Ann. Zool. Fennici 30:225–232
Helsinki 13 September 1993

ISSN 0003-455X

Foraging group structure among individuals differing in competitive ability

Kai Lindström & Esa Ranta[1]

Lindström, K. & Ranta, E., Integrative Ecology Unit, Department of Zoology, P.O. Box 17, FIN-00014 University of Helsinki, Finland

Received 24 April 1993, Accepted 31 May 1993

Foraging-group composition in the domain of an information-sharing model with individuals of distinct phenotypes differing in competitive ability was studied, using a simulation approach in which food-patch size and its predictability were varied. In addition, interference among individuals was introduced to reduce the efficiency of foraging groups. Foraging groups had a more homogeneous phenotypic composition than did randomly formed groups. Phenotypic heterogeneity as well as group size increased with food availability. The expected fitness of different phenotypes tended to increase with competitive ability, the largest fitness differences being between the best phenotype and all others. These differences, however, diminished as interference among individuals increased. In predictable environments fitness differences between phenotypes were at their greatest. Interestingly, in unpredictable environments poor competitors reached higher fitness levels than in predictable environments. Poorly performing individuals moved more between groups than did good competitors. Both increase in interference among individuals and decrease in food availability enhanced the frequency of movements.

1. Introduction

The research tradition regarding group foraging has divergences. Sutherland & Parker (1985, 1992) and Parker & Sutherland (1986) — using the concept of the ideal-free distribution, IFD — have studied how differences in competitive ability should affect the distribution of individuals, or phenotypes, among patches differing in productivity. The other tradition in group foraging (Bertram 1978, Vickery et al. 1991) emphasizes the importance of information-sharing among individuals, a mechanism that stabilizes and even enhances food intake of group members (Caraco 1981, Clark & Mangel 1986). These latter models, by treating all individuals as equal, mostly overlook food competition and its possible effects on group formation. In this domain Barnard & Sibly (1981) is a notable exception, allowing foraging groups to include scroungers exploiting the food-finding abilities of producers.

---

[1] Responsible Editor: Hannu Ylönen

The two traditions rarely meet, though, considering the phenotypic composition of foraging groups, there should be a common interface. It is clear that if individuals differ in competitive abilities a certain group foraging situation may imply advantages for some individuals but disadvantages for others. As put forward by Parker & Sutherland (1986), the question in group foraging is not only how should individuals distribute themselves over foraging environments differing in quality, but also what kind of individuals should we expect to find in those groups?

Recently Ranta et al. (1993) addressed the topic how size and phenotypic composition of foraging groups affect food acquisition of unequal competitors. The model, which we also shall make use here, is a variant of the information-sharing models (Vickery et al. 1991). By information sharing we mean that when an individual in a group locates a patch of prey, others gather around to benefit from the discovery (Ward & Zahavi 1973). This implies that the prey found have to be shared, but every individual in the group also gains from patch-discoveries by others. Thus, individuals, while foraging in groups, have to keep an eye upon the whereabouts and doings of others. This time is deducted from food-search time. Because of this the pooled searching efficiency of a group is assumed to be less than that of a similar number of solitary individuals. Finally, individuals are prone to differ in their abilities to compete for the food located. In terms of foraging returns, group foraging has to be profitable for an individual, otherwise solitary food seeking is an option worth considering. Our current scope is to unravel consequences stemming from unequal competitors effects on foraging group structure.

2. The simulation

This simulation is based on the group-foraging model by Ranta et al. (1993). The model incorporates three important elements of group foraging: sharing information about food location, interference among individuals while searching for prey patches, and differences in competitive ability among group members. Denoting by a the foraging efficiency (e.g., area searched per unit time) of an average solitary forager we get for a group of n foragers the pooled searching efficiency, $A(n)$, as (Ranta et al. 1993)

$$A(n) = an^{i}. \qquad (1)$$

Here i $[0 \leq i \leq 1]$ describes how search-efficiency changes as a function of group size. Complete additivity is reached when $i = 1$, whereas, if $i = 0$, the whole group will act as a single individual. With $0 < i < 1$ there is partial additivity.

The environment consists of randomly dispersed food patches numbering λ per unit area and containing X_j food items per patch. Their frequency distribution follows the negative binomial distribution with the parameters μ and k. The median, μ, describes the average amount of food items in a patch, and k is a measure of aggregation. With small values of k, the distribution is skewed to the right, and the predictability of patch content is very low. With increasing k the distribution concentrates more and more symmetrically around the median.

