Social organization of small heterosexual groups of Green swordtails (*Xiphophorus helleri*, Pisces, Poeciliidae) under conditions of captivity [2]

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INTRODUCTION

The classic works of Noble (1939), Noble & Borne (1940) and Braddock (1945, 1949) have shown that small isosexual and heterosexual groups of *Xiphophorus* fish form hierarchies based upon dominance submission relations which are established by challenging and fighting. The resulting dominance orders show a tendency toward the straight line type, although incomplete hierarchies and intransitive triangles are common, at least in platies, *Xiphophorus maculatus* (Braddock, 1945). Once the hierarchy is established, agonistic social behaviour of the fish is less reciprocal than during the formative period. Dominant individuals of either sex butt their subordinates differentially, as individuals; there is no systematic relationship between the difference in rank between individuals and the frequency of chases initiated by the dominant individual toward the subordinate one. The total amount of aggression shown by a fish, however, seems to correspond to his, own rank (Braddock, 1945). With two or three individuals of the same sex, dominance relations tend to be very stable, remaining unchanged for several weeks (Noble, 1939; Braddock, 1945) or even for much longer periods, up to six months in certain cases (Noble & Borne, 1938, 1940; Zayan, 1974). With four to eight individuals, dominance relationships tend to be more frequently reversed, apparently due to revolts of subordinates. Some evidence also indicates that the fish are able to recognize each other's in-dividual characteristics (Zayan, 1974, 1975b). This "individual recogni-tion" would be responsible for the stability of dominance relations within small groups. Poeciliid fish are not considered territorial. These ovoviviparous species have never been reported to establish and to defend individual territories (Braddock, 1942, 1945; Morris, 1955; Zayan, 1974, 1975a, b, c, 1976; Noble & Borne, 1940; Franck, 1964, 1973) as do cichlids, for example. One exception must be made, however, for Heuts (1968) has reported a presumed case of territoriality in two female swordtails. Observations made in the natural environment, although not clearly establishing the existence of territoriality, suggest that males can defend against intruding males, at least temporarily a feeding area or an area surrounding females. Zander (1967) has reported the case of an adult male *Xiphophorus helleri* patrolling an area of two square metres and chas-ing all intruding males. The same author has also noted that individuals distribute themselves within a pool or river according to size, larger in-dividuals occupying deeper waters and smaller fish living in more shallow zones, near the banks. The existence of a similar gradation in tropical streams is well documented, and has been noted in other poeciliids, *e.g.,* in *Poeciliopsis*

monacha and *Poeciliopsis lucida,* by Moore & McKay (1971), as well as for *Mollienesia latipinna* by Baird (1968). Although George (1960) has reported that both sexes in *Gambusia affinis* actively defended a territory under natural conditions, (1965) was not in a position to confirm this under laboratory conditions.

Laboratory studies of spacing out patterns in poeciliids have rarely been carried out in conditions clearly favouring competition for mates and space. For example, most studies were done either in the absence of females or in large aquaria not allowing visual isolation by dense vegeta-tion or rocks, as found in the natural habitat.

The present study was undertaken to determine whether green swordtails would defend individual territories when in competition for mates and for space in an aquarium permitting visual isolation. In addition, we were interested in knowing whether aggressive dominance would be related to priority of access to space and mates in this poeciliid.

METHODS

Subjects and material

Subjects used were adult male and female green swordtails, *Xiphophorus helleri* Haekel, originally obtained through a local dealer from Florida Fish Pounds, Tampa (Florida, U.S.A.) Before being used they were either maintained in three large tanks, each holding an heterosexual group of approximately 50 60 individuals, or kept in groups of two males and two females in smaller glass tanks (25 x 25 x 25 cm). All observations were done using eight 54 litre aquaria (60 x 30 x 30 cm) illustrated in Fig. 1. Each had a partition of opaque plexiglass separating the tank into two unequal volumes, the large compartment measuring 40 x 30 x 24 cm, and the small one 20 x 30 x 24 cm. Four of the tanks had the larger compartment on the left and four on the right. Each aquarium was gridded into 12 sectors, each of 20 x 15 x 15 cm. Three cm of white gravel covered the bottom of each aquarium. The level of water was adjusted daily and maintained at 2 cm above the plexiglass partition so that the fish could freely swim from one side to the other. One heater and Dynaflow filter was placed in the small com-partment of each aquarium. All sides, excepting the one reserved for observations, were painted white. Each observation tank was placed behind a plywood screen and observa-tions were carried out through a slot in the screen. A 12 h photoperiod was imposed throughout with initiation of the photofraction at 0800 h. Water temperature of all tanks was maintained between 25° and 30°C. All fish were fed dry food twice a day, once in the morning and once in the afternoon after completion of observations. The food was distributed equally between the two com-partments even though the fish were not themselves evenly distributed. The glass and plexiglass walls of the aquaria were also covered with green algae, except for the side through which the observations were made, and fish could graze on these for additional food. Four adult males and four apparently gravid females taken from different holding tanks were measured and placed into one aquarium and left undisturbed for at least five days before daily observations began. Between two and four periods of observation were com-pleted on each of the 16 populations for a total of 50 observation periods.
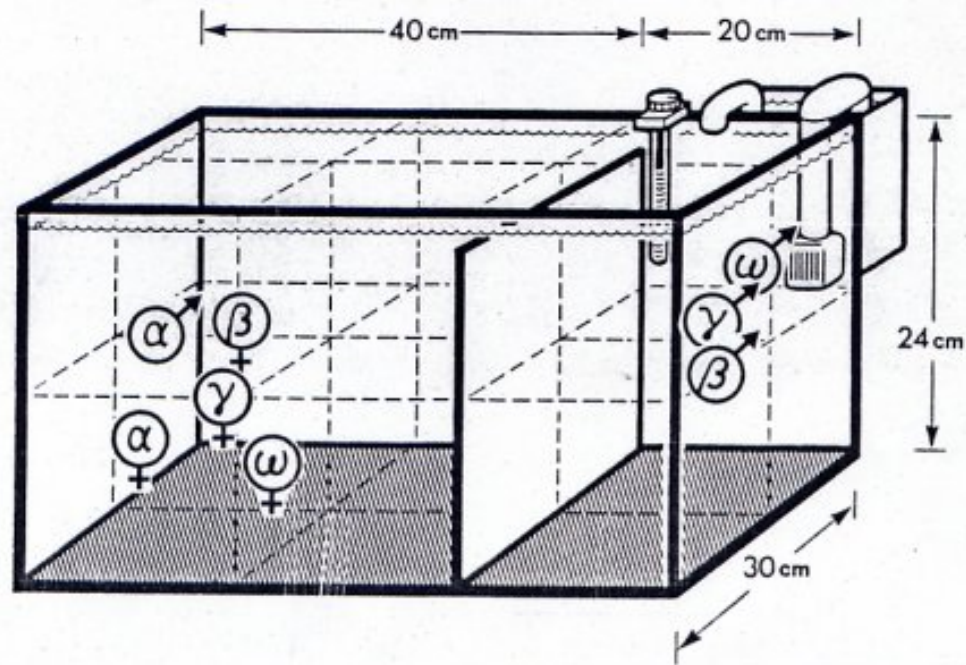
Fig. 1. Aquarium used in the present study and geometrical representation of the spatial association of the 8 types of fish. The tridimensional representation of the individual fish were obtained by the application of multidimensional scaling (KYST) to the mean of repeated sampling of inter-individual distances obtained for each observation period in which both female and male hierarchies were complete (N=16).

Observations

All observations were systematically recorded using two *Datamyte* ethographs (Model 916, Electrogeneral Co., Minnetonka, Minn., U.S.A.). The selected mode of entry allowed each event to be recorded with respect to its relative time of occurrence. The following observations were collected during each observation period:

1. Each of the eight fish was randomly focused upon for 15 min and all instances of relevant behaviour, initiated or received, were systematically noted, as well as the identity of the actor and of the receiver and the behaviour given "in response".

2. Eight samples of the instantaneous spatial positions of the 8 individuals in the aquarium were taken at 15 min intervals by systematically scanning the 12 sectors of the aquarium.

3. A sociometric matrix was also completed, tabulating aggressive chases noted during focal animal sampling and during an additional period of unrestricted observation. The aggressive asymmetries obtained were used to construct the chase order for each observa-tion period.

Dominance criterion

An individual was considered dominant over another if he or she successfully and unilaterally chased a given opponent on at least four consecutive occa-sions without, in the meanwhile, being chased in turn by the latter'). A chase was defined as the initiation of either one attack, bite, nip, lateral display, tail beat or approach by a given individual, and its temporal association with a defensive behaviour, or flight by the opponent.

Modal action patterns

The agonistic, sexual, and alimentary behaviour patterns and postures of *Xiphophorus helleri* have been described by Morris (1957), Wickler (1957), Franck (1964, 1968), Hemens (1968), Heuts (1968), Thinès & Heuts (1968), Franck & Hendricks (1973), Zayan (1974, 1975a, 1976) and Beaugrand & Zayan (1984). The following relevant units and categories were retained and encoded:

1. Offensive behaviour. This category includes attacking or charging, and biting the op-ponent. Attacking and charging entail the sudden acceleration of an individual toward his conspecific, the initial distance being at least equal to the length of the initiator. This unit may be followed by a bite. Biting consists of grasping, with the mouth, such anatomical parts of the other individual as the ventral or pectoral fins, gonopodium or even the mouth of the opponent (mouth fight).

2. Defensive behaviour. This category includes fleeing and submissive posturing. Fleeing is associated to an approach or attack or bite or lateral display or tail beat unit emitted by one individual. The threatened fish rapidly avoids the charging opponent or escapes his presence by a sudden acceleration separating both fish. This fleeing is sometimes accom-panied by a submissive posture. The submissive posture consists of the lowering of the dorsal and caudal fins and spreading of the ventral ones. It is sometimes accompanied by tilting on the side. The defensive unit is an interactive behavioural pattern since it entails the concomitant initiation of an aggressive act by the opponent.

3. Challenging behaviour. This category includes tail beating and lateral displays. Lateral display consists of the spreading of all fins, with the exception of the ventral fins which are kept close to the body. The body presents, most often, a typical sigmoid posture (S drohen). The orientation of the individual is usually perpendicular to and in front of the conspecific, or parallel to it, when both fish are mutually displaying. In tail beat, the initiator adopts lateral display posture, curves his body sharply, and rhythmically beats with his tail at a frequency of 2 10 units per minute. Tail beats are administered in the direction of the opponent, as if water currents were aimed at his head, flank or tail.

4. Approach. Slow movement of a fish toward his or her conspecific. It is initiated from a distance exceeding approximately twice the total length of the initiator.

5. Flutter. The fish is oriented and placed perpendicularly against one of the sides of the aquarium and swims laterally or up and down as if trying to get out of the aquarium.

6. Bottom and surface immobility. The immobile fish touches the bottom of the aquarium with his belly or sword, or is immobile at the surface, for a period longer than *5* sec.

7. Feeding. The fish grazes on the sides of the aquarium, or feeds on the bottom or at the surface. When at the surface, it is not differentiated whether the fish effectively eats or skims.

8. Hiding. The fish hides himself or is already hidden behind the heater or the siphon of the filter.

9. Sexual following and surveillance. The male approaches the female from behind, hovers, and/or follows her as she usually responds by accelerating or by moving a short distance forward and then stopping.

10. Sexual butting. The male (more rarely the female) butts gently with the tip of his jaws (nibbles) either in the vent region, usually behind or between the pelvic fins, or on the front or the side of the head.

11. Sexual waltz. Epigamic display in the male. It consists of the male positioning himself in front of the female, as if presenting a barrier to further forward or sideward movement of the female, and/or then "waltzing" up, down, sideways, forwards or in-versely so as to maintain his station, transverse to the female's head (blocking). He may facultatively back up rapidly, sideways to her, bringing his body to lie side by side with that of the female (gliding). These movements are so rapid as to be difficult to follow with the eye. The presence of one of these elements (blocking and/or gliding) is noted as "waltz".

