

## Intraspecific Aggression in the Colour Morphs of the Anemone *Phymactis clematis* from Chile

R. C. Brace

Department of Zoology, University of Nottingham; University Park, Nottingham NG7 2RD, England

### Abstract

The anemone *Phymactis clematis* exhibits intraspecific aggression. An investigation into dominance relationships amongst the 3 colour morphs collected from Viña del Mar, Chile, during June, 1980, revealed them to be equally aggressive. The outcomes of experimental contests appeared to reside solely with size-dependent differences in the threshold for the release of aggression. Contests were asymmetric and larger individuals displayed aggression earlier against smaller opponents, and won encounters. An analysis of times for the onset of aggression in contests showed that they were highly variable and were not a good indicator of the absolute aggressive ability of individuals as denoted by dominance rankings. It provided, however, evidence indicating a lack of assessment of opponent size during initial contact. This is discussed in relation to the evolution of aggression in anemones and to the concept of evolutionarily stable strategies in contest behaviour. It is concluded that future work on the apparent size-dependent threshold will most instructively be conducted at the neurophysiological level.

### Introduction

Attention has recently been focused on intraspecific aggression in the colour morphs of the anemone *Actinia equina* as part of a wider programme to investigate the behavioural ecology of this species (Brace and Pavey, 1978; Brace *et al.*, 1979). These studies demonstrated the existence of a size-dependent, dominance hierarchy amongst experimental individuals. Dominance ranking did not appear to depend upon assessment following initial contact, but rather on a size-dependent threshold for the release of aggression. Larger anemones attacked earlier than smaller opponents and won contests. The work also revealed a marked discrepancy in behaviour

between the colour morphs: red/brown individuals were highly aggressive, whilst green anemones rarely attacked and consequently lost contests against red/brown opponents.

The present paper provides comparative data on the aggressive sequence and interactions from an examination of *Phymactis clematis* (Drayton). In common with *Actinia equina*, this species is polymorphic with respect to colour, and possesses acrorhagi sited at the top of its column. These structures, which house batteries of nematocysts, are only found in the Actiniidae and appear to function solely in aggression (Äbel, 1954; Francis, 1973b; Bigger, 1976, 1980; Ottaway, 1978).

### Materials and Methods

#### Collection and Maintenance of Anemones

*Phymactis clematis* were collected from Montemar Beach, Viña del Mar, Chile, during June, 1980. Since *P. clematis* may form aggregations, each of which apparently constitutes a clone (W. Stotz, personal communication), not more than 1 individual was collected from any one site, thus minimizing any bias in results accruing from the possible genetic similarity of opponents. Although *P. clematis* adheres firmly to the substratum, it was found possible to remove individuals without damage; those damaged during removal were discarded.

In the Marine Laboratory at Montemar, the anemones were maintained within a circulating sea-water system in individual compartments, under non-tidal conditions. They were allowed to fasten either to small rocks or rough tiles. Following settlement, each anemone was fed a small quantity of *Mytilus* spp. This meal was subsequently presented at weekly intervals. Experiments were performed over a period of 3 wk commencing 3 d after initial settlement. Individuals were not re-employed in contests at intervals of less than 2 d. Anemones which

