

COMMUNICATION SYSTEMS AND SOCIAL INTERACTIONS IN A GOBY-SHRIMP SYMBIOSIS

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Abstract. Interphyletic communication is quantitatively shown to occur in a behavioural, mutualistic symbiotic association between the goby *Psilogobius mainlandi* and two species of shrimps, *Alpheus rapax* and *A. rapacida*, by the use of information theory and χ^2 analyses. Communication between gobies and shrimps is primarily tactual. Gobies use as shelter burrows dug and maintained by shrimps. Gobies sit at the burrow entrance and warn shrimps of danger by a flick of the tail. Shrimps communicate their presence outside the burrow by touching gobies with their antennae. Gobies never give warning signals in the absence of shrimps. It is postulated that the spacing of the burrows in nature is a result of the complex interaction of three communication systems: tactual communication among shrimps and between gobies and shrimps and visual communication among gobies. It is suggested that the analysis techniques used here be applied to the analysis of other symbiotic associations.

Communication has been defined as a process in which there is information exchanged between animals to the mutual adaptive advantage of both (Klopfer & Hatch 1968). Apparent interphyletic and interclass communication have been described in cleaning symbioses in which shrimps clean fishes (e.g. Feder 1966) and in which finches clean tortoises (MacFarland & Reeder 1974). The complexity of symbioses between sea anemones and pomacentrid fish (Mariscal 1972) or hermit crabs (Balasch & Mengual 1974) suggests that communication occurs in these associations. The communication within these symbioses has not, however, been quantified.

In this study communication in the behavioural mutualistic symbiosis between a goby, a small bottom-dwelling fish, and an alpheid, or snapping, shrimp is explored quantitatively. In this association gobies and shrimps communicate with each other tactually and possibly chemically. Gobies communicate with one another visually. The alpheid shrimps communicate with one another tactually and possibly visually.

Communication can be analysed at several different levels. At the syntactic level the signals, their variants, their frequency of occurrence, or their modification by environmental factors are determined. At the semantic level the meanings of the signals are determined. The significance of the signals to the receiver is determined at the pragmatic level (Morris 1946; Marler 1961; Cherry 1966; Smith 1968).

Communication signals have been analysed at the syntactic level using the concepts of information theory (e.g. Haldane & Spurway 1954; Wilson 1962; Altmann 1965; Hazlett & Bossert 1965, 1966; Dingle 1969, 1972; Chatfield & Lemon 1970; Steinberg & Conant 1974). In several of these studies the investigators also used χ^2 analyses to determine the effects of signals on responses. Although the χ^2 analyses also give a syntactic interpretation of signals, the significance of signals to the receivers and perhaps even to the emitters can be inferred from the results. These data analysis techniques are applied here to interphyletic communication.

The Goby-Shrimp Association

Goby-alpheid shrimp symbiotic associations, which have been observed pantropically (Bayer & Rofen 1957; Luther 1958; Harada 1969; Karplus et al. 1972, and many others), in general conform to the following description. The goby sits at the entrance of a burrow which the shrimp digs and maintains. The shrimp, when ploughing sand, exits from its burrow antennae first. The shrimp's antennae contact the tail of the goby, the shrimp continues to exit from the burrow, it drops its load of sand and withdraws into the burrow without turning around. If the shrimp is out of the burrow when an observer approaches, the goby flicks its tail. In response, the shrimp generally sits still or flees into its burrow. Depending on the nature of the disturbance, the goby may remain at the entrance of the burrow or may turn and flee head first into the burrow, always after the shrimp. The amount of time between the disappearance and reappearance of the goby at the entrance of the burrow

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varies greatly. The goby always reappears first. Thus the goby apparently profits from the ready-made shelter provided by the shrimp, and the shrimp apparently profits from the warning signals the goby provides as it sits at the opening of the burrow.

Exceptions to this description are gobies which hover over burrow entrances they guard, rather than sitting on the bottom (Klausewitz 1960; Harada 1969). Karplus et al. (1972) observed the shrimp cleaning its goby symbiont.

In shallow areas of Kaneohe Bay, Oahu, Hawaii, the goby *Psilogobius mainlandi* Baldwin (Baldwin 1972) guarded the interspersed burrows of *Alpheus rapax* Fabricius and *A. rapacida* de Man. Spacing between burrow entrances differed with the substratum and the size of the occupants. Where the substratum was extremely rocky, burrows were few, far apart, large, and occupied by large inhabitants. Where the substratum was silty with a thick coral rubble base, burrows were numerous and close together. Burrow entrance sizes, which reflected inhabitant sizes, differed greatly. There were many small burrows interspersed among larger ones. Marine resin casts showed that large burrows were similar to those described by Karplus et al. (1974). They were about 20 cm deep with several chambers and winding passages. The burrows lay under coral rubble and had sand floors. Burrow entrances collapsed readily when not attended by shrimps and new ones were formed in a short time.

