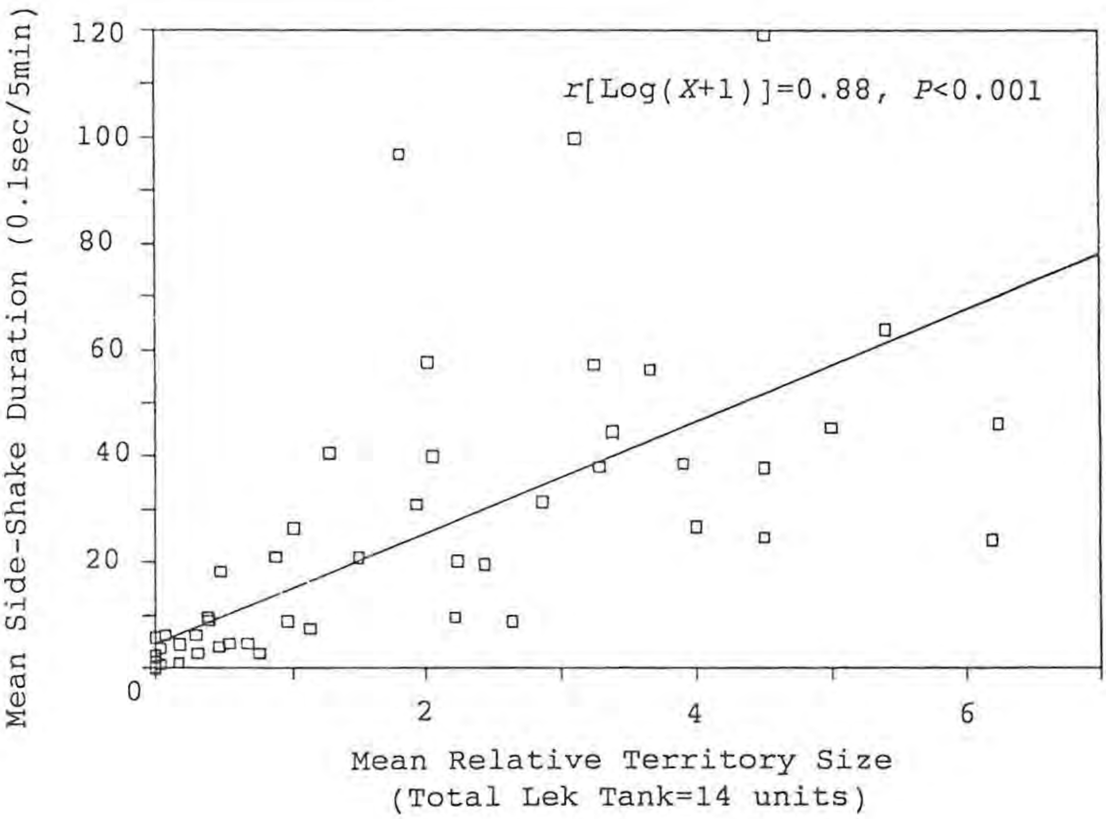


Fig. 29. Relationship between territory size and side-shake duration in 65 males on untransformed data. The linear regression line provided for the untransformed data is highly significant ($P<0.001$). Showing a strong positive correlation between territory size and side-shake frequency.

nest before spawning, even without experiencing interference, and their requirement for a prolonged pre-spawning courtship may suggest that females are indirectly assessing males and using certain subtle tactic (*sensu* Wittenberger 1983) to mate with dominant males. It has been suggested that by mating with dominant males, females can obtain direct benefits such as safer courtship (Trivers 1972; Halliday 1978, 1983; Borgia 1981; Foster 1983; Parker 1983; Partridge 1983) and/or better genes as dominant males are usually "fitter" and healthier (Trivers 1972; Slender 1972; Halliday 1978, 1983; Borgia 1979; Hamilton & Zuk 1982; Bradbury & Gibson 1983; Arak 1984).

Similar to the detector/detectee relationship (Barnard 1984), the mechanism of female choice will also involve costs (Halliday 1983; Parker 1983; Wittenberger 1983). To successfully maintain a territory in a lek is not easy for males. Therefore, the "genetic superiority" or fitness of the males has been largely sorted out by intensive male-male competition. Furthermore, owing to the changing dynamics of the males' status as a result of severe competition, it is very difficult and costly for females to directly and correctly assess the relatively small variation in fitness amongst T males at particular times. If the hereditability of additive genetic variance in fitness associated with dominance or other behavioural traits is very low as suggested elsewhere (Falconer 1960; Williams 1975; Maynard Smith 1978; O'Donald 1980), it further diminishes the potential benefit of choice amongst T males. The costs of choice alone, therefore, can make the maintenance of active choice entirely for "good-genes" difficult (Parker 1983). Thus, it does not become cost-effective for females to be extremely "choosy" by further developing a complex nervous system and the associated behaviour for superior male detection (see Parker 1983; Wittenberger 1983). Furthermore, the severe competition between males renders active female choice impossible (Trivers 1972; Diamond 1981; Borgia 1981; Arak 1983). The exercise of free choice by females amongst all males in the lek is inevitably restricted by the imposition of a dominance hierarchy by T males over subordinate males. Even though females apparently can choose amongst T males, the spawning interferences from subordinate fishes effectively modifies female choice. Therefore, only passive mate choice tactic by females would be favoured.