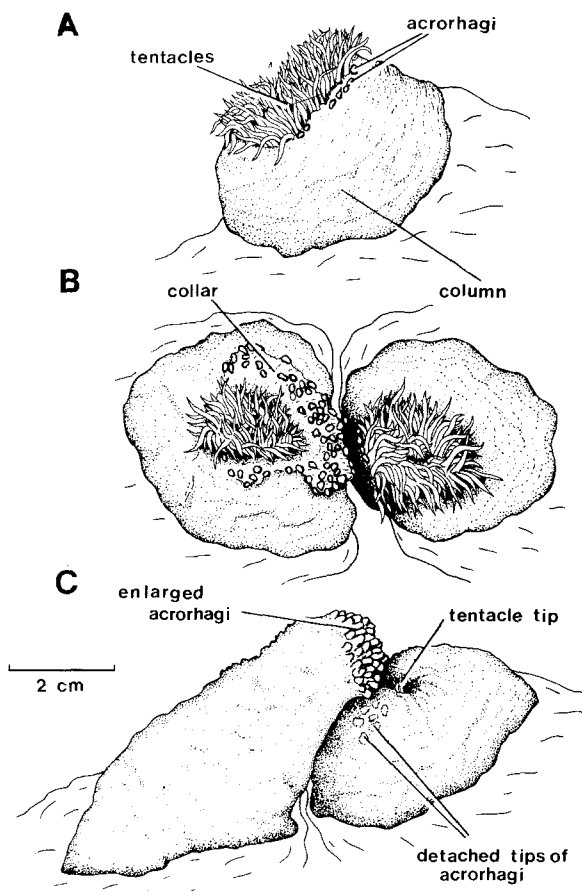


Fig. 1. *Phymactis clematis*. Morphology and aggressive behaviour. (A) Anemone with partially expanded tentacular crown, and some enlarged acrorhagi. (B) Immediately prior to delivery of a normal attack; attacker (on left) has a greatly enlarged collar and has partially withdrawn its tentacles, features, which are especially noticeable in the quadrant adjacent to the opponent; tentacles and upper column of potential victim are drawn away from aggressor. (C) Full attack, in which extreme contraction of upper column and postural changes to collar have resulted in "bunching" of the acrorhagi; note, following an earlier attack, fragments of acrorhagi adhering to victim

appeared unhealthy, or displayed extensive necrosis as a result of aggressive interactions, were removed.

Measurements of wet weight and pedal disk diameter were taken as indicators of anemone size. The latter values were obtained from attached individuals, and each measurement was the mean of the initial diameter, measured immediately after settlement, and of a second value obtained at the end of experimentation.

#### Observation of Aggressive Encounters

Experiments were performed *in situ*; i.e., in the compartments in which the anemones were maintained. Following initial, rapid transference between compartments, anemones were allowed to fully re-expand before contests commenced.

Contests were initiated by placing opponents adjacent to one another, ensuring that only minimal contact (up to 4 or 5 pairs of tentacle tips) was established. Excessive contact at this stage caused anemones to close, although normally only temporarily. During the first hour of interaction, observation was more or less continuous. Thereafter, contestants were observed at either 15 or 30 min intervals, depending on their respective postures. A contest was deemed to have finished when one or both opponents completely closed, moved away, or displayed no further aggressive activity over a period of 2 h.

#### Results

##### Littoral Distribution

Observations on the littoral distribution of *Phymactis clematis* on the exposed rocky shore at Montemar concurred with those of Carter (1965) and revealed that anemones occupied all levels from the top of the mid-shore downwards; they also occurred in the infra-littoral zone. Anemones were primarily found on bed-rock but, in less exposed regions, they also not infrequently occurred on the larger isolated rocks; in either case, the niches occupied were never in direct sunlight.

*Phymactis clematis* exists as three colour morphs: green, red/brown and blue. The former two colour morphs were found abundantly and intermixed at all tidal levels. Blue individuals were, in contrast, only found low on the shore where they were generally accompanied by green and red/brown anemones.

Although *Phymactis clematis* was found in loose, multi-coloured aggregations at Montemar, dense unicolour (clonal) groups characteristic of other localities in Chile (W. Stotz, J. Tomacich; personal communications) were not in evidence.

The geographic distribution of *Phymactis clematis* was given by Calgren (1949) as extending from California along the Pacific seaboard, south to Tierra del Fuego.

##### Gross Morphology

The general structure of an actiniid may be appreciated by reference to Fig. 1. The acrorhagi are located (in a ring) on the inner face of the collar which is sited at the upper end of the column. Larger individuals of *Phymactis clematis* (6 to 9 cm pedal disk diameter) bore up to 80 to 90 of these structures. Unlike *Actinia equina*, in which the colour (blue) is distinct from that of the column, that of the acrorhagi of *P. clematis* mirrors the colouration of the remainder of the body.

There is a good correlation between the two morphological parameters used below to examine possible links between times for aggression and body size (pedal disk diameter and wet weight), although a scatter in the data points relating to larger individuals is evident ( $Y = AX^B$ ,  $r = 0.9446$ ,  $P < 0.001$ ,  $n = 33$ ).

**Table 1.** *Phymactis clematis*. Behavioural characteristics of principal stages of aggressive sequence

Stage	Behaviour
(1) Initiation	increased tentacular movement following initial contact with opponent
(2) Inflation and extension	withdrawal of tentacles, and acrorhagial inflation in sector of ring adjacent to opponent; extension and bending of column, taking the now enlarged collar (with acrorhagi) up and away from the opponent
(3) Overtopping	further extension of column – often with considerable narrowing adorally. Continuing acrorhagial expansion
(4) Attack (see Fig. 1B,C)	acrorhagi make contact with opponent; resulting massive discharge of nematocysts frequently causes, upon retraction of aggressor, tips of the acrorhagi to break away and remain fastened to column of the opponent
(5) Recovery	return to resting posture. Deflation of acrorhagi and tentacle re-extension

### Aggressive Sequence

Since this behaviour closely resembles the aggressive behaviour of *Actinia equina* (Bonnin, 1964; Ottaway, 1978; Brace *et al.*, 1979) and *Anthopleura elegantissima* (Francis, 1973b) and can similarly be divided into 5 stages, only a summary is provided here (Table 1).

