

## Why is group size correlated with the size of the host sea anemone in the false clown anemonefish?

Jeremy S. Mitchell and Lawrence M. Dill

**Abstract:** When social groups monopolize discrete habitat patches, group size may be positively correlated with patch size. The correlation can be a direct consequence of limited resources. Alternatively, it can be an indirect consequence of patch-size effects on a dominant group member. We asked which of these two mechanisms was responsible for a positive correlation between the group size of false clown anemonefish (*Amphiprion ocellaris* Cuvier in Cuvier and Valenciennes, 1830) and that of the host sea anemone *Stichodactyla gigantea* (Forskål, 1775). We argue that some false clown anemonefish groups may have reached the carrying capacities of their hosts, but that the group size : patch size correlation in the population as a whole is best interpreted as an indirect consequence of a positive relationship between anemone size and the length of the dominant group member. The dominant's length in turn limits group size because dominant group members inhibit the growth of their subordinates. Thus, a correlation between group size and patch size need not imply resource limitation of subordinate group members.

**Résumé :** Lorsque des groupes sociaux monopolisent des parcelles séparées d'habitat, la taille du groupe peut être en corrélation positive avec la taille de la parcelle. La corrélation peut être une conséquence directe des ressources limitées. En revanche, elle peut aussi être une conséquence indirecte des effets de la taille de la parcelle sur un individu dominant du groupe. Nous avons vérifié lequel de ces deux mécanismes explique la corrélation positive qui existe entre la taille du groupe chez le poisson clown à trois bandes (*Amphiprion ocellaris* Cuvier en Cuvier et Valenciennes, 1830) et celle de l'anémone hôte *Stichodactyla gigantea* (Forskål, 1775). Notre argumentation est que certains groupes de poissons clowns ont atteint le stock limite de leurs anémones hôtes et que la corrélation taille du groupe : taille de la parcelle dans la population dans son ensemble s'explique mieux comme une conséquence indirecte d'une relation positive entre la taille de l'anémone et la longueur de l'individu dominant du groupe. La longueur du poisson dominant limite à son tour la taille du groupe, car les membres dominants du groupe inhibent la croissance des subordonnés. L'existence d'une corrélation entre la taille du groupe et la taille de la parcelle n'implique donc pas nécessairement une limitation des ressources pour les membres subordonnés du groupe.

[Traduit par la Rédaction]

### Introduction

In various reef fish species, individuals live in social groups. Each group monopolizes, and is restricted to, a discrete habitat patch. Group size and patch size are often positively correlated (e.g., Sale 1972; Fricke and Holzberg 1974; Fricke 1980; Donaldson 1989; Fautin 1992; Kuwamura et al. 1994). The correlation may result from a density-dependent process. For example, larger patches may be able to shelter more fish or may provide more foraging opportunities. A

correlation between patch size and group size can also result from effects of patch size on a dominant group member alone, even in the absence of resource competition. This possibility arises because the individuals occupying a habitat patch constitute a single social group, the composition of which may be dictated by the dominant group member.

In this study, we illustrate the effects of both mechanisms, but particularly the latter, on the group size of false clown anemonefish, *Amphiprion ocellaris* Cuvier in Cuvier and Valenciennes, 1830. Anemonefish live in obligate associations

Received 28 October 2004. Accepted 27 January 2005. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 29 April 2005.

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with sea anemones (reviews in Allen 1972; Mariscal 1972; Fautin 1991; Fautin and Allen 1992). Fish are not stung by their host anemone, and take refuge from predators among its tentacles. Anemones usually occur as isolated individuals, each occupied by a small group of anemonefish. With the exception of high-latitude populations (e.g., Moyer 1980), unoccupied anemones are typically rare. Thus, for anemonefish, an anemone constitutes a discrete habitat patch that provides a necessary and limiting resource. The number of anemonefish groups in an area is limited by the number of anemones (Allen 1972; Fricke 1979; Fautin 1992; Elliott and Mariscal 2001; but see Schmitt and Holbrook 2000). At a finer spatial scale, a positive correlation between anemonefish group size and host anemone size is a recurring theme in ecological studies of various anemonefish species (Allen 1972; Ross 1978; Fricke 1979; Hattori 1991, 2000; Fautin 1992; Elliott and Mariscal 2001), leading some researchers to conclude that space is limiting on an anemone and that larger anemones have a greater carrying capacity for anemonefish (Allen 1972; Ross 1978; Fricke 1979; Fautin 1992).