12. *Copulation attempt.* Usually following an epigamic display, the male swings his gonopodium forward and to the side nearest the female and then rolls his body away from the female at an angle of about 20 degrees. From this position, he makes forceful forward thrusts, aiming at the vent of the female.

13. Copulation. The two fish hover motionless with the gonopodium in the genital aper-ture for at least one second.

14. Acceleration. Possible response of a female to a courting male. The female clearly escapes the presence of the male by a rapid and prolonged acceleration away from him. Acceleration was arbitrarily distinguished from fleeing when it was

emitted by a female in response to a male.

15. Dotting. If the female responds by moving a short distance forward, not more than twice her own total length, and then stopping, her response to the male is noted as "dot-ting".

16. Changes of compartment. Each time a focal individual went from one compartment to the other, this action was noted as a special behaviour unit, specifying the destination.

') *Previous studies with this species have shown that the dominance decisions taken following the application of this criterion of 4 unilateral chases were disconfirmed only with a probability of P < 0.001 by continuing observations up to 10 unilateral chases (c.f.: Beaugrand & Beaugrand 1991).*

Size measurements

Before constitution of each group, the fish were immobilized on a sheet of paper in order to be measured with precision (1 mm). Two or three measures were taken according to the sex of the animal: 1) Body length: The distance between the snout and the extremity of the caudal fin. 2) Sword length: The distance between the extremity of the caudal fin and the sword end in the male. *3)* Flank width: The distance between the root of the dorsal fin and the origin of the gonopodium in the male and the vent in the female.

RESULTS

All generalizations presented here are based on results that are either self -evident or statistically significant (alpha = 0.*05).* Because there was a degree of mutual influence between the scores of different individuals within a population, and correlation between periods of observations ob-tained from the same population of individuals, tests for "correlated" measures were used when available. Six periods of observation were dropped from the analyses. In four cases one individual, considered at the start of the study as a female, matured into a male during the course of observations, and in two additional cases observations were in-complete due to errors in data transmission. A total of 50 observation periods were thus available for analysis.

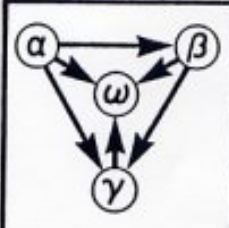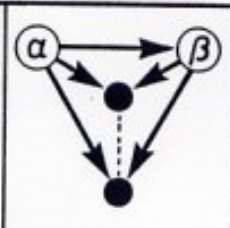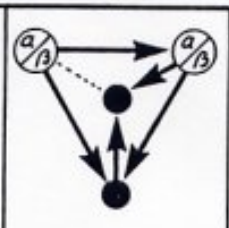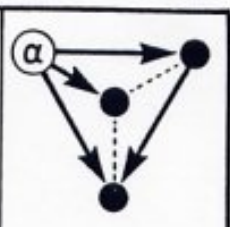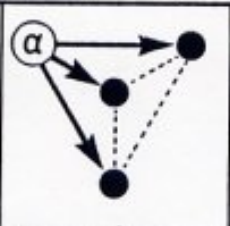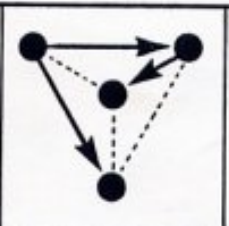*Occurrence of hierarchy types and of agonistic behaviour*
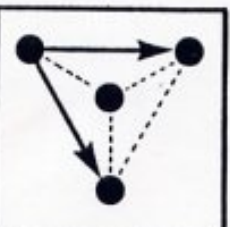
Table 1 presents the types of dominance orders that emerged from ag-gressive asymmetries obtained from observations after the application of the dominance criterion defined earlier. The most common type of hierarchy emerging from observations within sex subclasses was the true straight line type (transitive and complete), in which each individual dominated all others below it in rank. This represented 68% all obser-vation periods in males as compared to only 42 % *in* females. In several cases, observations did not permit inference of the existence of aggressive asymmetries between all intra-sexual pairs, and dominance orders were declared incomplete. An incomplete hierarchy is thus an order in which the positions of one or more individuals are still undetermined due to revolts, reverse chases, resistance, challenges, *etc. , or* to the absence or lack of a sufficient number of chases within an observation period, disallowing the attainment of the dominance criterion for all pairs.

Braddock's non straight line or triangular representation of intran-sitive dominance relationships were never noted. The emergence of true hierarchies departs significantly from equiprobability, with non true hierarchies in males ($X2 = 19.84, P < 0.01$), but not in females ($X2 = 0.43$, ns). Since the probability of obtaining, by chance alone, a complete linear structure or order between four elements is equal to *0.375,* the observation of *21* (i.e., *p = 0.42)* linear structures in female subclasses could be explained by chance alone. The despot males were neatly iden-tified in all *50* observation periods and both the alpha and beta males could be identified in *46* cases. Since *46%* of the orders emerging in females were either unstable or undefined in at least three out of a maximum of six possible asymmetries, one is tempted to conclude that the females are

ass structured than are the males in an heterosexual situa-tion. This is only an observer's point of view; female dominance structures could have relied on cues which the observer was not able to recognize as such.

TABLE 1

Frequencies of the various male and female dominance structures. The dominance relation between two individuals was obtained following the application of a criterion of four unilateral chases. A dotted line represents a missing asymmetry between two individuals. A black circle shows that it was not possible to infer the status of the corresponding individual. When two statuses are indicated within the same circle, it indicates that the concerned individual could have been of either of these statuses. In order to be declared alpha, an individual had to dominate all other individuals of the same sex in its population during a given period of observation.

ASYMMETRIES · unknown ------ missing asymmetries				
FREQUENCY FOR ♂♂	34	12	0	4
FREQUENCY FOR ♀♀	21	6	3	1
ASYMMETRIES · unknown ------ missing asymmetries				
FREQUENCY FOR ♂♂	0	0	0	0
FREQUENCY FOR ♀♀	5	2	3	9

In general, these results are not at variance with those of Cayron (1973) and Franck & Goldenbogen (1979). Cayron has worked on groups composed of three male *Xiphophorus helleri* and has found that 64% of the social structures were of the true straight line type, the rest being what she calls the "monarchistic" type, in which only one male clearly shows neat dominance relationships toward the two others. Franck & Goldenbogen (1979) have observed populations of six males and six females, as well as populations of eight male and eight female *Xiphophorus helleri*. They found that males were much more aggressive than females, which is confirmed by our results. In general, males were found to form linear structures in groups of six, but more non linear orders were noted in populations composed of eight fish. They also reported that orders were more frequently of the incomplete type in females than in males, again in agreement with the present results.

In the present study, green swordtail males did not assume the dominant position over the females as was reported for other poeciliids studied previously (Greenberg, 1947; Myrberg, 1972; Gorlick, 1976). Males and females apparently formed separate intrasexual hierarchies in all observation periods, and most (836 out of 939 occurrences) intersexual aggression involved females chasing males. In one case, a large female was observed killing a male; 392 of the 836 aggressive acts initiated by females toward males may be attributed to this particular interaction. Males engaged in sexual behaviour only with females, and directed ag-gressive behaviour almost exclusively toward other males.

Further detailed analyses of behavioural data in the present study will rely only on the observation periods of populations for which true straight line orders were obtained, i. *e.* 34 observation periods for males and 21 for females. Comparisons between sex subclasses will rely on the 16 observa-tion periods for which both females and males of the same population in-dependently formed true straight line orders.

The hierarchical structure of green swordtails kept in the laboratory condi-tions of the present study appeared to be based on chase right rather than the nip right relationships described for *X. maculatus* by Braddock (1945).

Fig. 2. Mean number of butting behaviours per observation period. Along the line extending from each fish are arrows pointing toward other fish either down the isosexual hierarchy and intersexual subgroup, or up the isosexual hierarchy or intersexual subgroup. The thickness of each arrow is directly proportional to the mean number of behaviours initiated by this type of individual toward the pointed one. In males and in females means are respectively based on 34 and 21 observation periods while intersexual means are based on the 16 observation periods for which complete hierarchies were obtained for both males and females.

First of all, nipping as described by Braddock (1945, p. 178) consisted of a quick bite, involving no noticeable harm to the fish bitten, and was directed upward and toward the ventral surface of the fish being nipped. This pattern as defined above was very rarely observed in the present study. We have observed it in previous studies done on the process of establishment of dominance orders in X. *helleri, i.e.* during fights for the establishment of dominance status, together with attacking and vicious biting (unpublished observations). In nipping, the target fish offers physical resistance to the contact. Once the dominance order is estab-lished between a pair, the superior individual shows the right to chase or drive away its subordinate, not to nip it. A chase implies one aggressive act, initiated by one individual, and is presumably responded to by flight and/or the adoption of a defensive posture on the part of the chased in-dividual. After several days, subordinates become well trained to retreat as soon as the superior moves in their direction. As a result, the dominant fish rarely physically touches its subordinates. A "chase order" (or "drive order" as suggested by Greenberg (1947) for *Lepomis cyanellus)* rather than a "nip order", as initially shown by Braddock (1945) for *X. maculatus,* would rather more rigorously correspond to what is observed in reality. A similar observation was made by Myrberg (1972) in a study on bicolour damselfish. He preferred to maintain the nip dominance rather than the chase dominance terminology for reasons of

coherence with the usage of previous authors. Butting, which is a motor pattern very similar to nipping, occurred very frequently in our fish, but was mostly associated with sexual behaviour, at least in males. Butting, done by males to females, consists in applying mouth parts or even the tip of the jaws (nibbling) either in the vent region, usually behind or between the pelvic fins or on the front or the side of the head of the female, to which the female may respond by dotting or acceleration. Butting done by females to males is usually more vigorous. Mouth parts are applied against the head (side or front) or on the flank, to which the male may respond by resisting, tilting or fleeing. This more readily corresponds to the definition of a nip. Individual means for butting or mouth contact behaviours are presented in Fig. 2. As can be seen, butting was a rather infrequent motor pattern within male and female subclasses. Following Hemens (1966), butting was con-sidered by the present study on X. *helleri* as a sexual behaviour, preliminary to copulation attempts in males, and sexually inciting when initiated by females toward males.
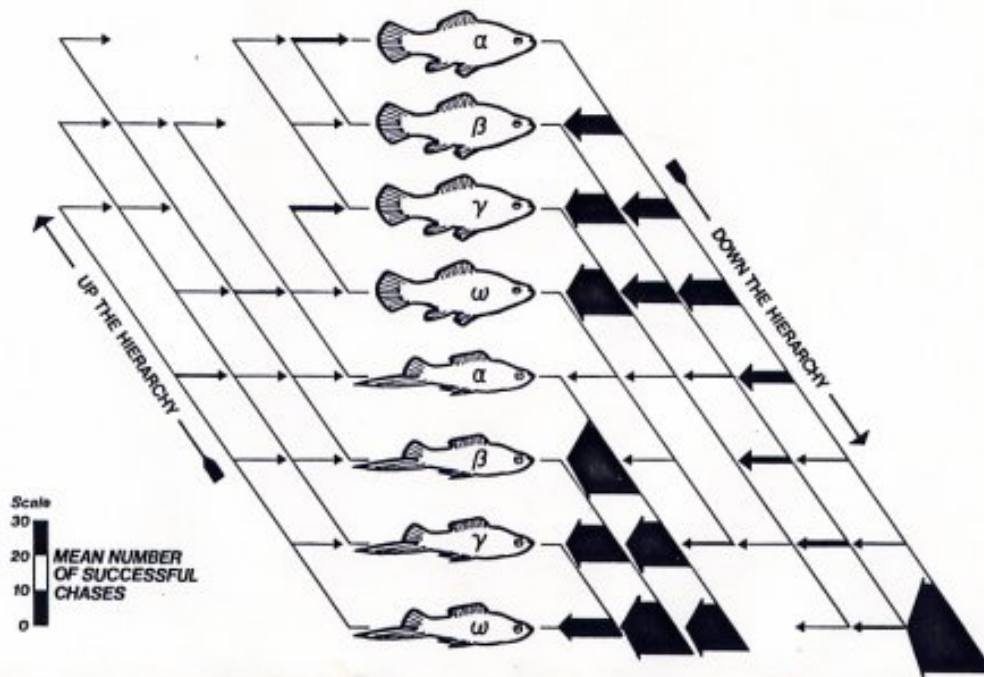
Fig. 3. Mean number of chases per observation period initiated by each individual. See Fig. 2 for further explanations.