Gobies were often observed without shrimps, but shrimps were observed without gobies only (1) on very hot days when the tide was low, at which time *A. rapax* were numerous on the surface of the substratum, or (2) when I had just captured a guarding goby. Shrimps guarded by gobies were extremely difficult to capture; those without gobies guarding were easily captured.

Pairs of gobies were observed throughout the year. Males and females could be distinguished in the field only if the two gobies were guarding the same burrow at the same time. Then the female had a white abdomen with a dark band around her body in the region of the anal fin. Interactions between gobies in the field were few. When they did occur, they were brief.

All goby-shrimp burrows were occupied by at least two shrimps. *A. rapacida* were found in male-female pairs only, whereas *A. rapax* were observed three to a burrow, two females and one male, or in pairs consisting of two females

or a male and a female. When pairs were observed, it is possible that a third shrimp was in the burrow. No interactions between shrimps other than their digging together were observed in the field.

Methods

Data for analyses of communication between gobies *P. mainlandi* and shrimps *A. rapax* and *A. rapacida* were gathered from field observations. Interactions were clearly visible from above the water on calm days during low tide. I chose a guarding goby to observe and began recording interindividual (interphyletic) two-act sequences immediately. I walked slowly toward the burrow. When the goby began to flick its tail, I stopped my approach in order to avoid frightening it into the burrow. When the tail flicking stopped, I continued my approach until I was stopped beside the burrow entrance. If the goby at that time did not flick its tail, I made movements until the goby withdrew or fled into the burrow. At that point observations on that pair ended. If two shrimps were out of the burrow at the same time, I discarded my observations since I was unable to observe the animals in sufficient detail.

A. rapax and *A. rapacida* are easily distinguished in the field since *A. rapacida* has a white abdominal band (which disappears in preservative) that is not present on *A. rapax*. One hundred and six goby-*A. rapax* pairs were observed for a total of 8.7 h. Sixty-six goby-*A. rapacida* pairs were observed for a total of 6.0 h. Durations of observations on goby-shrimp pairs ranged from 15 s to 28 min. No goby-shrimp pair was observed more than once.

Data Analyses

All acts performed by gobies and shrimps were coded and punched on IBM computer cards for analyses with an IBM 360/65 computer. Contingency tables (e.g. Table 1) were made for interindividual (interphyletic) two-act sequences having no minimum interval length. The total number of times each Initial Act (signal) occurred and the total number of times each Following Act (response) occurred were determined. The expected number of times that an act followed another act, assuming the Initial Act had no influence on the Following Acts, was calculated (Hazlett & Bossert 1965).

To test whether 'responses' followed 'signals' at random, a χ^2 value (χ^2_{table}) was calculated for the entire table. Columns or rows (whichever

produced the higher degrees of freedom) with any expected value less than one were lumped together.

Using the null hypothesis that responses followed each Initial Act with their overall frequency of occurrence, I applied a χ^2 analysis (χ^2_{row}) for each Initial Act. The observed and expected values were from the contingency tables of interindividual two-act sequences. In these calculations, if the expected number was less than one, both observed and expected numbers were lumped with all other categories in which the expected value was less than one for that Initial Act, that is, within one row. If the lumped sum of expected values was still less than one, the sums of observed and expected were added to the first figures in the row for which the expected value was greater than one. If there was not such a category, the χ^2 was zero. Lumped figures were counted as one category (Snedecor & Cochran 1967).

To determine whether an Initial Act was directive or inhibitive toward a given response, I compared the observed and expected values for each two-act sequence in the contingency tables. If the observed was greater than the expected, the signal was considered to be directive toward the response. If the observed was less than the expected, the signal was considered to be inhibitive toward that response (Hazlett & Bossert 1965). The statistical significance of the elicitation or inhibition was determined from the χ^2 value (χ^2_{act}) for each two-act sequence. In these calculations I used the observed and expected values for the given two-act sequence for one ratio. I subtracted these figures from the total observed value for

the given Initial Act for the second ratio. If the expected value in either ratio was less than one, the χ^2 for that act could not be calculated.

A number of two-act sequences were recorded for each pair of animals during observation periods which differed in length among pairs. As a result, not all two-act sequences are independent of one another and some pairs contribute more data to the overall two-act sequence data set than others do. Because of these problems and other questions as to the validity of χ^2_{row} and χ^2_{act} (Moehring 1972), χ^2 values were considered significant only if the probability of chance occurrence was less than 0.005.