However, a correlation between group size and anemone size can also result from effects of anemone size on the dominant member (hereinafter referred to as  $\alpha$ ) of an anemonefish group. An anemonefish group is a size-based dominance hierarchy (reviews in Allen 1972; Mariscal 1972; Fautin 1992; Fautin and Allen 1992). When a juvenile anemonefish settles on an anemone following a planktonic larval stage, it joins the resident group as the smallest, lowest ranking member. Subsequent growth, sexual maturation as a male, and male-to-female sex change are inhibited by the presence of larger, more dominant group members (Allen 1972; Fricke 1974; Fricke and Fricke 1977; Moyer and Nakazono 1978; Ross 1978; Hattori 1991; Buston 2003a). Since each group member's length sets an upper limit on the length of the next lower ranked group-mate, and since there will be a minimum size at which juveniles settle from the plankton,  $\alpha$ 's length will set an upper limit on group size (Fautin 1992). If  $\alpha$ s are smaller on smaller hosts (e.g., Fautin 1992; Elliott and Mariscal 2001; this study), then group size will tend to increase as host size increases, even if resources for the group are not limiting.

We asked whether a correlation between the size of a false clown anemonefish group and the size of the host sea anemone *Stichodactyla gigantea* (Forskål, 1775) arises because larger anemones can support more anemonefish (the carrying capacity explanation) or because dominant group members tend to be larger on larger anemones (the group structure explanation). To answer this question, we included both anemone size and the length of  $\alpha$  as predictors of group size in a multiple regression. The carrying capacity explanation predicts that, when  $\alpha$ 's length is included in a regression model, anemone size will continue to be positively correlated with group size. The carrying capacity explanation further predicts that, after controlling for the effect of anemone size, the correlation between group size and  $\alpha$ 's length will be negative, because a larger  $\alpha$  uses more of the available resources. The group structure explanation predicts that group size will increase with  $\alpha$ 's length and will be unaffected by variation in anemone size. We began by running this analysis using a "full" data set. We then re-ran the analysis using the subset of groups considered most likely to be approach-

ing the hypothetical carrying capacities of their host anemones. (The rationale for the latter analysis is presented in the Results.)

## Methods

We monitored false clown anemonefish groups occupying *S. gigantea* anemones at Bunaken Island, North Sulawesi, Indonesia, from September 1997 to March 1998. Population monitoring consisted of (at least) weekly visits to each anemone from September to March. Group size at each anemone was noted on each visit. In October and again in March, the residents of each anemone were captured using a hand net and measured (total length  $\pm$  1 mm). *Stichodactyla gigantea* occurred in near-shore seagrass, backreef rubble, and on the reef crest. These are all lower intertidal or marginally subtidal habitats. *Stichodactyla gigantea* did not extend down the reef face into deeper water. With the exception of a single juvenile *Amphiprion clarkii* (Bennett, 1830), no other anemonefish species was observed occupying *S. gigantea*.