Females appear to rely on a simple display-response system and use side-shake as a cue to indirectly assess males. The fact that females also alternatively leave and return to a male's nest during and after spawning suggests that such behaviour does not necessarily indicate that females are making a choice. The multiple visits by females before spawning probably is a mechanism which increases their chances of encountering higher ranking males, and does not represent an active comparison of males by females. Alternatively, such switching between males may assist females to acquire greater stimulation and accelerate the process leading to spawning (see Schwanck 1987). The requirement for a prolonged pre-spawning courtship may be an active filtering (*sensu* Lloyd 1979) by females to deliberately incite rivalry between males thus making it more difficult for subordinates to mate (see Borgia 1981; Partridge *et al.* 1987). The exaggerated courtship of females by males also attracts the attention of other males. Therefore, courtship by competitively inferior individuals could involve them in costly disputes, which they have little chance of winning and may in fact result in physical injuries. Even though less competitive individuals may adopt the alternative sneaking tactic to attempt to bypass the process of prolonged courtship during which females could potentially assess male status, the spawning pattern of females seriously limits the amount of fertilization they can steal. As in the more-refined version of the threshold criterion tactic described by Wittenberger (1983), females will spawn with any male, even other females, but this will occur only after she has reached a threshold level of courtship stimulus during visiting (Fig. 30). Thus, females appear to behave in a way which ensures that they mate with dominant males. No direct comparison of or discrimination between males is likely to be involved in the process although it cannot be dismissed entirely (see Borgia 1981; Partridge *et al.* 1987).