I applied a χ^2 analysis (χ^2_{req}) to two by two contingency tables to test whether the frequency of occurrence of each act for one type of interacting pair (goby-*A. rapax*) differed significantly from the frequency of occurrence of each act for the second type of interacting pair (goby-*A. rapacida*). In the contingency tables, one row was the observed number of times the act in question occurred for the two types of interacting pairs and the second row was the observed number of times all other acts occurred for the two types of interacting pairs.

Information as used here (Shannon & Weaver 1949) is defined as variation, or uncertainty. Information 'is measured . . . by its "news" value, that is, the extent of surprise it causes to the recipient' (Singh 1966, p. 9). Information values in this study were calculated from observed, interphyletic, two-act sequences, using the following formulae (Quastler 1958; Hazlett & Bossert 1965; Dingle 1969, 1972; Steinberg & Conant 1974).

Table I. Interindividual Two-Act Sequences in Interactions Between Gobies and *A. rapax*

Goby initial acts	<i>A. rapax</i> following acts						
	Flee	In burrow	Manipulate objects	No change	Plough	Sit	Withdraw
Dorsals erect	0	4	1	3	3	0	1
Flee	9	13	0	0	0	0	0
Guard	14	934	109	19	939	52	691
Move away	0	20	4	22	21	1	22
Nip sand	5	16	2	14	12	2	13
Pectorals wave	0	9	2	3	8	0	5
Sit away	3	8	0	0	7	1	4
Tail beat	3	0	1	1	0	0	1
Tail flick	119	17	3	134	22	82	65
Tail wave	0	22	3	25	15	1	38
Withdraw	1	15	2	3	10	2	6

1. Maximum information possible if all acts were equally probable: $H_{\max} = \log_2 N_j$, where N_j is the number of responses in the behavioural repertoire of the receiver.

2. Information Present: $H_B = -\sum p_j \log_2 p_j$, where p_j is the probability of occurrence of the response (j).

3. Conditional Information Present: $H_{B|A} = -\sum p_{ij} \log_2 p_{ij}$, where p_{ij} is the overall probability that a given two-act sequence (ij) will occur and $p_{j|i}$ is the probability that a given response (j) will occur provided that a given signal (i) has already occurred.

4. Information Transmitted:

$$H_t = H_B - H_{B|A}.$$

5. Contribution of a particular act to information transmission: $h_t = p_i \sum p_{j|i} \log_2 p_{j|i} / p_j$ (Blachman 1968; Steinberg & Conant 1974).

6. Normalized Transmission (Steinberg & Conant 1974; also called coefficient of constraint, Attneave 1959; per cent input, Herman 1965; per cent uncertainty reduction, Hazlett & Estabrook 1974a, b; Rubenstein & Hazlett 1974): $NT = H_t / H_B$, expressed as a percentage.

Goby-shrimp communication analyses are divided into two sections. For analyses in which shrimps perform Initial Acts and gobies' acts follow (shrimp communicates to goby), I used acts from the entire observation time since I observed the behaviour of the goby at all times. For analyses in which gobies initiate the behaviour and the shrimps' behavioural acts follow (goby communicates to shrimp), I excluded the behaviour of the goby when the shrimp was in its burrow since it was not possible to observe the shrimp's responses. The number of encounters occurring between gobies and shrimps was determined by the number of times shrimps entered their burrows.

Behavioural Acts of *P. mainlandi*

The behavioural acts of *P. mainlandi* are listed in alphabetical order.

Dorsals erect: The goby spread its dorsal fins.

Flee: The goby rapidly entered the burrow, generally head first.

Guard: Sitting still at the burrow entrance, the goby sat high on its pelvic fins with its pectoral fins extended to the side, its dorsal fins folded, and its caudal fin generally extending into the burrow.

In burrow: The goby was in the burrow and could not be seen.

Move away: The goby moved away from the burrow.

Nip sand: The goby turned its head to the side, moved slightly forward, took a quick bite of sand, then resumed its original position. The sand was filtered through the goby's gills and fell in small piles beneath each operculum.

No change: There was no change in the behaviour of the goby in 'response' to an act by the shrimp.

Pectorals wave: The goby moved its pectoral fins alternately in a rowing motion.

Sit away: The goby sat in any position more than 15 cm from the burrow entrance.

Tail beat: The goby moved its folded caudal fin to one side and back to its original position, usually hitting the shrimp with it.

Tail flick: The goby flicked its folded caudal fin about three times in a manner that was barely visually perceptible.

Tail wave: The goby moved its spread caudal fin back and forth.

Withdraw: The goby moved toward the burrow.