In this environment individuals of phenotypes 1 to m search for food. These phenotypes can be ordered into a linear competition hierarchy. If an individual searches for food in a group, its probability of obtaining food will depend on its competitive ability. An individual first in rank, on average, is among the ones sharing the food found by the group. When there is more than one individual of the phenotype m in the group, the rank values for these are tied analogously to test procedures in nonparametric statistics (see e.g., Siegel 1956). Following Ranta et al. (1983) we write s_m as the probability of an individual of phenotype m to be among the ones sharing the prey in the patch. Accordingly, the expected patch-finding time for that particular individual is

$$\mathrm{E}[T_j, m] = \frac{1}{\lambda s_m A(n)}\,. \qquad (2)$$

The inverse of Eq. (2) is the patch-finding rate (number of patches found per unit time) for an individual of phenotype m (Ranta et al. 1993). From now on this measure will be referred to as fitness. An individual's probability to get food depends not only on its absolute rank, but more importantly, on how many higher-ranked individuals are in the group. For example, in a group of phenotypes 1, 2, 2, 3 and 5 (note that there are two tied ranks) the individual of the competitive rank 5 has the lowest probability of getting food. The same individual, however, will be the one with the highest probability of obtaining food if the group consists, for instance, of phenotypes 5, 6, 7, 8, 8, 9 and 9. Since group size determines the rate of food patch locations a good competitor's fitness will be determined mainly by the size of the group it is in. The fitness of a poor competitor will also depend on the size of the group, but much more importantly, on its relative position in the group.

The simulation starts with 100 groups of equal size and composition. Each group contains one individual of each of the six phenotypes. As an alternative version we started from original foraging groups composed of six individuals of one of the phenotypes available. Our experimentation showed, however, that the initial situation is not important for the eventual outcome.

Each group is inspected in turn. First the algorithm checks for every group member how well it performs in its current group. This is then compared to the individual's expected fitness in all the other groups and when alone. If an individual gains by either changing groups or by being alone it either moves to the most profitable group or becomes a solitary forager. Otherwise the individuals will stay where they are. This procedure is then repeated 500 times for all the parameter combinations listed in Table 1.

At the end of the simulation rounds we calculated the following statistics to describe group composition:

1) The number of different phenotypes found in a group,
2) the coefficient of variation, CV, of phenotypes in groups (the six distinct phenotypes were given weights from 1 to 6),
3) foraging-group size, and
4) the total number of moves made by individuals shuttling between different groups.

Table 1. Parameter values used in the simulations.

Additivity coefficient, *i*	0.25, 0.50, 0.75, 1.00
Mode of the negative binomial, μ	1, 5, 10, 15
Coefficient *k* of the negative binomial	1, 20
Number of phenotypes	6
Initial number of gropus	100
Total number of individuals	600

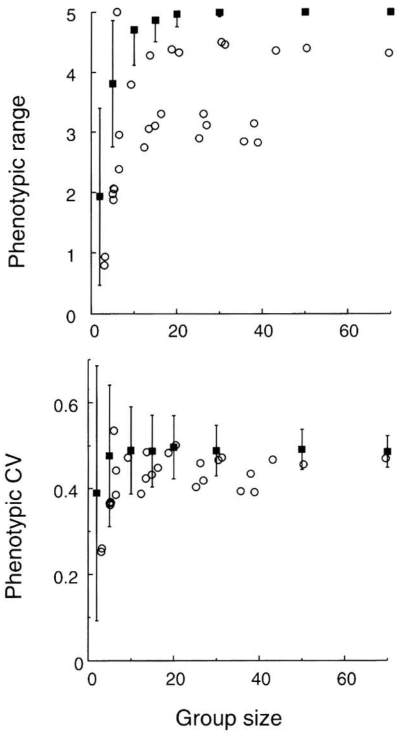

Fig. 1. Phenotypic range and CV in groups of different size. The open circles show groups formed by the simulation algorithm, while solid squares (in all graphs mean ± *SD*) refer to groups formed by random draws (details in text).

After each simulation round a grand mean was calculated for the three first variables. For each phenotype we calculated separately their expected fitnesses and the total number of moves made. The results of the above simulation were compared to those of random groups. These were formed by creating groups of 2, 5, 10, 15, 20, 30, 50 and 70 individuals drawn randomly from the pool of the six phenotypes.