In some instances, contraction of the circular muscles of the collar and upper column was extreme. This resulted in the formation of a tightly packed bunch of acrorhagi (Fig. 1C) which, with continuing column-bending, was effectively directed towards (and made contact with) the other contestant. This behaviour was termed "full attack" to distinguish it from the more frequently observed normal attack involving contact by a limited number of acrorhagi. This contrasts with *Actinia* and *Anthopleura* species, in which the "pointing" of acrorhagi always relies in part on postural changes to the collar. Although the collar of *Phymactis clematis* was often greatly protruded during attack (Fig. 1B), massive extension, characteristic of *Actinia equina* was never observed. The detached tips of the acrorhagi of *P. clematis* were easily seen adhering to the column of the victim (Fig. 1C).

Normally one individual displayed aggression first and attacked prior to the other. Retaliation was, however, frequent, and sometimes during a contest an individual anemone exhibited two or more attacks. During such a multiple attack sequence, an anemone, following the first attack, initially drew away from its opponent (component of Stage 2, Table 1), but then passed through Stages 3 and 4 again, thus completing a second attack.

The victim of an attack usually withdrew its tentacles, bent away from the aggressor, and contracted the upper end of the column and the oral disc, so causing the ring of acrorhagi to protrude upwards, partially concealed by the collar. Often the victim moved away from the site of the contest, or even completely detached from the substratum. Within a few days, areas of the column of the victim to which acrorhagi of the opponent had fastened, became necrotic and, if severe, this led eventually to the death of the anemone.

### Experimental Encounters

A total of 34 anemones was collected. Of these, 33 showed no immediate ill effects owing to collection and subsequent settlement in the aquarium, and thus were employed in aggression experiments: 11 were green, 15 were red/brown and 7 were of the blue morph. A breakdown of the 82 unique contests staged with the various colour combinations is given in Table 2. The maximum number of contests in which an individual anemone was employed was 7 (mean 5.0). Additionally, 16 repeat contests were undertaken (see below) following completion of the main series, using a total of 18 individuals. Of those anemones ( $n = 15$ ) not used in repeats, 7 became unhealthy (mean number of contests = 2.9), and 8 developed necrotic areas resulting from attacks delivered by opponents (mean number of contests = 4.8). Necrosis was exhibited from 2 to 11 d (mean 7.4) following the initial severe attack experienced. Full attacks were particularly potent in this respect. At the end of the series of repeat encounters, all the anemones remaining ( $n = 17$ ) appeared to be healthy, although some individuals displayed small necrotic areas.

An examination of the results of the series of contests undertaken by each anemone disclosed no obvious trends linked to the early removal of anemones, owing to either ill health or onset of necrosis. This implies that anemones were successfully removed prior to the appearance of any adverse effects on behaviour. The examination also indicated that the outcomes of early encounters did not obviously relate in any predictable manner to the results of later contests experienced by each anemone, and also that survival was independent of size.

Table 2 shows that there was a total of 49 encounters in which an attack took place, 23 of which included a full attack. Of these 49 encounters, 6 included retaliatory attacks, 10 entailed at least one anemone of the pair exhibiting two attacks (including 3 with two full attacks), and 4 included three attacks (not all full) delivered by a single anemone. All the colour morphs delivered some full attacks.

There was a uniformly high level of aggression observed (>90%; mean 97%), irrespective of the colour combination of contestants (Table 2), although the percentages of encounters incorporating attacks were considerably lower (38 to 73%; mean 59%). However, in those encounters in which attacks occurred, a defini-

**Table 2.** *Phymactis clematis*. Frequency of aggression within and between colour morph categories

Contest colour category <sup>a</sup>	No. of contests	No. of contests with aggression	% contests with aggression <sup>b</sup>	No. of contests with attack(s) <sup>c</sup>	% contests with attack(s)	No. of contests with definitive outcome (winner) <sup>d</sup>	% contests with winner	% contests in which attack(s) led to definitive outcome <sup>e</sup>
Green + Green	13	12	93	5 (1)	38	4	31	80
Red + Red	15	15	100	11 (8)	73	11	73	100
Red + Green	32	30	94	19 (7)	59	14	46	74
Red + Blue	13	13	100	9 (4)	69	9	69	100
Blue + Green	9	9	100	5 (3)	55	4	44	80
Totals and % means	82	79	97	49 (23)	59	42	53	87