Behavioural Acts of *A. rapax* and *A. rapacida*

The behavioural acts of the alpheid shrimps are listed in alphabetical order.

Flee: The shrimp rapidly entered its burrow, usually backward.

In burrow: The shrimp was in its burrow and could not be seen.

Manipulate objects: The shrimp picked up objects with its large chelipeds or walking legs.

No change: There was no change in the behaviour of the shrimp in 'response' to an act by the goby.

Plough: The shrimp exited from its burrow holding its large chelipeds forward and pushing sand, pebbles, or shells in front of it.

Sit: The shrimp sat still, apparently doing nothing.

Withdraw: The shrimp moved toward its burrow, generally backward.

Results and Discussion

The signals from one symbiont in a goby-shrimp pair decreased the amount of uncertainty in the occurrence of responses of its symbiotic partner by 13 to 15% (NT, Table II). That is, interphyletic communication between goby and shrimp in these associations did occur. The importance of each goby signal and each shrimp signal in their transmission of information is shown in Tables III and VI, respectively. The effects these signals had on the behaviour of the receiver are shown in Tables IV, V, VII and VIII.

Strong warning signals, defined here as goby acts directive toward 'flee' in the shrimps, are 'withdraw', 'tail flick', 'tail beat', and 'flee' (Tables IV and V). Using both qualitative and quantitative observations, I have listed these from weakest to strongest signal. Gobies 'withdrew' toward, but not into, the burrows when they sensed slight danger. 'Tail flick'

started when the danger was more imminent. If the shrimp did not respond to 'tail flick', the goby 'tail beat'. When danger was obvious and serious or if the shrimp did not respond to 'tail beat', the goby fled into its burrow. Shrimps always entered first.

The frequency of 'tail flick' was increased by the shrimp act 'plough' and decreased by the

Table II. Information Values for Communication Between Gobies and Shrimps

Category	H_B	H_t	NT	Acts	Encounters
Goby communicating to shrimp					
<i>A. rapax</i>	2.35	0.32	14%	2.2	1059
<i>A. rapacida</i>	2.34	0.35	15%	2.0	1005
Shrimp communicating to goby					
<i>A. rapax</i>	2.40	0.31	13%	3.2	1059
<i>A. rapacida</i>	2.21	0.31	14%	3.5	1005

H_B = Information present (bits/act); H_t = Information transmitted (bits/act); NT = Normalized transmission; Acts = Acts/signaller/encounter.

Table III. Contribution of Individual Goby Signals to Information Transmission

Goby to <i>A. rapax</i>		Goby to <i>A. rapacida</i>	
Signal	h_t	Signal	h_t
Tail flick	0.180	Tail flick	0.181
Guard	0.090	Guard	0.094
Flee	0.012	Tail wave	0.022
Tail wave	0.012	Move away	0.017
Moveaway	0.008	Flee	0.012
Tail beat	0.004	Withdraw	0.008
Nip sand	0.004	Tail beat	0.006
Dorsals erect	0.002	Dorsals erect	0.005
Sit away	0.002	Nip sand	0.003
Withdraw	0.001	Sit away	0.002
Pectorals wave	0.001	Pectorals wave	0.001

Table IV. Effects of Goby Initial Acts on *A. rapax*

Goby initial acts	<i>A. rapax</i> following acts		P for χ^2_{row}
	Directive	Inhibitive	
Dorsals erect			> 0.250
Flee	Flee, in burrow	Plough	< 0.005
Guard	Plough, in burrow	Sit, flee, no change	< 0.005
Move away	No change		< 0.005
Nip sand	No change		< 0.005
Pectorals wave			> 0.500
Sit away			> 0.500
Tail beat	Flee		< 0.005
Tail flick	Sit, flee, no change	Plough, manipulate, withdraw, in burrow	< 0.005
Tail wave	Withdraw, no change	Plough	< 0.005
Withdraw			> 0.750

$\chi^2_{\text{table}} = 1909$; $df = 36$.

shrimp acts 'withdraw', 'flee', and 'in burrow' (Tables VII and VIII). Apparently 'tail flick' functions only as a warning signal. *A. rapacida* was persistent in remaining out of its burrow primarily while it was 'manipulating objects'. Thus 'manipulate objects' was directive toward 'tail beat'.