We analyzed the results by using the technique of variance partitioning (Sokal & Rohlf 1981). This allowed us to evaluate the importance of different factors and their interactions on the total variation in response variables. We did not perform any tests of significance because, first, there is nothing stochastic in this simulation, and second, sample sizes could have been in-

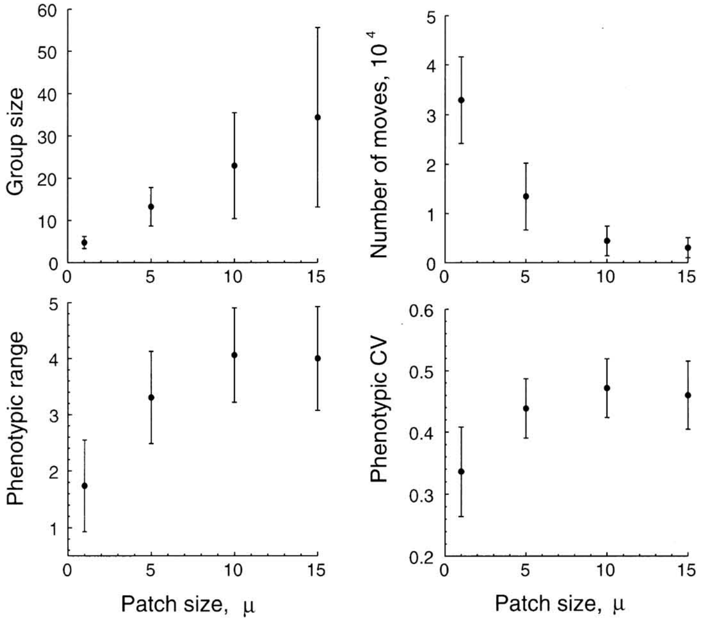

Fig. 2. Effect of patch size, μ, on variables describing group composition.

creased indefinitely to produce any significances that could be desired. These are also the reasons why we prefer to present data spread around the averages by using standard deviations.

3. Results

3.1. General

The foraging groups formed in the simulation showed a more homogeneous phenotypic composition than did those derived by the random model. Both the number of phenotypes found in a group and the CV for phenotype composition were smaller than in the random expectation (Fig. 1). This indicates that, overall, there is a tendency for assortative group formation with respect to competitive ability.

Food-patch size (or productivity of the environment), μ, had the strongest effect on simulation outcomes. It explained between 47% and 83% (Table 2) of the total variation in the four variables describing group composition (group size, phenotypic range, phenotypic CV, and total number of moves between groups). Increasing μ increased the size as well as the phenotypic heterogeneity of the groups (Fig. 2). Thus individuals tend to take advantage of grouping and move less among groups with increasing μ.

The predictability of food patch size, *k*, had a small effect on group composition and on the number of phenotypes in a group (Table 2). With *k* = 1 the average phenotype number in a group was 3.6 (*SD* = 1.4) whereas with *k* = 20 the number of phenotypes averaged 3.0 (1.0). For

Table 2. Variance partitioning for variables describing foraging group characteristic. The main factors are food patch size, μ, patch size predictability, *k*, and search area additivity, *i*. Columns indicate the percentage of the total variation in the different variables explained by the different factors.

Source of variation	Phenotype range	Phenotype CV	Group size	Moves
μ	58.1	50.5	46.9	82.7
k	5.0	1.4	0.7	0.5
i	1.8	4.1	26.7	3.4
Interactions				
μ × *k*	5.8	5.0	1.9	0.8
μ × *i*	22.6	33.4	16.8	9.6
k × *i*	3.6	1.5	4.3	1.0
Total	100.0	100.0	100.0	100.0

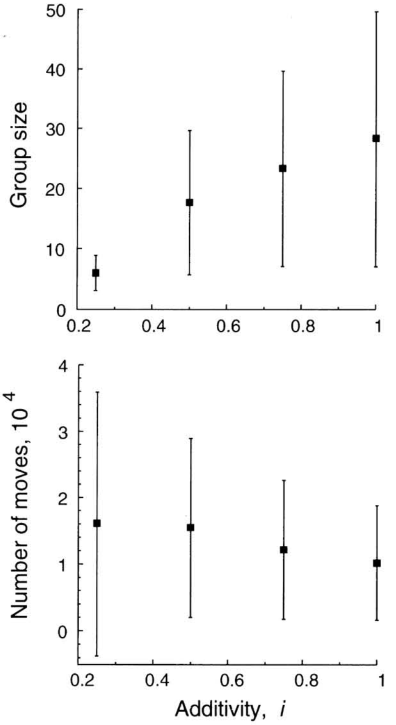

Fig. 3. Effect of search-area additivity, *i*, on group size and number of moves between groups.

the rest of the variables, *k* explained less than 1% of the variation (Table 2). The searching efficiency, characterised by the additivity coefficient, *i*, mainly affected group size. With increasing additivity group size also increased (Fig. 3). However, additivity had little effect on the rest of the variables characterising foraging group structure (Table 2).

