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SOME ASPECTS OF SOCIAL INTERACTION DURING FEEDING IN *SEPIA OFFICINALIS* (MOLLUSCA : CEPHALOPODA) HATCHED AND REARED IN THE LABORATORY

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SEPIA OFFICINALIS
REARING
BEHAVIOUR
FEEDING HIERARCHY
BODY PATTERNS

ABSTRACT – *Sepia officinalis* were reared in 2 groups of 4 individuals, and 4 individuals singly, from hatching to sexual maturity (7 months). During feeding, the animals were watched to find out whether they develop some kind of interactive behaviour, especially a feeding hierarchy. The following variables were recorded : (1) time needed for *Sepia* to attack a prey, (2) number of prey items caught, (3) rank order of individual catching prey, (4) possible changes in colour pattern during feeding. Individuals reared in groups attacked their prey about three times as fast and ingested more prey (up to twice as much) than individually reared animals. A feeding hierarchy was obvious after 4 months, then animals started to show a weak zebra-stripe pattern (mostly short bright stripes on brown/red skin), but only when feeding. When reared individually, animals showed this pattern only when they were fed in a group. In addition to showing a colour pattern, individuals of both sexes extended one or both ventral arms during feeding, thus preventing conspecifics from getting at the prey. After 5 months the feeding hierarchy was stable. The rank values were significant during the following 48 experimental days.

SEPIA OFFICINALIS
ÉLEVAGE
COMPORTEMENT
HIÉRARCHIE
LIVRÉE CHROMATIQUE

RÉSUMÉ – Deux groupes de 4 individus de *Sepia officinalis*, et 4 exemplaires isolés ont été élevés de la naissance à la maturité sexuelle durant 7 mois. Les Seiches ont été observées pendant qu'elles se nourrissaient en vue de constater si elles développent un comportement interactif, spécialement un comportement hiérarchique. Les variables suivantes ont été relevées : 1. temps nécessaire à une Seiche pour attaquer une proie ; 2. nombre de proies capturées ; 3. rang de capture d'une proie par individu ; 4. changements éventuels de la répartition des couleurs pendant la nutrition. Les exemplaires élevés en groupes attaquent leurs proies environ trois fois plus vite et ingèrent davantage de proies (plus de 2 fois plus) que les Seiches élevées séparément. Une hiérarchie dans la nutrition est observée au bout de 4 mois, puis les Seiches commencent à montrer un aspect rayé (le plus souvent, de courtes rayures brillantes sur fond brun-rouge), seulement pendant qu'elles se nourrissent. Les individus élevés séparément ne prennent un aspect rayé que lorsqu'ils sont nourris en groupe. Outre l'apparition de cette livrée rayée, les exemplaires des deux sexes allongent un ou deux bras ventraux pendant la nutrition, empêchant ainsi une autre Seiche d'attraper la proie. Au bout de 5 mois, la hiérarchie établie au moment de la nutrition reste stable. Les valeurs du rang de capture sont significatives pendant les 48 jours d'expérience.

INTRODUCTION

The common cuttlefish, *Sepia officinalis* L., is widespread in the Mediterranean Sea and the East Atlantic. It is known for its ability to change colours quickly and thus match various substrates.

Cuttlefish hatch as miniature replicas of the adult. Newly hatched cuttlefishes already have the basic behaviour traits of the adults, especially a benthic mode of life. The animals only swim up from the bottom to capture prey (Boletzky, 1983). Young *Sepia* are able to show body patterns as complex as those of adults (Hanlon & Messenger 1988). The body patterns consist of chromatic,

textural, postural and locomotor components. The chromatic component consists of chromatophore organs, leucophores (reflection of whole spectrum of incident light) and iridophores (light reflection and refraction producing iridescence).

In spite of extensive research covering courtship behaviour (Grimpe 1926 ; Tinbergen 1939), colour change and colour patterns (Holmes 1940 ; Hanlon & Messenger 1988), and predatory behaviour (Chichery & Chichery 1991) of *Sepia officinalis*, little is known about the social behaviour of juvenile *Sepia*. Zahn (1979) described occasional group formation in juvenile *Sepia officinalis*. Mather (1986) observed a female-dominated feeding hierarchy. In contrast, Hanlon & Messenger (1988) stated that there is no social behaviour up to an age of 4 months. In order to clarify this question, this study investigates the timing of the development of social behaviour in *Sepia officinalis*, with special emphasis on feeding hierarchy.

