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INFLUENCE OF FEEDING JUMPS ON THE EGG-CARING BEHAVIOUR OF MALE SERGEANT MAJOR *ABUDEFDUF VAIGIENSIS* (PISCES: POMACENTRIDAE)

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Rong-Quen Jan and Kun-Hsiung Chang (1984) Influence of feeding jumps on the egg-caring behaviour of male sergeant major *Abudefduf vaigiensis* (Pisces: Pomacentridae). *Bull. Inst. Zool., Academia Sinica* **23**(2): 159-171. Along northern coast of Taiwan, the damselfish Sergeant Major, *Abudefduf vaigiensis* (Quoy et Gaimard) is very abundant in the shallow waters. Its spawning season begins in April and heavy spawning occurs from May to August. In the majority of time before the fertilized egg hatches, the male which is responsible for egg-caring is dedicated to nesting site. However, conspicuous feeding jumps occur to the duty male when current brings the planktonic food. To examine a possible alternation of behaviour budget when feeding period commences, the actions of the egg-caring damselfish can be divided into the following items seperately: skimming, fanning, nipping, watching, chasing, cruising, feeding, staying, approaching and jaw locking. The occurring sequence of these actions was consistent. First order transition matrices showed that almost all motions were highly repetitive. It also showed that during non-feeding period, motions performed mostly were nipping, fanning and skimming, which comprised 63.9% of the total frequency. After planktonic food triggered the feeding period, the feeding action predominated over a relative frequency of as great as 59.2%. As time shifted from non-feeding period, the relative frequencies of skimming, chasing and approaching were less variable than were those of the other actions. The position of motions in a typical sequence shown in flow diagrams may be used to determining the level of activation of the behavioural system associated with those motions. Hypothetical control units are tentatively made to each action of the egg-caring male.

Parental care is a common phenomenon in a great number of fishes with demersal eggs (for reviews see Blumer, 1979; Perrone and Zaret, 1979; Barlow, 1981; Baylis, 1981). In pomacentrids, the information of egg-caring behaviour has also accumulated to a certain degree, since these fishes are highly associated with coral reefs and attractive to ethologists. However, most of previous studies were focussed on the description of the occurrence of intruder-defence and egg-cleaning actions rather than on the temporal sequence or activity budgets of egg-caring behaviour (Abel, 1961; Myrberg, *et al.*, 1967; Fishelson, 1970; Swerdloff, 1970; Clarke, 1971; Russell, 1971; Keenleyside, 1972; Fishelson, *et al.*, 1974; Moyer, 1975; Mapstone and Wood, 1975; Ross, 1978; Nakazono, *et al.*, 1979; De Boer, 1980, 1981; Chang and Jan, 1983; Thresher and Moyer, 1983).

In damselfishes, such as *Abudefduf zonatus* and *Pomacentrus nagasakiensis*, the egg-caring ones would sometimes leave their nesting sites for short-term feeding (Keenleyside, 1972; Moyer, 1975). In such case, we consider that an alternative strategy may exist for the feeding ones to invest their care, as compared with what had done by the fishes still staying around their nesting sites.

To examine this idea, the sequences of motions of egg-caring Sergeant Major *Abudefduf vaigiensis* (Quoy et Gaimard) were recorded *in situ*. Then, the activity budgets of the fish between non-feeding and feeding periods were compared.

MATERIAL AND METHODS

This study was done at Kwei-hou, the northern coast of Taiwan (121°41′E, 25°12′N). Underwater observations on the behaviours of egg-caring Sergeant Major, *Abudefduf vaigiensis*, were carried out intensively using scuba gears during May, 1982. The actions of the egg-caring males were further seperated into the following motion units (descriptions see Life history of the fish): skimming (SK), fanning (FA), nipping (N), watching (W), chasing (CH), cruising (CR), feeding (FE), staying (ST), approaching (A), and jaw locking (L). These units were written down in occurring sequence on a water-resistent notebook. All data were collected for two 40-min. periods on an egg-caring fish on the forth day after spawning.

In those motion units which, if occurred, were composed of several bouts of repetitive actions, each repetition was recorded seperately. For comparison, records of sequential behaviour were kept of the fish in two distinct different periods, (1) the non-feeding period, during which the egg-caring male was mostly busy with egg-nipping; and (2) the feeding period, which was characterized by conspicuous feeding jumps of the fish.