For two reasons I postulate that warning signals 'tail flick' and 'tail beat' have evolved from the goby act 'withdraw'. The most obvious reason is that gobies 'withdraw' or 'flee' into their burrows for their own safety. These then are positive indications of danger. When a goby swims backwards, its usual position for 'with-

Table V. Effects of Goby Initial Acts on *A. rapacida* Following Acts

Goby initial acts	<i>A. rapacida</i> following acts		P for χ^2_{row}
	Directive	Inhibitive	
Dorsals erect	No change		< 0.025
Flee	Flee, in burrow	Plough, withdraw	< 0.005
Guard	Plough	Sit, flee, no change	< 0.005
Move away	Withdraw, no change	Plough	< 0.005
Nip sand	No change		< 0.005
Pectorals wave			> 0.500
Sit away			> 0.500
Tail beat	No change		< 0.005
Tail flick	Sit, flee, no change	Plough, manipulate, withdraw, in burrow	< 0.005
Tail wave	Withdraw, no change	Plough, in burrow	< 0.005
Withdraw	Flee, no change	Withdraw	< 0.005

$\chi^2_{table} = 2423$; $df = 36$.

Table VI. Contribution of Individual Shrimp Signals to Information Transmission

<i>A. rapax</i> to goby		<i>A. rapacida</i> to goby	
Signal	h_t	Signal	h_t
In burrow	0.101	In burrow	0.084
Plough	0.086	Flee	0.074
Withdraw	0.064	Plough	0.073
Flee	0.045	Withdraw	0.065
Sit	0.012	Sit	0.006
Manipulate objects	0.004	Manipulate objects	0.006

Table VII. Effects of *A. rapax* Initial Acts on Goby Following Acts

<i>A. rapax</i> initial acts	Goby following acts		P for χ^2_{row}
	Directive	Inhibitive	
Flee	Guard	Tail flick, move away, no change	< 0.005
In burrow	Guard, nip sand, dorsals erect, tail wave, pectorals wave, move away, sit away, withdraw, flee, in burrow	Tail flick, no change	< 0.005
Manipulate objects			> 0.050
Plough	Tail flick, no change	Guard, nip sand, dorsals erect, move away, pectorals wave, withdraw, flee, in burrow	< 0.005
Sit	Guard, no change	Nip sand	< 0.005
Withdraw	No change	Guard, nip sand, tail wave, move away, flee, withdraw, in burrow, tail flick	< 0.005

$\chi^2_{table} = 2040$; $df = 55$.

draw', its tail makes a motion similar to 'tail flick'. 'Tail beat' looks like an exaggerated 'tail flick'. Thus, 'tail flick' and 'tail beat' may be intention movements, in the sense of Daanje (1950), which have derived signal function in this symbiosis.

'Tail wave' and 'move away' are weak warning signals, defined here as goby acts which were directive toward 'withdraw' in shrimps (Tables IV and V). 'Move away' was directive toward 'withdraw' only for *A. rapacida*. The antennae of *A. rapax* are longer than those of *A. rapacida* and thus may maintain contact with a goby that 'moves away' to a greater distance from the burrow entrance. Both shrimp species fled into or stayed in the burrow when the goby was far from the entrance.

The frequency of 'tail wave' increased when *A. rapacida* 'ploughed', but not when *A. rapax* ploughed. When *A. rapacida* 'ploughed', it almost always bumped the goby severely, generally ploughing sand in a path that went under the goby's tail. *A. rapax*, on the other hand, seldom bumped the goby. *A. rapacida* with its shorter antennae may maintain contact with the goby by using all parts of its body whereas *A. rapax* maintains contact primarily by using its longer antennae. This suggests that 'tail wave' may be a method by which gobies keep their balance. 'Tail wave' also occurred in the absence of *A. rapax*. Thus 'tail wave' may also be a means by which the burrow is aerated or it may be a signal which has no immediate effect on a shrimp but communicates the presence of a goby at the entrance of the burrow. Perhaps it was directive toward 'withdraw' only because it resembles warning movements.

Information present was higher when *A. rapax* communicated to gobies than when *A. rapacida*

communicated to gobies (Table II). That is, the gobies' behaviour was less restricted in their association with *A. rapax* than it was in their association with *A. rapacida*. At the same time the amount of information transmitted by shrimps to gobies was the same for both associations. The number of shrimp acts per encounter was slightly higher for interactions between *A. rapacida* and gobies, yet information transmitted per encounter was approximately the same for the two shrimp species. These results and the fact that only one bit of information was transferred per encounter support the idea that one yes-no question was answered for the goby in each encounter. This was independent of the number of shrimp acts performed to communicate the message and independent of the differences in the behaviour for the two shrimp species. More transmission probably would be wasteful.