MATERIAL AND METHODS

Sepia eggs were sent from the Laboratoire Arago, Banyuls-sur-Mer (France) to the Alfred-Wegener-Institut (AWI, Bremerhaven) and to the Zoology Department in Bremen (Germany). Twelve individuals were reared from hatching to 7 months (July 1991-February 1992) in the Alfred-Wegener-Institut. The animals were kept in circular glass aquaria (150 l) at a constant temperature of 19°C. A closed water system with artifical sea water (S 36 ‰) was used. The bottom of the aquaria was covered with 1-2 cm of Foraminifera-sand to allow the cuttlefish to bury ; it also assisted in stabilizing the pH value (pH : ca. 7.8). It is indeed important to check the water quality regularly, especially nitrite content (Boletzky & Hanlon 1983).

The aquaria contained plastic containers, the walls of which had numerous holes that were small enough to prevent the animals from escaping, yet large enough to allow the water to circulate. To insure an optimal oxygen supply, the plastic containers were placed below the water surface. These containers also made it easier for the freshly hatched cuttlefishes to catch their prey. A total of twelve individuals were reared : two groups of 4 in containers measuring 17.5 cm in diameter during the first 2 months, and in circular 150 l glass aquaria thereafter ; the remaining 4 animals were reared individually in containers measuring 9.5 cm in diameter during the first 2 months, and in larger containers (17.5 cm) thereafter. All the animals were kept in the same water system, but were visually separated from other containers.

The cuttlefish were fed every day at the same time. During the first 2 months, only live mysids (10-20 mm) were offered. Later the cuttlefish were fed mainly small *Crangon sp.* (10-30 mm). After 3 months deep-frozen dead *Crangon* were fed most of the time.

The time needed for prey attack, the number of prey items caught by each individual, and their respective order in catching prey were recorded. The attacking time was measured between introduction of a prey into the container and seizure by the cuttlefish. During feeding the behaviour and related body pattern was recorded. An average rank for each animal was determined and tested for significance using the Wilcoxon-U test (error = 5 %).

Photographs of the animals were taken with a Canon EOS 600 and a telephoto lens (105 mm). An electronic flash Speedlite 430 EZ was used for all photographic records.

After 3 months, it was possible to mark the individuals with a formaldehyde-free nail varnish. Animals were anaesthetized with 2 % ethanol in sea water to determine the sex (presence or absence of hectocotylus differentation). The body size of each individual was recorded by measuring the dorsal mantle length (ML) each month. Once the animals were marked, the respective rank order was determined by the order in which individuals caught prey items.

After the death of one animal in each of groups I and II, at ages 4 and 4.5 months, respectively, individually reared animals were used as substitutes (with new identifications Ib^2 and IIb^2, as indicated in Tables V and VI), and corresponding medians and averages were calculated.

RESULTS

A. Feeding and related behaviour during the first 4 months

During the first 4 months, individually reared animals took 228 seconds on an average (of 4 individuals) to catch prey. The number of prey items caught per day varied from 1 to 4 mysids (2 prey items on an average). A group reared animal needed only 74 seconds on an average (2 groups, each consisting of 4 individuals) to get the prey, and it seized 4-9 mysids daily (4 prey items on an average). Thus individually reared young animals needed on average three times as long to catch prey and took much less prey than group reared individuals. At age 5 months, however, there were only small time differences between individuals grown up under different conditions (Tables I and II).