Life history of the fish

Abudefduf vaigiensis (Quoy et Gaimard) is very abundant along northern coast of Taiwan. During winter when northeast monsoon prevails, the individuals of *A. vaigiensis* scatter around reef area. Individuals would aggregate in early spring, forming schools and feeding along channels between reef flats. Reproduction begins in April and heavy spawning occurs from May to August. While reproducing, the male in the spawning school would build nest on the slanting surface of reef outcrops, where it is possibly predominated by strictly territorial damselfish *Stegastes fasciolatus*. The ecology and reproductive behaviour of this local species is quite similar with that of the Red Sea ones (Fishelson, 1970). Breeding colonies are composed of tens of nesting males from place to place during the spawning season. After spawning, the male is responsible for taking care of eggs. The egg-caring behaviour is composed of the following elements:

Skimming (SK)—The fish swims laterally and rubs the egg layer with his body trunk.

Fanning (FA)—The fish swims near egg mass, then to fan the egg with pectoral fins or to swim backward to bring his caudal fin to the egg mass, then fanning with vigorous fin movements.

Nipping (N)—The fish bites something from the egg layer with his mouth.

Watching (W)—The fish remains in the water column a bit over the reef outcrop where the nest locates.

Staying (ST)—The fish stays simply beside the reef outcrop, and exhibits no other egg-caring motions.

Chasing (CH)—The fish dashes straightly toward intruders, such as *Stegastes fasciolatus*, *Pomacentrus coelestis*, etc., and chases them away.

Approaching (A)—The fish swims gently toward an intruder, then swims back no matter whether the intruder responds or not.

Cruising (CR)—The fish swims within a diameter of about 1.5 meters around the nesting site.

Feeding (FE)—The fish darts upward to the water column over his nest and swallows planktons as food.

Jaw locking (L)—The fish attacks trespassing conspecifics and grasps the jaws of the latter fish for a few seconds with his own jaws.

Abudefduf vaigiensis is a planktonic feeder. While feeding, the fish ascends in the water column, often rising three to five meters above his nest. In the daytime, the behaviour of an egg-caring fish can be divided into two patterns according to whether mass feeding excursion happens or not. In the majority of time, the nesting male is used to staying around spawning site, busy with egg-caring actions (Fig. 1). In this case, feeding only happens sporadically and the time is defined as non-feeding period. However, heavy feeding happens when tidal current brings planktonic masses to the shoreline. The egg-caring fish in the distant area would find the approaching plankton first and dash to the water column to collect planktons, such as *Sagitta* and hydromedusae, as food. Same action would be done later by other egg-caring individuals (Fig. 2). Then, the previous monotonous water column is filled with fish individuals busy with feeding. That is to say, feeding period commences. Feeding period stops about two hours later when planktonic mass moves away. From now on, non-feeding period begins again.

Data analysis

Data collected from the fish in both non-feeding and feeding periods are arranged to construct matrics after Kroll (1981). For those actions with a total frequency higher than ten, every two actions are treated with Spearman's rank correlation method (Sokal and Rohlf, 1969; De Boer, 1980) to test correlation between them. Furthermore, expected values of the cells in the matrix are calculated. Two kinds of expected values were deduced for each cell, they are expected value one (E1), calculated after Kroll (1981); and expected value two (E2), calculated by 'Quasi-independence' method (Everitt, 1977) after omitting the diagonal cells which present repetition of each action.

Fig. 1. During the non-feeding period the male *Abudefduf vaigiensis* centring the nesting site, is subject to egg caring. Egg patch is conspicuous on the slanting surface of the reef.