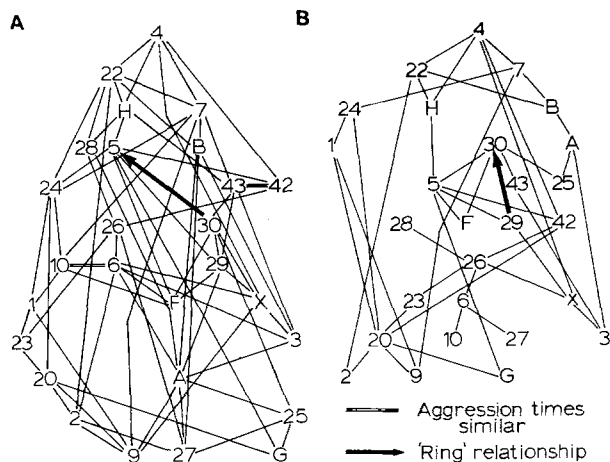
<sup>a</sup> Only 2 blue-blue contests were staged; both incorporated aggression but provided no attacks

<sup>b</sup> No significant difference between categories

<sup>c</sup> Values in parentheses: numbers of contests with full attack(s); values in brackets: numbers of contests in which green, red or blue individuals attacked (normal or full)

<sup>d</sup> Values in brackets: numbers of outcomes of encounters in favour of each colour morph

<sup>e</sup> Remaining percentage accounted for by contests in which both anemones were still open at the end of the encounter, including "stalemates" in which both opponents had attacked one another



**Fig. 2.** *Phymactis clematis*. Dominance hierarchies of anemones based on (A) first aggressor (acrorhagial expansion), and (B) first attacker. Vertical placings of anemones directly relate to assigned numerical ranks. Those anemones ( $n = 6$ ) whose ranks could not easily be assessed with respect to the above two hierarchies and the "winner" hierarchy (not illustrated) were omitted from consideration; 27 anemones were thus ranked. Letters and numbers identify individual anemones. "Ring" relationships were produced when particular individuals could not be arranged in a hierarchical manner, such that all anemones which were more aggressive reside higher in the hierarchy and all anemones which were less so, reside lower

tive outcome was frequent ( $> 70\%$ ; mean  $87\%$ ), indicating the potency of the completed aggressive sequence.

The data obtained from the total of 82 encounters were used to construct dominance hierarchies based on: (1) first aggressor; (2) first attacker; (3) winner. The former two hierarchies are illustrated in Fig. 2. Only one "ring" relationship (e.g. A beats B, B beats C, C beats A) was revealed in each of the three hierarchies. Using these hierarchies, ranking orders were established. Only those anemones which could be readily incorporated into all three hierarchies were assessed. Comparisons of the ranking orders clearly indicated that the first aggressor, as expected, attacked first ( $r_s = 0.7697$ ;  $P < 0.001$ ) and that first attackers subsequently won encounters ( $r_s = 0.619$ ;  $P < 0.001$ ). These correlations were equally well demonstrated when (vertical) compensation was applied to those anemones involved in "ring" relationships ( $r_s = 0.7929$ ;  $P < 0.001$ ;  $r_s = 0.7225$ ;  $P < 0.001$ ).

Analysis of the results accruing from the entire set of encounters (Table 3) showed that the larger opponent generally displayed aggression first, attacked first and subsequently won the contest. For particular combinations of colour morph interactions this result was not always found, probably owing, in some instances, to the small sample sizes involved.

**Table 3.** *Phymactis clematis*. Relationships between expected first aggressor, first attacker and winner based on larger size (wet wt), with actual behaviour observed in experimental contests of different colour morph combinations. (Only 2 blue-blue contests were staged, both of which incorporated aggression, but had no definite outcomes.) Chi-square values and numbers of observations (in parentheses) are tabulated (\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ). Also shown are correlations arising from the total set of data, using both wet wt and pedal disk diameter as indicators of anemone size