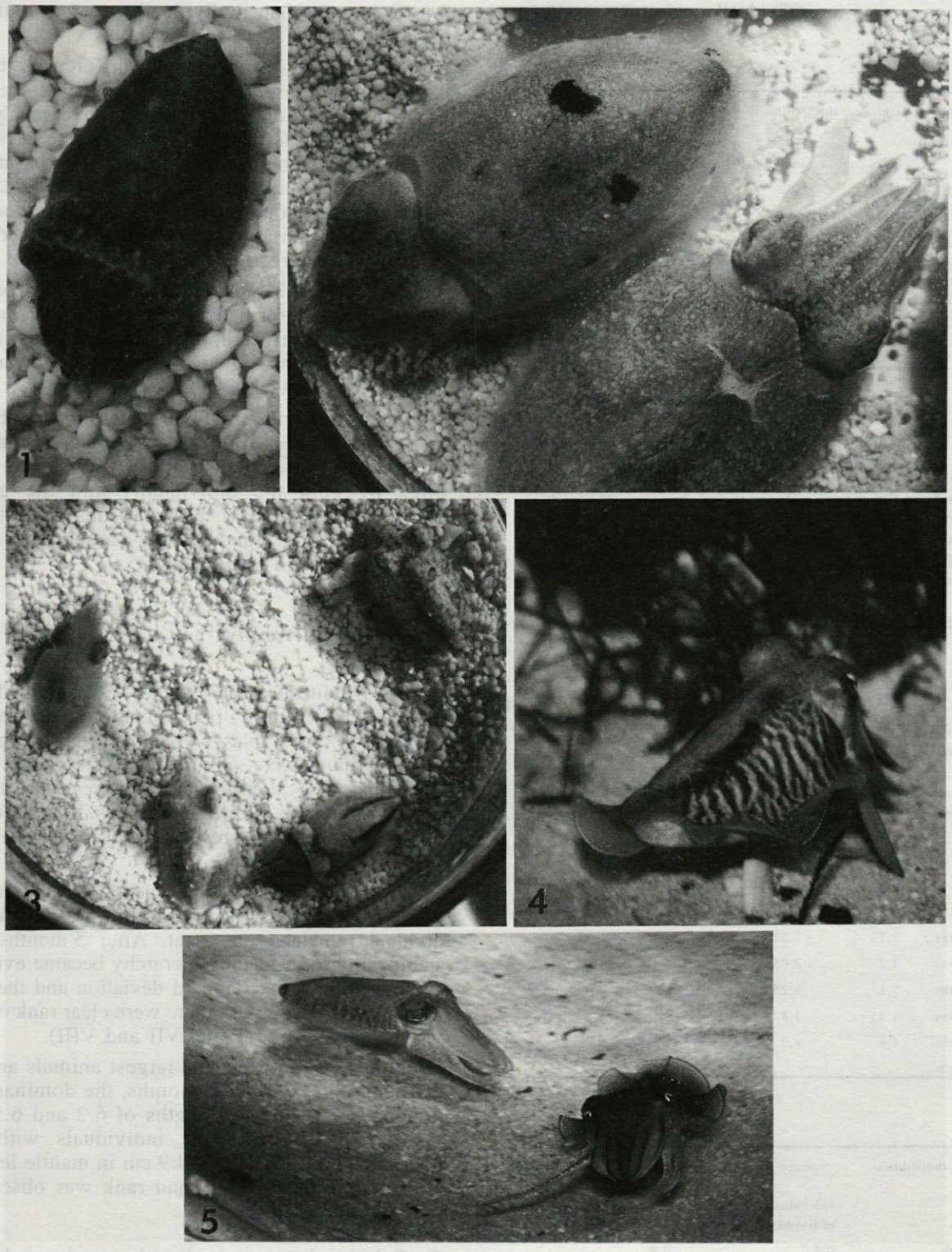

Fig. 1. Juvenile *Sepia officinalis* at the age of 1 month, turning dark brown after disturbance. Fig. 2. Two young *Sepia officinalis* 3.5 months old ; the upper individual shows paired dark spots on the mantle (for detail see text); the lower individual is freshly marked with nail varnish and does not exhibit spots. Fig. 3. Group of juvenile *Sepia officinalis* aged I month during feeding on mysids; one individual shows the longitudinal stripes on the mantle. Fig. 4. Subadult *Sepia officinalis* at age 8 months exhibiting longitudinal stripes in combination with zebra stripes. Fig. 5. Subadult *Sepia officinalis* at age 7 months in a feeding situation; the dominant animal at righ extends its right fourth arm towards the other individual, which will retreat shortly.

Table I. – Time to get the prey for individuals reared individually. Table II. – Time to get the prey and number of prey taken for individually and group reared animals.

I

age of individuals	average values (time in s)			
	individual a	individual b	individual c	individual d
1 month	120	300	301	275
2 months	237	381	344	273
3 months	218	283	174	206
4 months	149	151	-	103
5 months	35	76	-	30

II

age of individuals	time to get the prey average values (time in s)		number of prey taken average values	
	individually reared individuals	group reared individuals	individually reared individuals	group reared individuals
1 month	249	41	0.7	2.4
2 months	309	33	1.2	4.75
3 months	220	112	3	6.2
4 months	134	108	2.6	3.5
5 months	47	79	2.3	2.8
average value (first 4 months)	**228**	**74**	**1.9**	**4.2**

Table III. – Mantle length (ML) for individuals reared individually. Table IV. – Mantle length (ML) of individually and group reared animals.