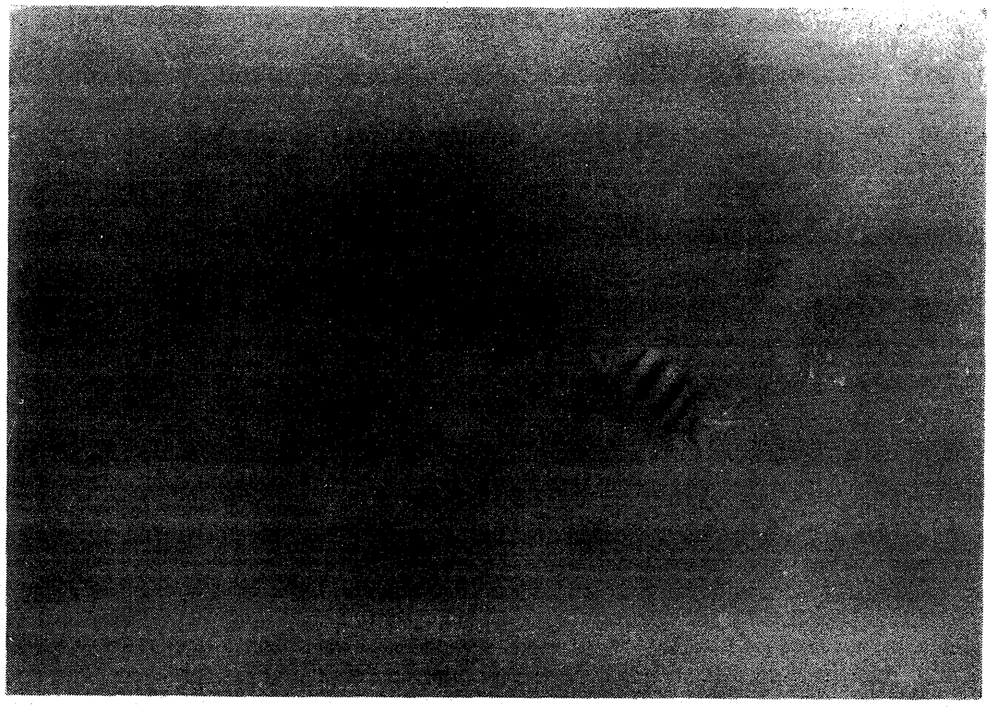

Fig. 2. When the planktonic mass arrives, the egg-caring male jumps to the water column for feeding.

For each frequency which occurs in the sequence preceding or following an action, adjusted values are deduced, to test if this frequency differs significantly from its expected values. Adjusted residuals are obtained from expected values except zero, then compared with 5% standard normal deviate, namely, 1.96, to test significance.

RESULTS

Sequential motions of egg-caring *A. vaigiensis* were recorded in a total of 577 units during non-feeding period (Table 1), and 542 units during feeding period (Table 2). Motor patterns are analyzed and the differences among them are studied.

The relative frequencies of different actions are shown in Fig. 3 to enable a comparison of fish behaviours between non-feeding and feeding periods. During non-feeding period, actions performed mostly were nipping, fanning and skimming, which comprised 63.9% of the total frequency. Other actions occurred less frequently as compared with the above actions. Feeding was very rare in this period but, predominated over a relative frequency of as great as 59.2% after planktonic mass triggered the feeding period. In comparison with the behaviour budgeted for different periods, it is found that the relative frequencies of FA, N, W, CR, and ST declined drastically as time shifted from non-feeding to feeding period. Among the rest actions SK and CH varied in a comparably small scale and jaw locking occurred only facultatively.

The significant positive correlations between actions recorded during non-feeding period is given in Fig. 4A. It shows that SK, FA and N can be arranged in a mutually positively correlated group, with few correlations with actions outside this group. SK, FA and N can be functionally considered as actions serving the care of fertilized eggs. All the three actions are performed on the nest. Analogous function

TABLE 1

Matrix of the number of times the different actions followed or preceded each other during non-feeding period

E1=indicates expected frequency of each cell. E2=indicates expected frequency without taking the repetitive frequency into account. SK=Skimming; FA=Fanning; N=Nipping; W=Watching; CH=Chasing; CR=Cruising; FE=Feeding; ST=Staying; A=Approaching.

		Following									
		SK	FA	N	W	CH	CR	FE	ST	A	Total
Preceding											
SK		46	11	16	13	10	0	0	5	4	105
	E1	19	20	28	13	9	5	0	9	2	
	E2		10	13	11	8	5	0	8	2	
FA		15	58	12	9	6	5	0	3	1	109
	E1	20	21	29	13	10	5	0	9	2	
	E2	10		11	10	7	4	0	7	2	
N		14	12	92	14	12	4	0	5	1	154
	E1	28	29	41	19	14	7	1	13	3	
	E2	13	11		12	8	5	0	8	2	
W		8	10	14	15	4	11	0	9	0	71
	E1	13	13	19	9	6	3	0	6	1	
	E2	11	10	11		7	5	0	7	2	
CH		13	5	5	5	13	2	0	6	2	51
	E1	9	10	14	6	5	2	0	4	1	
	E2	8	7	7	7		3	0	5	1	
CR		3	4	3	4	1	4	1	7	1	28
	E1	5	5	7	3	2	1	0	2	1	
	E2	5	4	5	5	3		0	3	1	
FE		0	0	0	1	0	0	0	1	0	2
	E1	0	0	1	0	0	0	0	0	0	
	E2	0	0	0	0	0	0		0	0	
ST		4	9	11	7	5	1	1	8	1	47
	E1	9	9	13	6	4	2	0	4	1	
	E2	8	7	7	7	5	3	0		1	
A		3	0	1	2	0	1	0	3	0	10
	E1	2	2	3	1	1	0	0	1	0	
	E2	2	2	2	2	1	1	0	1		
Total		106	109	154	70	51	28	2	47	10	577

TABLE 2
Matrix of the number of times the different actions followed or preceded each other during feeding period

L=Jaw locking; otherwise same as Table 1.