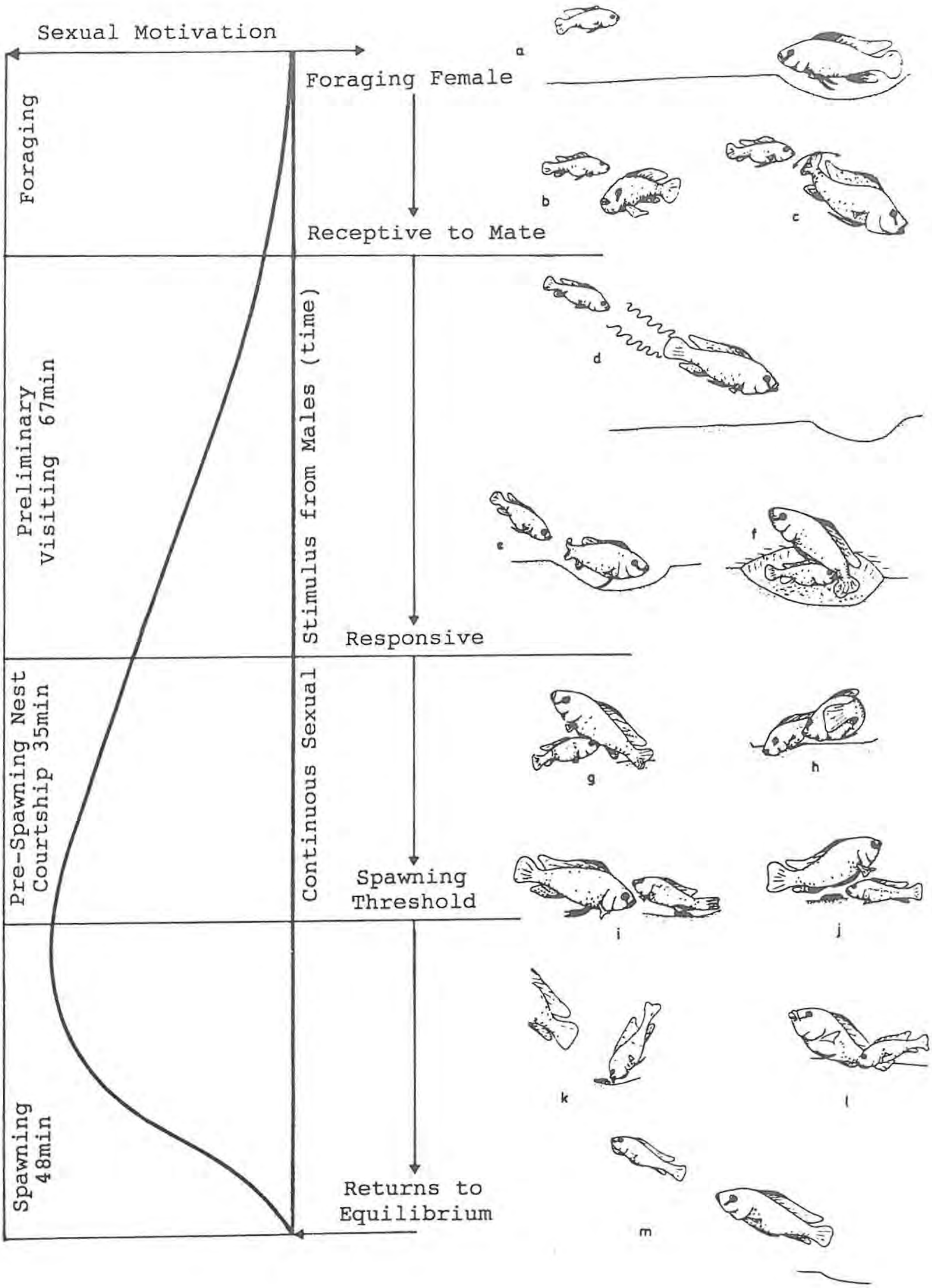


Fig. 30. A schematic description of the hypothetical threshold-criterion spawning response of females during mating. Figure is modified from Ribbink (1971). Sub-legends for behavioural sequence see Fig. 7.

Therefore, if females do obtain some benefits from mating with dominant males, probably mainly non-heritable environmental benefits (Parker 1983; McKaye 1984, but see Hamilton & Zuk 1982; Arak 1984), their simple stimulus-response to side-shake display will be further reinforced by selection. Moreover, further selection pressure to develop this simple display-response mating system in females is released both by the prevention by the mating males of spawning interference and by the strong male-male competition in sexual selection. This may provide an explanation for the widespread misdirected behaviour exhibited in both spawning and mouthbrooding females when responding to sexual stimuli. Even if male dominance is not directly selected by female choice or offspring fitness, the severe intrasexual selection alone still can strongly favour high aggression in males. This may be enough to explain the highly aggressive and strongly territorial nature of male *P. philander*.

Since side-shake is also the most immediate sexual stimulation received by females, it becomes directly selected by female choice (see Farr 1980). Similarly, female chasing by males has a direct repulsive effect on female choice, and hence poses a dilemma for males in territory defence. Besides lowering the threshold to chase females, males are inclined to lowering their threshold of sexual response to visiting females. Thus, they can compensate for the inhibiting effect of chasing to the sexual response in females by performing more side-shake. Therefore, in order to become more "attractive", males are selectively favoured to be highly sexually motivated by courting more and indiscriminately (see Selander 1972), and to become relatively more "tolerant" towards females in their territories. Such selection on males and the motivational constraint (simple display-response mating system) in females then facilitates the evolution of female egg-stealing and female-mimic sneaking in this fish. This scrounging behaviour of subordinate fishes may partly account for their gathering in leks (Arak 1983, 1984). Nevertheless, due to the high aggression level of T males and the spawning pattern in females, the amount of fertilization stolen by sneaking is negligible. Thus, the adoption of an alternative mating tactic by subordinate males is merely "making the best of a bad situation". Egg-stealing by females occurs more often than sneaking; however, the evolution of counter-selection in T males is restricted by the parasitic and net-beneficial nature of this behaviour (Dominey 1981; Barnard 1984). Besides altering female choice, the effect of interference can also lead to a longer pre-spawning courtship and even multiple-mating by females.

Similar to damselfish (Schmale 1981; Thresher & Moyer 1983) and pupfish (Kodric-Brown 1983), body size in *P. philander* does not directly affect male mating success, nor is it preferred by females. Although the trend is for large males to acquire territories more easily (Fig. 31), it does not necessarily follow that the larger the male the larger will be its territory, especially over the narrow size ranges which are typical for *P. philander* T males occupying a lek (Ribbink 1975). The frequent occurrence of territory displacement in the laboratory lek suggests that it is costly to maintain a territory. It has been suggested that a lek mating system is associated with a higher cost in competition than that of resource-defence mating system (Gosling *et al.* 1987). In the laboratory lek, threat displays and fights are common amongst T males and when they prevent subordinate males from settling, with the longest recorded escalated fight being about 6 minutes (Pl. 10). Furthermore, a considerable amount of energy will also be spent in undergoing lengthy courtship with females. Therefore, a rapid depletion of available energy may result in the T males being unable to maintain a territory any longer in the highly competitive environment. In other lek-breeding cichlids of Lake Malawi, males can only remain in the arena for less than 2 weeks (McKaye 1983, 1984). Since neither body size nor sequence of arrival have any significant effect on male mating success, the age of males probably also is not significantly related to male mating success.