Successful chases initiated by each individual are presented in Fig. 3. As can be seen, aggressive and approaching behaviour successfully followed by defensive behaviour on the part the target fish is mostly found to the right of the diagonal of each sex subclass, supporting the ex-istence of a chase right rather than a chase dominance in our fish. Fig. 4 presents aggression that was not followed by defensive behaviour on the part of the target fish. As shown in these figures, reverse chases (up the hierarchy) and unsuccessful attempts at rebellion were rather infrequent-ly noted. They represent less than 2 % of all chases and less than 5 % of all challenges. They were the result of yet unsettled disputes, of true rever-sals occurring during observation periods, of errors in encoding and also, probably, of errors in identification on the part of the fish. If we use the criterion of four successful, asymmetrical chases to decide, for each pair, which individual dominates the other, only two clear reversals of dominance status occurred within a given observation period during the total 100 hours of focal observation. Unsuccessful attempts at rebellion and resistance to a challenging or attacking superior were also noted. In males (N = 34 observation periods), this resistance was mostly directed toward the despot of the group (see Fig. 4).

Fig. 4. Mean number of aggressive behaviours not followed by de-
fensive behaviour on the part of the target fish. See Fig. 2 for
further explanations.
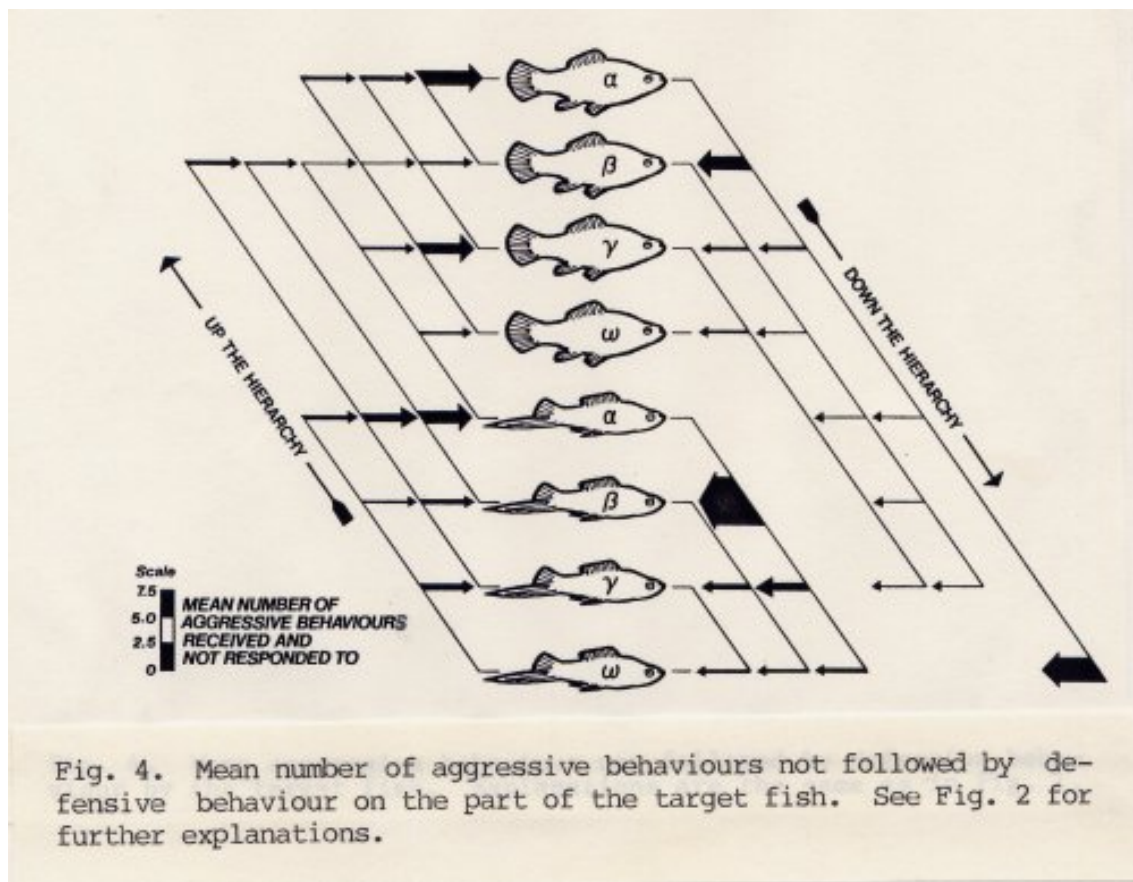
In females (N = 21 observa-tion periods), the same pattern was apparent. In general, however, subordinates did not necessarily rebel against their immediate superior but distributed rather evenly their resistance. Individual mean frequencies and proportions of aggressive behaviour are presented in Fig. 5. Frequencies of superiority were also obtained for each behaviour. They correspond to the frequency with which a given in-dividual type (e.g. alpha) was noted to have more frequently initiated the corresponding behavioural unit than rivals of the same sex in his own population, for one observation period. Spearman correlation coefficients between the corresponding unit and rank in the dominance structure are also presented. As suggested by Fig. 5a, aggression between males was characterized by the alpha male more frequently initiating the offensive (attacking, biting) and challenging (lateral display and tail beating) behaviour than any other male of the group. Alpha males were responsi-ble on the average for 49.2 (61.7 %) aggressive units while the beta were responsible for only 28 (26.7%). Differences in total frequencies of ag-gressive behaviour between the four rank orders in males all reached significance (min $t = 3.02$, $df = 66$, $P < 0.01$) and mean frequencies were proportional to the corresponding hierarchical status of the initiating in-dividual. The correlation between the individual total frequencies of ag-gressive behaviour and individual rank in the hierarchy in males reached statistical significance ($r = 0.68$, $df = 136$, $P < 0.01$). Alpha males had more frequently (70 %) the neat superiority in total frequency of ag-gressive acts initiated against their rivals than any of the subordinates. Beta males had superiority in 30% of the observation periods and the two lowest individuals had superiority in none of the periods. The alpha females were more frequently aggressive than subordinates (min $t = 2.02$, $P < 0.05$), while the beta and gamma ones seemed to be equally ag-gressive ($t = 1.67$, ns) and the omega females appeared significantly less aggressive than their superior rivals of the same sex (min $t = 2.89$, $df = 40$, $P < 0.01$). In female subclasses, initiated aggressive behaviour was proportional to rank, the alpha female having superiority in 48 % of the cases. A significant correlation was also found between the position occupied in the female hierarchy and the number of chases received ($r = 0.68$, $df = 84$, $P < 0.001$), females lower in the hierarchy more fre-quently responding to aggressive behaviour by flight than superior ones. This also applies to total aggression received ($r = 0.66$, $df = 84$, $P < 0.001$). As mentioned above, males chasing females were rarely seen. Most social behaviour initiated by males toward females were of the butting or mouth contact type (Fig. 2) or of the clearly sexual type (Figs. 3 and 6). Females offending and chasing males were more frequently seen, even if we except the case of a female killing a male. No systematic relation seemed to exist in the present study between the hierarchical position of a female initiator and a male receiver of aggressive behaviour. Reverse of-fences and challenges also occurred within sex subclasses. As shown by Fig. 3, successful chases up the hierarchy (subordinate chasing superior) were very rarely noted. Finally, the alpha males and none of the four females were ever observed hiding

behind the heater or siphon of the filter in the small compartment, contrary to the three subordinate males. As illustrated by Fig. 5, these males hid in direct proportion to their rank in the hierarchy.

BEHAVIOURAL UNIT	MEAN # PER OBSERVATION PERIOD				PATTERN TO 5% T TESTS	CORRELATION WITH DOMINANCE POSITION
♀♀ N=21						
CHALLENGES INITIATED	1.5	1.6	0.7	0.7	a = b = c = d	0.14
CHALLENGES RECEIVED	0.9	1.8	1.3	0.5	a = b = c = d	0.06
OFFENSES INITIATED	41.6	18.2	13.4	2.3	a>(b = c)>d	0.27**
OFFENSES RECEIVED	2.0 6.2	14.7	25.6		a < b < c < d	−0.66***
TOTAL AGGRESSION INITIATED	43.0	20.0	14.1	3.1	a>(b = c)>d	0.28**
TOTAL AGGRESSION RECEIVED	2.9 8.0	16.1	26.1		a < b < c < d	−0.62***
CHASES INITIATED	40.5	19.0	14.0	2.0	a>(b = c)>d	0.29**
CHASES RESPONDED TO	1.4 6.3	15.3	26.8		a < b < c < d	−0.68***
♂♂ N=34						
CHALLENGES INITIATED	8.5	2.8	1.5	0.9	a>(b = c = d)	0.36***
CHALLENGES RECEIVED	1.7	6.7	2.9	2.3	a<(b = c = d)	0.32
OFFENSES INITIATED	40.6	25.5	5.5	1.2	a > b > c > d	0.66***
OFFENSES RECEIVED	3.3 18.3	22.0	44.2		a<(b = c)<d	−0.35***
TOTAL AGGRESSION INITIATED	49.2	28.2	7.0	2.2	a > b > c > d	0.68***
TOTAL AGGRESSION RECEIVED	5.1 25.0	24.9	46.6		a<(b = c)<d	−0.34***
CHASES INITIATED	45.5	26.8	5.9	1.1	a > b > c > d	0.69***
CHASES RESPONDED TO	2.6 20.5	24.6	46.3		a<(b = c)<d	−0.40***
HIDING	0 1.0	2.2	3.4		a <(b = c)<d	−0.40***