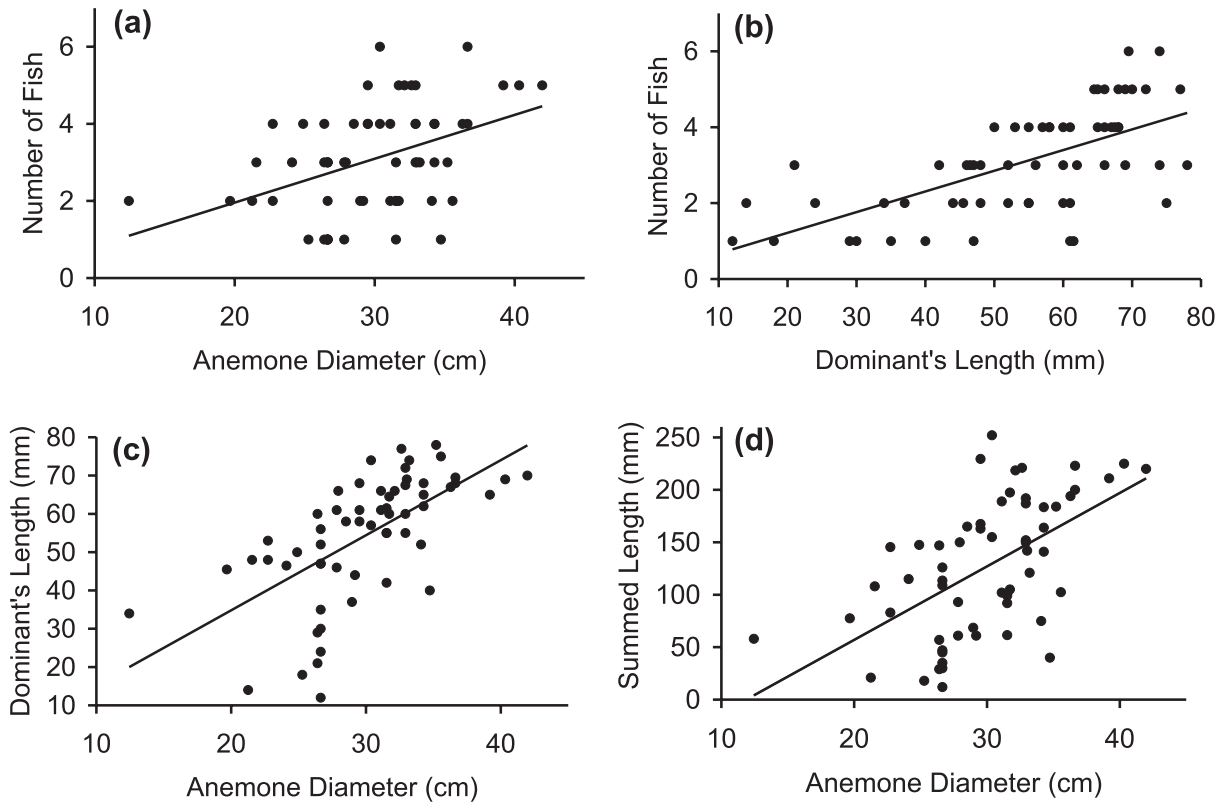
The long and short axes of each anemone's oral disc were measured on three occasions in February and March 1998. Under the assumption that oral discs are approximately elliptical, we estimated anemone diameter as the geometric mean of the lengths of the two axes (Hattori 1991). The largest of the three estimates was used as the estimate of an oral disc's expanded diameter. Unoccupied anemones were excluded from the analyses because we did not know whether their prolonged vacant status was a consequence of their size or of some other variable. Anemone species that harbour anemonefish are long-lived and slow-growing (Fautin and Allen 1992), so we have assumed that anemone growth was negligible over the course of the monitoring period. Over longer time frames, anemonefish can have a positive effect on the growth of their hosts (Schmitt and Holbrook 2003; Porat and Chadwick-Furman 2004). Such an effect would not alter our central conclusion (see Discussion).

We conducted less frequent surveys of a second study site, approximately 4 km from the primary study site described above. At the second site, there was no relationship between group size and anemone size, or between  $\alpha$ 's length and anemone size. Data for the second study site are not presented for two reasons. First, because the second site was not monitored as intensively as the first, we cannot make meaningful comparisons between the two sites. Second, our objective is to contrast two mechanisms that can give rise to the same positive correlation between group size and patch size. Data from a site at which there is no correlation cannot contribute to that contrast. Note that, given the distance separating the two sites, the exclusion of the second site is not equivalent to the inclusion of a biased subset of anemones from a single study site.

## Results

We began by establishing the pairwise relationships between initial group size, anemone diameter, and the length of  $\alpha$ . The initial group size was defined as the number of false clown anemonefish occupying an anemone on the date that the fish were captured and measured in October. We

**Fig 1.** Pairwise relationships between (a) false clown anemonefish, *Amphiprion ocellaris*, group size (number of individuals occupying an anemone) and anemone diameter, (b) group size and the length of the dominant group member (referred to in the text as  $\alpha$ ), (c) the length of the dominant group member and anemone diameter, and (d) the summed length of all group members and anemone diameter.



