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EFFECT OF COVER ON AGONISTIC BEHAVIOR OF A REEF FISH: A POSSIBLE SPACING MECHANISM[1]

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Abstract. Each *Dascyllus aruanus* shelters in a colony of coral on a reef. The fish restricts its movements to the vicinity of this colony, which may be shared with several other individuals. In areas where suitable coral colonies are in short supply, the fish are efficiently spaced over the available coral (Sale 1972). The mechanism by which this dispersion might be attained is examined in the present paper.

If the tendency of a fish to be aggressive were controlled by the degree to which it was crowded while sheltering in its coral, the pattern of emigration and immigration among neighboring groups would be influenced. Groups in one area would approach a common ratio between the number of fish they contained and the size of the coral they occupied.

An experiment tested whether the frequency or intensity of agonistic behavior of a group of *D. aruanus* was affected by the amount of shelter provided for them. Agonistic behavior was observed when groups of two, four or six fish were placed with one, two, or three units of synthetic coral. In addition to the expected effect of group size on the level of agonistic behavior ($P < 0.005$), a significant effect of the amount of shelter ($P < 0.005$) and a significant interaction ($P < 0.005$) were detected. The results are interpreted as supporting the proposed mechanism.

INTRODUCTION

Agonistic behavior within a social group may function to delineate a set of territories, to maintain mobile personal spaces, or to establish a hierarchy of dominance. One result of any such structuring is an ordering of the distribution of resources among the members of the group. It has long been held (Collias 1944) that another result of such structuring is a control of the density, or possibly the absolute size of the population involved.

Howard (1920) recognized that the separate breeding territories established by the males of many species of birds might limit density by spacing the animals over the available habitat. Present evidence indicates that this is so in some cases (e.g., Krebs, J. R. 1971), but it is not an incontrovertible rule (see reviews by Hinde 1956, Lack 1966, Watson and Moss 1970). The situation is still less clear when other types of territorial or hierarchical systems are considered (Watson and Moss 1970: 191, 207 et seq.). Although Wynne-Edwards (1962) suggests that the function of a hierarchy is to identify the surplus, or have-not, individuals of a population, strong evidence that this is so exists only for some rodents (Krebs, C. J. 1970; Myers and C. J. Krebs 1971).

Many fish hold individual breeding or feeding territories (e.g., Kalleberg 1958, Keenleyside and Yamamoto 1962, Reese 1964, Clarke 1970, Low 1971). It is a tenable hypothesis that by so doing the fish space themselves over the available habitat and thus limit their density. Many other fish, however, are aggressive without holding territories of this type. Juvenile *Lepomis* (Greenberg 1947, Miller 1964), *Oryzias latipes* (Magnuson 1962), and male poecilids (Baerends, Brower, and Waterbolk 1955, Hemens 1966) maintain dominance hierarchies, for example. Among the pomacentridae, several species of *Dascyllus* and *Amphiprion* occur as small groups of individuals that appear to maintain dominance hierarchies in the same way. In all such cases it is not clear how agonistic behavior might function to regulate population densities, or indeed, if it functions at all in this way.

Dascyllus aruanus is notably aggressive toward its own and other species. Such aggression is not limited to one sex, one age, or one time of year. Nevertheless, *D. aruanus* commonly occurs in small groups averaging two to five (maximum 25) individuals. Each group makes use of a colony of one of several species of branching coral as shelter. Fish shelter in the same coral colony for periods of at least 7 months and restrict their activities to the water immediately surrounding it (Sale 1971). Within a group, agonistic encounters are frequent and a dominance hierarchy exists, but there is no evidence of intragroup territoriality. All members of the group use all parts of the coral colony and the surrounding area.

In those areas of a reef where suitable corals are in short supply relative to the numbers of *D. aruanus*, a high correlation is found between the number of fish in a group and the size of the colony occupied by that group. The fish are thus efficiently spaced over the coral available in the area, and I have suggested that the agonistic behavior occurring among the members of a group might be responsible for this efficient dispersion (Sale 1972). In the present paper I shall amplify that hypothesis and present experimental evidence to test it.

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The members of a group of *D. aruanus* shelter together within their coral colony every night (and on most low tides in some shallow areas) as well as for brief periods during the day in response to passing predators. At such times each fish is crowded to a degree dependent upon the size of its group and the size of its coral colony.