		Following										
		SK	FA	N	W	CH	CR	FE	ST	A	L	Total
Preceding												
SK		31	6	4	0	6	0	43	1	1	0	92
	E1	16	6	5	2	7	0	55	1	1	0	
	E2		7	5	3	9	0	29	2	2	1	
FA		7	13	2	0	2	0	10	0	1	0	35
	E1	6	2	2	1	3	0	21	0	0	0	
	E2	7		2	1	3	0	10	0	0	0	
N		5	1	14	0	0	1	9	0	0	0	30
	E1	5	2	2	1	2	0	18	0	0	0	
	E2	5	2		1	2	0	8	1	0	0	
W		1	0	0	1	0	0	6	2	0	0	10
	E1	2	1	1	0	1	0	6	0	0	0	
	E2	3	1	1		1	0	4	0	0	0	
CH		9	2	3	0	12	0	11	1	0	1	39
	E1	7	3	2	1	3	0	23	0	0	0	
	E2	9	3	2	1		0	13	1	1	0	
CR		0	0	1	0	0	0	0	0	0	0	1
	E1	0	0	0	0	0	0	1	0	0	0	
	E2	0	0	0	0	0		0	0	0	0	
FE		36	13	7	5	18	0	238	2	3	0	322
	E1	55	21	18	5	23	1	181	4	3	1	
	E2	29	10	8	4	13	0		3	2	1	
ST		1	0	0	3	0	0	2	0	0	0	6
	E1	1	0	0	0	0	0	4	0	0	0	
	E2	2	1	1	0	1	0	3		0	0	
A		1	0	0	0	1	0	2	0	0	1	5
	E1	1	0	0	0	0	0	3	0	0	0	
	E2	2	1	0	0	0	1	0	2		0	
L		1	0	0	0	0	0	1	0	0	0	2
	E1	1	0	0	0	0	0	1	0	0	0	
	E2	1	0	0	0	0	0	0	0	0	0	
Total		92	35	31	9	39	1	322	6	5	2	542

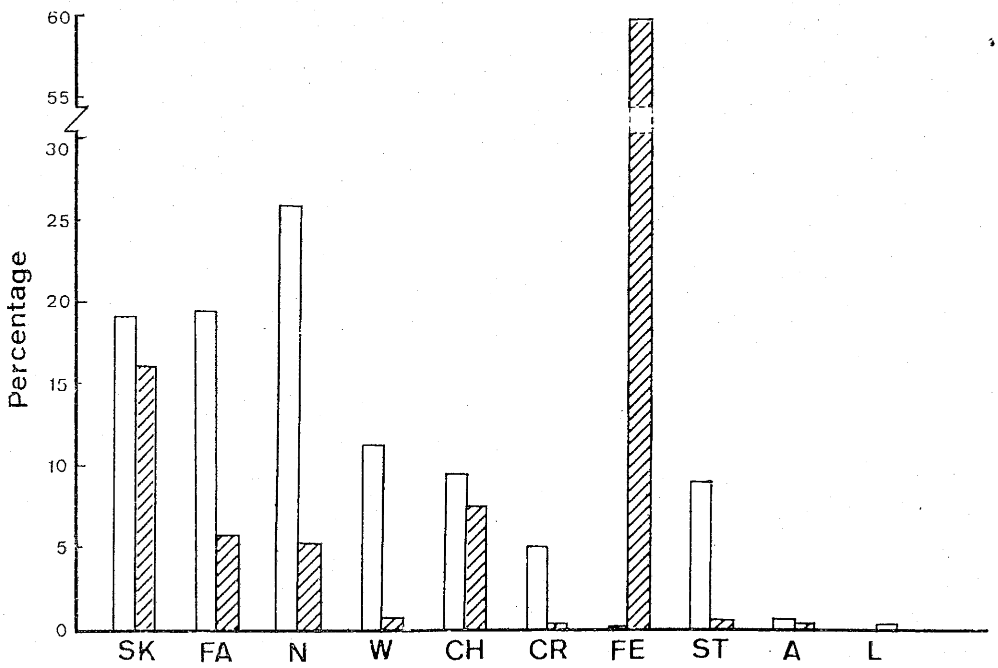

Fig. 3. Relative frequencies of behaviour (as percentage of total) of egg-caring *Abudefduf vaigiensis* during both non-feeding (blank column) and feeding (thatched column) periods. For abbreviations see Table 2.

and the same performing site could therefore cause the correlations between them. Watching in this case does not belong to the same group since it correlates with SK, FA and N only as a preceding action. With regard to other actions, it is found that there is no mutual positive correlation between each other.