III

age of individuals	average values (in cm)			
	individual a	individual b	individual c	individual d
1 month	0.8	0.8	0.8	0.8
2 months	1.17	1.31	1.27	0.98
3 months	2.2	2.05	2.15	1.6
4 months	3.1	3.25	3.15	2.48
5 months	4.35	4.8	4.5	3.85
6 months	4,8	4.9	-	4.3
7 months	-	-	-	4.5

IV

age of individuals	average values (in cm)	
	individually reared individuals	group reared individuals
1 month	0.8	0.8
2 months	1.18	1.3
3 months	2	2.2
4 months	2.99	3.25
5 months	4.37	4.96
6 months	4.66	5.76
7 months		6.37

Starting from identical hatching size (mantle length : 8 mm), group reared animals were always 8-9 % longer than individually reared animals (Table IV).

During the first 4 months, no differences in behaviour were observed between individually and group reared animals. Upon disturbance early juvenile *Sepia* turned dark in most cases, e. g. when a "threatening" object was moved towards an individual (Plate I, 1). Between alert individuals this uniform colour pattern was not observed. In feeding situations, group reared animals showed no signs of interaction between individuals.

After 2 months the animals showed paired Black Spots (described by Holmes 1940) on the dorsal mantle surface upon disturbance, but at this age there were no signs of this pattern towards a conspecific (Plate I, 2).

Only in feeding situations were dark longitudinal stripes expressed on the mantle surface at age 1-3 months. This colour pattern was shown very often by both the individually and the group reared animals (Plate I, 3). Later this pattern was shown only rarely and then in combination with the Zebra pattern (Plate I, 4).

B. Feeding hierarchy

The overall observation time of the marked animals covered 81 days ; rank values were determined on 59 days (see Tables V, VII). In each group, the 59 rank values were significantly different between individuals. No significant differences were found for the same rank in different groups. The variances of rank 1 and 4 were respectively smaller than the variances of rank 2 and 3.

During the first 40 experimental days, frequent rank changes were noticed in both groups ; no individual remained dominant. After 5 months, the stabilization of a feeding hierarchy became evident. In both groups, the standard deviation and the variance values decreased ; there were clear rank orders in both groups (see Tables VII and VIII).

Table IX shows that the largest animals are the dominant ones. At age 5 months, the dominant individuals have mantle lengths of 6.2 and 6.5 cm, respectively, whereas the individuals with the lowest rank measure only 4.9 cm in mantle length. No relation between sex and rank was observed.

C. Relation between feeding hierarchy and body patterns

After 4 months, when the animals began to show a feeding hierarchy, they started to exhibit a weak zebra-stripe pattern, but only in a feeding situation. First there were only bright spots on a

Table V. – Feeding rank order of marked animals, group I.

V

experimental day	date	individual a	individual b[1]	individual b[2]	individual c	individual d
1	06.11.91	3	1	-	2	4
2	07.11.91	2	4	-	1	3
4	09.11.91	2	4	-	1	3
5	10.11.91	4	3	-	1	2
6	11.11.91	4	3	-	1	2
7	12.11.91	3	4	-	2	1
9	14.11.91	4	3	-	1	2
10	15.11.91	2	4	-	3	1
11	16.11.91	3	4	-	2	1
13	18.11.91	3	4	-	2	1
14	19.11.91	3	4	-	2	1
15	20.11.91	3	4	-	2	1
16	21.11.91	2	4	-	1	3
18	23.11.91	3	4	-	2	1
19	24.11.91	3	4	-	2	1
20	25.11.91	3	4	-	2	1
22	27.11.91	1	4	-	3	2
24	29.11.91	2	3	-	4	1
25	30.11.91	2	3	-	4	1
27	02.12.91	2	3	-	4	1
28	03.12.91	2	3	-	4	1
30	05.12.91	2	4	-	3	1
32	07.12.91	2	3	-	4	1
33	08.12.91	1	4	-	3	2
34	09.12.91	2	4	-	3	1
36	11.12.91	2	4	-	3	1
37	12.12.91	2	4	-	3	1
38	13.12.91	3	-	4	2	1
40	15.12.91	4	-	3	2	1
42	17.12.91	2	-	3	4	1
43	18.12.91	2	-	4	3	1
45	20.12.91	2	-	3	4	1
47	22.12.91	2	-	4	3	1
48	23.12.91	2	-	4	3	1
49	24.12.91	2	-	4	3	1
51	26.12.91	3	-	4	1	2
53	28.12.91	1	-	2	4	3
54	29.12.91	2	-	3	4	1
55	30.12.91	2	-	3	4	1
56	31.12.91	2	-	4	2	1
58	02.01.92	2	-	4	3	1
59	03.01.92	1	-	4	3	2
61	05.01.92	2	-	4	3	1
62	06.01.92	3	-	4	2	1
63	07.01.92	2	-	3	4	1
65	09.01.92	2	-	4	3	1
66	10.01.92	3	-	4	2	1
67	11.01.92	2	-	4	3	1
68	12.01.92	2	-	4	3	1
70	14.01.92	1	-	4	3	2
71	15.01.92	2	-	4	3	1
72	16.01.92	2	-	3	4	1
73	17.01.92	2	-	4	3	1
75	19.01.92	2	-	3	4	1
76	20.01.92	2	-	4	3	1
77	21.01.92	4	-	3	2	1
79	23.01.92	2	-	4	3	1
80	24.01.92	2	-	3	4	1
82	26.01.92	2	-	3	4	1
84	28.01.92	2	-	3	4	1