Let us suppose that the tendency of each fish to show aggression is regulated by the degree of crowding it experiences at these times so that more crowded fish tend to be more aggressive. It follows that in groups that are large relative to the size of the colony they occupy, fish will be more aggressive than those in other groups and will fight more frequently and/or intensely with each other. In any place on a reef, neighboring groups will show levels of intragroup fighting that vary with the degree to which their members are crowded while sheltering. Those groups showing higher levels of such fighting will be less successfully joined by newly metamorphosed juveniles than their neighbors. Furthermore, they will be more likely to lose members because their low-status fish, subject to constant attack, will be more likely to fall to predators or to leave the group. In time, all groups in an area will move toward the same ratio of number of fish to area of coral and the same level of intragroup fighting. This will be particularly so where coral colonies are in short supply, and hence, where the degree to which sheltering fish are crowded is greatest.

The crucial point on which this hypothesis is based is that the level (= frequency and/or intensity) of agonistic behavior shown by a group of *D. aruanus* depends upon the amount of shelter available to them. This possibility is tested in the following experiment.

Materials and Methods

The experiment consisted of a series of tests in which varying numbers of fish and quantities of shelter were brought together in a glass-fronted aquarium 90 by 50 by 50 cm deep provided with a subsand filter. I measured the resulting agonistic behavior.

Fish were collected from the reef and held in 100-liter plastic containers of aerated seawater prior to use. They were not given any coral in the holding containers and were not held longer than 2 days before use. Synthetic wooden "corals" of a standard type (Fig. 1) were used to provide cover in the experimental tank. These were readily accepted as shelter by *D. aruanus,* and if fish were left overnight with them, they slept among the branches.

Each test began between 0730 and 0830 hr when a group of two, four, or six fish of similar size was placed in the experimental tank. A single cluster of one, two, or three units of synthetic coral provided shelter. The coral was in the center of the floor of the tank, and when two or more units were used they were arranged in a row parallel to the front of the tank, with the branches of adjacent units just in contact. The fish were observed for four 15-min periods beginning 1, 3, 5, and 7 hr, respectively, after the start of the test. At the completion of the fourth observation period the fish were removed from the tank, measured, and discarded. Fish used ranged in size from 3.1- to 5.9-cm fork length (mean size = 4.17 ± 0.25 cm SD). The range of size within a group was kept small. The maximum range within a group was 1.4 cm, and mean ranges were 0.37 ± 0.34 cm SD for groups of two fish, 0.48 ± 0.23 cm SD for groups of four fish, and 0.92 ± 0.40 cm SD for groups of six fish.

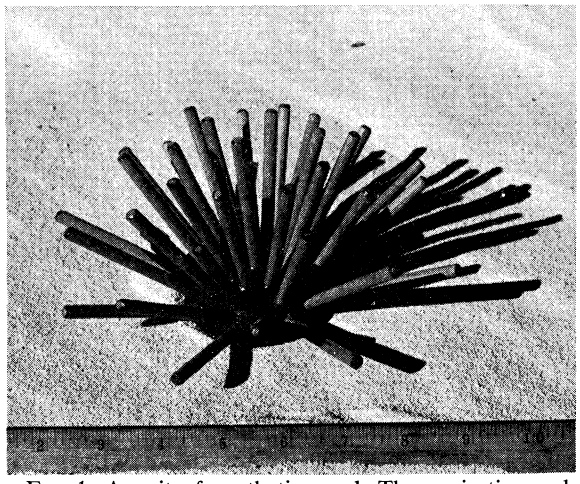

FIG. 1. A unit of synthetic coral. The projecting rods are 0.63 cm in diameter and extend 10.0 cm from the base. The scale shown is graduated in inches (1 in = 2.54 cm).

Agonistic encounters occurring during observation periods were recorded in one of two categories. Class I encounters, believed to be the more intensely aggressive interactions, always involved raising of the dorsal fin by both combatants, and, in their more common form, one fish rapidly pursued the other and nipped at its anal region. The alternative form, mouth-biting, occurred very rarely. Class II encounters, considered to be less intensely aggressive, were more variable. At least one fish raised its fins, but either lateral display, turning away by one fish, or a chase with little acceleration and no attempted nip followed.

