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FLOCK SIZE OF BIRDS WINTERING IN A CULTIVATED AREA. INFLUENCE OF VEGETATION STRUCTURE AND TYPE OF DIET ***

ABSTRACT: Mean flock size of the species wintering in farmlands in the North of the Iberian Peninsula was inversely correlated with vegetation density in the areas that they occupied and positively correlated with the degree of granivory in their diets, granivorous species aggregating in large flocks and insectivorous species being solitary. These results can be interpreted as a consequence of predation risk and spatial dispersion of food resources and show that it is unnecessary to consider predator avoidance and increasing feeding efficiency as mutually exclusive.

KEY WORDS: Birds, diet, farmlands, flock size, habitat structure, winter.

1. INTRODUCTION

Predator detection and avoidance together with food exploitation efficiency are two interacting factors determining flocking (Pulliam 1973, Powell 1974). An increase in the number of individuals in flock enables birds to devote more time to searching for food and less time per individual to predator vigilance; the overall vigilance of the members of the group combined being similar to that shown by solitary individuals. In this way survival is maximized by increasing food intake rate, a consideration of great importance when food resources are scarce or limited. On

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the other hand flocking can result from the clumping of food resources in space and group size can influence the rate at which food patches are discovered, whilst the time required to discover a food patch may decrease as group size increases. Nevertheless flocking may carry associated costs in resource exploitation related to interference competition and to intraspecific aggression that may be balanced by flocking behaviour (see reviews of Bertram 1978, Krebs and Davies 1981, Pulliam and Caraco 1984).

Flocking in relation to structutral characteristics of the habitat has been rarely studied. Grzybowski (1983a, 1983b) has obtained inverse relationships between flock size of North American granivorous birds and vegetation density. Caraco (1979) has demonstrated experimentally that the addition of shrub patches, which provide refuges to escape predators, produced a reduction in the size of flocks of North American sparrows. However Lima et al. (1987) obtained somewhat conflicting results suggesting that birds perceive cover as providing a source of attacks as well as a refuge against predators.

In the present study flocking was studied in an overwinter community of birds in Atlantic farmlands in the north of the Iberian Peninsula in order to assess the role of habitat structure and the spatial distribution of food on the flocking behaviour of species. For this we used a comparative approach adopting the suggestions made by Clutton-Brock and Harvey (1984).

2. MATERIAL AND METHODS

The study was undertaken between December 1984 and January 1985 in five areas at the Basque Country (Spain; 42°50′N, 2°40′W). The study areas were of fields with scattered hedgerows, pasture land predominating. In some scarce places and only over small areas, there were ploughed fields or stubble fallows.

The five areas were surveyed by two observers who noted birds observed up to a distance of 50 m to the right and left of their path in order to control the incidence of flock size on detectability (Samuel and Pollock 1981). For each contact the following was noted: the number of birds, the shrub cover, the cover of small trees less than 3 m in height and the cover of trees more than 3 m in height within a plot of 25 m radius aroung the individual or flock center. Cover was estimated visually according to the method proposed by Prodon (1976). As a measure of the vegetation density the sum of the cover of the three strata was used. The great majority of flocks were of single species.

Using published information on the winter food of the species observed (Gil Lleget 1927, 1928, Witherby 1965, Dementiev and Gladkov 1967, Guitián 1984, 1985, Herrera 1984a, 1984b, Sánchez-Aguado 1986, Jordano 1987) a rough granivory-insectivory index was calculated (based on the extent to which seeds compared to insects or other invertebrates contributed to the diet): 3 (essentially granivores not taking insects or fruits), 2 and 1 (mixed diets), 0 (diet almost exclusively composed of insects and other invertebrates).

Table 1. Mean flock size (*FS*), insectivory-granivory index (*G*) and mean vegetation density (shrub and tree cover; *STC*) of the habitat occupied by twenty species wintering in farmlands
Only species asterisked were used to analyse the relationship; *FS*, *STC* and *G*; *n* — sample size

Species	*FS*	*STC*	*G*	*n*
* *Alauda arvensis*	8.4	0.1	3	34
Anthus pratensis	4.7	1.9	2	75
* *Motacilla alba*	1.8	1.2	1	14
Prunella modularis	1.0	24.3	2	11
* *Sylvia atricapilla*	1.2	28.1	0	6
Regulus ignicapillus	1.0	24.0	0	7
* *Saxicola torquata*	1.4	4.2	1	11
Erithacus rubecula	1.0	26.0	1	35
* *Turdus merula*	1.2	25.8	1	26
T. iliacus	8.2	8.8	2	22
* *T. philomelos*	1.3	13.2	1	29
Parus major	1.4	25.1	1	28
* *P. caeruleus*	1.1	44.6	1	9
Certhia brachydactyla	1.0	60.4	0	6
* *Troglodytes troglodytes*	1.0	29.5	0	12
Fringilla coelebs	5.6	6.8	3	41
* *Carduelis carduelis*	2.7	5.7	3	18
Acanthis cannabina	14.0	0	3	7
* *Passer montanus*	10.0	6.8	3	18
P. domesticus	13.8	2.1	3	19