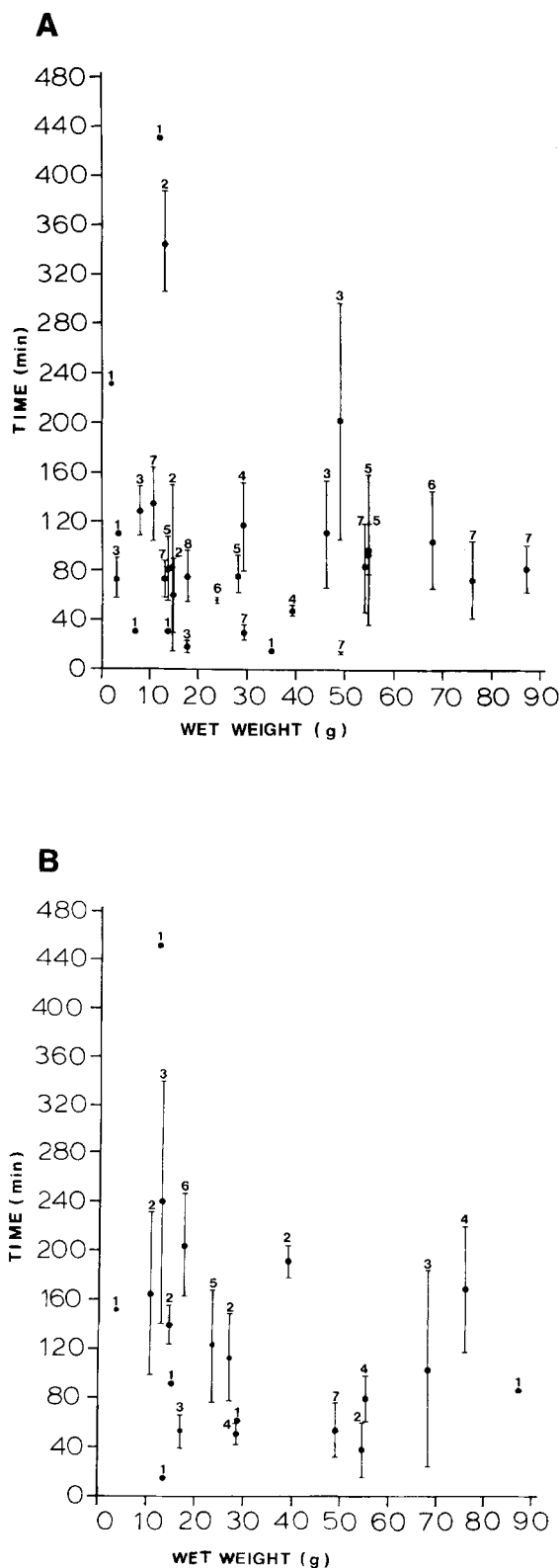
	First aggressor		
	Red	Green	Blue
Red	3.27 (15)	4.17 (29)*	0.08 (13)
Green		8.33 (12)**	5.44 (9)*
	First attacker		
	Red	Green	Blue
Red	2.21 (11)	0.22 (18)	0.11 (9)
Green		5.00 (5)*	5.00 (5)*
	Winner		
	Red	Green	Blue
Red	4.50 (11)*	2.57 (14)	0.11 (9)
Green		4.00 (4)*	4.00 (4)*
Total data set			
	First aggressor	First attacker	Winner
Wet wt	15.51 (79)***	5.33 (48)*	9.52 (42)**
Pedal disk diam	9.47 (77)**	2.57 (47)	5.49 (41)*

**Table 4.** *Phymactis clematis*. Outcomes of contests in which smaller individuals displayed aggression first (excluding data from repeat contests). Mean size-ratios of pairs of contestants are given in parentheses; note that these ratios are lower when anemone size is based on pedal disk diameter

	No. of contests	No. of contests with definitive outcome (win) by smaller opponent	No. of contests in which the larger individual won despite first aggression by smaller opponent
Smaller on basis of wet wt	24	11 (2.45)	2 (2.09)
Smaller on basis of pedal disk diam	25	11 (1.52)	2 (1.24)

It should be emphasised that in those contests in which the smaller individual displayed aggression earlier, a proportion ( $\approx 45\%$ ) of outcomes were in favour of the smaller contestant (Table 4).

In order to assess whether times for (1) onset of acrorhagial expansion and (2) attack following initial contact between the opponents were related to absolute anemone size (weight), these parameters were graphed (Fig. 3). Regression analysis failed to reveal any correlation between anemone weight and the sets of temporal data. Nevertheless, both data sets show an increase in scatter to the left (smaller individuals) where the longest



**Fig. 3.** *Phymactis clematis*. Times for (A) onset of aggression and (B) attack in relation to anemone size (wet wt). Vertical bars and numbers denote standard errors and numbers of observations, respectively. Times recorded for acrorhagial expansion or attack occurring after receipt of an attack from an opponent are not included