The strongest first order interaction was between patch size, μ, and the additivity coefficient, *i*, explaining 33% of the variation in phenotypic CV of groups (Table 2). In an environment with small patches an increase in *i* tended to increase the phenotypic heterogeneity of groups (Fig. 4). With large food patches there was initially a much larger heterogeneity of groups and it decreased with increasing *i* (Fig. 4).

3.2. Individuals of different phenotypes

In general, the fitness of each phenotype tended to be directly related to its respective competitive rank, explaining 26% of the total variation in fitness (Table 3). There were some unexpected situations, however, where a phenotype of lower competitive rank had higher fitness than a superior competitor (Fig. 5). The absolute differences in these situations where minute, though, and it is likely that, had the simulation run for a longer time, these differences had disappeared.

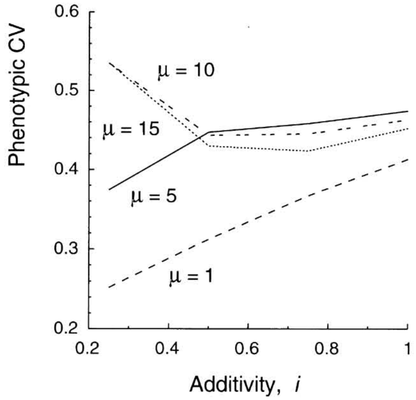

Fig. 4. Interaction between search-area additivity, *i*, and phenotypic coefficient of variation of foraging groups in environments with differing food-patch size, μ.

Fitness differences quickly levelled off with decreasing competitive rank of phenotypes (Fig. 5). The importance of competitive rank was not independent of the environment. Interaction between average patch size and phenotype explained 14% of the total variance in fitness (Table 3).

Table 3. Variance partitioning for fitness and movements (%). For other explanations, see Table 2.

Source of variation	Fitness	Movements
μ	0.9	57.6
k	3.8	0.3
i	5.3	2.4
Phenotype	25.5	18.8
Interactions		
μ × *k*	1.1	0.6
μ × *i*	5.3	6.7
μ × phenotype	14.2	8.8
k × *i*	0.8	0.7
k × phenotype	4.5	0.1
i × phenotype	21.1	0.6
Total	100.0	100.0

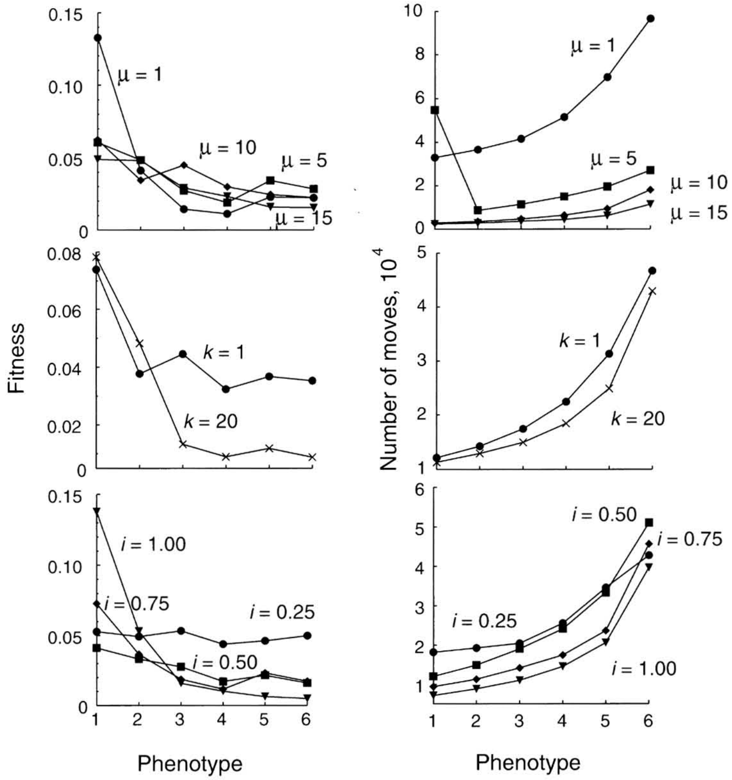

Fig. 5. Fitness of and number of movements made by phenotypes differing in competitive ability (μ = food-patch size, *k* = predictability of the food environment, *i* = search area additivity).