α   β   γ   ω

CORRELATIONS
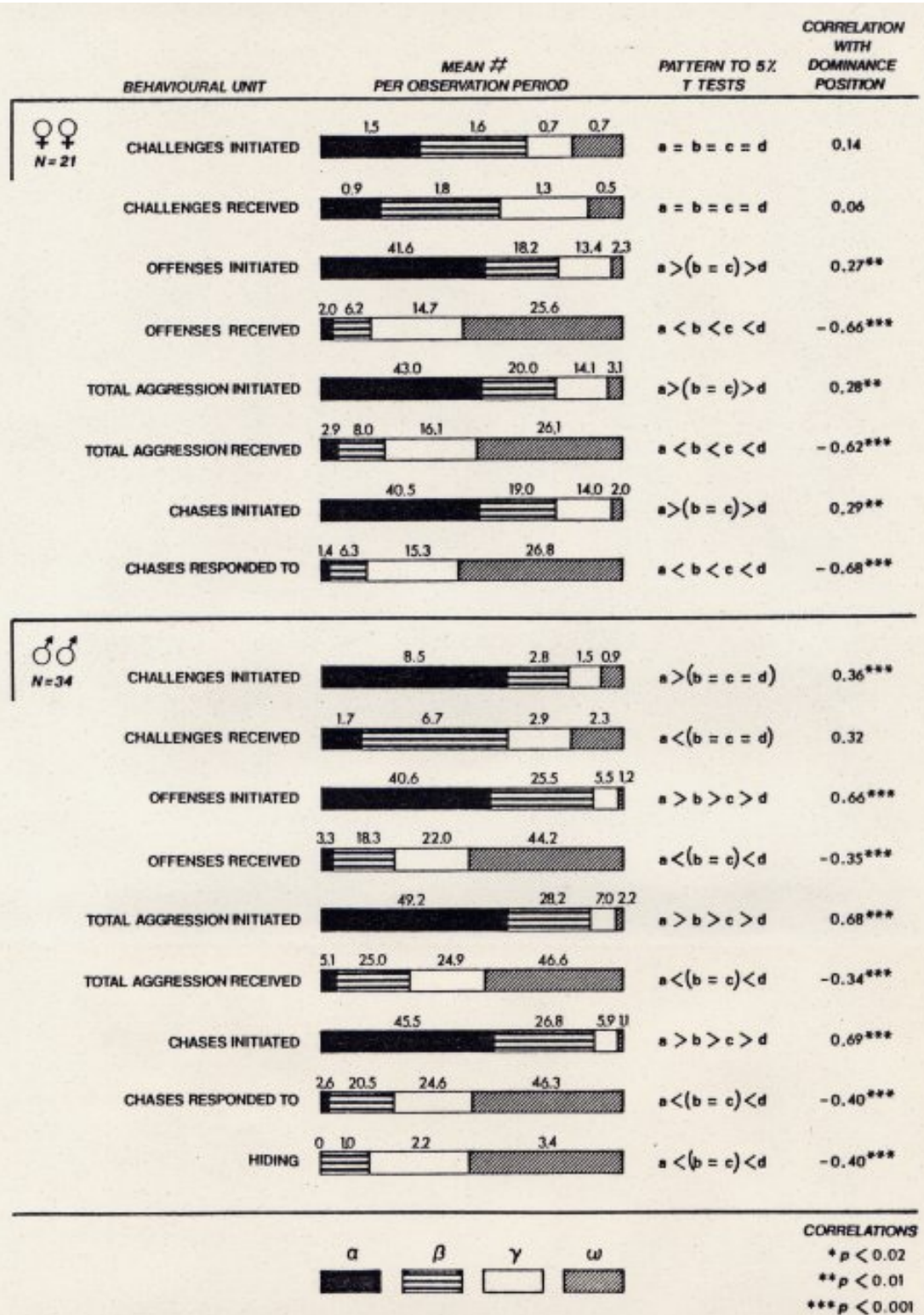*p < 0.02
**p < 0.01
***p < 0.001

Fig. 5. Mean frequency and proportion of aggressive behaviours. For each behavioural unit, the mean frequency of occurrence is presented. The length of each bar is proportional to the relative frequency with which each individual status-type either initiated or received the unit concerned. Pair comparisons between each of the status-types were done using t tests, and the patterns of difference at a 5% level thus obtained are presented together with the correlation (Spearman's Rho) of the behavioural unit and the corresponding dominance position in the hierarchy. A negative

coefficient of correlation indicates the existence of an inverse correlation between the frequency (or duration in certain cases) and the corresponding individual position in the hierarchy.

Epigamic behaviour

Clark & Aronson (1951), Barends et al. (1955), and Liley (1966) have established that a small percentage of gonopodial thrusts and short con-tact attempts in some poeciliids were in fact successful inseminations, a relatively small amount of sperm being transferred to the female. Farr (1980) has also demonstrated that the primary factor influencing male mating success in guppies was the frequency, relative to that of other males, with which males courted females, for males which more frequent-ly court females have a higher probability of encountering a receptive female and are preferred by females. Therefore, in the present study, we reasoned that the frequency of all epigamic behaviour, obtained from the records of each male and female, could provide an index of sexual activity in males and of sexual appetence in females, and of possible reproductive success.
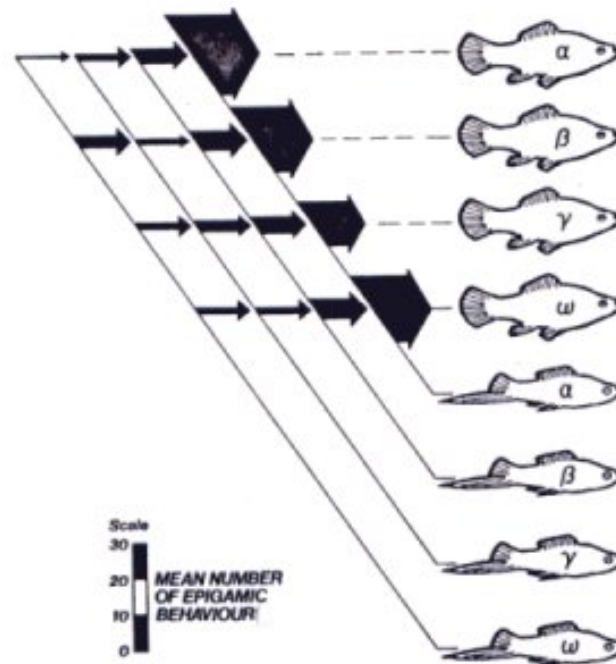

Fig. 6. Mean number of epigamic behaviours. See Fig. 2 for further explanations.

Distribution of epigamic behaviour initiated and received by the various individuals is presented in Figs 6 and 7. As can be seen from these figures, the alpha male was much more sexually active than rivals; in general, however, the total number of epigamic acts was related to rank in males (r= 0.60, P < 0.001). The alpha male showed superiority in courting the females in 81 % of the observation periods retained, and had privilege in attempting insemination (and eventually transferring

sperm).This superiority of the alpha males increased to 85 % when all 50 periods of observation were considered. Only one true copulation was noted during the 200 hours of focal and unrestricted observation. The mean frequency of male epigamic displays was superior for the alpha in-dividuals (84.8 acts) over all other males (21.4, 8.0 and 7.5) (min t = 7.60, df = 66, P < 0.001). The beta males, on the average, also in-itiated significantly more behaviours of this category than their gamma and omega rivals (min t = 4.12, df = 66, P < 0.001). The alpha individuals were also found to have much more frequent superiority within their populations in the initiation of sexual following, butting and waltzing than the three male subordinates. Copulation attempts were infrequently noted, compared to sexual following, butting and waltzing. However, in the eight out of 12 populations in which this pattern was once or more fre-quently observed, the alpha males had superiority in the initiative. In females, no regular sexual pattern seemed to emerge (Fig. 7). Females were not preferentially courted or receptive to male courtship according to their position in the hierarchy. Crow & Liley (1979) have demonstrated that there is a chemical factor associated with the behaviourally receptive period in female guppies. The fact that, in the present study, no significant correlation was found between positions in the dominance structure and frequency of epigamic behaviour received by females suggests that position in the hierarchy and sexual receptivity (as measured by the preference showed by males) were controlled by in-dependent factors.

Spacing patterns

Spacing patterns were first studied using individual positions obtained at 15 min intervals during observation periods for the 16 periods in which both male and female hierarchies were complete. Individual cartesian coordinates obtained from the samples taken at each 15 min interval were transformed into Euclidean distances between subjects, and the resultant daily mean matrices were submitted to multi dimensional scaling using KYST (Young, 1970). A one dimensional representation reached a satisfactory stress of 0.10. A three dimensional representation was chosen to be presented in Fig. 1 for the sake of visual clarity (final stress of 0.01). This figure strongly suggests that the eight fish can be divided into two different groups: the alpha male and the four females form a first group in the large compartment, while the three subordinate males form the second group in the small compartment. The fact that multidimensional scaling successfully collapses, without too much stress, the original three dimensions into two, and finally into a single one, suggests that distances within the dimensions of height and depth of the aquarium are not very important. Individual positions can be best resumed into a single dimen-sion, representing most realistically the length of the aquarium, i. e. oc-cupation of the small compartment as occupation of the large one.
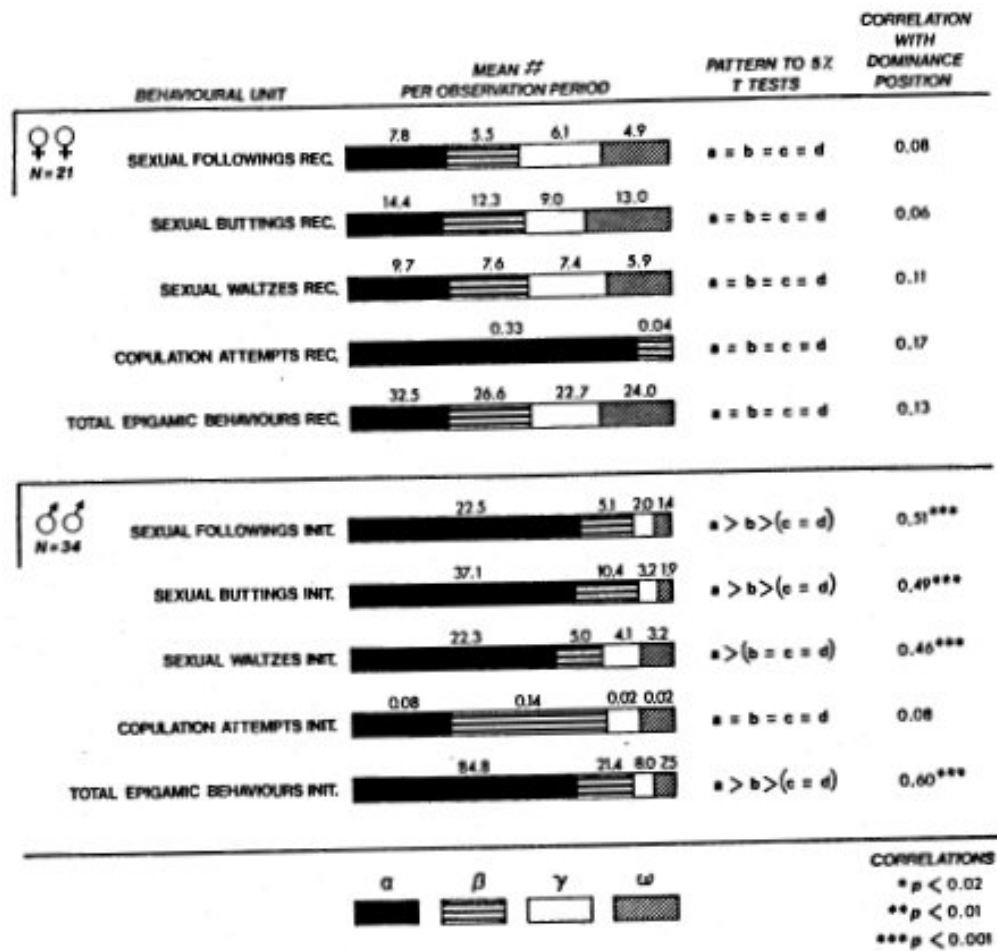
Fig. 7. Mean frequencies and proportions of epigamic behaviours initiated by males (a) and received by females (b). See Fig. 5 for further explanations.

This preliminary description of the data gains support from more specific analyses of the results. Firstly, as shown by Fig. 8, alpha males and all females were significantly more frequently seen (max 8) in the large compartment at sampling time. The large compartment of the aquarium was twice as large as the small one; so, the probability of being there at the moment of sampling was equal to p = 0.66. It was found that the alpha males and the females were in the large compartment more often than predicted by chance ($X2 = 42.82$, df = 4, P < 0.0001), while the other males were more often seen in the small compartment ($X2 = 275$, df = 2, P < 0.0001). All four females were more often seen in the large compartment of the aquarium (min Z = 9.05, P < 0.001) than in the small one. These results are confirmed by the total time spent in the large com-partment by each of the eight individuals during their respective 15 min focal observation period. On the average, the alpha individuals spent 10.5 out of 15 min in the large compartment (see Fig. 8) while the three other males spent in that same compartment, on the average, no more than 4.8 min during the same period. This difference between the alpha males and the other three males was found to be statistically significant (min t = 6.36, df = 66, P < 0.001). The three subordinate males were not different, among themselves, in this respect (max t = 0.27, ns). The alpha males spent more time in the large compartment than did their rivals in 70 % of the observation periods (N = 34) as opposed to 10 % for the beta individuals ($X2 = 54.16$, P < 0.001). Although the four females also spent most of their time in the large compartment (average 11.6 min), there are differences between the various females according to their rank. For ex-ample, the alpha females spent more time in the large compartment than beta and omega ones (min t = 2.18, df = 40, P < 0.036), but not more time than the gamma (t = 1. 22, df = 40, ns). The fact that no female was found more often in the large compartment at sampling time and that no rank had more frequent superiority in this respect over other ranks within the various populations ($X2 = 2.258$, ns), suggests that these differences in total time are not reliable. Nevertheless, the correlation between total time spent in the large compartment and rank in the female hierarchy reaches significance (r = 0.23, df = 84, P < 0.02).