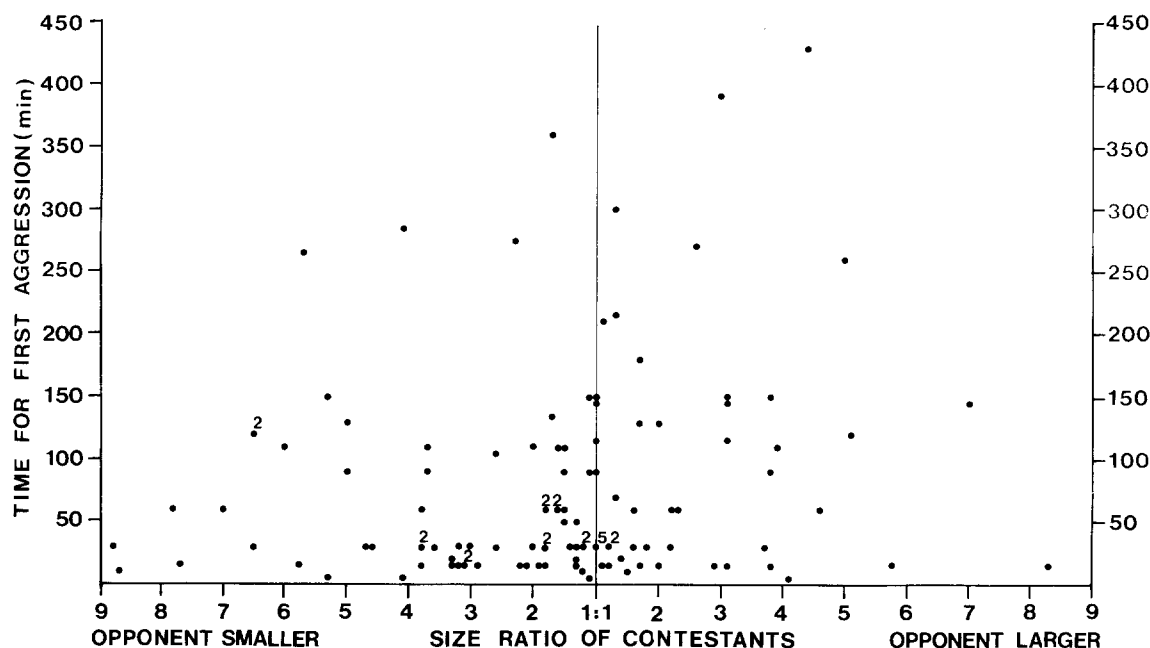


Fig. 4. *Phymactis clematis*. Times for onset of aggression against size (wet wt) ratio of pairs of opponents. When more than one observation is represented, number of replicates is given in graph. Only those times pertaining to acrorhagial expansion occurring prior to attacks delivered by opponents are considered

recorded times are located. The extents of the standard error bars demonstrate the extensive variability observed in both sets of data.

The behaviour of anemones could also have been influenced by the relative sizes of opponents, and thus the distributions of times for first aggression against (1) the size (weight) difference, and (2) the size (weight) ratio (Fig. 4) of opponents were examined. No significant trend was noted in either case, nor when pedal disk diameter was used as the morphological parameter.

The series of repeat contests comprised 8 encounters in which the larger individual of the pair had previously displayed aggression earlier, and 8 contests in which the reverse was true. Of these, aggression was observed in 15 contests. The first aggressor was the same as in the prior experiments on 13 occasions. Less consistency was apparent with respect to the repeatability of the later components of the aggressive sequence. However, in several instances the discrepancy between the original and repeat encounters entailed only a change from "stalemate" (see footnote to Table 2 for definition), or a situation in which there was a change from no definitive winner emerging following an attack to a contest providing an outright winner. Since the sizes of the members of several pairs of contestants were not markedly dissimilar, these changes in the final outcome of contests were not totally unexpected.

As an indication of the healthy condition of the anemones used in repeat experiments, there were 8 contests in which an attack took place, which compares reasonably well with 11 such encounters in the main series of experiments. Thus, in common with earlier conclusions (see above), the behaviour of anemones

used in this late stage of experimentation did not appear to have been adversely affected by the prior experimental regime which included up to 7 encounters for an individual anemone.

Analysis of the data pairs of times for first aggression of individual anemones in specific contests, by ranking, indicated that the repeat times were not significantly different from those of the main series ( $r_s = 0.7588$ ;  $P < 0.001$ ;  $n = 19$ ).

