

Ecological aspects of heterospecific flocks formation in a Mediterranean passerine bird community

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Mixed-species bird flocks were studied in a southern Spanish evergreen-oak woodland. Of the eight flock-participating species, four ('flock-positive') tended to take part in flocks more frequently, and four ('flock-negative') less, than expected on a random basis. Flock-positive species tended to broaden their utilization of feeding sites (in height and substrate) when participating in flocks, whereas flock-negative species showed the opposite trend. For all flock-positive species combined, foraging success while in flocks was about twice that for solitary foraging birds. Among flock-negative species no significant difference in foraging success existed between the solitary and flocking situations. During the flocking period (autumn-winter), if not in flocks, flock-positive species needed more time to find a given number of prey items than during the remainder of the year. When in flocks, they were able to improve significantly their foraging performance. Flock-negative species improved in autumn-winter their foraging success regardless of whether they participated in flocks or not. It is shown that these results can be interpreted as evidence supporting both the predation- and feeding-related hypotheses proposed for the evolution of flocking behaviour. The nature and degree of the advantages gained by participating in flocks must vary according to species, food availability and, presumably, other factors.

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Стаи птиц смешанного видового состава исследованы в южной Испании в лесу вечнозеленого дуба. Из 8 видов, составлявших стаю, 4 ("стаино-положительные") чаще включаются в стаю и 4 ("стаино-отрицательные") – реже, чем предполагалось заранее. Стаино-положительные виды имеют тенденцию к расширению кормовых участков (по высоте и характеру субстрата) при стаином образе жизни, а у стаино-отрицательных видов наблюдалась противоположная тенденция. Для всех стаино-положительных эффект сбора пищи в стае вдвое выше, чем у одиночных особей. Среди стаино-отрицательных видов нет существенных различий в активности сбора пищи в одиночной и стаиной ситуациях. В течение стаино-положительного периода (осень – зима) вне стаи стаино-положительные виды тратят больше времени на добычу определенного количества пищи, чем в остальную часть года. В стае они способны активизировать свою фуражировку. Стаино-отрицательные виды активизируют осенью и зимой сбор пищи, независимо от того, входят ли они в состав стаи. Показано, что эти результаты могут быть интерпретированы как доказательство, подтверждающее гипотезу хищничества и гипотезу питания, предложенные для объяснения эволюции стаино-поведения. Характер и количественная оценка преимуществ стаино-поведения могут различаться в зависимости от видовой специфики птиц, доступности пищи и, по-видимому, от других факторов.

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1. Introduction

Flocking behaviour in birds is a widespread phenomenon which has received much attention in the last few decades. A considerable amount of literature exists with results of both field and laboratory investigations, and many factors have been proposed as responsible for the formation of bird flocks. These factors fall into two major sets of hypotheses, which have been usually proposed to explain the evolution of flocking behaviour: improved feeding efficiency and increased protection from predators (see review in Morse 1977). Evidence supporting each of them has been obtained for many different habitats, species and geographical areas. In general, 'predation' and 'feeding' hypotheses have too often been regarded mutually exclusive, thus giving rise to controversies (e.g. Murton 1971a, Lazarus 1972), although some authors have pointed out the likely compound nature of the selective factors promoting flocking behaviour (e.g. Lazarus 1972, Buskirk 1976, Morse 1977).

I present in this paper some results (see also Herrera 1977, 1978a) suggesting that flocking behaviour may be explained by considering simultaneously the selective forces derived from predation-related and feeding-efficiency advantages.

2. Study area and methods

2.1. Study area

The study area was located on the northeasternmost part of the province of Huelva, Andalusia, southern Spain. Altitude of the area ranges from 350 to 550 m a.s.l., and general characteristics are rounded hills covered by extensive evergreen-oak *Quercus ilex* L. woodlands of differing ages, degree of conservation and management (see Rivas-Martínez 1974 and ICONA 1976). Like nearly all habitat types around the Mediterranean Basin, the vegetation in the present study area is rather degraded. Climate is of Mediterranean type, characterized by hot and extremely dry summers, and rainy mild winters (Emberger et al. 1963). Annual rainfall is 785 mm, with nearly 77% during November-April. Mean annual temperature is 15.4°C, the highest occurs in July (24.8°), the lowest in January (8.5°).

Two study plots, 10.9 and 18.9 ha in size, located in north-facing, gentle slopes covered by pure stands of evergreen-oak woodland and less than 2 km apart on a straight line, were chosen. Detailed descriptions can be found elsewhere (Herrera 1977). Although data were originally kept apart for the two plots, they have been pooled in the present study, since there are no differences between their respective bird communities regarding composition and structure.

2.2. Methods

Between March 1975 and April 1976, censuses and observations were regularly carried out in the study plots. The results reported in this paper refer, however, mainly to the period in which flocking behaviour occurred (October-February).

Bird densities were determined by means of the Emlen's (1971) linear transect method (see e.g. Nilsson 1974, Robinette et al. 1974, Franzreb 1976). Two transects 700 m long were walked 6-7 times each per month during the first three hours after sunrise.

Observations on feeding-site utilization were carried out during periods of variable length uniformly distributed from sunrise to dusk. Within a given month, observations were made during all times of the day. I walked slowly across the plots with periodic stops of 10-15 min. The whole plots were surveyed several times per month, deliberately avoiding any concentration of observational effort on particular areas. When an actively foraging bird was sighted, I recorded species, feeding-site used (see below), time (in seconds) spent in the same feeding-site (measured with a stop-watch) and height above ground estimated by eye to the nearest 0.25 m). Any individual was observed for no more than three consecutive minutes. In many cases, I was able to assess with certainty whether the bird under observation made an attempt of prey capture (at least) or not in the course of the observation period, and in these instances the observation was recorded as either feeding-positive or feeding-negative, respectively.

Eight feeding-site categories were distinguished: ground, shrubs (less than 2 m in height), trunks, branches (larger than 5 cm in diameter), small branches (diameter 0.5-5 cm), twigs (with no leaves), leaves, and air volume between and above the trees. Foraging height data, on the other hand, were grouped into seven classes for the analyses: 0-1, 1-1.5, 1.5-2.25, 2.25-3.0, 3.0-5.0, 5.0-7.5 and 7.5-11 m.