BEHAVIOURAL UNIT	MEAN # PER OBSERVATION PERIOD	PATTERN TO 5% T TESTS	CORRELATION WITH DOMINANCE POSITION
♀♀ N=21 TOTAL TIME IN LARGE COMP. (max 15 min.)	13.7 10.4 12.0 9.3	a > (b = c = d)	0.23 *
FREQUENCY OF TRANSIT (for each 15 min. sample)	1.5 2.7 1.9 2.1	a = b = c = d	-0.06
M̄ NUMBER OF ♀♀ AT PROXIMITY	2.2 1.8 2.1 2.0	a = b = c = d	0.00
M̄ NUMBER OF ♂♂ AT PROXIMITY	1.7 2.0 1.8 1.8	a = b = c = d	0.07
M̄ FREQUENCY IN LARGE COMP.	7.1 5.5 6.3 5.6	a = b = c = d	
♂♂ N=34 TOTAL TIME IN LARGE COMP. (max 15 min.)	10.5 4.4 4.4 4.8	a > (b = c = d)	0.32 ***
FREQUENCY OF TRANSIT (for each 15 min. sample)	6.0 3.8 2.8 2.8	a > (b = c = d)	0.26 **
M̄ NUMBER OF ♀♀ AT PROXIMITY	2.7 1.4 1.8 1.6	a > (b = c = d)	0.32 ***
M̄ NUMBER OF ♂♂ AT PROXIMITY	1.0 1.6 1.7 1.8	a < (b = c = d)	-0.48 ***
M̄ FREQUENCY IN LARGE COMP.	6.1 2.1 2.4 2.0	a > (b = c = d)	
M̄ FREQUENCY IN LARGE COMP. WITH 3 - 4 ♀♀ AND NO OTHER ♂	3.1 0.1 0.1	a > (b = c = d)	
M̄ FREQUENCY IN SMALL COMP. WITH 3 ♂♂ AND ≤ 1♀	0.5 3.4 3.5 3.6	a < (b = c = d)	

α   β   γ   ω

CORRELATIONS
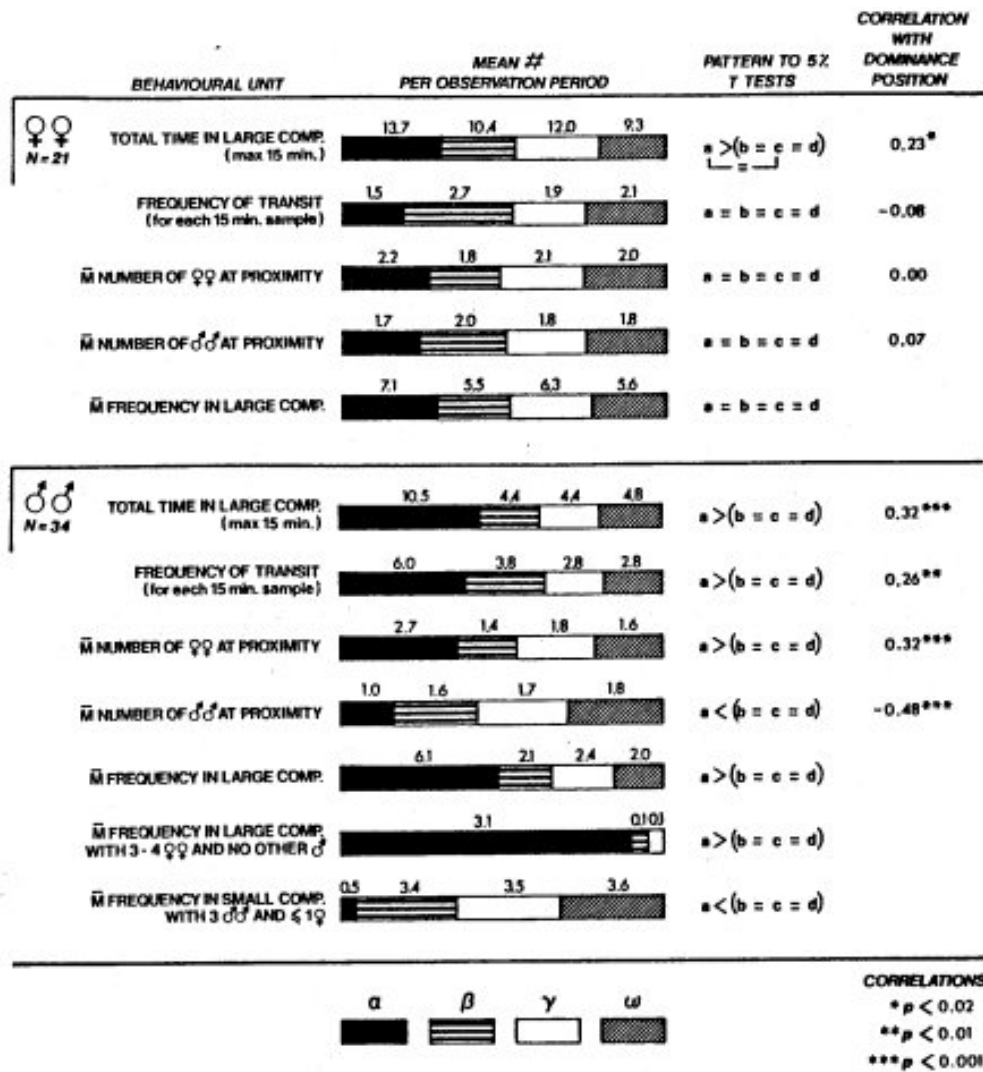* p < 0.02
** p < 0.01
*** p < 0.001

Fig. 8. Mean values and relative individual status proportions for several behavioural units related to the utilization of space. Explanations are presented in the text and in Fig. 2.

It was also found that the alpha male had, more frequently, exclusive access to 3 4 females in the large compartment, without any male com-pany (Fig. 8). In addition, the beta, gamma and omega individuals were more frequently seen together in the small compartment with less than two females, than they were in the situation of having exclusive access to 3 4 females in the large compartment (X2 = 8.669, df = 2, P = 0.01). An toward the small one. In 204 cases (83 %), the initiator was the alpha in-dividual, while only 30 (4%) were initiated by the beta. The difference reaches statistical significance and suggests that the alpha males more fre-quently actively defended the larger space than rivals did. If one con-siders the compartment where each male has spent more than 8 min dur-ing one observation period as his "residence" area (Table 2b), it is found that 89 chases were in fact initiated from a compartment in which the alpha individual did not have "residence". This suggests that the chased individual escaped the presence of the alpha male rather than a specific "territory". But, one cannot discard the hypothesis that the whole aquarium was the "territory" of the alpha male.

A similar analysis was done for aggressive excursions. An aggressive excursion had to satisfy the following sequence of events: a male in-dividual had to go to the other compartment, aggress, at least once, one or more male rivals already there, and come back to the original com-partment within 60 sec. As can be seen from Table 2c, most aggressive behaviour qualifying as aggressive excursions were initiated by the alpha male and were directed from the large compartment of the aquarium to the small one. The beta individual received 54% of these alpha aggres-sions.

As a conclusion on spacing patterns, the following regularities were supported by the data: Firstly, the alpha males spent most of their time in the large compartment with a majority of females while their three subor-dinate rivals stayed together in the small compartment, without females. Secondly, the alpha males more frequently actively defended the large compartment of the aquarium than rivals did. Thirdly, the alpha males more frequently initiated aggressive excursions into

the small compart-ment than male rivals did.

TABLE 2

Frequency of active defences and of aggressive excursions. In (a), only the compartment where the chase was initiated and where it terminated was taken into account. In (b), the compartment where each male had spent more than 8 min during one observation period was considered as its "residence" area. Frequency of aggressive excursions are presented in (c).

(a) ACTIVE DEFENCES

	INITIATOR				
	α	β	γ	ω	
FROM LARGE TO SMALL	204	30	8	3	245
FROM SMALL TO LARGE	83	68	10	4	165
	285	98	18	7	410

(b) ACTIVE DEFENCES AND RESIDENCE

	INITIATOR				
	α	β	γ	ω	
FROM RESIDENCE	198	86	18	7	309
FROM NON-RESIDENCE	89	12	0	0	101
	287	98	18	7	410

(c) AGGRESSIVE EXCURSIONS

	INITIATOR				
	α	β	γ	ω	
FROM LARGE TO SMALL	155	8	1	0	164

FROM SMALL TO LARGE	8	2	5	2	17
	163	10	6	2	181

Diversity of the behavioural repertoire

It has frequently been suggested that the already, or eventually, more dominant individual in a population or a pair of animals, has a less stereotyped and predictable behaviour than do subordinates (Hazlett & Bossert, 1965; Dingle, 1969; Frey & Miller, 1972; Barlow, 1968; Zayan, 1975a). In order to test the existence of such a regularity in our data, an index of the variability of the individual repertoire was calculated. This index was obtained by counting the number of different categories of behaviour that were used by an individual, including alimentary and hiding behaviour. Social categories were given a weight equal to the number of different individuals in the population to which this behaviour had been addressed during an observation period. Also, the total number of behavioural acts initiated by each individual was calculated, including agonistic and epigamic behaviour, as well as alimentary and hiding behaviour, and the number of transits done by each individual during an observation period. These measures are graphically illustrated in Fig. 9. It was found that superior individuals displayed a behavioural repertoire which was more diversified than was that of subordinates, in the number of distinct motor patterns used, in the frequency with which they were used, and in the variety of conspecifics to which the social behaviour was addressed. In males, except between the gamma and omega fish types, all ranks differed in their index of diversity (min t = 5.85, df = 66, P < 0.01), the fish higher in the hierarchy having the higher scores (r = 0. 74 with rank order, P < 0.001). In addition, in 85 % of the observation periods the alpha male had a higher index of diversity. The alpha male was also the most active individual of the group (min t = 5.33, df = 66, P < 0.001) and the one that most frequently tran-sited from one compartment to the other (min t = 3.30, df = 66, P < 0.001), while still totaling a longer time period spent in the large com-partment (min t = 5.90, df = 66, P < 0.001). In general, the level of activi-ty of the four males was related to their hierarchical status (r = 0. 70, P < 0.001). In 77 % of the observation periods, the alpha male still was the most active individual in its own male subclass ($x2$ = 77.48, df= 3, p<0.001).