Shrimp signals apparently informed gobies whether or not an actively digging shrimp was present, that is, whether or not warning signals were necessary in the event of danger. The shrimp act 'in burrow', the main act signalling that a warning signal would be unnecessary, contributed the most to information transmission from shrimp to goby (Table VI). When the shrimp was in its burrow, the goby guarded and was active in its interactions with other gobies and in feeding (Tables VII and VIII). When the shrimp 'withdrew' or 'fled', warning signals were unnecessary since the shrimp was entering its burrow anyway. Warning signals were, in fact, inhibited. The shrimp acts 'sit' and 'flee' were directive toward 'guard' in the goby. This suggests that the goby sat alert to danger which it may have just signalled was present. The shrimp act 'sit' combined with the

Table VIII. Effects of *A. rapacida* Initial Acts on Goby Following Acts

<i>A. rapacida</i> initial acts	Goby following acts		<i>P</i> for χ^2_{row}
	Directive	Inhibitive	
Flee	Guard	Tail flick, withdraw, no change	< 0.005
In burrow	Guard, nip sand, dorsals erect, move away, pectorals wave, sit away, withdraw, flee, in burrow	Tail flick, no change	< 0.005
Manipulate objects	Tail beat		< 0.025
Plough	Tail wave, tail flick, no change	Guard, nip sand, withdraw, in burrow	< 0.005
Sit	No change		< 0.005
Withdraw	No change	Guard, nip sand, tail wave, tail flick, move away, withdraw, in burrow	< 0.005

goby act 'guard' may be a strategy for concealment. 'Tail flick' was the only act directive toward 'sit' (Tables IV and V). Shrimps and gobies are difficult to see when they are still. If the goby 'guards' and the shrimp 'sits', and if the pair was not seen previously, they may not be detected by an observer. Thus warning signals would be unnecessary for a 'sitting' shrimp. 'Sit' and 'guard' consume less energy than 'withdraw' or 'flee' if the animals sit still until danger passes and then continue their activity. Thus, 'sit' and 'guard' appear to be highly adaptive behavioural acts.

'Guard' was the only goby act directive toward digging behaviour in shrimps (Tables IV and V). 'Guard' was directive toward 'in burrow' for *A. rapax* but not for *A. rapacida*. *A. rapacida* often stayed out of its burrow, 'manipulating objects', until it 'fled' in response to a warning signal. *A. rapax*, on the other hand, 'manipulated objects' for shorter periods (qualitative observations), although with the same frequency as *A. rapacida* ($P > 0.250$), and entered its burrow without necessarily having been warned of danger. In fact, 'flee' contributed quite a bit more to information transmitted from *A. rapacida* to gobies than from *A. rapax* to gobies (Table VI). For both species of shrimps, 'guard' was inhibitive toward inactivity and 'flee' (Tables IV and V). This suggests that 'guard', in certain contexts, communicates to shrimps that there is no danger.

Certain goby acts appear to have no significant effect on shrimp behaviour (insignificant χ^2_{row} or directive toward 'no change') for one of several reasons. (1) The goby act may actually have had no effect on shrimp responses, i.e. it had no communicative function. (2) The number of times responses occurred may have been too small to show the true effect of the initial act. (3) The goby act may have had an effect that was not immediately expressed, i.e. there may have been a latency in the characteristic response. (4) The shrimp's previous response may have been the act with which it would normally respond to the goby's new signal. It therefore continued to perform that act and registered 'no change' in response to the goby's act. (5) The observer was unable to detect a response which actually occurred, for example, a chemical response.

'Sit away' had no significant effect on the behaviour of either *A. rapacida* or *A. rapax* (Tables IV and V), yet it showed a significant effect when the data for the two species were

combined ($P < 0.025$). This suggests that the number of times it occurred for the separate species of shrimps was too small to show the effect. In the combined data analysis, 'sit away' was directive toward 'flee'. Although it was relatively unimportant in the overall transmission of information from goby to shrimp (Table III), 'sit away' may communicate the absence of a warning system.

Goby signals 'withdraw' and 'move away' had significant effects on *A. rapacida* responses and no significant effects on *A. rapax* responses. 'Tail beat' had significant effects on *A. rapax* responses and no significant effects on *A. rapacida* responses (Tables IV and V). For 'withdraw' the combined data analysis shows the same effect as for *A. rapacida* alone. 'Tail beat' and 'move away' have the same effect as for *A. rapax* alone. This suggests that the goby acts 'withdraw' and 'tail beat' actually did have an effect on the responses of both shrimp species. At least it indicates that the responses of *A. rapax* to 'withdraw' and of *A. rapacida* to 'tail beat' were not sufficiently different to alter the significance of the signals. The shrimps tended to 'flee' in response to both signals. The goby act 'move away' apparently had an effect on the behaviour of *A. rapacida* but not on the behaviour of *A. rapax*. That is, the response of *A. rapax* was sufficiently different from that of *A. rapacida* to alter the results. This follows since *A. rapax*, with its long antennae, could maintain contact with the goby even when it 'moved away'. *A. rapacida*, with its shorter antennae, would lose its warning system when the goby 'moved away'. *A. rapacida* would thus 'withdraw' into its burrow.