Male colour is also not subjected to female choice. Although the coloration of a male is behaviourally controlled and can change abruptly depending on its ecological and social conditions, the basic colour pattern amongst males within a

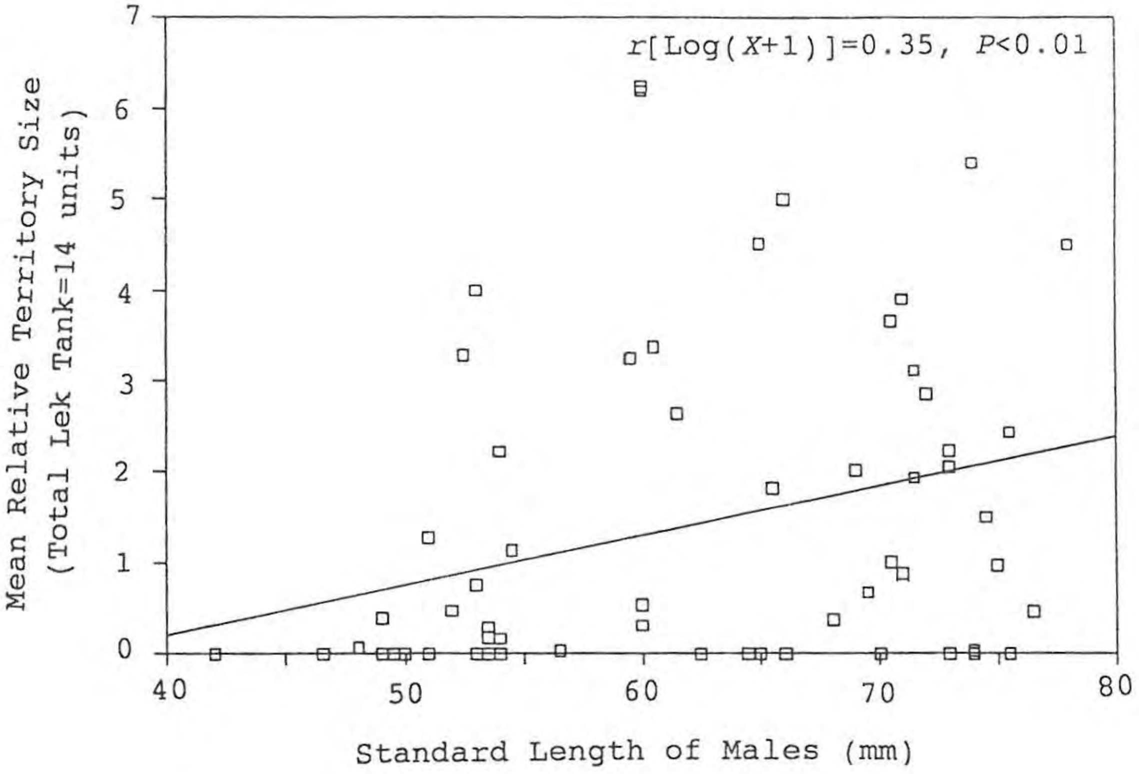
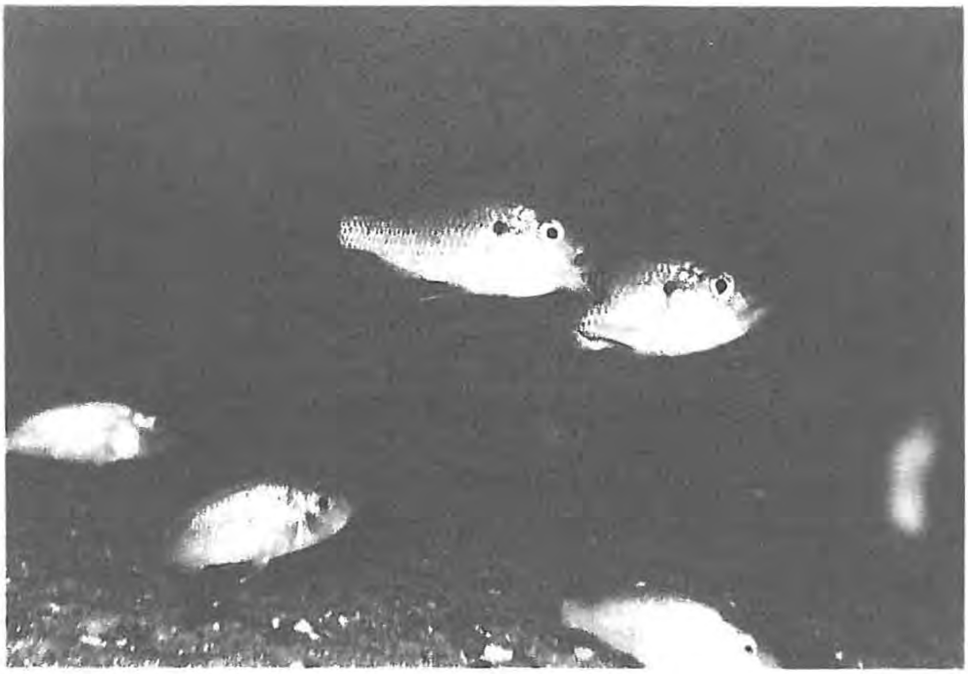