The experiment was a 3 (fish) × 3 (coral) × 4 (observation) factorial and was replicated twice. The sequence of tests was randomized. Since Bartlett's test demonstrated significant heterogeneity among variances for the counts of encounters, a square root transformation ($\sqrt{X+1}$) was applied to the data. This successfully removed the heterogeneity, and

TABLE 1. Analysis of variance for total agonistic encounters (square root transform)

Source	df	Sum of squares	Mean square	F	P
Replicates	1	0.1653	0.1653		
Treatments:					
Size of group	2	236.8155	118.4077	212.8	<.005
Cover	2	37.5702	18.7851	33.8	<.005
Observations	3	0.5338	0.1779		
S x C	4	14.8154	3.7038	6.7	<.005
S x O	6	2.6924	0.4487		
C x O	6	3.4785	0.5797		
S x C x O	12	4.0504	0.3375		
Error	35	19.4807	0.5565		

analysis of the transformed data was carried out by standard methods (Snedecor and Cochrane 1967).

TABLE 2. The linear and quadratic components of the sum of squares for cover for each size of group considered, and their associated regression coefficients. The relation between cover and fighting for groups of one size is of the form $Y = a + b\sqrt{X} + cX$, where $Y =$ total agonistic encounters and $X =$ number of units of cover

	Linear effect		Quadratic effect	
Size of group	Sum of squares	b	Sum of squares	c
2 fish	18.04***	−1.06	8.83***	−0.43
4 fish	0.53	−0.18	19.01***	−0.63
6 fish	0.41	+0.16	5.58***	−0.34

***effect is significant at $P < 0.005$, F-test.

RESULTS

The fish spent most of their time swimming in the vicinity of the synthetic coral but made frequent excursions to other parts of the tank. They sheltered occasionally among the coral's branches but seldom did all of them do so at the same time or did any one remain there for long periods. Agonistic encounters took place in mid-water as well as within the coral.

Separate analysis of the two classes of encounter gave very similar results. Only an analysis of total encounters is considered here. As expected, analysis of variance (Table 1) showed a highly significant effect of size of group on the number of agonistic encounters ($P < 0.005$). More encounters occurred in groups of six fish than in groups of two. That no significant variation occurred among observation periods demonstrates that the levels of agonistic activity seen were effectively stable over the period of a test.

Of greater interest is the highly significant effect on agonistic behavior of the amount of cover provided ($P < 0.005$). In addition a significant interaction existed ($P < 0.005$) between the effects of cover and of group size. The existence of this interaction suggested further analysis, and since the cover provided in any test was in the form of up to three identical units of coral, I was able to examine the regression of the frequency of agonistic encounters against the amount of cover provided for each of the three sizes of groups used (Table 2).