Likewise, there was an important interaction between additivity and competitive rank (21%). With low additivity the phenotypes showed clear differences in fitness values, while with high additivity little differences apared among individuals of differing phenotype (Fig. 5).

Increased predictability of food-patch size increased the difference between phenotypes, whereas a less predictable environment resulted in smaller fitness differences between phenotypes (Fig. 5). In a stochastic environment individuals of low rank also fared better than did individuals of the corresponding phenotypes in a predictable environment.

Poor competitors systematically moved more between groups than did good competitors (Fig. 5). Average patch size had the strongest effect on the total number of movements (58%, Table 3), with more than a ten-fold increase in movement numbers from the most productive to the least productive environment. Competitive rank was the second most important variable, explaining 19% of total variance in number of movements (Table 3). Number of movements increased with decreasing additivity (Fig. 5). Predictability of food-patch size, however, had a minor effect on movement behaviour. It thus seems that individuals increase their tendency to switch when either the food environment or the social context becomes less favourable. Individuals of the worst-performing phenotypes tend to behave poorly regardless of the environmental or social context they are in.

4. Discussion

Our research has shown that the effect of competitive differences among individuals will result in foraging groups that are more homogeneous with respect to competitive abilities than randomly formed groups. This applies, provided that individuals perform ideally, i.e., they know all options available, and are free to move into any of the existing foraging groups or to establish their own group. Apparently, the current approach is an extension of the Fretwell & Lucas (1970) Ideal Free Distribution model, with the notable simplification that our model (Ranta et al. 1993, Ranta 1993) does not imply any spatial differences in habitat quality (the food-patches in the foraging environment of the current model obey the negative binomial distribution). As the global food environment is the same for any individual, heterogeneity — the relevant element in the IFD — emerges from the differences in foraging performance of individuals. These results show that low-ability competitors tend to move away from groups which include good competitors. Eventually, if the right possibilities exist, individuals of different phenotypes form their own homogeneous groups. This pattern — individuals forming groups composed of competitively matching individuals — was termed assortative schooling by Ranta & Lindström (1990).

An approach similar to the present one was taken by Pulliam & Caraco (1984). They modelled a two-person game with a dominance hierarchy and two different habitats. With certain combinations of payoffs they could show that the dominant individual would always benefit from the presence of the subdominant and for the subdominant it always paid to escape the better competitor. We have extended the situation to n individuals and m competitive abilities. The situation is also more general, as habitat differences need not be incorporated.

In the present model most of the groups are unstable, i.e., the rearrangement of individuals rarely reaches a situation where it no longer would benefit any individual to move. However, in a more realistic situation, moving between different groups should have its price, e.g., increased predation risk for the group-switchers. Experimentation along this line indicates that existence of a switching cost tends to stabilize the system.

The fact that foraging groups in our simulations tend to become sorted (Ranta & Lindström 1990, Ranta et al. 1993) with respect to phenotypic composition is due to unequal gains from moving. A less well performing individual often finds itself in a situation which it can improve by moving either to a group with fewer superior competitors, or to groups where its relative rank is higher or even to become solitary. However, a good competitor may have little to win by moving from its present position, as only group size would affect its performance. The significance of group size may not, however, be very high, especially if the additivity in search-efficiencies of individual foragers is low. A possible mechanism keeping one of the best competitors from joining a group of poorly performing foragers might be the fact that an aberrant individual in a group is an easy target for a predator (Landeau & Terborgh 1986).

A desirable feature of theoretical work is to make predictions that can be tested on real systems (Levins 1968). A major prediction of the current simulation is that competitively inferior individuals should move more often than good competitors do. Milinski's (1984) stickleback work on the distribution of individuals among food-patches in conjunction with the IFD studies show that poor competitors move more between the food patches than do good competitors. His research also indicates that such individuals have smaller food-intake rates, as well.