Fig. 31. Relationship between male body size and territory size in 65 males on untransformed data. The linear regression line provided for the untransformed data is significant but weak (*P*<0.05). Indicates that there is only a weak correlation between male size and territory size.



Pl. 10. An escalated fight between two males, with one biting the other. In the laboratory lek, due to fighting, males are often scarred on the lips and/or scales are detached.

population does not vary considerably (Ribbink 1971, 1975). In the choice-chamber experiment, males in plain colour, and sometimes even in stress colour, might court females although during the course of courtship their colour will become brighter. But in the laboratory lek, the expression of nuptial coloration in males depends on the possession of a territory, and it is maximally expressed during escalated mouthfights, but rapidly becomes pale immediately after a fight is lost (also see Ribbink 1971, 1975). The colour of males with well established territories is not particularly deep and generally only becomes slightly deeper during courtship. Therefore, it appears that colour in *P. philander* is mainly used as an aggressive and social signal between males by advertising their status (see Kodric-Brown 1977, 1978, 1983; Thresher & Moyer 1983; Mckaye 1984). Thus, the change to nuptial coloration not only provides a signal to potential mates, but also triggers aggressive behaviour from other males.

A summary of the hypothetical evolution of the mating behaviour in *P. philander* is illustrated in Figure 32. The present conclusion that male competition is the major driving force in sexual selection of this fish is contradictory to the traditional interpretation that active female choice is prevalent in lek species (eg. Darwin 1871; Lill 1974a; Harvey & Arnold 1982; Foster 1983; Arnold 1983; Bradbury & Gibson 1983). Since those females which do not choose to spawn with T males will be harassed by continuous interference and will lose eggs due to egg-stealing, female choice will not be selectively neutral, at least in the sense of immediate benefit (see McKaye 1984). Furthermore, as females have no prior preference and exercise their choice by responding more readily to males which court more frequently and longer to compete for their attention, differences in male behaviour due to male-male competition chiefly determine the operation of sexual selection (O'Donald 1983; Parker 1983; Partridge 1983). A runaway selection (which is formulated primarily on active female choice) on male characters, including side-shake display here (see Farr 1980; Partridge *et al.* 1987), through female choice will be greatly limited by the counter-