Twenty species were considered for which more than six contacts were recorded. These were then arranged in the taxonomic order used in Heinzel et al. (1975). From this taxonomic list two groups of the species were obtained arbitrarily to avoid bias. One of these groups (species asterisked in Table 1) was used to analyse the relationship between flocking (average flock size; see *FS* in Table 1) and vegetation density (shrub and tree cover; *STC*) and degree of granivory-insectivory (*G*). The second group (the control; species not asterisked) was used to test the models and the predictions obtained from the first group.

Finally the patterns relating flocking to vegetation cover and granivory-insectivory degree were considered for all twenty species together. The statistical procedures that have been employed are simple, partial and multiple correlation and regression analyses (see Sokal and Rohlf 1979). All correlations have been made using the logarithmic transformation ($z' = \log(z + 1)$).

3. STATEMENT OF HYPOTHESIS AND PREDICTIONS

In the following the hypothesis and the predictions based on them which are tested in the results are outlined (see Krebs and Davies 1981, Pulliam and Caraco 1984 for a review of flocking).

Hypothesis 1 (Hl): The average group size increases with the predation risk perceived by birds.

Assuming that the risk of predation decreases with the density of shrub and tree cover through providing concealment and a refuge to escape to (Grzybowski 1983b, Lima 1987, Hogstad 1988) the following prediction can be made (Pl): those species which exploit the structurally most simple habitats should have larger average flock sizes than those which use areas with greater cover and quantity of vegetation, through being exposed to a greater risk of predation.

$$\text{correlation } FS-STC\text{: negative}$$

Hypothesis 2 (H2): The spatial clumping of resources should lead to behaviour tending towards aggregation in flocks.

The following assumptions are accepted as valid. Seeds are more abundant in structurally simple habitats, where they present a strongly clumped distribution (Schenkeveld and Verkaar 1984, Symonides 1986, Thompson 1986). In cultivated areas, adventitious plants can produce large seed banks (see among others Roberts 1981, Froud-Williams et al. 1983) which seem to be more accesible to birds than those stored in grasslands (Newton 1972, Brownsmith 1977 and Wiens and Johnston 1977 for a discussion of the obstructive effect of grass on the foraging ability of granivorous birds). Therefore, it can be assumed that, in the study area, cultivated patches within the grasslands produce an additional clumping in the distribution of seeds. This assumption is consistent with the fact that bird densities are greater on those substrates (170.7 birds/10 ha on cultivated patches vs 36 birds/10 ha on grasslands) (unpublished data; see Telleria and Santos 1985). Hence, the prediction derived from hypothesis 2 is that a greater level of granivory in the diet of the species should be associated with a trend towards the formation or larger flocks (P2):

$$\text{correlation } FS-G\text{: positive}$$

4. RESULTS

Using the species indicated in Table 1 by an asterisk a significant negative correlation was found between flock size (FS) and the density of shrub and tree vegetation (STC; one-tailed test, $r = -0.630$, $p < 0.05$). The correlation between flock size (FS) and the granivory-insectivory degree (G) was positive (one-tailed test, $r = 0.785$, $p < 0.01$). That is flock size of the species increases as vegetation cover decreases and as the degree of granivory increases. The following regression equations were obtained (log-log regression):

$$FS = (6.79 * (STC + 1)^{-0.32} - 1$$
$$FS = 1.54 * (G + 1)^{0.97} - 1$$

Using these equations the flock size of the control group of species (those not asterisked in Table 1) was calculated taking into account the average vegetation cover in the area where they occurred and their degree of granivory-insectivory. The expected values derived from the regression equations strongly correlated with those observed both for the vegetation cover ($r = 0.864$, $n = 10$, two-tailed test, $p < 0.01$) and for the degree of granivory-insectivory ($r = 0.778$, $p < 0.01$). Thus the relationships between flocking and vegetation cover and diet can be generally extended to those species which overwinter in farmlands at the Basque country, and the predictions derived from the antipredator defence and the food searching dispersion hypotheses are fulfilled.