Superior females in the hierarchy were also found to have a more diversified repertoire than inferior ones and addressed their behaviour to a greater number of different individuals, including males. Although the difference in the index of diversity between the alpha and beta females did not reach significance (t = 1.36, ns), both were superior, in that respect, to the two lowest individuals of the hierarchy (min t = 3.21, df = 40, P < 0.003) and the correlation between the individual coefficient of diversity and the corresponding rank in the hierarchy was found to be statistically significant for females (r = 0.64, P < 0.01). A significant cor-relation was also found between the total number of behavioural units in-itiated by a female and her position in the hierarchy (r = .36 with rank order, df = 84, P < 0.01). The alpha female was also found to be more ac-tive than subordinates (min t = 2.96, df = 40, P < 0.001). These results were confirmed by analysing the superiority frequencies ($x2$ = 15.0, df = 3, P < 0.01). The beta and gamma individuals were not found to be different between themselves in this respect (t = 0.16, ns).
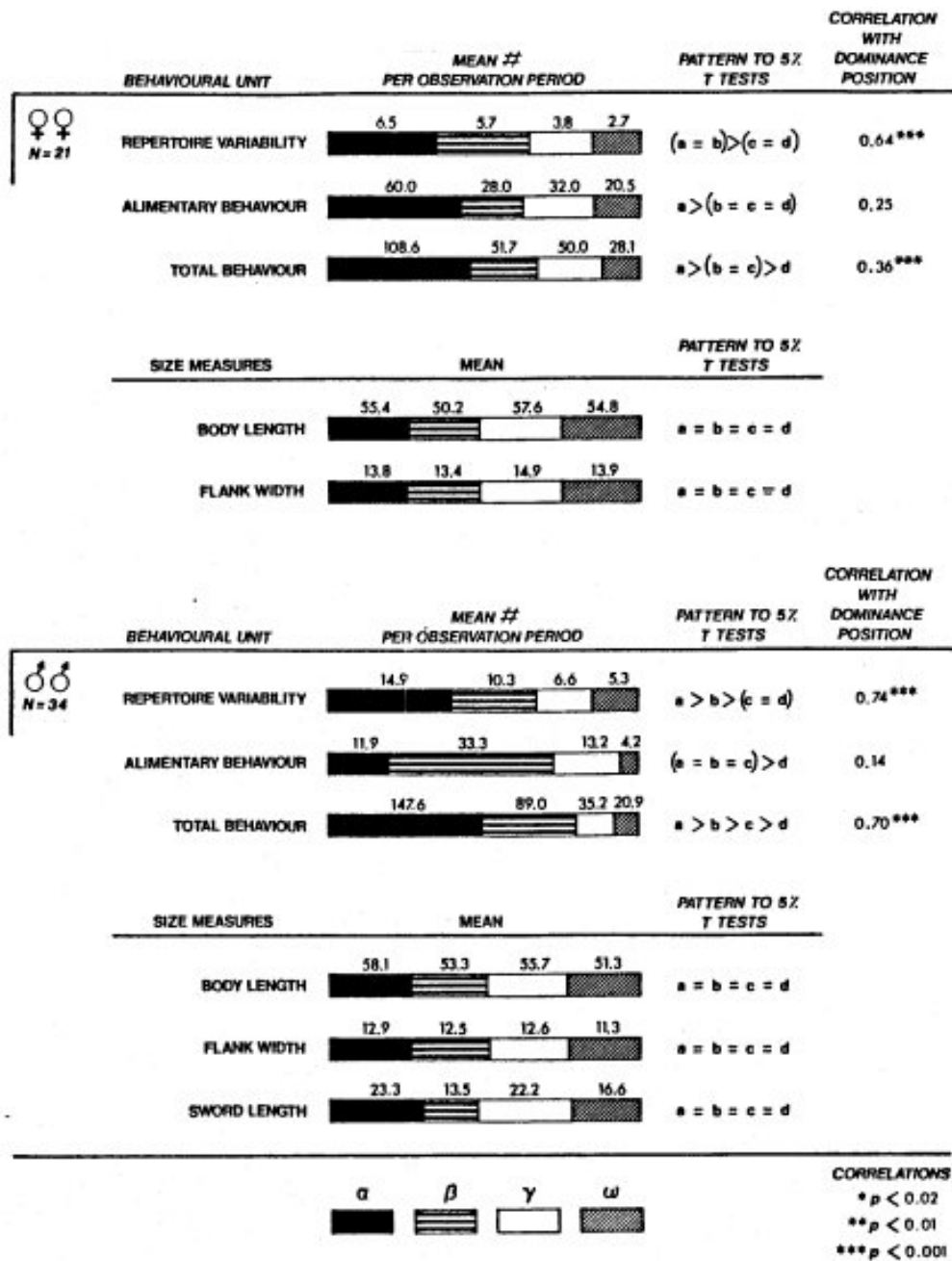
Fig. 9. Mean values for repertoire variability, alimentary behaviours, total number of behaviours and size measures. Size measures are in mm. Further explanations may be found in Fig. 2.

Size, dominance status and received epigamic behaviour

It is a well accepted fact in ethological literature that differences in size, strength between opponents constitute the decisive factor in the outcome of aggressive duels in animals. In experiments simultaneously introduc-ing two or more fish to an unfamiliar milieu, it can be predicted that the larger individual will occupy a higher hierarchical position than will smaller individuals. This conviction is well established for several species of Teleost (Noble & Curtis, 1939; Greenberg, 1947; Braddock & Braddock, 1955; Newman, 1956; Huck & Gunning, 1967). It is known since the works Of Zayan (1974, 1975a, 1975b, 1975c, 1976) and of Beaugrand & Zayan (1984) that dominance relationships between *Xiphophorus helleri* fish of about the same size mostly depend upon previous ecological and social experiences related to dominance or sub-mission and familiarity with conspecifics or the given space, or to Isola-tion, and not especially on size differences. In the present research, size was not controlled and we were legitimately expecting that differences in size would explain social order within sex subclasses. The basic 16 in-dependent populations of eight individuals settled upon in this research were thus used to study the relation between size differences and position in the dominance structure revealed. Mean size

measures and their stan-dard deviations are presented in Fig. 9. Multiple comparisons have revealed that superior individuals in the hierarchy were not significantly larger than subordinates (max t = 1.09, P < 0.28). This holds true for both males and females. If we compare superiority measures, it is found that alpha males are more frequently the larger individuals in their populations in body length (9 out of 16) and flank width (8.3 out of 16), but not in sword length (6 out of 16). In females, no systematic pattern emerges for superiority in body length and flank width that could not be explained by chance alone. A tentative conclusion on size measures, would be that individuals that are larger in body length tend to occupy higher ranks in male hierarchies but not in female ones. That fact can be explained by the play of different factors such as, for females, their posi-tion in the breeding cycle. It is possible, as first suggested by Noble & Borne (1938), that hierarchical position in females is related to the breeding cycle. Clark *et al.* (1954) have also found that female receptivity in X. *helleri* affected copulation frequency in males. The fact that we did not find any systematic relationship between epigamic behaviour re-ceived by the females and their momentary position in the hierarchy does not support the hypothesis of the existence of a relation between position in the hierarchy and female receptivity. In addition, no systematic cor-relation was found between the size of the female and the frequency of epigamic behaviour received from males, as is known to exist in guppies (Barends *et al., 1955),* in sculpins, *Cottus bairdi,* (Downhower & Brown, *1981)* and in *Gasterosteus aculeatus* (Rowland, *1982).* In the present study, the correlation found between rank order in females and size measures were respectively of r = 0.*12* for body length and r = 0.10 for flank width.

Alimentary behaviour

The correlation between rank order in males and alimentary behaviour was not significant (r = 0.*14,* Fig. *9),* suggesting that rank in the hierar-chy was not systematically associated with the privilege of eating more frequently. Although Fig. *9* suggests that individuals having the beta rank ate more frequently than all male rivals, this difference in total fre-quencies was not statistically confirmed by further analyses done on the original frequencies of superiority in eating behaviour for the *34* observation periods. When the analyses are done on the *46* observation- periods for which both alpha and beta individuals were clearly identified, this impression is confirmed (min t = 1.*97,* df = 90, *P < 0.05).* In *17* out of *46* observation periods, the beta individual ate more frequently in his own population than male rivals, but this superiority did not reach statistical significance (X2 = 5.*16,* ns). Our results do not unequivocally support the hypothesis that the beta individual, in eating more frequently than the despot, prepares himself to overthrow him. Females having the alpha rank were responsible for *42 % of* all eating behaviour. When analyses were based on superiorities in their own population on a given observation period, it was found that the alpha and beta individuals were more often superior to their omega and gamma rivals than explainable by chance alone, and that the alpha females were even more highly superior to the betas in that respect (overall X2 = 12.*33,* df = 3, *P < 0.001).*
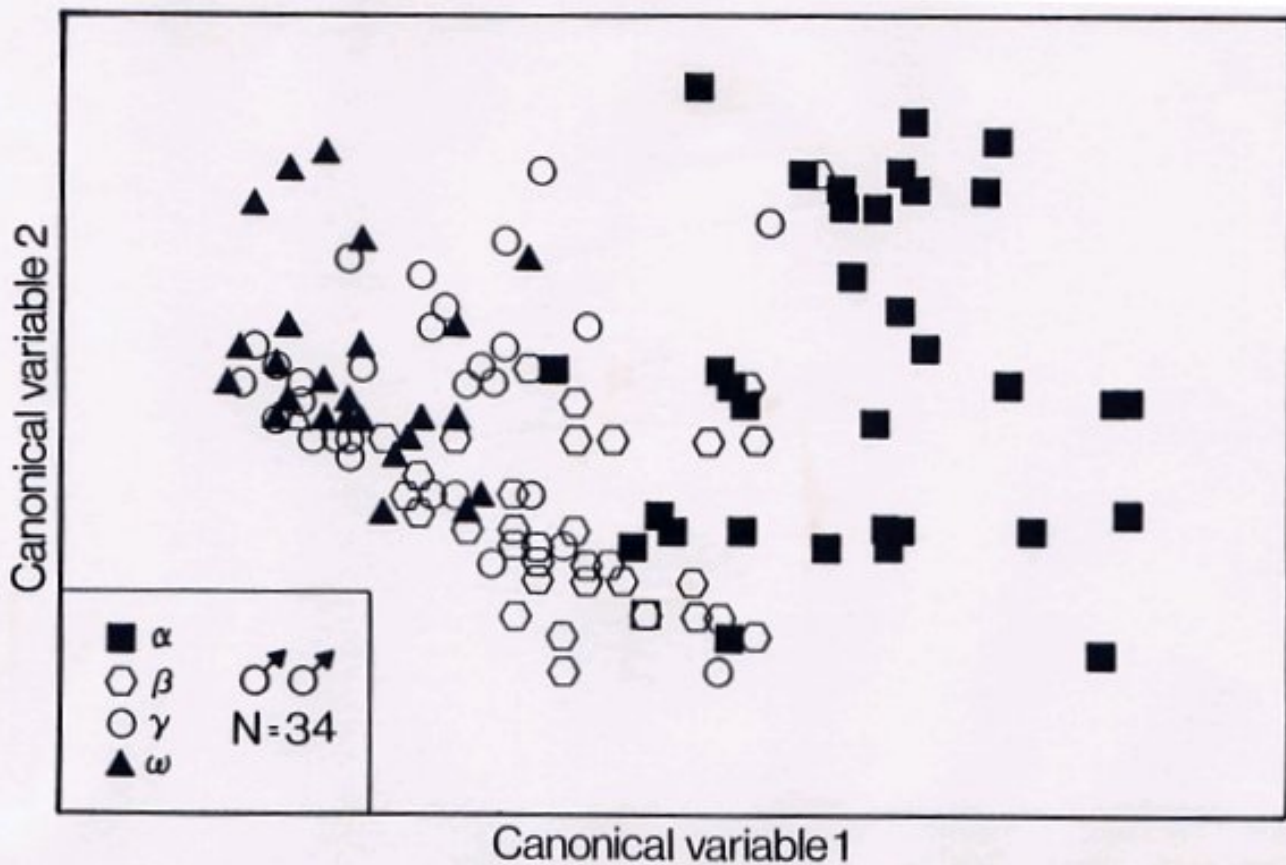
Fig. 10. Plot of individual male cases against the two canonical variables best correlated to repertoire variability, frequency of initiated (successful) chases, frequency of epigamic behaviour and relation of co-occurrence in the large compartment together with females.