Whenever a heterospecific flock was sighted, its composition and size were recorded. A flock was considered to be any group of two or more individuals in which at least two species were present, and whose individuals were following each other along the same path. The open nature of the habitat and the small size of the flocks made it possible to determine accurately their size and composition in all cases. Single-species groups were very rarely seen, being invariably formed by long-tailed tits *Aegithalos caudatus* L. They have been excluded from the analyses.

3. Results

3.1. Composition of flocks

Heterospecific flocks were found only during the period October-February. In these months, the passerine bird community in the woodlands is composed of fourteen

Tab. 1. Composition of the 48 heterospecific flocks recorded, contribution of each of the eight flock-participating species to the observations of alone and flocking individuals, and their densities in the study area. Density figures are derived from census results and represent average values for the five-months periods in which flocks occurred.

	% flocks in which found	Average number when present	% individuals		Density (birds/10 ha)
			In flocks (n = 225)	Not in flocks (n = 856)	
Blue tit <i>Parus caeruleus</i> L.	79.2	1.71	14.6	44.3	14.7
Crested tit <i>P. cristatus</i> L.	39.6	1.16	28.2	6.5	1.7
Great tit <i>P. major</i> L.	47.9	1.65	48.1	4.8	1.5
Nuthatch <i>Sitta europaea</i> L.	54.2	1.31	26.0	11.3	2.2
Longtailed tit <i>Aegithalos caudatus</i> L.	14.6	1.86	26.0	4.3	1.1
Short-toed treecreeper <i>Certhia brachydactyla</i> Brehm	22.9	1.00	16.4	6.5	1.3
Firecrest <i>Regulus ignicapillus</i> Temm.	22.9	2.09	29.9	6.3	1.6
Chiffchaff <i>Phylloscopus collybita</i> Vieil.	31.3	1.27	12.3	15.9	3.4

species, only eight of which were recorded taking part in multispecies flocks (Tab. 1). The remaining six were the thekla lark *Galerida theklae* Brehm, woodlark *Lullula arborea* L., blackbird *Turdus merula* L., mistle thrush *Turdus viscivorus* L., robin *Erithacus rubecula* L. and chaffinch *Fringilla coelebs* L. All these are species foraging mainly on the ground (Herrera 1977), whereas all the eight flocking species forage primarily or exclusively in trees.

A total of 48 heterospecific flocks comprising in all 225 individuals was observed in the course of 136 hours of field observations. In the same observation period 856 nonflocking individuals of the same eight flock-participating species were observed (Tab. 1), thus only 20.8% of total observations referred to flocking individuals. Flocking behaviour appears then to be fairly uncommon among the passerine species inhabiting the woodland studied. Flocks are also of very small size. Three-birds groups were the most frequently seen and mean flock size was 4.7 individuals (Fig. 1).

All flock-participating species are resident in the area

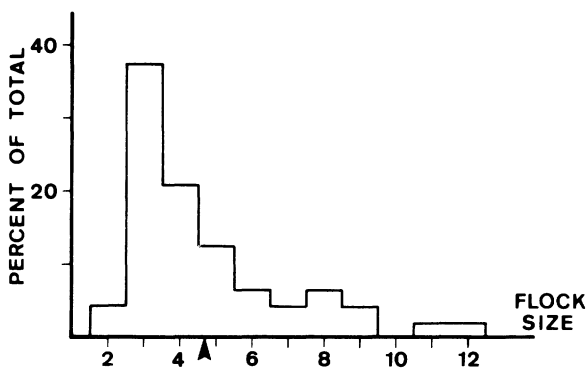


Fig. 1. Size frequency distribution of mixed-species flocks observed (N = 48). Arrow denotes mean flock size.

except *R. ignicapillus* and *P. collybita*, which are winter visitors which leave the woodlands in early spring (Herrera 1977). Frequency of occurrence in flocks (Tab. 1) varies between 79.2% (*P. caeruleus*) and 14.6% (*A. caudatus*). When present, the species contributing to the flock with most individuals was *R. ignicapillus* (2.09 birds/flock), and that with the least was *C. brachydactyla* (1.00 birds/flock).

There exists a significant correlation between the relative abundances of flock-participating species in the woodland, and their relative frequencies with respect to the total number of non-flocking individuals observed ($r_s = 0.899$, $n = 8$, $p < 0.01$). However, when the relative frequencies of individuals of these species in the 48 flocks pooled and either their frequencies in non-flock observations or in the habitat (censuses), are compared, results are nonsignificant ($r_s = 0.304$, $r_s = 0.571$ respectively, $p > 0.05$). This shows that birds in the flocks represent a nonrandom sample, with respect to the relative frequencies of the various species, of the birds in the habitat. In other words, among flock-participating species, there are some species tending to take part in flocks more frequently, and others less, than expected on the basis of their frequencies in the habitat.

To investigate this point further, a simulation of flocks was performed by a Monte Carlo method (see e.g. S6bol 1976). Cut-points for probabilities were chosen according to the relative densities of each species derived from census results (Tab. 1). The significant agreement found between the latter and the not-in-flocks frequencies shown above suggests that density estimates are fairly accurate. The frequency distribution of the sizes of simulated flocks was chosen to match exactly that of observed flocks (Fig. 1), and total number of simulated flocks was four times the number of observed flocks in the field (= 192). Each flock was simulated in an independent trial, generating