Using all twenty species the predictions (P1 and P2) continue to be fulfilled ($FS-STC$: $r = -0.754$, $p < 0.001$; $FS-G$: $r = 0.770$, $p < 0.001$; one tailed tests). In the same way the predictions are fulfilled when partial correlation analysis is used to exclude the effect STC has over G and vice versa ($FS-STC$: $r = -0.487$, $p < 0.05$; $FS-G$: $r = 0.529$, $p < 0.01$; with one tailed tests and $n = 20$ in both cases). Overall the vegetation cover (STC) and the type of diet (G) explains 69% of the variation observed in the average flock size of the species living in farmlands during the winter ($r = 0.830$, $n = 20$, $p < 0.001$). In Figure 1 a graphic model is illustrated which predicts winter flocking of birds as a function of the protection offered by vegetation cover and the type of food eaten.

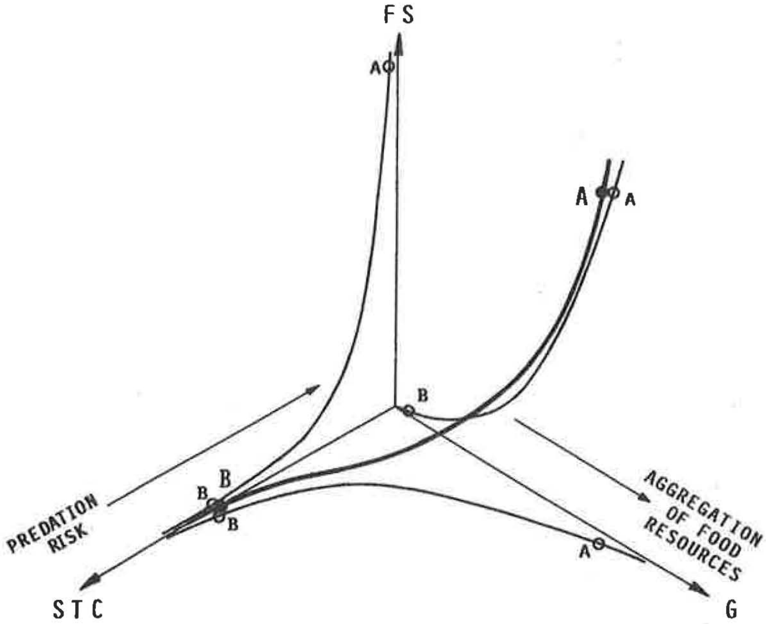

Fig. 1. Graphic model showing the relationship among flock size (FS), vegetation density (STC) as an inverse measure of predation risk, and type of diet (insectivory-granivory index, G) in farmlands during winter

5. DISCUSSION

Just as Grzybowski (1983a, 1983b) has found for North American grasslands, gregarious species occur in habitats with sparse shrub and tree cover, and solitary passerines never occur in sparsely vegetated areas. The inverse reltionship between average flock size and vegetation cover, given the common assumption that distance to cover determines the probability of escaping an attack (Lima 1987), must be related to predation risk (Grzybowski 1983b). Birds in or around hedges would be less conspicuous and/or would reach safety more quickly than birds feeding in open country (see Barnard 1983 for a similar view for house sparrow *Passer domesticus* (L.) and Caraco et al. 1980. Grubb and Greenwald 1982, Schneider 1984 and Hogstad 1988). Thus in hedgerows areas a reduced need for vigilance would bring with it a reduced tendency towards grouping in large flocks in order to maximize survival by means of the balance between foraging and vigilance. In this way some of the costs associated with flocking like aggresive interactions and interference competition between individuals while foraging would be reduced (Fretwell 1972, Fleischer 1983).

On the other hand flocking can be seen as favoured in open areas allowing birds to maintain high foraging rates with low individual vigilance intensity, yet keeping high rates of overall group vigilance. Additionally in large flocks there would be a stronger effect of "dilution" (Hamilton 1971, Bertram 1978, Parker 1985). Other factors influencing the increase in flock size in areas lacking cover would be the effect of predator confusion and risks to a predator of injury through collision with birds that were not the target prey (Treisman 1975, Bertram 1978, Barnard 1983).