Fig. 4B presents the significant positive correlation among actions recorded during feeding period. It shows that the group consisting of SK, FA and N in the non-feeding period no longer exists. However, among them, SK and FA are still highly correlated with each other. Conjecturally, they could be again arranged in a group. Additionally, another group comprising CH and FE is also found in the feeding period.

Direct association between every two actions for the egg-caring *A. vaigiensis* in the non-feeding period is shown by flowdiagrams in Fig. 5. The diagrams which show the temporal pattern of behaviours of an individual fish, are prepared from the matrix presented in Table 1. Since the purpose of the diagram is to present typical sequences of behaviour, only the cells reaching a value more than ten are included in the flowdiagram. Two diagrams, one for actions with repetition (Fig. 5A) and the other for actions without the repetition frequency (Fig. 5B), were prepared. In Fig. 5 it shows that actions, namely, FA, SK, N, CH and W, have significantly higher repetition frequency than the expected values (refer to Table 1). And among six transiting frequencies of the FA, N, SK group, four of them, viz., N⇄FA, FA→SK, N→SK, were significantly lower than expected values. When the repetition frequency are excluded (Fig. 5B), it is found that transitions within FA, N, SK, group occurred not significantly different from the expected values. Therefore, it is concluded that during non-feeding period each action of the SK, N, FA group tends to occur repetitively. But the change of actions would be