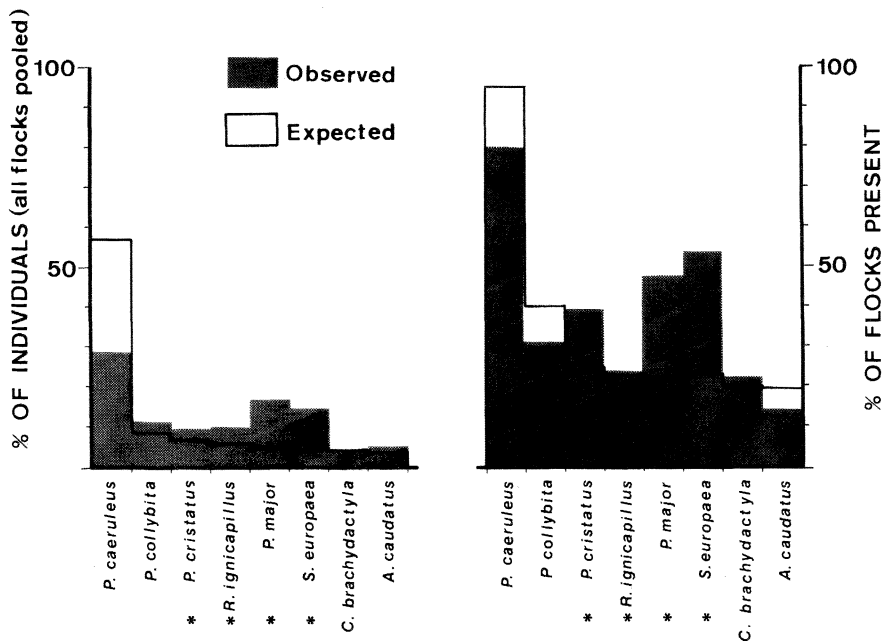


Fig. 2. Percentage represented by each flock-participating species with respect to the total number of flocking individuals (left) and frequency of occurrence in flocks (right). The actual figures derived from field data (shaded bars) are compared with the results of a simulation on a random basis (white bars). Asterisks mark those species for which their participation in flocks is much more important than expected ("flock-positive" species, see text).

successively a certain number (=flock size) of random numbers (between 0–1). Each number (equivalent to a bird individual) was assigned to the appropriate bird species according to its value in relation to the cut-point probabilities. Results are shown in Fig. 2.

Four species (*P. cristatus*, *P. major*, *R. ignicapillus*, *S. europaea*) participated in flocks appreciably more often and in larger numbers than expected on a random basis. Two species (*P. collybita*, *A. caudatus*) took part in flocks less frequently than predicted but, when present, their numbers were slightly higher than expected. Observed figures for *C. brachydactyla* were close or equal to those predicted and, finally, the participation in flocks of *P. caeruleus* was much less than expected, both in number of individuals and frequency of occurrence.

Thus, two groups of species can be distinguished: those participating in flocks more often than expected (hereafter named 'flock-positive', *P. cristatus*, *P. major*, *R. ignicapillus* and *S. europaea*), and those 'indifferent to' or 'avoiding' flocks (hereafter named 'flock-negative', the remaining four species). These two groups will be used consistently in the following analyses. Tab. 2 shows some ecological characteristics of the species in each group. On average, flock-negative species are lighter and more specialized in foraging tactics than flock-positive ones, and they tend to use foraging substrates in a more specialized fashion. They also are morphologically more differentiated within the whole-year bird community inhabiting the woodlands. The small number of species makes statistical comparisons between groups difficult, and no difference reaches significance.

3.2. Utilization of foraging sites

The relative use of the various substrates and height zones by flock-participating species is shown in the Ap-

pendix. From these data, values of feeding site breadth were computed (Tab. 3). When in flocks, flock-negative species tend to decrease their feeding-site breadth, both with respect to height and substrate. On the other hand, flock-positive species tend to broaden their utilization of feeding sites (height and substrate) when foraging in flocks. When the variations in height and substrate breadth (flocking vs. alone) of all species are pooled, this trend reaches statistical significance ($U=11$, $n_1=n_2=8$, $p=0.014$, Mann-Whitney test), thus demonstrating an effective difference between flock-positive and flock-negative species regarding the nature (sign) of the shift they experience when participating in heterospecific flocks.

Interspecific overlap values in feeding height and substrate are shown in Tab. 4. In the set of overlap figures between flock-positive and flock-negative species (lower-left and upper-right quarters of each matrix), the highest value for each species pair tends to occur significantly most frequently in the not-in-flock situation (lower-left quarter) ($\chi^2=6.13$, $df=1$, $p<0.02$; $\chi^2=4.5$, $df=1$, $p<0.05$, height and substrate respectively). This reveals that individual species of the flock-positive group are more similar in foraging to those of the flock-negative one when alone than when they participate in multispecies flocks.

For the overlap of the flock-negative species among themselves (lower-right quarter of each matrix, Tab. 4), the highest value of each pair occurs significantly more often in the not-in-flock situation ($p=0.039$ in both substrate and height, Fisher test). This suggests that flock-negative species, when in flocks, forage in such a way that decrease their mutual overlap in height and substrate use.

In the case of the overlap among flock-positive species, a trend towards largest values in the in-flock

Tab. 2. Some ecological characteristics of flock-negative and flock-positive species (groups defined in the text). Based on data in Herrera (1978a), except for the far-right column (see Appendix). Main foraging substrate has been considered as that accounting for at least 50% of total foraging time recorded.

	Body weight (g)	WSFD ¹	DC ²	DNN ³	Main foraging substrate
Flock-negative species					
Blue tit <i>Parus caeruleus</i> L.	9.4	1.29	1.49	0.17	Leaves
Short-toed treecreeper <i>Certhia brachydactyla</i> Brehm	8.0	1.15	4.06	0.56	Trunks
Longtailed tit <i>Aegithalos caudatus</i> L.	6.8	1.02	2.89	0.33	Twigs
Chiffchaff <i>Phylloscopus collybita</i> Vieil.	7.7	2.30	1.51	0.08	Leaves
Average	7.98	1.44	2.49	0.29	
Flock-positive species					
Crested tit <i>P. cristatus</i> L.	10.1	1.59	1.14	0.13	Twigs
Great tit <i>P. major</i> L.	16.9	2.40	0.93	0.17	Twigs, ground, small branches
Nuthatch <i>Sitta europaea</i> L.	20.5	1.88	2.11	0.23	Large branches
Firecrest <i>Regulus ignicapillus</i> Temm.	6.0	1.57	1.60	0.08	Twigs, leaves
Average	13.38	1.86	1.45	0.15	

1. Diversity of foraging tactics (on a year-round basis).
2. Distance to the centroid in a reduced-dimensionality morphological space.
3. Distance to the nearest neighbour species in the same space.

Tab. 3. Feeding-site niche-breadth values with respect to foraging height and substrate for the eight flock-participating species. Breadth values were computed from the data in the Appendix by using Shannon's information function (logarithms to base e).