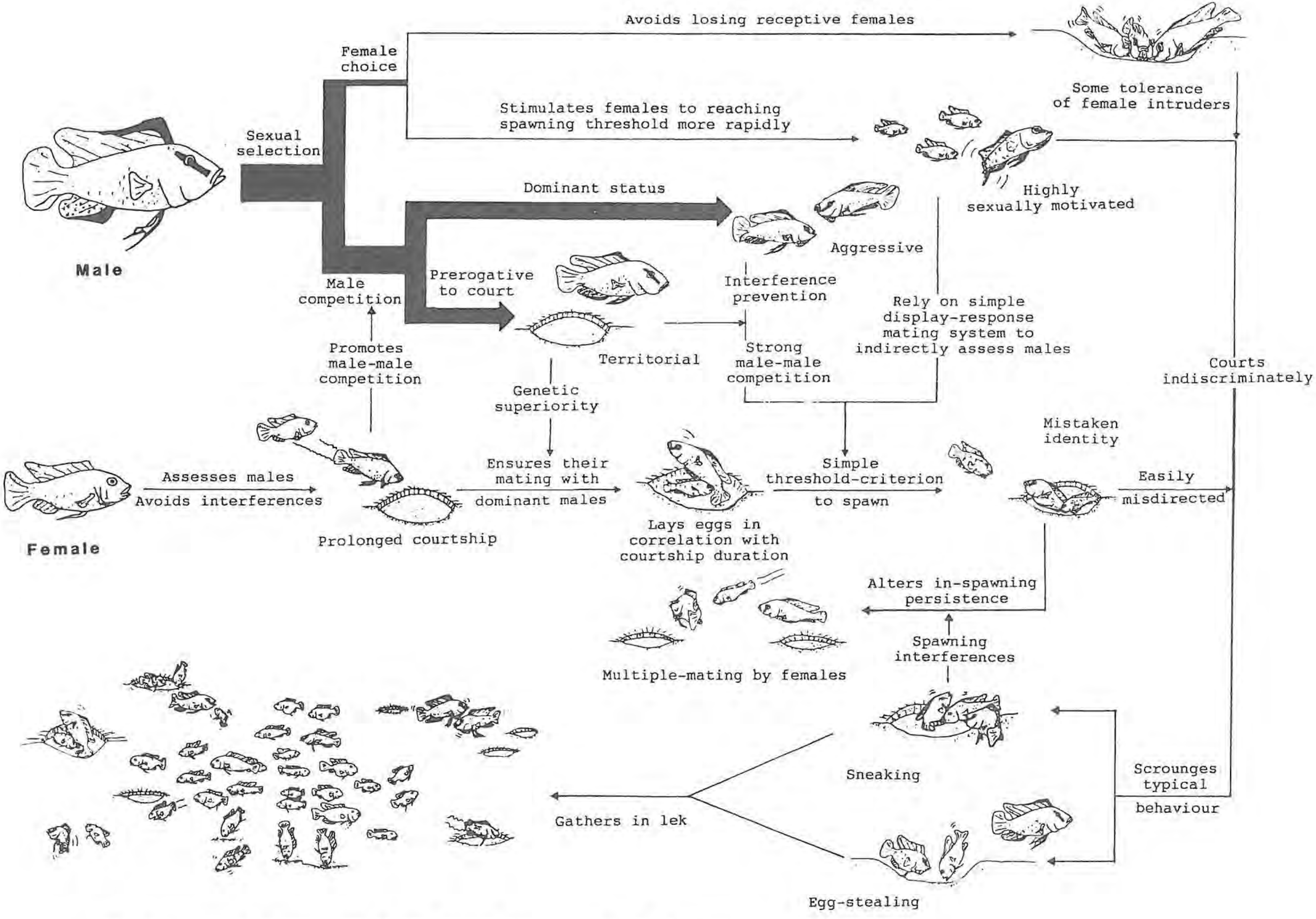


Fig. 32. A schematic explanation of the mating behaviour in *P. philander*.

selection from severe male-male competition, although it is unlikely that the effect of male-male competition would run completely opposite to female preference (Borgia 1981; Partridge *et al.* 1987).

The inclination of females to mate with males which are superior in combat, and the variation in competitive ability of males results in variation in mating success in males. This appears to support the "war propaganda model" (Borgia 1979, also see optimal sexual advertisement model by Parker 1983), which considered that the effect of mating competition is more realistic than female choice. Similar to Wallace's (1889) argument and the evolution of thread signals proposed by Huxley (1938), Borgia suggested that vivid and active courtship displays which demonstrate a male's dominance should be favoured by females as long as the mating process is not thus seriously threatened by predators. He considered structures and behaviours which evolve in such a context to be products of selection under the war propaganda model. Thus, exaggerated characters should function to signal male dominance both to females and rival males in the same degree, eg. colour and side-shake display in *P. philander*. Furthermore, since females are choosing a male who has earned his right to display, their encouragement of behaviour which tests a male's dominance would promote not only extravagant displays but a sufficiently long courtship to insure that the behaviour of her prospective mate has not gone unnoticed by other males.

Runaway selection proponents argue that the evolution of signals involved in male-male competition is not exaggerated enough to account for the development of extraordinary traits in males, because their evolution is constrained to reflect the true superiority of their bearers (Fisher 1930; Otte 1979; Lande 1981, 1982; Arnold 1983; West-Eberhard 1983). However, there are suggestions that the effect of social selection can also greatly accelerate and amplify the development of characters in a population due to the constant and unending social conflict between conspecifics (West-Eberhard 1979, 1983; Thornhill 1979; Lande 1980; Thornhill & Alcock 1983; Dominey 1984b) under "evolutionary arms races" (Dawkins & Krebs 1979; Dawkins 1982; Barnard 1984; Weldon & Burghardt 1984). Thus, the war propaganda model combined with the sexual advertisement model (Parker 1983, also see Hamilton & Zuk 1982) may be enough to account for the extreme and rapid divergence of social signals and behaviour used in sexual selection for lekking species.

The present interpretations, nevertheless, needs further confirmation from field data, especially on the formation and evolution of the lek structure in this species. The difference in fitness of offspring from females which are mated with dominant males and subordinate males, as well as the life-time reproductive success of individual males will also be of great interest.