That the regression coefficient for the quadratic

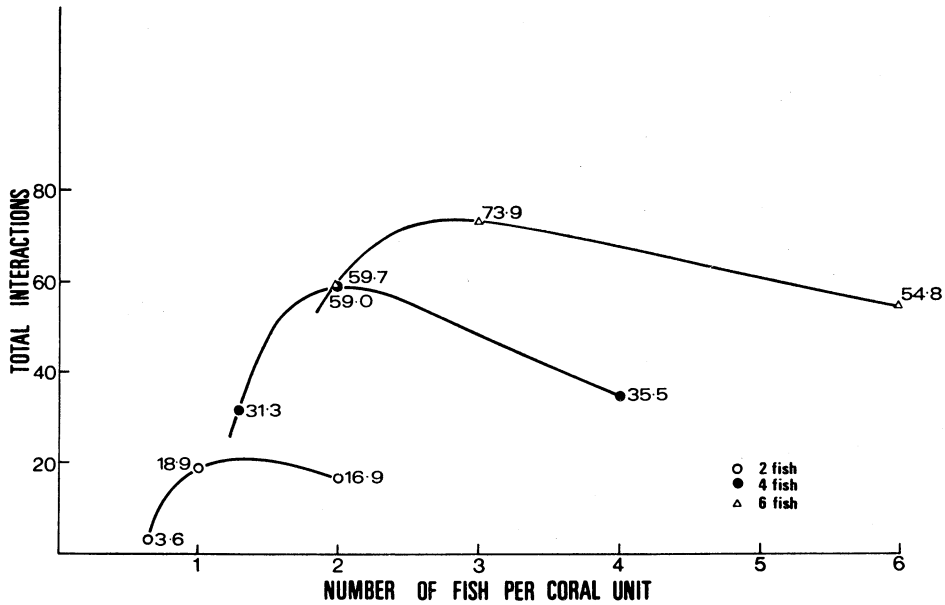

FIG. 2. The relation between the total agonistic encounters per observation period, and the degree of crowding as measured by the ratio of the number of fish to the number of units of coral. The three curves are those calculated from Table 2 for the three sizes of groups used. Each point is the mean value for a particular tested combination of fish and coral units.

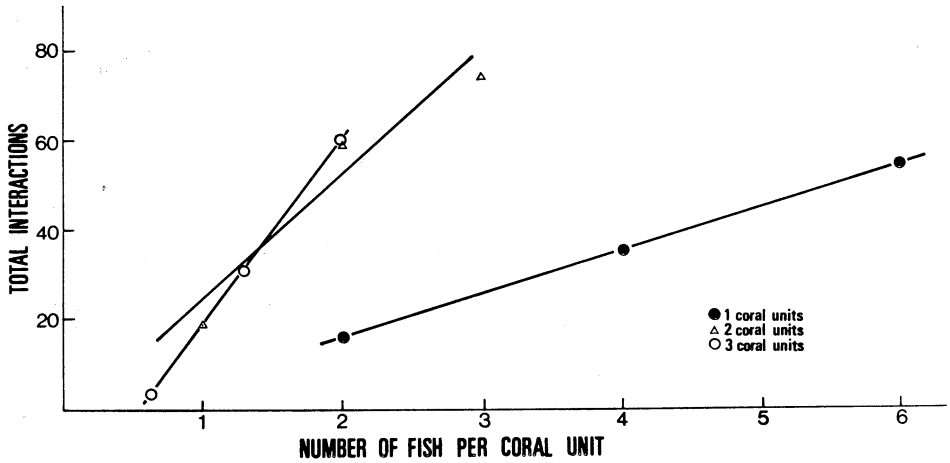

FIG. 3. A comparison of the relation between agonistic encounters and crowding in experiments in which different numbers of coral units were supplied. Results of tests in which a single unit was used differ markedly from the others.

term is significant for all three sizes of groups indicates a curvilinear relationship between the number of agonistic encounters and the amount of cover provided. The interaction between size of group and amount of cover results from the differences among the linear and quadratic coefficients for groups of different size.

Figure 2 shows the results plotted in terms of the number of fish per unit of coral supplied. The curves shown are those calculated from the analysis in Table 2. Of particular interest in Fig. 2 is the way in which the three curves are nearly coincident on the left-hand side. This suggests that there is a single positive relationship between the frequency of encounters and the degree of crowding entailed by sheltering within the cover provided, but that groups of different sizes depart from this relationship at different levels of agonistic behavior. Figure 3 contains the same points as Fig. 2 but points from tests using the same quantity of coral are joined by straight lines. It is clear that tests in which only a single unit of coral was used present a relationship between agonistic activity and crowding very different from that in the other tests.

DISCUSSION

A group of *D. aruanus* will shelter together in a single structure whether in a tank or in the field. The degree of crowding each fish experiences while sheltering will depend upon the size of this structure and the number of fish in the group. The present results demonstrate that by controlling the degree of crowding that fish experience, one produces a significant effect on the frequency with which they fight. I suggest that this effect can best be understood as a direct result of the degree of crowding fish experience while sheltering. Apparently, in *D. aruanus*, intermittent crowding of this sort has a pronounced effect on agonistic behavior, and this effect extends over intervening periods when the fish are not sheltering.

Many authors have demonstrated a relation between agonistic behavior and the degree of crowding to which fish are subjected. The relation is not simple. In general, increased crowding results in increased agonistic activity (Erickson 1967, Frost and Kipling 1967). Increased crowding has also been correlated with a decrease in this behavior (Gibson 1968). Keenleyside and Yamamoto (1962) demonstrated a rise in the rate of nips per fish as the sizes of groups of Atlantic salmon (*Salmo salar*) were increased to eight fish. Groups of more than eight fish showed fewer nips per fish and fewer total nips. Their results were not influenced by the floor area of the tank (4,630 or 7,500 cm^2) in which the observations were made.