	Height			Substrate		
	alone	in flocks	variation	alone	in flocks	variation
Flock-negative species						
Blue tit <i>Parus caeruleus</i> L.	1.28	1.12	+0.16	1.22	1.01	+0.21
Short-toed treecreeper <i>Certhia brachydactyla</i> Brehm	1.78	1.50	+0.28	1.21	1.09	+0.12
Longtailed tit <i>Aegithalos caudatus</i> L.	0.68	0.82	-0.14	0.04	0.18	-0.14
Chiffchaff <i>Phylloscopus collybita</i> Vieil.	1.41	1.17	+0.24	1.29	1.05	+0.24
Average	1.29	1.15	+0.14	0.94	0.83	+0.11
Flock-positive species						
Crested tit <i>P. cristatus</i> L.	0.95	1.23	-0.28	1.01	1.51	-0.50
Great tit <i>P. major</i> L.	1.53	1.49	+0.04	1.57	1.41	+0.16
Nuthatch <i>Sitta europaea</i> L.	1.59	1.64	-0.05	1.23	1.23	0.00
Firecrest <i>Regulus ignicapillus</i> Temm.	1.01	1.10	-0.09	0.69	1.02	-0.33
Average	1.27	1.37	-0.10	1.13	1.29	-0.16

situation can be suggested, but it does not reach an overall statistical significance ($p=0.244$, Fisher test).

All these results show that, when participating in flocks, the foraging patterns of flock-negative and flock-positive species experience qualitatively different changes. The former narrow their feeding niches and decrease their similarity with all the other species, while the latter tend to broaden their niches and, much less markedly, increase their mutual overlap.

3.3. Foraging success

The percentage of foraging observation period during which at least an attempt of prey capture takes place ('percent of success', PS hereafter) was used to investigate whether birds in heterospecific flocks have a greater foraging efficiency than solitary foraging individuals. However, as observation periods are of variable length and it is more likely to record a prey finding in longer than in shorter periods, I compared the lengths of observation periods for birds in flocks and alone prior to comparing PS values (Tab. 5). There is no significant

Tab. 4. Overlap in foraging height and substrate between the eight flock-participating species. In each matrix, the upper-right half represents overlap values when birds are in flock, and the lower-left half shows similarity values when alone. Figures in italics are the highest value of the two possible, symmetrical ones within each species pair. Overlap was computed from the data in the Appendix by means of the expression $a_{ij} = 1 - 0.5 \sum_h |p_{hi} - p_{hj}|$, where $h = 1, 2 \dots 8$ = number of foraging zones considered (in height or substrate) and p_{hi}, p_{hj} are the frequencies of utilization of zone h by species i and j respectively (Schoener 1968).

Overlap in height	Flock-positive species				Flock-negative species			
	1	2	3	4	5	6	7	8
1 <i>P. cristatus</i>	—	<i>0.53</i>	<i>0.73</i>	0.56	0.43	<i>0.58</i>	0.62	0.64
2 <i>P. major</i>	0.39	—	<i>0.58</i>	0.33	0.34	0.71	0.26	0.48
3 <i>S. europaea</i>	0.68	0.57	—	<i>0.67</i>	0.52	0.57	<i>0.62</i>	0.63
4 <i>R. ignicapillus</i>	<i>0.97</i>	<i>0.36</i>	0.66	—	0.81	0.45	<i>0.85</i>	<i>0.85</i>
5 <i>P. caeruleus</i>	<i>0.85</i>	<i>0.39</i>	<i>0.64</i>	<i>0.87</i>	—	0.42	0.66	0.79
6 <i>C. brachydactyla</i>	0.47	0.72	0.78	0.46	<i>0.51</i>	—	0.38	0.57
7 <i>A. caudatus</i>	<i>0.78</i>	0.37	0.48	0.75	<i>0.73</i>	<i>0.40</i>	—	<i>0.78</i>
8 <i>P. collybita</i>	<i>0.78</i>	<i>0.52</i>	<i>0.66</i>	0.79	<i>0.85</i>	<i>0.59</i>	0.66	—

Overlap in substrate	Flock-positive species				Flock-negative species			
	1	2	3	4	5	6	7	8
1 <i>P. cristatus</i>	—	<i>0.79</i>	<i>0.40</i>	0.64	0.62	0.17	0.39	<i>0.52</i>
2 <i>P. major</i>	0.59	—	<i>0.37</i>	<i>0.54</i>	0.45	0.17	<i>0.45</i>	0.36
3 <i>S. europaea</i>	0.33	0.32	—	0.12	0.14	0.55	0.07	0.14
4 <i>R. ignicapillus</i>	<i>0.67</i>	0.52	<i>0.18</i>	—	<i>0.74</i>	0.04	0.49	<i>0.70</i>
5 <i>P. caeruleus</i>	0.52	<i>0.58</i>	<i>0.26</i>	0.55	—	0.08	0.32	<i>0.85</i>
6 <i>C. brachydactyla</i>	<i>0.28</i>	<i>0.24</i>	<i>0.74</i>	<i>0.12</i>	<i>0.18</i>	—	0.00	0.08
7 <i>A. caudatus</i>	<i>0.56</i>	0.38	0.09	<i>0.81</i>	<i>0.36</i>	<i>0.02</i>	—	0.21
8 <i>P. collybita</i>	0.49	<i>0.61</i>	<i>0.16</i>	0.54	0.83	<i>0.12</i>	<i>0.40</i>	—

difference in the length of observation period between flocking and alone birds for any species, so foraging success can properly be compared by means of the relative frequency of feeding-positive observations (PS).

Considering species individually, sample size is in many cases insufficient to perform adequate statistical comparisons of PS values. Nevertheless, among flock-positive species, the only possible comparison (*S. europaea*) came out significant, showing that PS was higher for birds participating in flocks (Tab. 5). No significant difference appeared in the two only possible comparisons among flock-negative species (*P. caeruleus*, *C. brachydactyla*), PS values in flocks being indistinguishable from PS's for alone birds.