As Krebs (1987) has indicated, flocking in birds is also associated with diet, so that seed eating species form larger flocks than birds that eat animal matter. This idea is supported by the results noted in the present study, since the insectivorous birds were usually solitary while the strict granivores were flocking. The explanation of this phenomenon must be related to the spatial distribution of food. Seeds tend to occur unpredictably in defined patches in the cultivated plots. When birds eat this type of food, the limiting factor is to find the patches rich in food. Under these circumstances it is beneficial to come together in flocks since it increases the probability of an individual finding a good feeding site, there being many birds searching (Barnard 1983, Krebs 1987 and Alonso et al. 1987 for common cranes wintering in cultivated areas). Alternatively another possible advantage of being in groups is that the birds reduce the probability of looking for food in previously exploited areas with low food availability due to foraging depletion (Cody 1974, Morse 1980). Furthermore, on joining a flock a bird can observe other individuals with high food intake rates and hence increase its probability of finding a sufficient quantity of food (see Krebs et al. 1972, Ward and Zahavi 1973, Morse 1980, Barnard 1983 and Pulliam and Caraco 1984 for information relevant either to such social facilitation or local enhancement). Although the high average flock size of the granivorous species can also be explained by an aggregation effect at sites of high food availability because birds track the places with the highest food density (see Barnard 1983, for house sparrow), the groups of birds in the cultivated fields must be considered as flocks and not as aggregations of individuals. The groups of birds observed are in flocks because individuals show cohesive movements in travelling and escaping from predator attacks (in the study area principally *Falco tinunculus* L., *F. peregrinus* Tunst., *Accipiter nisus* and *Circus cyaneus* (L.); see Krebs 1987).

Contrary to that of seeds, arthropods and other invertebrates are less clumped. Thus, insectivorous birds are unable to come together in flocks, as if they did there would be high levels of interference as they competed for the same prey items. Birds in these circumstances can be territorial if it pays energetically to defend a specific area against other individuals (e.g. Pulliam and Caraco 1984). This appears to be the case with blackbirds *Turdus merula* L., robins *Erithacus rubecula* (L.) and wrens *Troglodytes troglodytes* (L.) in the farmlands in winter since they sing and there are hostile interactions between conspecifics. None the less the territorial behaviour of wintering birds can vary with changing conditions of food availability as has been found for pied wagtails (*Motacilla alba* L.) by Davies and Houston (1981, 1983).

The results of the present study show the importance of food distribution, diet and predator avoidance in the forming of winter bird flocks in cultivated areas. These three factors appear to work together to determine flock size and it is unnecessary to consider predator avoidance and increasing feeding efficiency as mutually exclusive (Morse 1977) (Fig. 1).

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6. SUMMARY

Flock size was studied in an overwinter community of birds in Atlantic farmlands in the North of the Iberian Peninsula. Mean flock size of twenty species (Table 1) was inversely correlated with the density of shrub and tree vegetation in the areas occupied by these species. Given the common assumption that distance to cover determines the probability of escaping a predator attack, this result is seen as a consequence of predation risk. The type of diet of the species, measured as an ordinal gradient between insectivory and granivory was positively correlated with mean flock size, showing that spatial dispersion of food is important for explaining foraging behaviour.

Overall the vegetation density and the type of diet explains 69% ($p < 0.001$) of the variation observed in the average flock size of the species studied living in farmlands during the winter (Fig. 1).

These results corroborate the predictions derived from flocking behaviour theories, and show that it is unnecessary to consider predator avoidance and increasing feeding efficiency as mutually exclusive.

7. POLISH SUMMARY

Badaniami objęto zespół gatunków ptaków zimujących w krajobrazie rolniczym w północnej części Półwyspu Iberyjskiego. Stwierdzono, że u dwudziestu gatunków przeciętna wielkość stad była ujemnie skorelowana z zagęszczeniem drzew i krzewów (tab. 1). Przyjmując ogólnie akceptowane założenie, że odległość osobnika od stanowiących schronienie zakrzewień lub zadrzewień określa prawdopodobieństwo uniknięcia ataku drapieżcy, uzyskany wynik interpretować można jako efekt działania drapieżcy. Z kolei stwierdzono, iż przewaga udziału nasion w stosunku do pokarmu zwierzęcego w diecie jest dodatnio

skorelowana z wielkością stada. Wskazywałoby to pośrednio, że charakter przestrzennego rozmieszczenia pokarmu ma istotne znaczenie dla zrozumienia sposobu odżywiania się ptaków. Ogólnie stwierdzić można, że zagęszczenie drzew i krzewów oraz typ diety określały łącznie 69% ($p < 0{,}001$) zmienności przeciętnej wielkości stada gatunków występujących na polach w okresie zimy.

Powyższe wyniki są zgodne z przewidywaniami opartymi na teorii zachowania stadnego i wskazują na konieczność rozpatrywania tendencji do unikania drapieżcy i wydajności odżywiania się związanej ze stadnością jako wzajemnie wykluczających się czynników.

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