Note, however, that the classical IFD works (Sutherland & Parker 1985, Milinski 1984 and references in both) differ in a fundamental way from the present simulation, because, in those studies food-input rates are independent of group size. In a foraging situation obeying information-sharing model, food-input (food-finding) rates will be crucially dependent on group size unless additivity in search-efficiency (our parameter i) is very low. Secondly, research on the IFD addresses how *individuals differing* in foraging performances should distribute themselves over *good and poor habitat patches* in terms of food production (Fretwell & Lucas 1970, Milinski, 1979, 1984, 1988, Sutherland & Parker 1985, 1992, Parker & Sutherland 1986). This assumption is relaxed in the current model (Ranta et al. 1993).

A second set of predictions for movement patterns comes from changes in the features of the environment, and especially attractive are the predicted interactions between environment and phenotype. Thus, for example, with decreasing patch-size individuals should change groups much more frequently than with larger food patches. Also, good competitors should show a much more pronounced response to changes in environmental productivity than do poorly performing individuals. Currently these predictions remain to be tested.

Acknowledgements. We thank Bill Sutherland for whiskey and many discussions on the fate of unequal competitors. Anssi Laurila, Nina Peuhkuri and two anonymous referees improved this paper with their comments and suggestions.

References

Barnard, C. J. & Sibly, R. M. 1981: Producers and scroungers: a general model and its application to captive flocks of house sparrows. — Anim. Behav. 29:543–550.

Bertram, B. C. 1978: Living in groups: predators and prey. — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: an evolutionary approach: 64–96. Blackwell, Oxford.

Caraco, T. 1981: Risk sensitivity and foraging groups. — Ecology 62:527–531.

Clark, C. & Mangel, M. 1986: The evolutionary advantages of group foraging. — Theor. Popul. Biol. 30:45–75.

Fretwell, S. D. & Lucas, H. L. 1970: On territorial behaviour and other factors influencing habitat distribution in birds. — Acta Biotheor. 19:16–36.

Landeau, L. & Terborgh, J. 1986: Oddity and the 'confusion effect' in predation. — Anim. Behav. 34:1372–1380.

Levins, R. 1968: Changing environments. — Princeton University Press, Princeton.

Milinski, M. 1979: An evolutionary stable feeding strategy in sticklebacks. — Zeitschr. Tierpsychol. 51:36–40.

— 1984: Competitive resource sharing: an experimental test of a learning rule for ESSs. — Anim. Behav. 32:233–242.

— 1988: Games fish play: making decisions as a social forager. — Trends Ecol. Evol. 3:325–330.

Parker, G. A. & Sutherland, W. J. 1986: Ideal free distribution when individuals differ in competitive ability: phenotype-limited ideal free models. — Anim. Behav. 34:1222–1242.

Pitcher, T. J. 1986: Functions of schoaling behaviour in teleosts. — In: Pitcher, T. J. (ed.), The behaviour of teleost fishes: 294–337. Croom Helm, London.

Pulliam, H. R. & Caraco, T. 1984: Living in groups: is there an optimal group size? — In: Krebs, J. R. & Davies, N. B. (eds.), Behavioural ecology: an evolutionary approach. 2nd ed.: 122–147. Blackwell, Oxford.

Ranta, E. 1993: There is no optimal foraging group size. — Anim. Behav. 46 (in press).

Ranta, E., Rita, H. & Lindström, K. 1993: Competition versus co-operation: success of individuals foraging alone and in groups. — Amer. Nat. 140: 42–58.

Ranta, E. & Lindström, K. 1990: Assortative schooling in three-spined sticklebacks? — Ann. Zool. Fennici 27:67–75.

Siegel, S. 1956: Nonparametric statistic for the behavioral sciences. — McGraw-Hill, Tokyo.

Sokal, R. & Rohlf, F. J. 1981: Biometry, 2nd ed. — Freeman, San Francisco.

Sutherland, W. J. & Parker, G. A. 1985: Distribution of unequal competitors. — In: Sibly, R. M. & Smith, R. H. (eds.), Behavioural ecology: ecological consequences: 255–273. Blackwell, Oxford.

— 1992: The relationship between continuous input and interference models of ideal free distributions with unequal competitors. — Anim. Behav. 44:345–356.

Vickery, W. L., Giraldeu L.-A., Templeton, J. J., Kramer, D. L. & Chapman, C. A. 1991: Producers, scroungers and group foraging. — Amer. Nat. 137:847–863.

Ward, P. & Zahavi, A. 1973: The importance of certain assemblages of birds as 'information centers' for food-finding. — Ibis 115:517–534.