Combining all flock-positive species in one single sample, PS in flocks was about two times higher than for solitary birds, the difference being statistically significant. For flock-negative species, the combined sample does not reveal any significant difference between PS in flocking and alone birds. This suggests that flock-positive species really obtain an improvement of their foraging success when participating in flocks, while flock-negative ones do not get any benefit of this kind (on the basis of the foraging success measure used here).

To assess variations of success in the course of time, foraging observations were classified into eight classes according to their length in seconds. The percentage of feeding-positive observations was determined within

every time class and its variation with time analysed. However, to account for the nature of the data, original figures were transformed as follows. Since any negative-feeding observation extending over, say, 50 s, necessarily implies successive negative-feeding observations of 10, 20, etc (up to 50) s, negative observations were accumulated from high- through low-length time classes. That is, the number of negative observations in time class i was transformed according

$$\text{to } NF_i = \sum_{j=1}^i NFO_j \quad (NF = \text{transformed data, } NFO = \text{original ones}).$$

The number of positive-feeding cases in class i (YF_i) was not transformed. Percent success in class i (S_i) then became $S_i = YF_i / YF_i + NF_i$. As the number of observations was fairly low in some species, data were pooled in a single sample within the same species group (flock-positive and flock-negative). Results are shown in Fig. 3. The curves depicted represent cumulative probabilities of finding prey during a time period shorter or equal than that given on the horizontal axis.

S_i increases steadily with time of foraging in all cases, from about 0.05 in the class 0–10 s to nearly 1.00 in the period 90–110 s. For flock-positive species, S_i is always greater when in flocks than when alone ($T=1$, $p=0.008$, Wilcoxon test). For flock-negative species, there are no differences in S_i values between flocking and solitary individuals ($T=8$, $p>0.05$). This demonstrates that, during a foraging period of a given length, flock-positive species have a greater probability of finding food when

Tab. 5. Length of observation periods and foraging success of flock-participating species. PS = percent of observations in which at least an attempt of prey capture took place. Observations longer than 110 s have been excluded.

	Observation periods				Foraging success		
	N	Mean length (s)	Student's <i>t</i>	p	PS	χ^2	p
Flock-negative species							
<i>P. caeruleus</i>							
In flocks	22	29.8	0.543	>0.5	50.00	0.078	>0.5
Alone	115	33.1			46.96		
<i>C. brachydactyla</i>							
In flocks	10	30.0	0.674	>0.5	40.00	0.043	>0.5
Alone	59	24.3			44.07		
<i>A. caudatus</i>							
In flocks	3	16.0	1.014	>0.2	33.33	-	-
Alone	4	37.2			50.00		
<i>P. collybita</i>							
In flocks	7	19.9	1.520	>0.1	42.86	-	-
Alone	45	37.2			62.22		
All combined							
In flocks	42				45.24	0.238	>0.5
Alone	223				49.33		
Flock-positive species							
<i>P. cristatus</i>							
In flocks	14	23.8	0.031	>0.9	28.57	-	-
Alone	30	24.0			30.00		
<i>P. major</i>							
In flocks	23	27.8	0.583	>0.5	21.74	-	-
Alone	20	23.5			5.00		
<i>S. europaea</i>							
In flocks	30	26.2	0.629	>0.5	56.67	3.902	<0.05
Alone	55	23.4			34.55		
<i>R. ignicapillus</i>							
In flocks	9	46.7	0.958	>0.5	88.89	-	-
Alone	18	33.8			27.78		
All combined							
In flocks	76				44.74	6.102	<0.025
Alone	123				27.64		

in flocks than when alone. Flock-negative species do not increase their probability of finding food during a time period of given length by participating in heterospecific flocks.

As a standard with which to compare autumn-winter (flocking period) conditions, S_i values were computed as above for the whole period March-September (spring-summer, all months combined) (Fig. 3). In this period *R. ignicapillus* (flock-positive) and *P. collybita* (flock-negative) are absent from the study area, so the two species groups are reduced to three components each.

For flock-positive species, the in-flocks profile of S_i is above ($T=3$, $p=0.019$, Wilcoxon test) and the not-in-flocks profile is below ($T=3$, $p=0.019$) the S_i curve for the remainder of the year. For flock-negative species, both the not-in-flocks and in-flocks S_i curves are significantly above that for the remainder of the year ($T=1$, $p=0.008$; $T=3.5$, $p=0.039$, respectively). These results reveal further important differences between flock-positive and flock-negative species. In au-

tumn-winter, if not in flocks, flock-positive species need more time to find a given number of prey items than during the remainder of the year. However, when in flocks, they are able to improve significantly their foraging performance as compared to the other periods of the yearly cycle, finding food items more frequently. On the other hand, flock-negative species improve in autumn-winter their foraging success regardless of whether they participate or not in flocks.

4. Discussion

4.1. Size and frequency of flocks

Interspecific flocks in my study area are the smallest among those reported so far for non-tropical forest habitats in winter. Mean size was 4.7 individuals, as compared, for example, with figures of 21.3 (England, Morse 1973), 8.5 (Sweden, Ulfstrand 1975), 11.6 (England, Gibb 1960), 13.2–22.8 (Louisiana, Morse 1970), 12.6–17.9 (Maryland, Morse 1970), 9.2–10.8 (Maine, Morse 1970) and 14.1 (Arizona, Austin and