Conclusion:

The present study shows that there is only passive choice in *P. philander* females and the strongly skewed mating success amongst males in the laboratory lek is mainly a consequence of intensive male-male competition. The fact that dominance is the most important determinant of male mating success and the possession of a territory is essential to successful spawning probably can explain the highly aggressive and strongly territorial nature of male *P. philander*. Male size and colour, as well as some other physical features and behaviours, were not subjected to female choice. Their evolution under sexual selection, therefore, is likely due to their association with male dominance. However, although females do not actively discriminate amongst males but rely on a simple display-response system to mate, it appears that their coy behaviour encourages male rivalry and has the effect of favouring mating by dominant males. Since side-shake is the immediate sexual stimulation received by females, it becomes directly selected by female choice and probably also indirectly becomes a cue used by females to assess males. Female chasing has a directly repulsive effect on female choice and hence contributes negatively to male mating success. Thus, selection favours highly sexually motivated males which are also relatively tolerant of females. The indiscriminate eagerness of males to mate and the simple display-response effected in females facilitate the occurrence of female egg-stealing and female-mimic sneaking in *P. philander*. Although the effect of spawning interference can contribute to a longer pre-spawning courtship and multiple-mating in females, spawnings are still monopolized by a small number of dominant males due to the spawning pattern of females.

The roles of male and female behaviour in producing the strongly skewed mating success in males of this lek mating fish do not conform with the principle of the runaway selection model, which assumes that the disparity in male mating success is chiefly attributable to the exercising of active choice by females. The behavioural evidence, however, agrees with the prediction of the war propaganda model (Borgia 1979), which regards male-male competition as more effective than female choice for lekking species.

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APPENDIX

Natural Selection and Sexual Selection:

Darwin did not view sexual selection as a subcategory of natural selection and frequently pointed out that sexual selection may oppose natural selection. With the introduction of the gene concept in evolution, natural selection is now generally considered to be an all encompassing force which also contributes to the differential reproductive success of genotypes (eg. Williams 1966; Alcock 1975; Otte 1979; Thornhill 1979; Futuyma 1979; West-Eberhard 1979; Lambert *et al.* 1982; Thornhill & Alcock 1983; Dunbar 1983; Stebbins & Ayala 1985). Then the ability to survive and the ability to obtain more mates are merely different aspects of the same goal, for the ultimate function of survival is also to reproduce (Halliday 1978; Otte 1979; West-Eberhard 1979; Thornhill & Alcock 1983). Therefore, sexual selection can be considered as a subcategory of natural selection (Williams 1966; Otte 1979; West-Eberhard 1979; Barnard 1984; Thornhill & Alcock 1983, but see Arnold 1983; Arnold & Wade 1984b). The confusion created by Darwin is mainly due to his usage of the term "Fitness" because of the lack of genetic knowledge at his time (Mayr 1972; Halliday 1978). Nevertheless, since the effect of mating is so pervasive, most evolutionists agree that Darwin is right and the term sexual selection is useful in explaining evolutionary possesses (eg. Mayr 1972; Otte 1979; West-Eberhard 1979, 1983; Thornhill & Alcock 1983; Arnold & Wade 1984b).

Unfortunately, the terms employed in describing natural and sexual selection by many modern biologists are still not specific and are often confused, especially when discussing their relationship. However, implying that natural selection is for the maintenance of variability only (eg. Fisher 1930; Selander 1972; Lande 1980, 1981, 1982; Kirkpatrick 1982; Harvey & Arnold 1982; Arnold 1983; Endler 1983; Dominey 1984b; Arnold & Wade 1984b; Heisler 1984; 1985). Some authors infer that sexual selection is the selection of reproductive characteristics (eg. Selander 1972), others suggest that selection may cause deviations from panmixia (Ehrman 1972), and that there is frequency-dependent selection (Lande 1980), or even female choice only (Farr 1977). Such confusion has subsequently contributed to many misrepresentations and mishandlings of Darwinian sexual selection, especially on the mathematical definition of sexual selection (see Mayr 1972; Halliday 1978; West-Eberhard 1979; Burley 1986; Koenig & Albano 1987; Zuk 1987). Burley (1986) even claimed that some authors (eg. Kirkpatrick 1982; Arnold 1983) have tended to restrict the concept of sexual selection to female sexual preference of aesthetic traits.

In order not to run into the same difficulties, the definition of natural selection and sexual selection are specifically stated and it will be attempted to avoid using these by replacing them with more pertinent terms (see Fig. 33), in later discussions:

Natural Selection: The differential reproductive success of individuals.

Sexual Selection: The advantage of one individual over other members of the same sex in acquiring mating opportunity(ies).