'Pectorals wave' has insignificant χ^2 values in the combined analysis, as well as in the separate analyses (Tables IV and V), for its effect on the shrimps' behaviour. Although the frequency of 'pectorals wave' is not great, it is probably large enough for an effect to be indicated. This is suggested by the fact that other acts ('tail beat', 'sit away') with lower frequencies of occurrence did show significant effects on responses. 'Pectorals wave' may have had no effect because it may not be a display with communicative signal value. It did, in fact, contribute the least to information transmission from goby to shrimp (Table III). It occurred with significantly greater frequency in gobies associated with *A. rapax* than in those associated with *A. rapacida* ($P < 0.025$). Because *A. rapax* is generally larger than *A. rapacida*, it may

consume more oxygen and thus more rapidly deplete the oxygen supply in the burrow. 'Pectorals wave' may be a method of accelerating ventilation in the goby's gill slits (Kinzer 1960), or it may be a means of aerating the burrow. On the other hand, it could have had an effect on the shrimps' behaviour that was not immediately expressed. The shrimp act 'in burrow' was directive toward 'pectorals wave' (Tables VII and VIII). It may have communicated to a shrimp inside the burrow that a goby was present at the burrow entrance. The goby may have performed other acts before the shrimp actually exited, in which case the effect would not be indicated in this type of analysis.

'No change' is an unusual category since it indicates the continuation, rather than the initiation, of any act. The frequency of 'no change' in the shrimp's behaviour was increased by 'dorsals erect', 'move away', 'nip sand', 'tail beat', 'tail flick', 'tail wave', and 'withdraw' (Tables IV and V).

'Dorsals erect' is a visual signal. The shrimp could not feel that the goby's dorsal fins were erect since they did not wave and the shrimp did not place its antennae on them. This act was probably not sensed by shrimps and, therefore, directed 'no change'.

'Nip sand' is a feeding and perhaps a displacement act which occurred when one goby interacted with another goby. It may be sensed by a shrimp since it is a jerky movement of the body which could be detected with the shrimp's antennae. It may have communicated 'no danger' since a goby that nipped sand was generally either feeding or interacting with another goby. The shrimp's behaviour would thus go unchanged.

When 'no change' followed any warning signal, weak or strong, I think the signal was ignored, not sensed, or the shrimp was already 'withdrawing', 'sitting', or 'fleeing'. If the shrimp was not touching the goby with its antennae or if the shrimp was too far away from the goby to sense the water displacement, warning signals probably were not sensed. Shrimps may have ignored a signal if the goby had signalled many times in sequence and did not flee itself.

The goby act 'no change' occurred with a significantly higher frequency in gobies associated with *A. rapacida* than with *A. rapax* ($P < 0.005$). This suggests that *P. mainlandi* was less responsive to the movements of *A. rapacida* than to the movements of *A. rapax*. Perhaps this results from the gross body contact

between *A. rapacida* and the goby, making different body movements of the shrimp difficult to distinguish. Thus the shrimp's behaviour might change without the goby's sensing the change. Or, more likely, the messages that were of significance to the goby were the presence or absence of an actively digging shrimp near the burrow entrance. Thus the goby responded one way to the presence of the actively digging shrimp and the goby's behaviour did not alter while the shrimp continued digging, independent of the specific act the shrimp was using.

In its interactions with gobies, *A. rapacida* performed the acts 'plough' and 'flee' with significantly higher frequencies than did *A. rapax* ($P < 0.050$ and $P < 0.005$, respectively). *A. rapax* responded to the goby by 'no change' in its behaviour with a significantly higher frequency than did *A. rapacida* ($P < 0.005$). Although the elicitation of the responses was not statistically significant, *A. rapacida* frequently responded to generalized movements of the goby by fleeing whereas *A. rapax* continued what it was doing in response to the same movements.

In the analysis for gobies communicating to shrimps, information present is essentially the same for the two species of shrimps (Table II). Information transmitted and normalized transmission were only slightly higher for gobies communicating to *A. rapacida*. On average, gobies performed slightly more acts per encounter when associated with *A. rapax* than when associated with *A. rapacida*. Although in some cases the differences between the two species are small, the combined results from this study suggest that *A. rapacida* was more sensitive to the gobies' movements whereas the behaviour of *A. rapax* appeared to be more independent from the gobies' behaviour. At least three possible interpretations of these associations can be made.