Table VI. – Feeding rank order of marked animals, group II.

VI

experimental day	date	individual a	individual b[1]	individual b[2]	individual c	individual d
1	06.11.91	3	4	-	1	2
2	07.11.91	3	1	-	4	2
3	08.11.91	1	4	-	3	2
4	09.11.91	1	4	-	2	3
5	10.11.91	4	3	-	1	2
6	11.11.91	4	3	-	1	2
7	12.11.91	1	4	-	2	3
9	14.11.91	2	1	-	4	3
10	15.11.91	4	2	-	3	1
11	16.11.91	1	4	-	3	2
13	18.11.91	2	4	-	3	1
14	19.11.91	4	2	-	3	1
15	20.11.91	3	1	-	2	4
16	21.11.91	1	4	-	3	2
18	23.11.91	2	3	-	1	4
19	24.11.91	2	4	-	1	3
20	25.11.91	1	4	-	2	3
22	27.11.91	2	3	-	4	1
24	29.11.91	1	4	-	2	3
25	30.11.91	3	-	2	1	4
27	02.12.91	1	-	3	4	2
28	03.12.91	1	-	2	4	3
30	05.12.91	1	-	4	3	2
32	07.12.91	3	-	2	4	1
33	08.12.91	1	-	4	3	2
34	09.12.91	2	-	4	3	1
36	11.12.91	1	-	4	3	2
37	12.12.91	3	-	4	1	2
38	13.12.91	1	-	4	3	2
40	15.12.91	1	-	4	3	2
42	17.12.91	1	-	3	4	2
43	18.12.91	1	-	3	4	2
45	20.12.91	1	-	4	3	2
47	22.12.91	1	-	4	2	3
48	23.12.91	1	-	3	4	2
49	24.12.91	1	-	4	2	3
51	26.12.91	1	-	4	2	3
53	28.12.91	1	-	4	3	2
54	29.12.91	1	-	3	4	2
55	30.12.91	1	-	4	3	2
56	31.12.91	1	-	3	4	2
58	02.01.92	1	-	2	4	3
59	03.01.92	3	-	4	1	2
61	05.01.92	1	-	4	3	2
62	06.01.92	1	-	4	3	2
63	07.01.92	1	-	4	3	2
65	09.01.92	1	-	3	4	2
66	10.01.92	2	-	4	3	1
67	11.01.92	1	-	4	3	2
68	12.01.92	1	-	4	3	2
70	14.01.92	2	-	4	1	3
71	15.01.92	1	-	3	4	2
72	16.01.92	1	-	4	3	2
73	17.01.92	1	-	4	3	2
75	19.01.92	1	-	4	3	2
76	20.01.92	1	-	4	3	2
77	21.01.92	1	-	3	4	2
79	23.01.92	1	-	4	3	2
80	24.01.92	1	-	3	4	2
81	26.01.92	1	-	3	4	2

dark or dark spots on a bright mantle surface ; later the spots changed to actual stripes, and the pattern became increasingly distinct.

The animals became very active when they were fed. They often ejected masses of ink and they chased each other. Some animals jetted against the tank wall and injured themselves at the tip of the mantle. In addition to showing particular colour patterns, males and females extended one or both of the ventral arms, thus apparently inhibiting conspecifics from getting at the prey. In combination with the zebra pattern the animals often showed a dark unilateral eye circle and a dilated pupil towards the opposite individual.