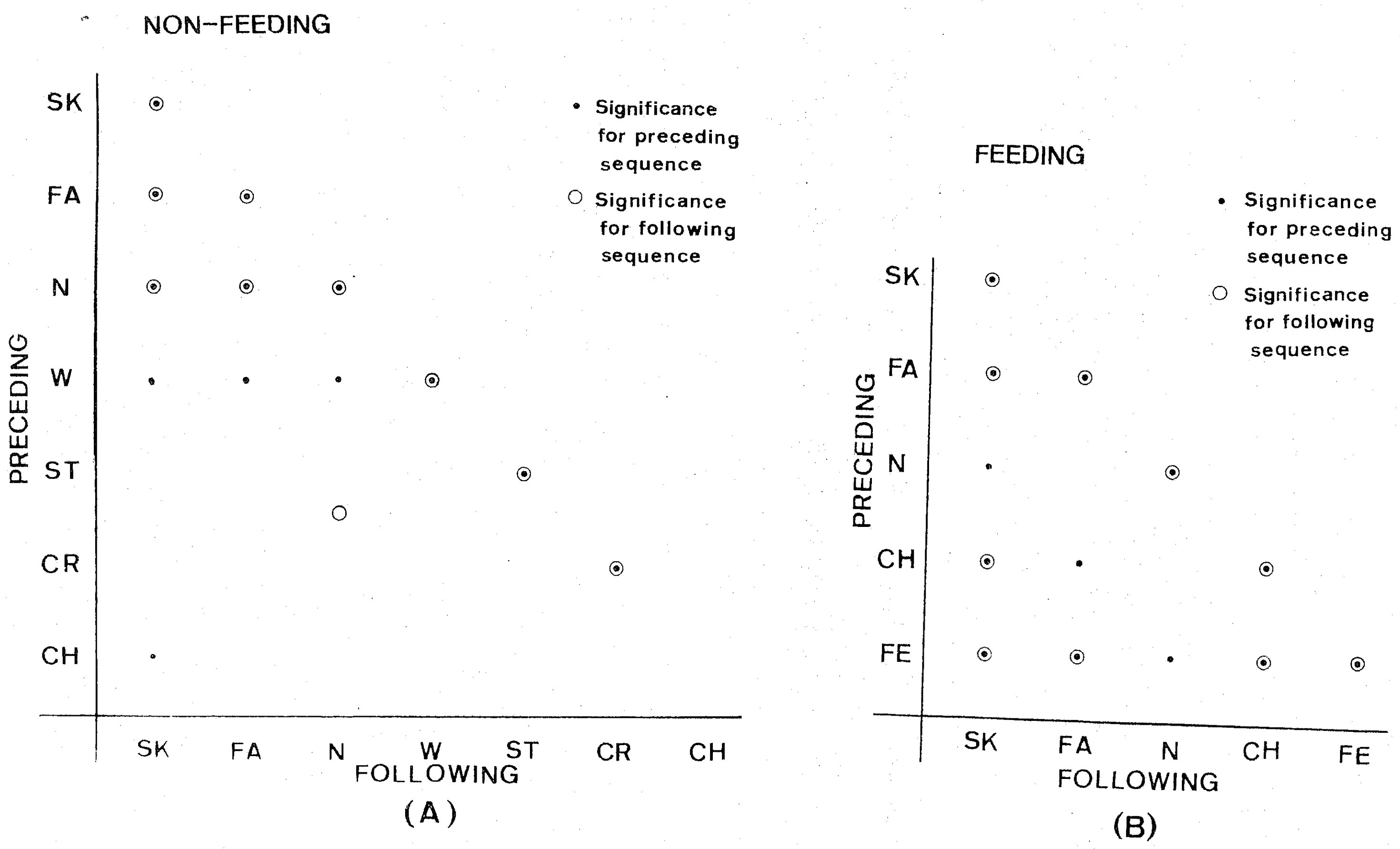

Fig. 4. Significant positive correlations between motions occurred during (A) non-feeding period, and (B) feeding period. For abbreviations see Table 2.

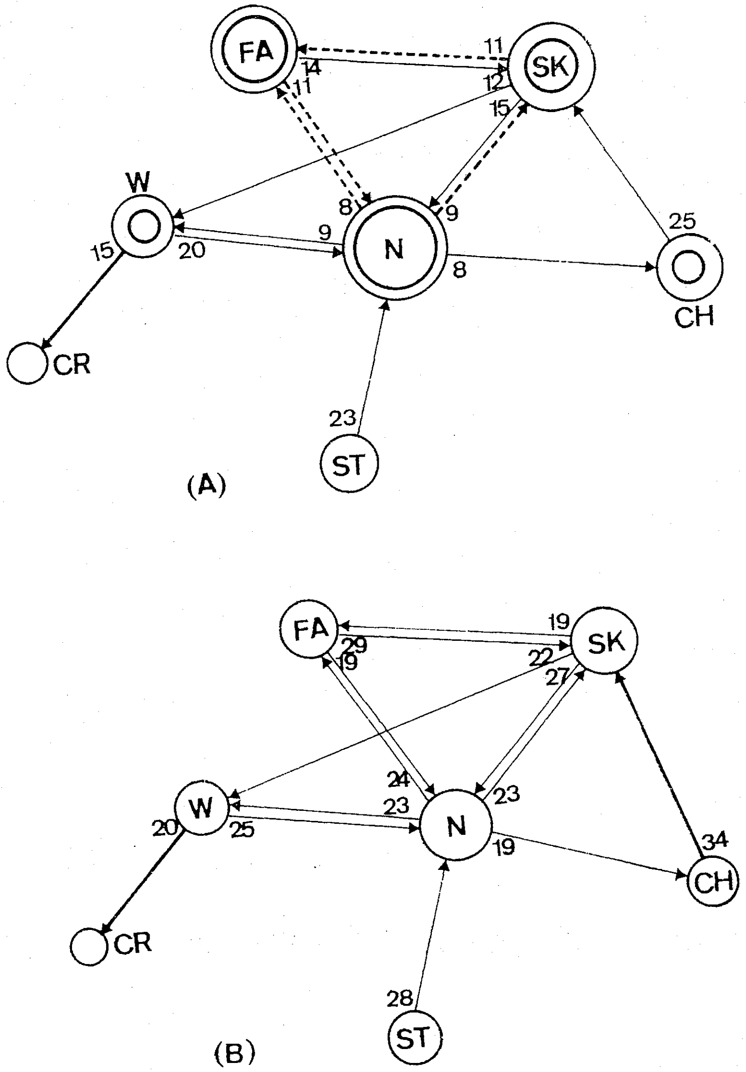

Fig. 5. Behavioural flowdiagrams for the egg-caring *Abudefduf vaigiensis* during the non-feeding period. Cells less than ten are omitted. (A) Repetitive actions included, (B) Repetitive actions excluded. A bold arrow connecting two actions indicates a transition in which the adjusted residual $d_{ij} \geq 1.96$, a dashed arrow indicates $d_{ij} \leq -1.96$, and a plain arrow indicates $-1.96 < d_{ij} < 1.96$. Numbers over the arrows indicate percentage of times the first behaviour is followed by the second. Diameter of the circle indicative relative frequency of the behaviours. The percentage of a repetitive action is presented as a circle inside the preceding action. For abbreviations see Table 2.

controlled by the weights of actions themselves.