(1) The symbiosis between gobies and *A. rapacida* is more highly developed than the symbioses between gobies and *A. rapax* since *A. rapacida* responds to generalized, as well as to specialized, movements of gobies. *A. rapax*, in contrast, is less dependent on the goby's behaviour. This interpretation would lead one to believe that the *A. rapax*-goby symbiosis is more recently developed than the *A. rapacida*-goby symbiosis.

(2) The symbiosis between gobies and *A. rapax* is more highly developed since *A. rapax* responds primarily to specialized warning signals of gobies whereas *A. rapacida* responds also to more

generalized goby movements. With this interpretation, one would be led to believe that the *A. rapacida*-goby symbiosis is more generalized and, therefore, more recent.

(3) Because of differences in the length of antennae of the two species of shrimps, two slightly different behavioural symbioses may have developed. *A. rapax* with its long antennae can dig at a relatively greater distance from a goby and still maintain contact. Its antennae distinctly detect a difference between a generalized movement of a goby and a 'tail flick'. *A. rapacida* with its relatively short antennae has more body contact with the goby. Generalized and specialized movements of gobies cannot be easily distinguished by this more gross contact. With this interpretation, a statement as to which symbiosis is more recent or more specialized is unjustified.

Not all methods of communication were considered in these analyses. Almost certainly there was no auditory communication between gobies and shrimps. I would have heard the shrimps snap. In laboratory observations in which a hydrophone was used, I never heard gobies make sounds either when with other gobies or when with shrimps.

Karplus et al. (1972) note that, in a goby-shrimp symbiosis similar to the one reported here, the shrimp *Alpheus djiboutensis* is chemically attracted to the goby *Cryptocentrus cryptocentrus*. A similar chemical communication may occur between *P. mainlandi* and its symbiotic partners. However, considering the speed with which responses to warning signals took place, I doubt that they involved chemical communication. It is possible that a goby's presence or absence from the burrow entrance was transmitted to shrimps by chemical means. Also, a goby, having sensed danger while the shrimp was in its burrow, may have communicated danger to the shrimp by chemical means. It is clear, nevertheless, that the tactual communication system in itself can adequately explain the warning behaviour.

Karplus et al. (1972) also report that *C. cryptocentrus* is visually attracted to its shrimp symbiont. *P. mainlandi* and its symbionts may also communicate visually. In the warning system, however, the communication of shrimp to goby is most likely to be tactual, since during most of their communication the shrimp is behind the goby. Tactual communication of shrimp to goby would free the goby's visual

senses for attention to predators or to intruding gobies.

After careful observation and analyses, it seems clear that because the goby uses the burrow prepared by the shrimp, the energy the goby would otherwise need to spend in building a shelter can go into guarding the burrow against predators and into defending its shelter against the takeover by another goby. With the presence of the goby to warn it of predators, the shrimp can put more energy into shelter preparation and maintenance. There may, however, be other ways that the goby and shrimp benefit from one another.

Karplus et al. (1974) found that gobies, in the goby-shrimp associations they studied, controlled to some extent the location of a burrow entrance by pushing through the substratum to the surface where burrows were not located. Gobies also determined the direction their shrimp would plough by the orientation of their body in the burrow. Gobies would orient away from prospective goby opponents. Shrimps generally ploughed sand in a line parallel to the body of the goby.

Judging from this and from my field and laboratory studies, I feel that the spacing of goby-shrimp burrows in nature is a result of the interweaving of three communication systems: communication between gobies and shrimps, communication between gobies, and communication between shrimps.

Gobies placed in a large aquarium with no shelters increase distances between individuals by going up onto the sides of the aquarium or even jumping out. When provided with shelters, each goby sets up a territory with its shelter as the focal point. By entering their shelters, gobies avoid or escape from visual contact with an opponent. Since these shelters are provided in nature by shrimps, it can be concluded that because of their association with shrimps, gobies live closer together than they could without shelters, but only as close together as their visual communication system will allow.

When shrimps are placed in a large aquarium, they walk around examining the substratum and generally touch one another before they move apart. Thus, they frequently dig burrows close to one another. In nature, if their burrow entrances are too close together, shrimps will not have a goby guarding them. Because they then lack tactual communication from gobies about the presence of danger, they are taken

readily by predators, as indicated by the ease with which I could capture unguarded shrimps. The result is a compromise between maximal dispersion of gobies without shelters and clumping of shrimps in the absence of predators. Thus the complex communication system in this mutualistic symbiosis not only provides the goby with shelter and warns the shrimp of predators, but also results in optimal spacing of burrows.

The insights obtained from the use of information theory and associated χ^2 analyses in this study of interphyletic information exchange suggest that the use of these techniques should not be restricted to intraspecific studies. Much knowledge about other symbioses, from mutualistic to parasitic associations, could be gained by their use.

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