It is apparent that an understanding of such complex and often contradictory results will require closer attention to the manner in which fish use the space available to them and less emphasis on the simple relation between the number of fish and the amount of space supplied. Keenleyside and Yamamoto (1962), for example, considerably clarified their results by noting that although all members of groups of eight or fewer salmon competed for territorial space on the floor of the tank, only the few most dominant fish of larger groups did this. In these cases the less dominant fish schooled in mid-water. Apparently no more than eight salmon were able effectively to hold territories on the relatively unstructured floor of a tank, whether it be 4,630 or 7,500 cm^2 in area. When more than eight fish were present some were forced into mid-water and acted as a nucleus to attract more of the less successful competitors. Since the fighting observed was largely in

defense of territories, schooling fish were rarely participants.

The importance of the way in which fish use the available space is also seen in the present results. All fish in groups of a given size were uniformly crowded in the sense that they were confined in a 225-liter tank; nevertheless, controlling the degree of additional crowding to which they were subjected when sheltering significantly influenced the frequency of their agonistic encounters. Species which, unlike *D. aruanus,* will not share a shelter probably would not respond in the same way to variation in its size, although they might still respond to an alternative treatment producing intermittent increased crowding. The effects of intermittent crowding have not been examined in fish.

Up till now I have considered only the fact that some relationship exists in *D. aruanus* between the degree of crowding incurred by fish while sheltering and the level of agonistic activity. The nature of this relationship (Fig. 2) is not as simple as might have been desired, and I want now to seek explanations for this. While there is evidence (see also Fig. 3) of a single positive relation between crowding and fighting up to the levels of crowding produced by a ratio of two to three fish per unit of coral, it is clear that the smaller groups depart from this relationship at different maximum frequencies of encounters. It is also true that at still higher levels of crowding the frequency of encounters decreases.

There presumably exists an upper limit to the rate at which agonistic encounters can occur among the fish of a group. I would expect this limit to be set by the size of the group, and the maxima in Fig. 2 may represent these limits for groups of two, four, and six fish.

All the data indicating a decreased rate of encounters under very crowded conditions were obtained in tests in which only a single unit of coral was supplied, and, as noted (Fig. 3), the relation between crowding and fighting in these tests was markedly different from that in the others. In the field I have never seen more than one fish in a colony as small as a single coral unit. It is worth bearing in mind, therefore, that in these tests with only one unit the fish were being subjected to far more intense crowding while sheltering than ever occurs naturally.

There is some evidence that under these extreme conditions the fish had reorganized the way in which they used the coral. In a couple of tests of groups of four or six fish I noted that one fish was effectively excluded from the group. Exclusion, presumably by means of aggression, usually occurred before the first observations period of the day, and the excluded fish thereafter rarely interacted with the remainder of the group. It avoided, to a varying degree, the substratum and the central region of the tank and sought shelter in the corners of the tank rather than in the coral. The remaining fish thus experienced less crowding when sheltering and belonged to an effectively smaller group. Correspondingly they showed fewer agonistic encounters. Any tendency of a group toward the exclusion of a particular individual from the coral would result in a reduced level of fighting. In a sense this phenomenon is analagous to the shift toward mid-water schooling by intensely crowded salmon (Keenleyside and Yamamoto 1962).

If the results obtained using a single coral unit are put aside, the experiment demonstrates a relationship between crowding and fighting of the type required by the hypothesis. The proposed mechanism could function as suggested to space *D. aruanus* over the available coral on the reef. The frequency, but apparently not the intensity, of agonistic encounters will be set by the degree of crowding experienced by the fish while sheltering in their colony.

If crowding in the field ever leads to exclusion of fish, these presumably would move to neighboring corals. Since exclusion only occurred in some experimental groups subjected to very intense crowding, it may be an unimportant phenomenon in nature. Adults on the reef move little (Sale 1971), and it seems likely that the main effect of the regulation of agonistic behavior will be to prevent the addition of juvenile fish to groups that are already more crowded than their neighbors. In time, this effect should achieve an efficient dispersion of fish among available colonies of coral. Such efficient dispersion is observed on those areas of a reef where suitable corals are in short supply (Sale 1972).