## Discussion and Conclusions

This study has demonstrated that the aggressive sequence of *Phymactis clematis* is strictly comparable to that of other actiniids bearing acrorhagi: *Actinia equina* (Bonnin, 1964; Brace *et al.*, 1979), *A. tenebrosa* (Ottaway, 1978), *Anthopleura elegantissima* (Francis, 1973a,b), *A. artemisia* (Francis, 1973b), *A. krebsi* (Bigger, 1980). The only noteworthy additional feature is that there is variability in the mode of attack. Not infrequently, *P. clematis* showed extreme narrowing and elongation of the upper part of the column, such that the individual acrorhagi approached one another and then collectively were directed at an opponent. All size classes exhibited this behavioural variation, although it was more frequently observed in larger anemones.

The physical results of attacks, especially those involving the entire ring of acrorhagi, were readily apparent from the occurrence of necrosis which, in some instances, led to the death of the victim. Tissue in the affected area was, however, often sloughed off and damage quickly repaired by regeneration, as shown for *Anthopleura elegantissima* by Francis (1973b).

It is probable that the artificial positioning of anemones in the laboratory, contiguous to one another, provided conditions which, in respect to the field situation, accentuated the opportunities for inflicting severe damage. Nevertheless, that the aggressive sequence clearly provided a strong deterrent to approaching conspecifics, was demonstrated by the rapid movement of many victims away from the contest site following receipt of an attack. The wide separation of most individuals observed on the beach at Montemar supports this observation. This overall distribution pattern was, however, complicated by the presence of small, tightly packed aggregations, each of which probably represented a single clone since, elsewhere in Chile, large clonal aggregations are not uncommon (W. Stotz, personal communication). In agreement with the behaviour of clonal individuals of *Anthopleura* species (Francis, 1973a, 1976; Bigger, 1980), and some individuals within loose aggregations of *Actinia equina* (own personal observations), anemones within each of the small aggregations of *Phymactis clematis* were found to display little aggression towards one another.

Particular attention was focused on discerning whether or not there were any differences in the degree or manner of aggression between the red/brown and green morphs of *Phymactis clematis* which might mirror those existing between the corresponding colour morphs of *Actinia equina*, but no obvious discrepancies in behaviour were observed. Moreover, blue individuals were also equally aggressive.

The dominance relationships established show that a group of captive *Phymactis clematis* can be accurately ranked, and that individuals which display aggression first normally go on to attack first and win contests. There was no apparent modification of aggressive ability following previous experience of staged encounters (inter-contest period of 2 d), but additional, more controlled experimentation is desirable to confirm whether this is indeed always the case. That further work might reveal the presence of a general "memory" of past events is suggested by data on *Actinia equina*, which showed sensitization with repetition (inter-trial period of 10 min) of determinations of the threshold for the release of aggression (presentation of an amputated tentacle acting as a stimulus) (Brace *et al.*, 1979). Bigger (1980) has also detected a similar sensitization in *Anthopleura krebsi* using inter-determination periods of up to 2 h. Moreover, Ottaway (1978), working on a field population of *Actinia tenebrosa*, reported changes in the degree of locomotion lasting months after receipt of an attack. He noted, however, that there was no evidence to suggest "that victims 'learnt' to stay away from aggressors".

A search for relationships between the expected first aggressor, first attacker and winner based on larger size, and the observed results provided three significant correlations when anemone weights were assessed and when two pedal disk diameters were considered. The size-dependent nature of the outcome of contests, together with the observation that minimal, initial

contact (generally followed by a period out of contact with the opponent) is sufficient to "trigger" the entire aggressive sequence, leads one to expect a strong correlation between anemone size and times for both onset of aggression (acrorhagial expansion) and attack. However, regression analyses amply demonstrated that this was not the case, and indirectly showed that the speed of attack itself, was not a simple function of anemone size. Presumably the extensive variation in these times for individual anemones largely reflects the specific duration and sequence of contacts experienced by each opponent at the start of contests. In view of this variability, it was intriguing to find that a comparison of times for onset of acrorhagial expansion between repeat contests and the initial experimental meetings yielded data pairs which were significantly similar. Despite this similarity, the overall conclusion is that times for first aggression (and attack) are not valid indicators of absolute aggressive ability.

Notwithstanding this failure, it is nevertheless easy to appreciate that given a size-dependent release of aggression, larger individuals should, everything else being equal, display aggression earlier and more frequently against smaller opponents than against larger anemones. Furthermore, the lack of correlation found between the times for onset of aggressions and the relative sizes of pairs of contestants strongly indicates that the size-dependent dominance hierarchy is solely dependent on these thresholds. There may, however, be quantitative or qualitative differences in surface-bound substances that could provide information as to the size of an opponent (but such a possibility seems unlikely).