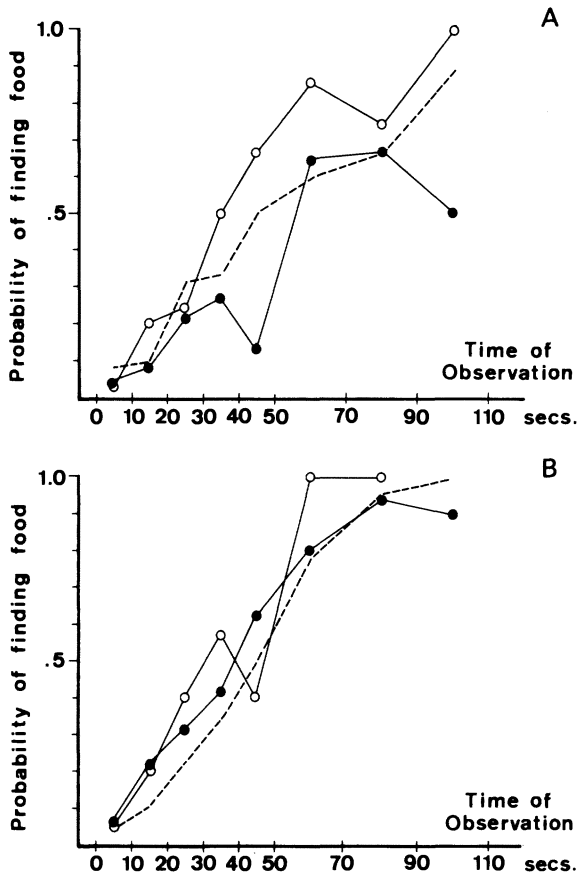


Fig. 3. Probability of an individual bird attempting a prey capture and its variation with time of observation. A, flock-positive species; B, flock-negative species. Unbroken lines, during autumn-winter: white circles while in flocks, filled circles when alone. Broken lines, during the remainder of the year. See text for details of computations. Flock-positive and flock-negative species groups are as defined in the text.

Smith 1972). Furthermore, the percent of individuals observed in flocks with respect to the total of observations denotes that flocking behaviour is fairly uncommon within the community as a whole (see e.g. Figs 3 and 4, Morse 1970).

Size and frequency of occurrence of flocks have been found sometimes to be directly related to the harshness of the environmental conditions faced by the birds (e.g. Morse 1967, 1970, Cody 1971, Pulliam et al. 1974) and my results may be interpreted similarly. Although food availability varies seasonally in the oak woodlands studied, practically all food categories are actually present in the habitat throughout the year (Herrera 1977, 1978a). Active insects occur throughout winter in the air, ground, bark and foliage, and several aerial and foliage-gleaning insectivores spend the winter in the woodlands. The most likely reason for this apparent winter favourableness, which affects many aspects of the structure of local bird communities (Herrera 1978b), is that the mean temperature of the coldest

month of the year is as high as 8.5°C (mean of maxima 15.0°, mean of minima 2.0°). This causes both an increase in food supply for insectivores and a decrease in their energy demands. The reduced tendency for flocking in my study area as compared to more northern ones may be related to this fact.

On the other hand, heterospecific flocks seem to be uncommon in tropical forest habitats on three islands. (Willis 1972, 1973 Diamond 1972). The two former cases were explained by the absence or rarity of bird predators, but this argument does not apply to the latter, since several predatory *Accipiter* species were frequent in that area (Diamond 1972: 104–108). In my study area avian bird predators are extremely infrequent in winter. The sparrowhawk *Accipiter nisus* L. is the only species known to occur, although I never saw it in the course of my field work. However, the extensive studies of Morse (1970) in several North American areas revealed a high frequency of flocking behaviour despite a general scarcity of bird predators.

4.2. Ecological correlates of the various flocking tendencies

Three groups of species can be distinguished in relation to their frequency of occurrence in heterospecific flocks, (1) species never found in flocks, (2) species which participate in flocks, but which do it less frequently than expected, and (3) species participating in flocks more frequently than expected. These groups are not sharply distinct, for an almost continuous gradient of flocking propensity is most likely to occur. Nevertheless, the categories may be useful for comparative purposes.

The finding that ground foragers were never recorded as flock members, while species feeding in trees are the only ones participating in flocks, agrees with Buskirk (1976). In a tropical bird community in Central America, he found that the species presumably most vulnerable to predators (actively feeding in trees) were precisely those participating most commonly in mixed flocks, and he interpreted these results as predation playing an actual role in the evolution of flocking behaviour.

Trends of different nature are revealed when the two groups of flock-participating species, flock-positive and flock-negative, are considered. These groups differ in species-specific attributes and in their responses when participating in flocks. Flock-negative species tend to be more specialized in their use of foraging substrates, and more differentiated in morphology, than flock-positive ones. When in flocks, flock-negative species shift and narrow their foraging niches, decreasing the overlap with all other species. Narrowing of feeding niches when in flocks has been frequently reported (e.g. Morse 1967, 1970, Austin and Smith 1972, Hogstad 1978), and it has been interpreted as supporting the role of predation as a selective pressure promoting flocking behaviour (Morse 1977). Furthermore, the fact that those species in my study narrowing their niches and minimising

overlap are precisely those which do not obtain any feeding-efficiency advantage when in flocks, also suggests that these species are obtaining in the flocks other benefits than feeding-related ones.

Among flock-positive species, the trend is towards broader feeding niches and, although statistically non-significant, slightly higher mutual overlap when participating in flocks as compared to the solitary situation. A result of this kind, to which I have found no previous reference in the literature, has been postulated by Morse (1977) to reveal food-mediated heterospecific flocks. This is clearly supported by the finding that flock-positive species in this study have a higher rate of prey encounters when in flocks than when foraging by themselves. Enhanced feeding efficiency in flocks has been reported previously for rather diverse situations, both in the field and the laboratory (e.g. Murton 1971a, b, Krebs et al. 1972, Krebs 1973, Silliman et al. 1977).

4.3. A synthetic view of the advantages gained by flocking individuals

The somewhat conflicting results presented suggest that, (1) not all species which participate in flocks are gaining advantages of the same kind and/or magnitude, and (2) the formation of flocks is not an all-or-nothing process in which the entire set of potentially involved species in a habitat respond in the same discrete fashion to one or several causal factors, whatever they are. The gradient of flocking responses, from no participation at all to participation much more frequently than expected, strongly suggests that the participation in flocks by any species is the result of a compromise between the various advantages and disadvantages derived from flocking behaviour, that these advantages and disadvantages may vary among species, and that the critical point of the compromise (disadvantages equalling ad-

vantages) must be affected both by the specific attributes of the species and the environmental conditions. If only advantages were derived from flocking (whatever they are), no matter how small they are in absolute value, only all-or-nothing responses among the species involved should then be found.

The probably compound nature of the selective pressures promoting the evolution of bird flocks has been pointed out by some authors (e.g. Lazarus 1972, Buskirk 1976, Morse 1977). There must be a fairly high number of counteracting selective pressures involved whose relative importance presumably varies among species. In any case, however, the long-term evolution of social feeding necessarily requires a positive balance in a cost-benefit equation for the individual. The terms in the equation may be reduced to four, three positive (advantageous) and one negative (disadvantageous).