Acknowledgments

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Literature Cited

Baerends, G. P., R. Brouwer, and H. TJ. Waterbolk. 1955. Ethological studies on *Lebistes reticulatus* (Peters) 1. An analysis of the male courtship pattern. Behaviour **8**:249–334.

Clarke, T. A. 1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, *Hypsypops rubicunda.* Ecol. Monogr. **40**:189–212.

Collias, N. E. 1944. Aggressive behavior among vertebrate animals. Physiol. Zool. **17**:83–123.

Erikson, J. G. 1967. Social hierarchy, territoriality, and stress reactions in sunfish. Physiol. Zool. **40**:40–48.

Frost, W. E., and C. Kipling. 1967. A study of reproduction, early life, weight-length relationship and growth of pike, *Esox lucius* L., in Windermere. J. Anim. Ecol. **36**:651–693.

Gibson, R. N. 1968. The agonistic behaviour of juvenile *Blennius pholis* L. (Teleostei). Behaviour **30**:192–217.

Greenberg, B. 1947. Some relations between territory,

social hierarchy, and leadership in the green sunfish (*Lepomis cyanellus*). Physiol. Zool. **20**:267–299.

Hemens, J. 1966. The ethological significance of the sword-tail in *Xiphophorus hellerii* (Haekel). Behaviour **27**:290–315.

Hinde, R. A. 1956. The biological significance of the territories of birds. Ibis **98**:340–369.

Howard, H. E. 1920. Territory in bird life. Murray, London. 308 p.

Kalleberg, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Rep. Instit. Freshw. Res. Drottningholm **39**:55–98.

Keenleyside, M. H. A., and F. T. Yamamoto. 1962. Territorial behaviour of juvenile Atlantic salmon (*Salmo salar* L.). Behaviour **19**:139–169.

Krebs, C. J. 1970. *Microtus* population biology: behavioral changes associated with the population cycle in *M. ochrogaster* and *M. pennsylvanicus*. Ecology **51**: 34–52.

Krebs, J. R. 1971. Territory and breeding density in the great tit *Parus major* L. Ecology **52**:2–22.

Lack, D. L. 1966. Population studies of birds. Clarendon, Oxford. 341 p.

Low, R. M. 1971. Interspecific territoriality in a pomacentrid reef fish, *Pomacentrus flavicauda* Whitley. Ecology **52**:648–654.

Magnuson, J. J. 1962. An analysis of aggressive behavior, growth, and competition for food and space in medaka (*Oryzias latipes* (Pisces, Cyprinodontidae)). Can. J. Zool. **40**:313–363.

Miller, H. C. 1964. The behavior of the pumpkinseed sunfish, *Lepomis gibbosus* (Linneaus), with notes on the behavior of other species of *Lepomis* and the pigmy sunfish, *Elassoma evergladei*. Behaviour **22**:88–151.

Myers, J. H., and C. J. Krebs. 1971. Genetic, behavioral, and reproductive attributes of dispersing field voles *Microtus pennsylvanicus* and *Microtus ochrogaster*. Ecol. Monogr. **41**:53–78.

Reese, E. S. 1964. Ethology and marine zoology. Oceanogr. Mar. Biol. Annu. Rev. **2**:455–488.

Sale, P. F. 1971. Extremely limited home range in a coral reef fish. *Dascyllus aruanus* (Pisces, Pomacentridae). Copeia **1971**:324–327.

———. 1972. Influence of corals in the dispersion of the pomacentrid fish, *Dascyllus aruanus*. Ecology **53**:741–744.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames. 593 p.

Watson, A., and R. Moss. 1970. Dominance, spacing behaviour, and aggression in relation to population limitation in vertebrates, p. 167–218. *In* A. Watson [ed.] Animal populations in relation to their food resources. Br. Ecol. Soc., 10th Symp. Blackwell, Oxford.

Wynne-Edwards, V. C. 1962. Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh. 653 p.

Errata

In the paper "An ordination of phytoplankton populations in ponds of varying salinity and temperature" by M. Levandowsky, Volume 53, Number 3, pages 398–407, the captions for Figures 2 and 3, page 403, should be interchanged.