Factors related to dominance

What are the factors most closely related to the position in the dominance order held by males and females? Several factors are well cor-related with the position in the dominance structure of females and that of males. In males, it seems that the coefficient of diversity of the reper-toire (r = 0. *74), frequency of chasing behaviour (r = 0.69),* and the fre-quency of epigamic behaviour (r = 0.61) are all significantly correlated to rank. We also have seen that staying in the large compartment with a majority of females was related to position in the male dominance structure. This social and spatial pattern was translated into a quantitative variable by taking, for each male, the ratio between the number of females and the number of males present with him in the same compartment at sampling time, and by giving a greater weight to the ratio when co-occurrences happened in the large compartment than when they happened in the small one. As expected, the resultant ratio was significantly correlated to rank (r = 0.53, P < 0.001), with males higher in the dominance structure having a larger ratio. When this factor, and the four previously mentioned, were simultaneously included in a regression analysis, they explained 67 % of the observed variance. Using discriminant functions, obtained through a stepwise procedure, these factors can be used to correctly classify 74.4% of the alpha males in their proper alpha category (jacknife technique). Individual male cases are plotted in Fig. 10 against the canonical variables to which these five factors are best correlated. Canonical variable 1 is the linear combination of the five variables that best discriminate among the various statuses (largest oneway ANOVA F), the second canonical variable is the next best combination of variables orthogonal to the first one. The first canonical axis accounted for most of the total variation (74%) and had an eigenvalue of 2.73. In contrast, the second

axis had an eigenvalue of .22 and accounted for only 17 % of the variation, and added little discriminatory power to the analysis. As can be seen from this figure, although there was con-siderable overlap between ranks, especially lower ones, more fish were reclassified correctly into their proper rank than into any of the three classes, suggesting the existence of lawful patterns related to position in the dominance structure of these fish. A similar analysis was also carried out for females. In females, the best retrodictors of dominance status in-cluded the frequency of received chases (r= .6847, P < 0.001) and the coefficient of repertoire variability (r = 0.64, P < 0.001), both positively related to position in the female dominance structure. When these variables were progressively included, together with measure of time spent in the large compartment and frequency of alimentary behaviour, in a stepwise regression analysis they helped to explain 67 % of the total variance in ranks, and to correspondingly classify 58% of the females into their correct rank category. However, 81 % of the alpha females were correctly re classified. As in males, only the first canonical axis of Fig. 11 was significant, having an eigenvalue of 2.03 and a canonical correlation of 0.82. Only the coefficient of repertoire variability and number of chases received contributed significantly to this canonical variable. The combination of these factors does not explain why a given in-dividual became dominant in the first place. They are properties associated with the state of having a more or less elevated status in the ag-gressive dominance structure, once the dominance relationships have stabilized.
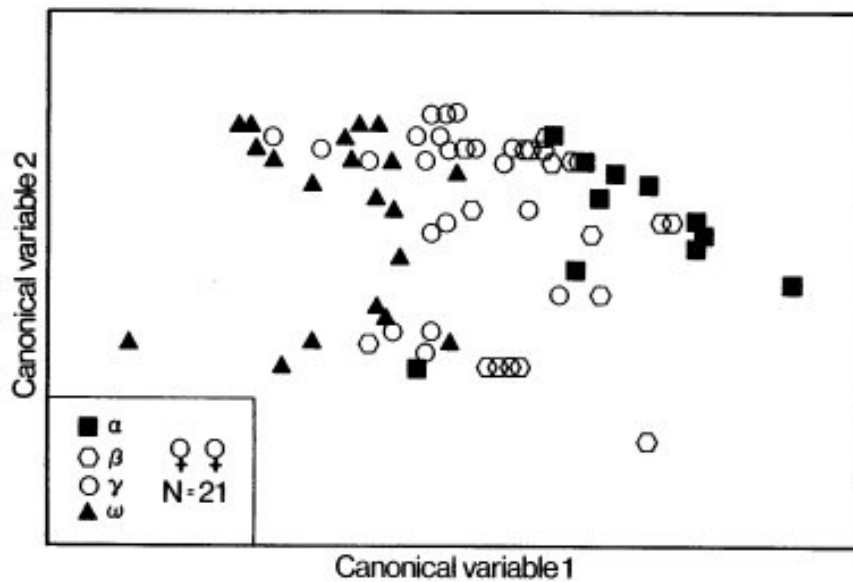

Fig. 11. Plot of individual female cases against the canonical variables best correlated to the frequency of received chases and the coefficient of repertoire variability. Only the first canoni-cal axis was significant.

That the coefficient of repertoire diversity be one of the best correlates of position in the dominance structure is intuitively sound since it is to be expected that individuals having higher coefficients also have more in-fluence than lower ones. But we are intruding into the following discus-sion.

DISCUSSION

In the two compartment situation of the present study, which allowed spacing out and visual isolation of the individuals, the alpha males oc-cupied the larger area of the aquarium in the company of the four females while the three subordinate males

were restricted to the smaller area, unaccompanied by any females. This spacing out pattern emerged with neat regularity from the data and was apparently caused and maintained by aggressive behaviour, especially by charges, initiated by the alpha male toward male rivals, but also by other behaviour leading to cohesion in females. It is however evident that the behaviour of the alpha males did not qualify as true territorial defence. In addition to site tenacity, advertisement of the presence in a given site, successful site defense (at least putatively), and exclusive use of the defended area, conditions that were all satisfied by the behaviour of the alpha males in the present study, a fifth criterion of putative reversibility of exclusion was not obtained. True territoriality implies putative reversibility of exclusion of the con-cerned individual when it becomes an intruder for an adjacent site -holding male (Tinbergen, 1953; De Boer & Heuts, 1973; Zayan, 1974). In the fish *Hemichromis bimaculatus,* territorial defence could be induced at will by alternatively provoking intrusion into each of two fish's residence areas (De Boer & Heuts, 1973). This specific area linked dominance was never realized in the present laboratory study. The alpha male holding the large compartment was never seen being charged by rivals when entering the small compartment and was never seen expelled from it.

The spacing out pattern obtained here is probably the expression of competition between males but also of cooperation among the females. As stressed recently by Zayan *et al.* (1983), spatial relations are a full component of social systems. They should be discussed in the light of cooperation and competition which are basic forces fashioning social systems.

Some preliminary concepts, borrowed from Bunge (1979, 1980) and Zayan *et al.* (1983) will help to characterize the social and mating schemes most readily conforming to the regularities obtained in the present study.

A set of socially linked or connected animals can be considered as a social system, or as a sociosystem. Social links, bonds and connections are special cases of social relations, but, unlike a mere relation, a connection makes some difference to the individual to which it is related. If a link holds between two individuals, then at least one of them will behave dif-ferently from the way he or she would behave if not so coupled. On the other hand, a noncoupling relation makes no difference to the thing to which it is related. When a connection effects two group members, it im-plies that one of them, or both (reciprocally), act upon the other and can, potentially at least, modify the tatter's behavioural trajectory. This is the basic notion of influence. A sociosystem also includes connections with the environment; its immediate environment or milieu (i. *e.* the composi-tion of the next supersystem) must be included in the description of a sociosystem because the behaviour of the latter individual depends critically on the nature of its milieu. The total structure of a system will thus be defined as the set of all connections among the system's com-ponents, namely group members, as well as among these and the things in the system's immediate environment.

It is necessary to distinguish a system's internal structure from its ex-ternal one. The internal structure of a sociosystem is the subset of rela-tions among internal parts of the sociosystem, namely group members. The configuration or spatial structure of a sociosystem is the subset of the total structure composed of the spatial relations among the group- members. Sociosystems have no shape but they have a spatial configura-tion since they are made up of living beings that stand in definite spatial relations to one another (Bunge, 1979). The external structure is the complement of the internal structure. It is composed of relations existing between the elements of the environment and the elements composing the internal structure. In the present research we were mainly interested in the internal structure of a sociosystem; but internal and external struc-tures are closely interdependent *(e.g.*, scarceness of resources influences aggressive behaviour and spacing out).

The social or internal structure among group members can be con-sidered as the result of a balance of forces that act in opposed directions: cooperation between group members tends to social cohesion and com-petition between them to social dispersion. Cooperation can be said to oc-cur when members in a group of socially connected individuals share goods for defence against predation, in order to increase their foraging ef-ficiency, or to ease reproduction between mates, for mutual defence against parasites and infestations (Wittenberger, 1981). Competition is repulsive and highly dispersive in nature, both socially and spatially. In-dividuals compete for food, shelters, females, sites for reproduction; in a nutshell, they compete for differential reproduction. If the inner connec-tions in a structure are attractive and strong, the degree of integration is high; if the links are still positive but weak, the degree of integration is low; and if the links are very repulsive, there is no systemicity or integra-tion at all (Bunge, 1979). The highest level of integration corresponds to no differentiation at all: all individuals are equivalent. The lowest level of integration corresponds to complete differentiation, for example, in a ter-ritorial situation where individuals do not participate truly in a society. However, intermediate levels of differentiation exist in a true straight-line hierarchy or even in despotism.

There is no doubt also that social structure influences spatial structure (and probably vice versa also) and that spatial

relations must be con-sidered as full components of social systems (Murchison, 1935; Zayan *et al.,* 1983). Hence, as stressed by Zayan *el al.* (1983), in the context of social activities, participation of individuals in a common activity such as feeding, copulation, rest, mutual preening, flocking and group defence against predation, implies mutual tolerance, namely synchronism and sharing of objects and especially space. On the contrary, competition im-plies spatiotemporal incompatibility, particularly in the execution of in-dividually valuable activities (Zayan *et al.,* 1983). While cooperation and participation implies decrease of interindividual distances and cohesion, spacing out is the result of competition. Ultimately, extreme competition can lead to complete differentiation, namely to complete disconnection from the social structure, as in territorial expulsion and emigration. In our results, although the females less frequently showed complete and linear agonistic dominance structures than males did, they nevertheless formed more compact configurations and, hence, showed more cohesion, more integration and systemicity than males. Since cooperation implies the formation of a social system and creates cohesion and integration, female X. *helleri* may be considered to be more sociable than males. In males, competition overrode cooperation and sociability was lower. The social fabric in males was more loosely woven than in females due to the dispersive influences of competition. The apparent cohesion of subor-dinate males was due to the despotic activity of the alpha male and to the situation of confinement.

Male X. *helleri* would have shown a much lower level of dominance "organization" if observations had been carried out in the wild or at least in larger tanks. Male aggressive dominance structures emerging from the present study are the result of fish forced to interact within a closed en-vironment without the possibility to regulate (through social positive and negative feedbacks) their own dispersion and their own social interac-tions. But, some interesting hypotheses on social structures can be drawn from these artifacts.

In the present study, the social scheme that best describes the dominance structure emerging in males is the monarchistic or despotic one. Essentially, it entails that one individual becomes very dominant over others and drives the latter of the same sex away from the resources. Monarchistic structures have been reported in many vertebrates (Collias, 1944; Wynne Edwards, 1962; LeBoeuf & Peterson, 1969) in-cluding the poeciliid fish *Gambusia affinis* (Caldwell & Caldwell, 1962) and unisexual bisexual Poeciliopsis (McKay, 1971; Moore & McKay, 1971). In natural conditions where animals can control their degree of spacing and social interactions, it is to be expected that a monarchistic social system will also entail the presence of a shallow hierarchy where one individual, the hierarch (Dawkins, 1976), clearly dominates, while subordinates occasionally have fleeting aggressive encounters among themselves, but seldom often enough to establish fixed and stable rela-tionships. However, as mentioned above, in conditions of confinement, individuals are forced to make their relations clear and the full criterion of shallow hierarchy cannot be expected to hold under these conditions. A monarchistic structure can, next to no structure at all, be best characterized by a very low degree of cohesion of inner elements and poor inner systemicity. The absence of a hierarchy among subordinate elements is not an essential characteristic.

The intensity of interindividual asymmetries, corresponding to dif-ferences between group members in a social structure with respect to in-fluence, can be represented by distances between points representing in-dividuals in a digraph. In the case of agonistic asymmetries and in-fluences, the greater the influence, the larger the distance between the in-fluencing subject and the influencee. Intuitively, what is expected from a despotic scheme is a configuration in which the distances obtained be-tween the despot and all subordinates should appear much larger than the distances among points corresponding to the subordinates. But the various distances between the despot and subordinates should remain more or less equivalent. A distance is, by definition, a relation. The con-cept of despotism refers not only to dominance relationships between in-dividuals of the same set (does individual A exceed individual B in some specified property ?), but also to dominance relations between distances bounded by points from the same set, having or not a common terminus (does the distance from individual A to individual B exceed the distance from individual C to individual D ?). This syntactical aspect of despotism can be explicitly interpreted by differences in control of the valued resources. Despotism usually interprets itself in terms of exaggerated ac-cess or disproportional exploitation of resources by the despot as com-pared to the exploitation allowed by the latter to its subordinates. However, in our fish at least, control over resources can only be obtained and secured by direct influence and control of competitors, through their impairment, alienation and eventual elimination, and rarely by direct ac-cess or exploitation alone. For example, the monarch might be the sole individual to court females and to supply sperm for insemination, or might have exclusive access to a given valued resource such as space, but only at the expense of having eliminated and disqualified all rivals.