Flocking will occur if $\sum_{i=1}^3 I_i > I_4$, where the I_i 's mean the

variations in survival rate when participating in social feeding as compared with the solitary situation. The I_i 's represent:

I_1 = increase in survival due to improved protection against predators (e.g. Moynihan 1962, Pulliam 1973, Powell 1974, Goss-Custard 1970, Page and Whitacre 1975, Siegfried and Underhill 1975, Buskirk 1976, Drent and Swierstra 1977).

I_2 = increase in survival due to an increase in the amount of food eaten, derived indirectly from reduced surveillance to predators (e.g. Murton et al. 1971, Lazarus 1972, Powell 1974).

I_3 = increase in survival due to improvement in feeding rates, derived from local enhancement, imitation, formation of search images, minimizing duplication of effort, etc. (e.g. Morse 1970, Murton

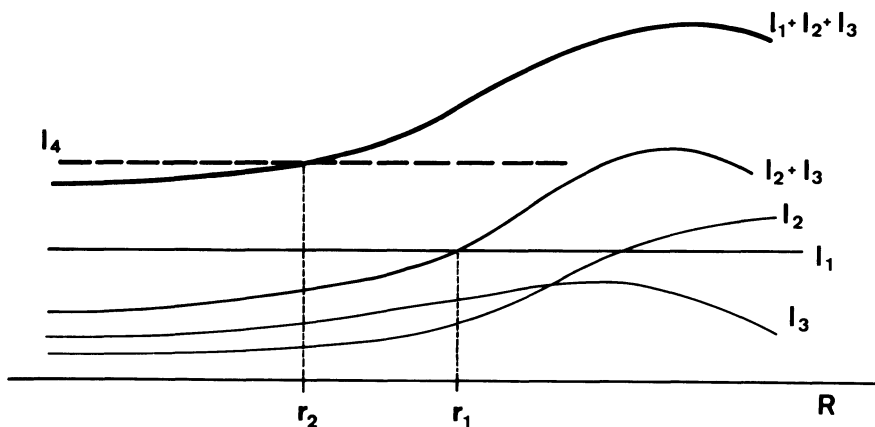


Fig. 4. Variation with the demand/supply ratio (R) of the advantages (I_1, I_2, I_3) and disadvantages (I_4) derived from heterospecific flocking by a hypothetical bird species. The I_i 's are described in the text, and are expressed as variations (increase or decrease) in the individual survival rate when participating in heterospecific flocks as compared to the solitary situation. The species concerned will participate in flocks when R is greater than r_2 . These flocks will be predominantly food-mediated if $R > r_1$, and predator-mediated if $r_2 < R < r_1$. See text for further details.

1971b, Cody 1971, Krebs et al. 1972, Krebs 1973, 1974, Greig-Smith 1978).

I_4 = decrease in survival rate due to interactions between individuals (aggression, displacement), mutual disturbance while foraging, etc. (e.g. Lockie 1956, Moynihan 1962, Recher and Recher 1969, Goss-Custard 1970, 1976, Jones 1977, Samson 1977, Smith 1977).

I_i 's values for any species will depend on whether they are referred to intra- or inter-specific situations. In the latter case, I_i 's must depend also on the identity of the coexisting species with which it is potentially feasible to form flocks. The variation of I_i 's with the ratio energy demand/food supply in a defined heterospecific context has been represented for a hypothetical species in Fig. 4.

The species referred to in the graph will participate in heterospecific flocks in its habitat when $R > r_2$. The relative importance of the advantages will vary depending on R , and flocks for the species involved will be predominantly food-mediated if $R > r_1$, and predator-mediated if $r_1 > R > r_2$. A given species may be participating in flocks mainly for either predation- or food-derived advantages, depending on the demand/supply ratio. Even assuming that both predation and feeding-efficiency are simultaneously playing a role in flock development, it is easy to imagine situations of alternative dominance for either factor in as simple a design as that of Fig. 4.

The I_i 's curves in Fig. 4 might be changed to depict diverse situations. However, the two main points I wish to emphasize here are, (1) the various species in a habitat are most likely to show different critical points (r_2 's) along the R axis, and (2) in a given habitat, the environmental conditions faced by every species at a given time (described in terms of their respective demand/supply ratios) must presumably bear different topological relationships with their respective r_2 's and r_1 's values. These facts may be used to understand the contradictory results of this study by considering, in a qualitative fashion, the relative positions of r_1 , r_2 and R_j along the R axis for the three species groups which I have distinguished in the woodland community (Fig. 5).

Those species which never participate in flocks are presumably less vulnerable to predators (lower I_1 and I_2), and their foraging methods and prey types probably increase substantially the negative effects of social feeding (higher I_4). Accordingly, $R_j \ll r_2$ (Fig. 5A).

Flock-negative species are probably more vulnerable to predators (higher I_1 and I_2), they are fairly specialized in morphology and substrate use, and thus presumably less able to obtain advantages from 'copying' the activity of other species (lower I_3). Species of lower body weight, they are probably subordinate in aggressive interactions (higher I_4). Probably their R_j values are fairly high even in winter (see Fig. 3), and these must lie close and around their r_2 's. Infrequent partici-