The type of hierarchy described here for experimental individuals, with its apparent lack of extensive information exchange during contests (see above), and lack of modification of behaviour as a result of past aggressive experiences, corresponds to the "statistical" hierarchy of Barnard and Burk (1979). A hierarchy of this nature should theoretically be stable, but as emphasised earlier, damage was frequently inflicted during encounters and thus there was some "turn-over" of contestants.

It is pertinent now to examine fighting strategies in sea anemones in the context of the evolution of contest behaviour and "evolutionarily stable strategies" (ESSs) (Maynard Smith and Price, 1973). In common with most intraspecific conflict (Maynard Smith and Parker, 1976; Maynard Smith, 1979), contests in *Phymactis clematis* are predominantly asymmetrical, and fighting ability is directly linked to size. In the field there may be additional asymmetries, including resident/intruder effects. Indeed, Ottaway (1978), working on *Actinia tenebrosa* noted that contest winners were usually "residents" (non-mobile) rather than "intruders" (mobile). Whatever asymmetries are involved, game theory predicts that they should be used as cues to settle contests, thus avoiding lengthy encounters which could prove costly. In *Phymactis clematis* all individuals appear to adopt the strategy of: if bigger, attack, but if smaller, do not attack.

Use of the word "cue" immediately suggests the occurrence of information exchange during fights but, as emphasised above, we are dealing here with a novel situation in which this is apparently not the case. What we have instead, is an overtly "physiological" convention rather than cue perception by information transfer.

An important question now arises: is the size-dependent threshold likely to have been selected for in conjunction with aggressive behaviour, or might it simply be a consequence of body size and thus be unrelated to fighting strategies? These alternatives can be examined by considering a situation in which all size classes of anemones initially possess similar thresholds. From this original state, it is to be expected that any mutants arising with lower thresholds would be preferentially selected. However, we may imagine that if smaller individuals were selected for, then it is likely that during contests they might easily sustain damage following even minimal retaliation from a larger individual, a cost which could easily outweigh any benefit from having attacked first. The opposite situation in which the "convention" swings in favour of larger individuals does not present the same theoretical drawback, and therefore we may predict that selection should indeed favour the evolution of *lower* thresholds in *larger* individuals. Thus, it seems logical to conclude that the proposed "physiological" differences are likely to have resulted from selection to maximise individual fitness during intraspecific conflict. In common with the behaviour of other animals, it is to be expected that the "size convention" in *Phymactis clematis* will have been refined only up to a certain point. That is, we might expect to find similarly sized individuals attacking each other at the same time. Further, we can expect to find in those instances where minimal, initial contact favours the anemone having the higher threshold, considerably smaller individuals occasionally attacking first. Indeed, the results obtained here include such examples (Table 4). By virtue of the stereotyped nature of the entire aggressive sequence once triggered, these smaller individuals may subsequently win contests.

Within the context of ESSs, the apparent existence of a behavioural polymorphism in *Actinia equina* accompanying the colour polymorphism (see "Introduction") is a complicating factor, since it provides a situation in which there may be a combination of pure and mixed strategies (Maynard Smith and Parker, 1976). This is an interesting area for further investigation. From the theoretical point of view, it is noteworthy that Hines (1977) has analysed possible ESSs under severe environmental conditions, such as those pertaining to the upper littoral sites occupied by *A. equina* (*Phymactis clematis* has a lower distribution), and has indicated that mutants employing a non-aggressive strategy could easily establish themselves. Future work will also have to take into account the feature that in both *P. clematis* and *A. equina*, adjacent anemones may well be related and thus the relevant ESS should be a function of the average degree of relatedness of opponents within any population (Grafen, 1979).

Finally, it has become apparent from this work that any further investigation of the size-dependent release of aggression in anemones is best attempted by a combined electrophysiological and behavioural approach rather than by purely behavioural means. Such a dual approach has already yielded results with *Actinia equina*, but as yet this work is at a preliminary stage (Donoghue and Brace, in preparation). Anemones appear to possess at least three discrete conduction systems (G. R. Arthur, unpublished data; McFarlane, 1969, 1976; Shelton, 1975), all of which are good candidates for the neuronal locus sought, since their morphologies reflect well the overall size and shape of the body, especially that of the ectodermal neuroid system. Moreover, a neurophysiological approach should yield information on self/non-self recognition in anemones (Bigger, 1976, 1980), and its possible relationship to immunocompetence which has already been demonstrated to exist in some corals (Hildemann *et al.*, 1977).

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