Both the repetition and non-repetition data show that a significantly higher frequency is contributed to the sequence of W→CR. This result suggests that CR action may occur subordinately after W. In other words, the fish would get a higher probability to perform CR if the preceding action is W. In addition, as repetition is not taken into account, CH gets a significant tendency to send out SK

(Fig. 5B).

A flow chart of behaviour of the egg-caring male in feeding period is illustrated in Fig. 6. Feeding may precede or be followed by a sequence of behaviours which typically includes FE, SK, FA and CH. As the result in non-feeding period, a high repetition of action unit also happens to the fish in the feeding period (Fig. 6A). Due to diminishment on frequencies of some actions in this period, only five actions viz., SK, FE, CH, FA and N, with frequencies of more than 10, compared to seven actions in the non-feeding period. Strong exhibition of FE characterizes the action of this period. The frequency of the sequences in the repetition data, such as FE⇄SK, CH→FE, is lower than its expected value (Fig. 6A). Nevertheless, the significant difference is no longer exist (Fig. 5B) in the non-repetition data. During feeding period, the frequencies of those actions preceding or following N are less than ten, therefore their relative frequencies are not indicated in the figure.

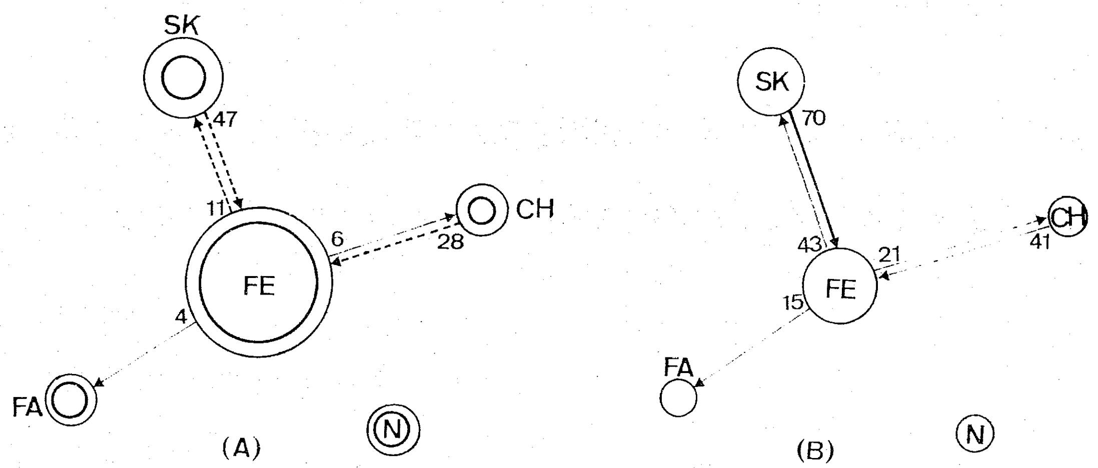

Fig. 6. Behavioural flowdiagrams for the egg-caring *A. vaigiensis* during the feeding period. (A) Repetitive actions included, (B) Repetitive actions excluded. For abbreviations see Table 2.

DISCUSSION

Parental investment of bony fishes has been currently focussed in recent years. Most studies on damselfishes have aimed at both pre-fertilization and post-fertilization investment. The reproductive success of the former is strongly emphasized (De Boer, 1981; Schmale, 1981; Thresher and Moyer, 1983). Nevertheless, the budget of the investment has not yet been sufficiently studied. In the present study, we describe that how the care is invested by *A. vaigiensis* when conflict occurs between care investment and energy gain.

Description of motion units of *A. vaigiensis* shows what occurs rather explains how or why. However, these motion units can be further divided into four categories according to the function currently known to each motion unit (Fishelson, 1970; Blumer, 1979). These categories are:

Type I—acts benefiting to egg development, and hatching. These acts include skimming, fanning and nipping.

Type II—acts to guard the eggs from predation by intruders. These acts include chasing, approaching and jaw locking.

Type III—acts to gain energy, feeding is the only motion unit here.

Type IV—acts not attributing to Type I, II and III, but may elaborate into these action types. These acts include watching, staying and cruising.

The egg-caring behaviours of the duty male centre around the nesting sites where the female spawns. When the fish jumps to feed in the mid-water, it would run risks of leaving his eggs unprotected. Therefore, it is undoubtedly that during the approach of planktonic mass, the fish has to make a decision whether to feed or to take care of eggs. It is found that FE (Type III) in this case takes priority over Type I and IV actions, as compared to what happened in the non-feeding period. Still, not all type I motions were neglected since the relative frequency of SK is nearly similar to that in the non-feeding period. For SK, which contributes 18.3% of the frequency in non-feeding period and 16.9% in feeding, seems to get an activity budget independent of whether food mass comes or not.