To this pattern of despotism is most frequently contrasted another "vue de 1'esprit", namely that of true hierarchy or straight line social order as known since classic works on fowls and platies. Here, each in-dividual dominates all others whose ranks are lower than his own. Since inter individual differences with respect to belligerence are not so great, individuals are said to

be more evenly spaced in the dominance scale. In addition, they are expected to participate in the utilization and exploita-tion of resources in direct proportion to their respective rank. If we refer to the present results, this kind of social organization would more ade-quately fit the case of females than that of males of the same species. However, the hypothesis that resource priority should depend on in-dividual status is not supported by the females' data.

The mating scheme is another structural facet of a sociosystem. A "one male to several females" scheme, or more briefly stated, a "haremic" scheme, most readily conforms to the results obtained here. In a harem polygyny, a single male defends access to a group of females either by defending the group itself or by defending the group home range where females congregate (Wittenberger, 1981). When females are spatially cohesive, as suggested by the present results, one male may join the group and systematically chase rivals out when they try to ap-proach the females. However, when females are not cohesive spatially, the male may attempt to keep females from leaving the group by herding them together, but rarely succeeds when they persist in their attempts to leave. Since it is ineffective to defend the whole group, it becomes more economical to defend spaces where female groups are to be found or to be attracted. In the natural environment, where space is not as limiting a factor as in the laboratory, it is to be expected that males would defend a harem whose quality depends on qualities of both the male and the site. Females could base their mating choices on male quality as well as on ter-ritory quality. Experiments are in progress to test rival hypotheses con-cerning the mechanisms for site and mate choices in this species.

In summary, the monarchistic, haremic and linear hierarchical schemes are, together with spatial configurations, subsets of the structure of the sociosystem of small populations of *Xiphophorus helleri* kept in a restricted space. Monarchistic relations qualify the structure of relations within male members, while the linear hierarchy represents relations oc-curring within the female group members. But, in a more generic theory, these two schemes would be special cases of agonistic structures applying to either sex or to both simultaneously. These connections regulate access to resources. The haremic scheme already includes or presupposes the monarchistic and true hierarchical structures. Exclusive, simultaneous access of a single male to several females was obtained through at least three mechanisms: Firstly, despotism led to almost total differentiation, *i.e.* to the neat emergence of a despot and to the almost complete discon-nection of potential competitors. Secondly, sociability led to cohesion and to a compact configuration among females, attesting to the fact that cooperation was overriding competition in this case. Thirdly, social preference of the alpha male for (valued) females, or social preference (or at least tolerance) of females for the (valued) alpha male, or both simultaneously, led to the formation of a configuration integrating the alpha male and the females. Space is also an essential element of the social system since spatial relations create and control social connections (and are part of their definition); eventually, space also contributes to the dissolution of social connections.

To conclude, alpha males were found to have priority of access to a larger space and to females, and were also almost the sole individuals to court the females and, presumably, to supply sperm for insemination. Females, on the other hand, formed a cohesive group that, behavioural-ly, preferred or tolerated the proximity and the sexual advances of the alpha male. The results are in accordance with accumulating evidence supporting the sociobiological theorem that to dominate is to possess priority of access to the necessities of life and reproduction (Wilson, 1975).

SUMMARY

Sixteen populations, each of four male and four female green 'swordtail fish, were ob-served in 54 litre tanks separated into two unequal volumes by a partition allowing swim-ming from one area to another only at the surface. Each population was observed on 2 4 occasions, making a combined total of 50 observation periods of 2 hours each. Chase right orders, spatial positions as well as several agonistic and epigamic behaviour units were noted during each period of observation. Males and females apparently form distinct hierarchies which are perfectly linear and transitive in 68% and 42% of the cases respec-tively. Some dominance structures are incomplete, but no intransitivity is noted. Alpha males are much more aggressive than their isosexual subordinates. In females, the fre-quency of aggressive behaviour appears to be more proportional to the social rank of the initiator, but the number of chases received from other females is the best indicator of rank in the female hierarchies. Alpha males are responsible for 80% of all sexual activity and have privilege to behaviour leading to insemination with a high probability in 85 % of the cases. Females are not courted according to their position in the female hierarchy, nor to their size. In the two compartment situation of the present study, which allowed spacing out and

visual isolation of the individuals, the alpha males occupied the larger area of the aquarium in the company of the four females while the three subordinate males were restricted to the smaller area, unaccompanied by any females. This spacing out pat-tern emerged with neat regularity from the data and was apparently caused and main-tained by aggressive behaviour, especially by charges, initiated by the alpha male toward male rivals. However, it is not evident that the behaviour of the alpha male should be neatly qualified as territorial defence, since specific area linked dominance was never realized in the present study. The social scheme most readily applicable to the present social and spatial organization is the "one male to several females" system or monar-chistic male hierarchy, in which one male becomes very dominant over the others, oc-cupies the larger area and is also the sole individual to court the females and to attempt in-semination (haremic). These results support the sociobiological theorem that to dominate is to have priority of access to the necessities of life and reproduction.

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RÉSUMÉ

Depuis les travaux classiques de Noble & Borne (1940) ainsi que de Braddock (1945) sur *Xiphophorus,* les poecilidés sont souvent cités comme des espèces s'organisant de façon hiérarchique, formant des ordres de dominance linéaires semblables à ceux décrits pour les poules par Schjelderup-Ebbe (1922) et reposant sur des relations asymétriques et transi-tives. On mentionne aussi que ces espèces ovovivipares ne défendent pas de territoire comme le font, par exemple, les cichlidés. Par contre, des observations, réalisées en milieu naturel, rapportent que les mâles de certaines espèces défendraient contre les intrus une aire de nutrition temporaire ou encore un périmètre autour des femelles (Baird, 1968; George, 1960; Caldwell & Caldwell, 1962; Zander, 1967). D'autres espèces de la même famille des poeciliidés ont été qualifiées de monarchiques, ou despotiques avec harem, comme c'est le cas des espèces du complexe des Poeciliopsis, ne formant pas des ordres de dominance du type "privilège de morsure" (*nip right*), mais des hiérarchies peu profondes (Moore & McKay, 1971; McKay, 1971). Nous avons donc réalisé une série d'observations dans le but de voir si *Xiphophorus* était pour défendre des territoires individuels clans une situation où 1'on favorisait la compétition pour 1'espace et les parte-naires reproducteurs. Aussi, nous voulions éprouver chez cette espèce 1'hypothèse socio-biologique que la dominance agressive procure la priorité d'accès aux nécessités de la vie et de la reproduction (Wilson, 1975). Seize populations composées de 4 mâles et 4 femelles adultes *Xiphophorus helleri* ont été observées. Elles avaient été établies depuis quelques jours clans des aquariums de 54 litres séparés par une cloison en deux volumes inégaux communiquant entre eux à la surface de 1'eau comme s'il s'agissait de deux flaques reliées par un filet d'eau. Au cours de trois ses-sions d'observation réparties sur deux semaines, nous notions systématiquement les ordres de dominance, les positions spatiales ainsi que divers comportements agonistiques, épigamiques, alimentaires, etc., émis par chacun des individus dune population. Nos résultats se résument ainsi: Les mâles et les femelles forment des hiérarchies apparemment distinctes, du type parfaitement linéaire dans 68% des cas chez les mâles, et 42 % chez les femelles. Les autres ordres de dominance sont incomplets, mais aucune intransitivité n'est notée. Le mâle alpha est beaucoup plus agressif que les mâles subalter-nes. Chez les femelles, la fréquence des comportements agressifs est proportionnelle au rang social. Le mâle alpha est responsable de 80 % de toute activité sexuelle et il a le privi-lège des comportements conduisant (avec une grande probabilité) à 1'insémination dans 85 % des cas. Les femelles ne sont pas courtisées en relation de leur position hiérarchique, ni de leur taille. Le mâle alpha occupe avec les 4 femelles le grand compartiment de 1'aquarium et poursuit systématiquement les autres mâles lorsqu'ils pénètrent dans le grand compartiment ou s'approchent des femelles.

ADDENDUM

The following text on *the advantages of site holding* was not included by the editor in the Behaviour 1984 publication, though references found within this addendum were included in the original publication.

About the advantages of site holding

Even though ovoviviparous fish do not require a fixed territory for reproduction, one can nevertheless formulate the hypothesis that site tenacity influences reproductive success in *X. helleri*. Amore or less permanent site tenacity and defence might be beneficial for the ovoviviparous species in several respects which are not mutually exclusive. The first concerns efficient exploitation of food resources when food is distributed in a predictible but irregular manner. Efficient exploitation becomes possible through knowledge of the area and from the dispersion afforded by spacing. A second benefit is efficient escape from predation. Fish appear to develop a strategy for escape after a period of residence in a given place, whether it be darting to a sheltering hole or undercut bank, or flying in one direction until out of danger (Jenkins, 1969). The efficient defence against predation by the use of familiar landmarks, crevices and holes in order to evade and hide, concerns not only the male gender but also the females that dwell with him in the same space, and eventually the young he has most probably sired. Third, the site is instrumental in competitive interaction for mates. Assuming that females are attracted to the defended site, it permits interference with the sexual efficiency of other males by directly or indirectly limiting a competitor's access to a necessary resource such as females and exploitation of the resources, once access to them has been secured. By settling on a fixed site, at least temporarily, the male becomes more efficient in guarding the females than if the females had to be

constantly rounded up. The existence of sperm displacement in poeciliids is well documented. Guarding, then, represents an adaptive pattern, since the male attempts to prevent his mate from accepting another male or from being forcedly inseminated (Farr, 1980a), which would result in a reduction in egg fertilization by her original mate (Parker, 1970). Thus, site holding not only reduces courtship interference from rival males but it can also serve to eliminate sperm displacement and insure the paternity of the site holder. In the present study, the alpha individual was, in general, much more sexually active than were his rivals. This can be explained, together with the spacing-out pattern observed, since occupation of the large compartment with the four females, together with the absence of any male rival, greatly reduced interference with sexual behaviour of the alpha male. Alpha males were responsible for 81% of all epigamic behaviour initiated during the 100 hours of focal observation and had privilege in attempting insemination, and eventually in transferring sperm, in 85% of the cases. The territory influences the frequency and success of sexual behaviour since, once it is established (i.e. females are attracted there to form a harem and adjacent males have been sufficiently conditioned to respect the defended site), the sexual behaviour of the alpha male can be very efficient as females are not dispersed or refractory to courting, and satellite males do not interfere with parades and insemination. Finally, a fourth advantage involves energy balance. Movements take energy, especially when they are made against a current, which, in the Atoyac River, varies between 20 and 40 cm per sec. Spatially stable fish are able to avoid undue swimming, especially when the position chosen and held maximizes food intake, defence of females, attraction of new ones and protection against strong currents, and minimizes risks of predation. It cannot be excluded, nevertheless, that site tenacity in *X. helleri* is a remnant of oviparity or a by-product of selection, acting through other consequences, still unclear. For example, individuals capable of selecting and defending an adequate site could be systematically chosen by females, or in a better position to test a female's readiness to copulate. Hence, if a male's reproductive success hinges on his aggressive capabilities, males might be aggressive and defend a space to advertise superior competitive abilities in other contexts, and females might prefer to mate with "territorial" males. On the other hand, a male can gain a definite competitive advantage over other males if he can avoid wasting time courting unreceptive females. By defending a fixed space, a male increases a female's investment by forcing her to clearly manifest her choice and by remaining with him. This investment should induce her not to come or to leave immediately if she is not interested in him.