Furthermore, with the realization of the necessity to distinguish between the effect of ecological selection and social selection in analyzing the natural selection process (Wynne-Edwards 1962; Crook 1972; West-Eberhard 1979, 1983; Thornhill & Alcock 1983, described in different terms -- Huxley 1938; Mayr 1972; Otte 1979; Lande 1980; Wallace 1981), sexual selection can also be inferred as the social selection exclusively for mating (Wynne-Edwards 1962; Crook 1972; West-Eberhard 1979, 1983; Thornhill & Alcock 1983; Dominey 1984b). The idea of "sexual selection can oppose natural selection" and "females prefer to mate with maladaptive males and ignore fitter males" (*sensu* Lande 1981; Harvey & Arnold 1982; Kirkpatrick 1982; Arnold 1983) can then be easily clarified if the various terms used in discussing natural selection process have been specifically defined beforehand.

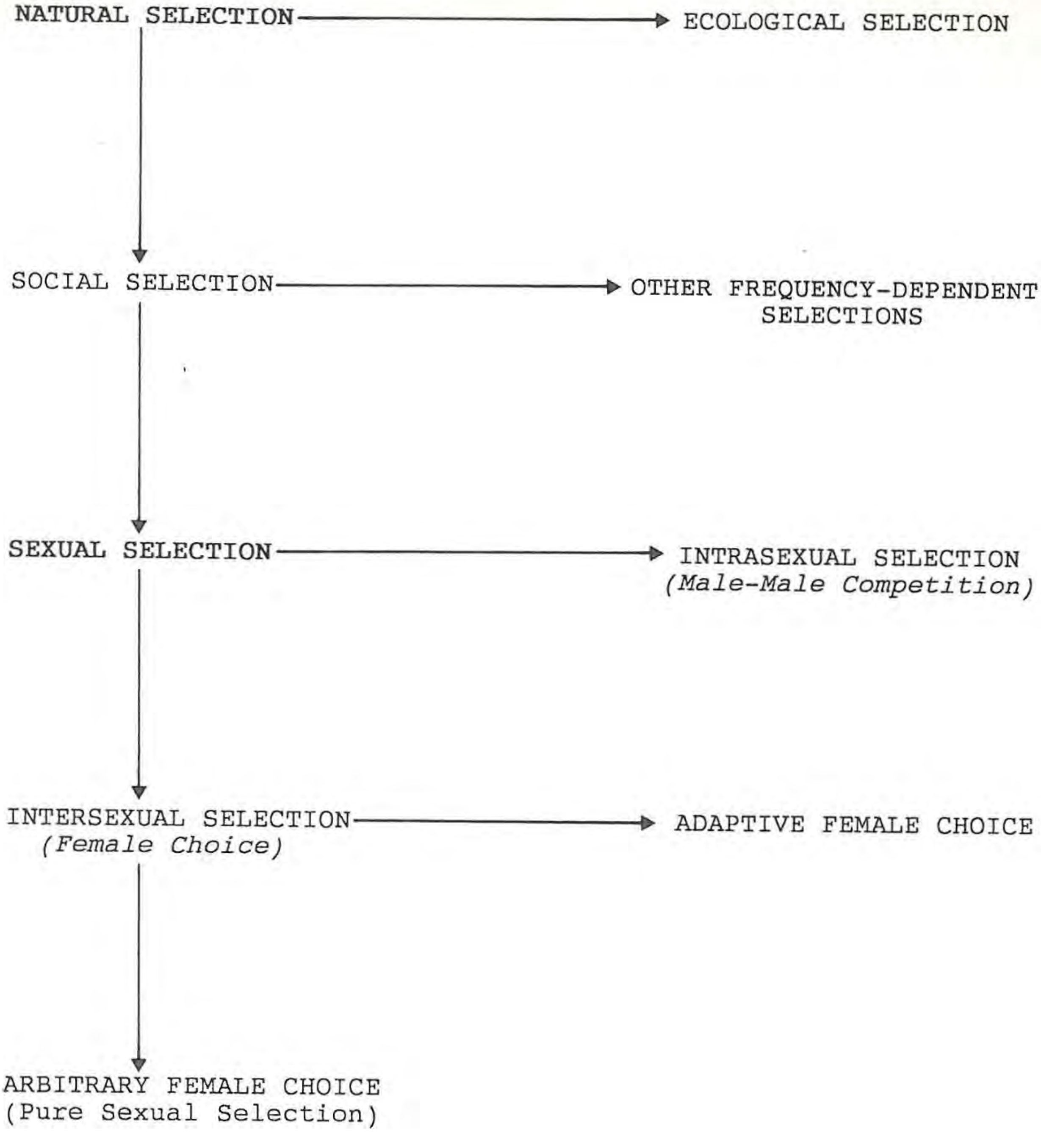

Fig. 33. The hierarchy of selection forces discussed in the present report.