The function of Type IV actions is still obscure. Though a high relative frequency of 25.3% in the non-feeding period drops drastically to 3.1% when feeding period commences, existence of sequence of unexpected frequency, e. g., W→CR may imply there between the units to be certain linkage. In consideration of the characteristic of Type IV actions such as highly supressible, these actions may be termed as 'intermediate' actions.

As to Type II actions they are mostly elicited by trespasses of intruders, such as *Stegastes fasciolatus*, *Pomacentrus coelestis*, *Labroides dimidiatus* and some other wrasses, which inhabit neighbouring area and tend to rob eggs. The similar relative frequencies of Type II actions recorded in both the feeding and the non-feeding periods, may imply that these motions are important to egg-protection. Since these actions are mainly elicited by external stimuli, they correlate with other actions only in few cases. When the duty male left for feeding, the trespassers would take the opportunity to steal eggs. Though he seldom failed to defend the intruders, he lost some eggs during his absence. Therefore, the budget for defending the intruders during the feeding period seems to be limited.

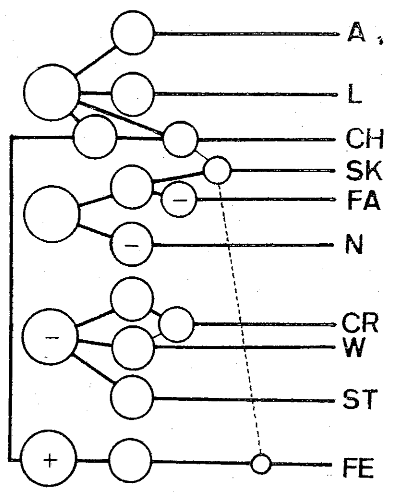

Fig. 7. Hypothetical model for organization of egg-caring behaviours of *Abudefduf vaigiensis*. Where, circle indicates control unit; control output transits from a circle to a smaller one. A plain line indicates that the control out-put functions only during the non-feeding period, whereas a dashed line indicates the control output functions only during feeding period. Bold lines fabricate the basic control system available during both periods. Signals in some circles present budget changes when feeding jump is activated, where plus sign indicates frequency reinforced, and minus sign indicates frequency suppressed.

A hypothetical model for the organization of egg-caring behaviour of *A. vaigiensis* is tentatively prepared in Fig. 7. In this model existence of control units is based on both non-repetition flowdiagram and correlation analysis. Outputs of control units pass from circles to the smaller ones, and end with action(s). When the feeding behaviour is activated, an alternate budget is triggered passively as shown in the figure.

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條紋雀鯛 *Abudefduf vaigiensis* (Quoy et Gaimard) 的離巢攝食對其護卵行爲的影響

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在本省北部沿海水域之中，條紋雀鯛 *Abudefduf vaigiensis* (Quoy et Gaimard) 的數量非常多。條紋雀鯛在每年的四月份開始有生殖的現象，而在五月至八月爲產卵盛期，它們所產的卵爲黏性卵，這些魚卵在產出之後，會黏附在礁石的表面。在受精卵的孵化期間，雄魚負責護卵的工作。在此孵化的大部份時刻，雄魚會停留在巢邊護卵，不過當海流帶來濃密的浮游生物餌料時，護卵的雄魚會短暫地游到巢上水層中攝食這些浮游生物。爲了檢視這些護卵魚體在離巢攝食時，其行爲上的可能變化，我們先把他的行爲分成如下各種動作：擦卵 Skimming、扇卵 Fanning、啄卵 Nipping、觀視 Watching、追逐 Chasing、巡游 Cruising、攝食 Feeding、停貯 Staying、前迎 Approaching 及鎖顎 Jaw Locking 等等，然後依其各種動作的發生次序，加以記錄，以做分析整理之用。

以矩陣分析的結果，顯示大部份動作都有顯著連續發生的現象。此外，在非攝食時期，啄卵、扇卵以及擦卵等三個動作的發生頻率所佔最多，約占此一時期中所有動作的 63.9%。至於當海流帶來浮游生物團之後，離巢攝食的動作會增加到 59.2% 之多。當護卵雄魚由非攝食時期轉換到攝食時期，在行爲上他在擦卵、追逐及前迎等這三個動作上，發生頻率只有些微的變化，至於其他動作的發生頻率則變化甚大。經以流程圖來表示時，各種動作的相關位置可以顯示出整個行爲系統運作的決定情形，文中並嘗試擬定一個條紋雀鯛各種護卵活動的行爲控制系統。