used group size in October rather than time-averaged group size, because the length, and in some cases the identity, of  $\alpha$  changed at some anemones during the course of the field season. Initial group size increased with anemone diameter ( $F_{[1,58]} = 13$ ,  $p < 0.001$ ,  $R^2 = 0.17$ ) (Fig. 1a). Group size was also larger when  $\alpha$  was longer ( $F_{[1,58]} = 40.1$ ,  $p < 0.001$ ,  $R^2 = 0.40$ ) (Fig. 1b). The length of  $\alpha$  increased with increasing anemone diameter ( $F_{[1,58]} = 38$ ,  $p < 0.001$ ,  $R^2 = 0.39$ ) (Fig. 1c). The summed lengths of false clown anemonefish group members also increased with anemone diameter. This relationship was considerably stronger than that using initial group size ( $F_{[1,58]} = 27$ ,  $p < 0.001$ ,  $R^2 = 0.31$ ) (Fig. 1d). (The summed lengths of group members have been used as an index of group size in several previous studies (Allen 1972; Ross 1978; Hattori 1991; Fautin 1992; Elliott and Mariscal 2001; Buston 2003b).) Thus, group size,  $\alpha$ 's length, and anemone diameter were "tangled". However, correlations were not so strong that they could not be teased apart by multiple regression. The multiple regression of group size in October on anemone diameter and on the length of  $\alpha$  reduced to the simple linear regression of group size on the length of  $\alpha$  (Fig. 1b). Anemone diameter did not add additional predictive power, either as an interaction with  $\alpha$ 's length ( $t_{[1,56]} = 1.5$ ,  $p = 0.15$ ) or as a main effect ( $t_{[1,57]} = 0.3$ ,  $p = 0.74$ ).

We repeated the multiple regression analysis using group composition data from March and excluding anemones at which either group size or  $\alpha$ 's length decreased between October and March. (The latter situation arose at some anemo-

nes where the identity of the dominant individual changed during the course of the field season.) The intent of these restrictions was to limit the data set to groups that potentially approached the hypothetical carrying capacities of their hosts. If anemones have a carrying capacity for anemonefish, then a group that was smaller in March than it was in October was not at the carrying capacity of its host at the time of the March sample, whereas a group that was as large, or larger, on the second sampling date may have been approaching the carrying capacity of its host. Thirty-two groups met these criteria.

The result of this analysis was quite different from that using the October data. Using the March data, variation in group size was best explained by following model:

$$\text{Group size} = 2.02 - 0.05(\alpha\text{'s length (mm)}) \\ + 0.15(\text{anemone diameter (cm)})$$

This model was statistically significant ( $F_{[2,29]} = 4.5$ ,  $p = 0.02$ ) and explained 19% of the variation in group size. The interaction between anemone diameter and  $\alpha$ 's length was nonsignificant ( $t_{[1,28]} = 0.4$ ,  $p = 0.66$ ). Anemone diameter itself, though, was a useful predictor of group size ( $t_{[1,29]} = 3.0$ ,  $p = 0.006$ ) — controlling for the effect of  $\alpha$ 's length, groups were larger on larger anemones. The effect of  $\alpha$ 's length remained significant ( $t_{[1,29]} = 2.0$ ,  $p = 0.05$ ), but the coefficient was negative — after controlling for the effect of anemone diameter, group size decreased as  $\alpha$ 's length increased.

Thus, the data from March suggest that anemones do have a carrying capacity for anemonefish. However, patterns of variation in group size in October indicate that most groups in the study population did not approach the carrying capacities of their host anemones. Instead, group size was limited by the length of  $\alpha$ .

## Discussion

Analysis of the March data indicates that it is possible for false clown anemonefish groups to reach a point at which resources become limiting. Among groups considered most likely to be approaching the carrying capacities of their hosts, group size was positively correlated with anemone diameter and negatively correlated with the length of the dominant group member, just as the carrying capacity explanation would predict. However, differences in anemone carrying capacities were not responsible for the variation in group size in the population as a whole. Instead, a positive correlation between group size and anemone diameter in the full (October) data set was best attributed to the underlying correlations of both variables with  $\alpha$ 's length. Anemone diameter was not a significant predictor of group size when  $\alpha$ 's length was included in the regression model.

The greater strength of the relationship between summed lengths of group members and anemone diameter, compared with that between number of group members and anemone diameter, is consistent with this interpretation. Summed length incorporates both the effect of anemone size on  $\alpha$ 's length and the separate effect of  $\alpha$ 's length on the size, and hence number, of subordinate group members. The theoretical rationale for using summed lengths as an index of group size has been that summed lengths better account for the greater resource requirements of larger fish (Allen 1972; Buston 2003b). That rationale rests on the assumption that the group as a whole, including subordinates, is resource limited. The results of this study do not support that assumption. The empirical justification for using summed lengths has been that anemone size is more strongly correlated with the summed lengths of group members than with the number of group members (Allen 1972; Ross 1978; Hattori 1991; Fautin 1992; Elliott and Mariscal 2001; Buston 2003b). Overall (i.e., in the October analysis), false clown anemonefish at Bunaken followed that pattern. But the strength of the summed length correlation reflected underlying relationships with  $\alpha$ 's length, not resource limitation of subordinates. A relationship between summed lengths of group members and anemone size is not evidence that patch size (directly) limits group size.