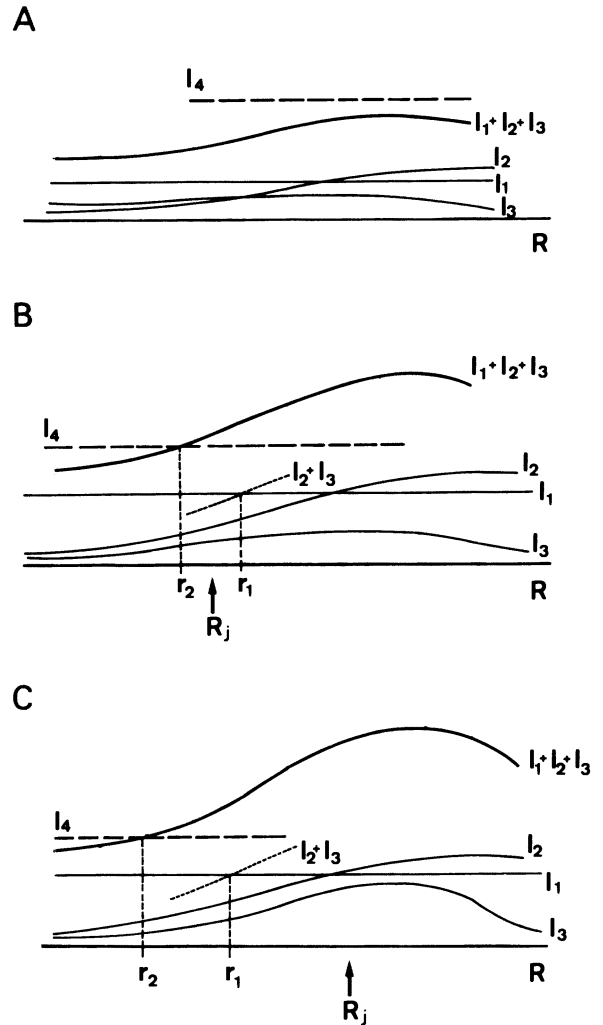


Fig. 5. Application of the model in Fig. 4 to explain the results found in this study. A: species which never were found in flocks. B: flock-negative species. C: flock-positive species. R_j denotes prevailing environmental conditions faced by species j (demand/supply ratio).

pation in flocks, and these apparently predator-mediated ($r_2 < R_j < r_1$), are to be expected (Fig. 5B).

Flock-positive species must be about as vulnerable to predators as the former group, but less specialized in morphology and substrate use, and thus probably able to gain more feeding advantages from 'copying' other species (higher I_3). Species of greater size are presumably dominant in aggressive encounters (lower I_4). Their R_j values must decrease in winter as compared to the remainder of the year. The R_j 's are probably much greater than both r_1 and r_2 , thus most frequent flocking, and obvious feeding-efficiency advantages must be expected (Fig. 5C).

The model presented here, although admittedly crude and oversimplified, serves to emphasize the complex

nature of the pressures involved in the evolution of bird flocks, as well as the serious shortcomings which may derive from considering the unravelling of these ecological mechanisms as a single choice between two alternatives. As Justus Liebig pointed out many years ago, 'the greatest difficulty comes from the fact that we are too accustomed to attribute to a single cause that which is the product of several, and the majority of our controversies comes from that' (after Allee et al. 1949, p. 729).

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A. Substrate categories

	N	Categories ¹							
		G	S	T	B	SB	T	L	A
<i>P. caeruleus</i>									
In flocks	786	11.6	0	0	0.9	1.3	27.5	58.8	0
Alone	12644	1.4	1.1	0.2	5.1	9.5	35.2	47.5	0
<i>C. brachydactyla</i>									
In flocks	503	6.2	0	51.3	33.8	8.8	0	0	0
Alone	3766	0.7	0.1	33.9	41.0	21.9	2.2	0.2	0.1
<i>A. caudatus</i>									
In flocks	305	0	0	0	0	0	95.7	4.3	0
Alone	810	0	0	0	0	0	99.3	0.7	0
<i>P. collybita</i>									
In flocks	219	8.7	6.9	0	0	2.3	16.4	65.7	0
Alone	5748	9.5	5.0	0.7	0.4	3.1	39.7	41.2	0.5
<i>P. cristatus</i>									
In flocks	531	12.0	3.8	0	2.3	26.2	35.0	20.7	0
Alone	2623	2.6	0	0	3.0	36.4	54.9	3.2	0
<i>P. major</i>									
In flocks	1130	26.1	4.8	1.1	0.7	22.8	40.4	4.2	0
Alone	1221	26.9	9.5	0	7.6	13.1	37.1	5.8	0
<i>S. europaea</i>									
In flocks	876	5.0	0	7.1	54.2	26.7	6.3	0.7	0
Alone	3214	0.6	1.5	9.7	58.6	19.9	8.2	1.3	0.3
<i>R. ignicapillus</i>									
In flocks	779	0	6.0	0	0	4.2	44.3	45.4	0
Alone	3108	0.1	0	0	1.4	7.9	79.8	10.9	0

1. G, ground; S, shrubs; T, trunks; B, branches; SB, small branches; T, twigs; L, leaves; A, air.

B. Height categories

	N	Categories ²						
		1	2	3	4	5	6	7
<i>P. caeruleus</i>								
In flocks	786	11.6	0	0	5.7	7.5	64.8	10.4
Alone	12644	0.4	0.4	1.3	9.3	29.0	46.5	11.2
<i>C. brachydactyla</i>								
In flocks	503	45.7	4.4	8.0	8.1	16.7	17.1	0
Alone	3766	14.3	10.5	14.4	22.2	23.8	14.3	0.5
<i>A. caudatus</i>								
In flocks	305	0	0	0.5	2.6	40.3	55.1	0
Alone	887	0	0	0.4	2.9	22.0	74.6	0
<i>P. collybita</i>								
In flocks	219	15.5	0	0	10.0	20.1	54.3	0
Alone	5748	15.1	0.3	0.4	5.2	29.9	40.9	8.1
<i>P. cristatus</i>								
In flocks	531	15.8	0	0	14.9	50.8	18.5	0
Alone	2613	0.4	0	0.9	6.2	39.3	51.0	0
<i>P. major</i>								
In flocks	1130	31.8	2.2	7.5	36.6	12.5	9.5	0
Alone	1221	37.8	7.3	18.7	1.2	20.7	14.3	0
<i>S. europaea</i>								
In flocks	876	7.0	1.9	6.1	20.9	32.8	25.7	5.7
Alone	3214	6.9	6.6	7.5	19.1	37.0	22.8	0.2
<i>R. ignicapillus</i>								
In flocks	779	6.0	0	0	5.0	26.7	58.8	3.5
Alone	3108	0.1	0	0	7.1	39.6	50.3	2.9

2. 1, 0–1 m; 2, 1–1.5 m; 3, 1.5–2.25 m; 4, 2.25–3.5 m; 5, 3.5–5.0 m; 6, 5.0–7.5 m; 7, 7.5–11.5 m.

Appendix. Relative use of the various substrate and height categories by flock-participating species (percent of total observation time in secs). N, total observation time (s).