Sometimes the paired dark spots, in combination with a flattened body posture and a dark stripe along the body at the mantle end, were shown during feeding situations. Hanlon & Messenger (1988) described this pattern as Deimatic. In addition, the animals sometimes raised the first pair of arms towards a conspecific or towards their own picture reflected by the aquarium glass wall. Individually

Table VII. – Feeding rank order of group I. Average, median, variance and standard deviation of rank values from 1-27 and 27-59, respectively.

VII

Individual	average values experimental days1-27	average values experimental days27-59	median values experimental days1-27	median values experimental days27-59
a	2.48	2.16	2	2
b^1	3.59	-	4	-
b^2	-	3.59	-	4
c	2.41	3.06	2	3
d	1.52	1.16	2	1

Individual	variance values experimental days1-27	variance values experimental days27-59	standard deviation values experimental days1-27	standard deviation values experimental days27-59
a	0.64	0.46	0.80	0.68
b^1	0.48	-	0.69	-
b^2	-	0.31	-	0.56
c	1.10	0.64	1.05	0.80
d	0.72	0.20	0.85	0.45

Table VIII. – Feeding rank order of group II. Average, median, variance and standard deviation of rank values from 1-18 and 18-59, respectively.

VIII

Individual	average values experimental days1-18	average values experimental days18-59	median values experimental days1-18	median values experimental days18-59
a	2.2	1.27	2	1
b^1	3.0	-	3.5	-
b^2	-	3.54	-	4
c	2.33	3.07	2	3
d	2.33	2.12	2	2

Individual	variance values experimental days 1-18	variance values experimental days18-59	standard deviation values experimental days1-18	standard deviation values experimental days18-59
a	1.39	0.40	1.18	0.63
b^1	1.35	-	1.17	-
b^2	-	0.45	-	0.67
c	1.17	0.82	1.08	0.90
d	0.94	0.31	0.97	0.56

reared animals normally showed no zebra pattern until the age of 6 months ; however, they did show the pattern when they were fed in a group.

After 5 months, when the feeding hierarchy was stable, the animals became less aggressive. They were only rarely chasing each other, and there were no more injuries. The extended fourth arm and the weak zebra pattern were shown all the time during a feeding situation (Plate I, 5).

DISCUSSION

In feeding situations, group reared animals showed no signs of agonistic behaviour between individuals during the first 4 months, but there must be some kind of inter-individual influence, because the group reared animals caught much more prey in half the time compared to the individually reared animals.

Holmes (1940) desribed the pattern of longitudinal stripes in adult *Sepia* in relation to disturbance ; in this work the pattern was observed only during feeding situations in 1-3 months old animals. In the present study it is not possible to determine the stimulus necessary for the appearance of this pattern, which is shown by *Sepia* fed both in groups and individually, because the individually reared cuttlefish were all kept in the same water system so an influence of olfactory cues cannot be excluded. But it can be surmised that the releasing factor for the zebra pattern until the age of 6 months is indeed visual, because during this period only those animals which were fed in a group showed the pattern.

A feeding hierarchy with significant ranking was observed. Once the hierarchy was stable, the weak zebra pattern with one fourth arm extended towards a conspecific was shown only as a "status-signal" pattern. The dominant individual in group II swam regularly with extended fourth arm to the feeding spot, even if there was no prey. No individual was ever observed to oust a dominant animal with extended fourth arms. The weak zebra pattern was shown by both sexes and in each rank. In most cases the colour was brown with short bright stripes. Probably this pattern is a response to disturbance by a conspecific. Deimatic pattern was also shown as an intraspecific "signal" pattern. Schröder (1966) described the dark spots as a defence pattern or threat "signal".

The rank seems to be size dependent. In both groups the animals with the highest rank were also the biggest (mantle length at 5 months 6.2 cm and 6.5 cm, respectively) ; the animals with the lowest rank (mantle length at 5 months 4.9 cm) are smaller than the rest.

Table IX. – Mantle length and head width of 5 months old group reared *Sepia*.

IX

Rank	Group	Individual	sex	mantle length in cm	head width in cm
1	I	d	male	6.2	3.1
1	II	a	male	6.5	3.8
2	I	a	male	5.8	3.2
2	II	d	male	5.6	3
3	I	c	female	6	3
3	II	c	male	5	3
4	I	b^2	female	4.9	2.9
4	II	b^2	female	4.9	2.8

There is no link between rank and sex. Mather (1986) suggested a female-dominated feeding hierarchy. In the experiments described here males were dominant. This result is not surprising given the general experience from rearing experiments showing that males are more aggressive and tend to live longer than females in captivity.

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