We emphasize the importance of group structure because it explains some of the variation in group size in our study population and, more importantly, because we would like to see the role of group structure given greater consideration in work with other systems. However, our results do not exclude carrying capacity as an explanation for variation in group size in other circumstances. Rather, our results demonstrate that both mechanisms can bring about the same correlation between group size and patch size. Patterns of variation in group size in other anemonefish species further illustrate this point. Fautin (1992) found that group size of *Amphiprion percula* (Lacépède, 1802) was correlated with

*Heteractis magnifica* (Quoy and Gaimard, 1833) anemone diameter but not with  $\alpha$ 's length, and that  $\alpha$ 's length was not correlated with anemone diameter. In contrast, Elliott and Mariscal (2001) found that  $\alpha$ 's length did increase with anemone diameter in *A. percula*. (Elliott and Mariscal (2001) did not assess the possibility that this relationship was responsible for a correlation between group size and anemone size.) Both Fautin (1992) and Elliott and Mariscal (2001) also examined variation in group size in *Amphiprion perideraion* Bleeker, 1855. Fautin (1992) concluded that, as in this study, the correlation between group size and anemone diameter in *A. perideraion* resulted from the correlation of both variables with  $\alpha$ 's length. Elliott and Mariscal (2001) reported that *A. perideraion* group size was strongly correlated with anemone size, even though the relationship between  $\alpha$ 's length and anemone size was weak and non-significant. Thus, whether anemone size or  $\alpha$ 's length limits anemonefish group size can vary both among and within species. Group size can also vary independently of both anemone size and  $\alpha$ 's length — at our secondary study site, we found no relationship between group size and either anemone size or  $\alpha$ 's length. Even at our primary study site, much of the variation in group size remains unexplained.

Predicting the pattern of variation in group size in a particular species and habitat requires some understanding of the processes responsible for that pattern. We do not yet have a clear understanding of the nature of space limitation on an anemone. Anemones clearly provide their residents with protection from predators, so a plausible interpretation of anemone carrying capacity is that refuge space itself, i.e., oral disc surface area, is a limiting resource. However, anemone size may also affect food availability; an anemonefish may require a minimum length of the oral disc margin of its host as a foraging station. When  $\alpha$ 's length determines group size, as in this study, understanding the process responsible for a correlation between anemone size and  $\alpha$ 's length is equally important. The pattern of variation in a relationship that involves the growth rate of  $\alpha$  may be quite different from that of a relationship that involves the dominant member's risk of mortality. Finally, we have assumed that an anemone's size affects the number or size or resident anemonefish, but the direction of causation can also be reversed: anemonefish can affect the growth rate of their host sea anemone (Schmitt and Holbrook 2003; Porat and Chadwick-Furman 2004). Our central argument (that interactions between  $\alpha$  and its subordinates can result in correlations between group size and anemone size in cases where no direct causal link exists) applies regardless of how a correlation between anemone size and  $\alpha$ 's length comes about.

We have shown that, in false clown anemonefish, a correlation between group size and patch size results, not from density dependence, but from interactions among group members. We conclude by observing that the importance of social structure is not limited to anemonefish. Size structure is evident within social groups of many species. Moreover, while size differences facilitate the description of group structure, the more general argument does not require size-structured groups. If a dominant individual can dictate group size, and if patch size affects that dominant individual, then a correlation between group size and patch size can result even when resources on a patch are not limiting.

## Acknowledgements

This study was approved by the Simon Fraser University (SFU) Animal Care Committee (proposal No. 572B). The Eastern Indonesia University Development Project (EIUDP) and Universitas Sam Ratulangi, Manado, provided logistic support during the field season. The EIUDP, Natural Sciences and Engineering Research Council of Canada (operating grant A6869 to L.M.D. and postgraduate scholarship to J.S.M.), the Canada – Association of Southeast Asian Nations Centre, SFU, the Garfield Weston Foundation, BC Packers, and the Steele Foundation all assisted with research or personal (J.S.M.) funding. Kodak Canada and Bonica Precision donated field equipment. B.J. Crespi, D.G. Fautin, D.J. Green, S.J. Holbrook, D.B. Lank, and anonymous reviewers offered insightful comments on earlier drafts of the manuscript. B. Pratasik introduced the field site to us.

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