

# The establishment of foraging flocks in house sparrows: risk of predation and daily temperature

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Received April 1, 1986 / Accepted August 14, 1986

**Summary.** The foraging decisions of animals often reflect a trade-off between the risk of predation and efficient foraging. One way an animal may reduce the risk of predation, and hence exploit a resource patch in relative safety, is by foraging in a group. Solitary 'pioneer' sparrows often recruit others to a food source by making chirrup calls in order to establish foraging flocks. This study describes the decisions of house sparrows that arrive at food resources of different risks of predation. Four feeding sites at different distances from a perching site and from an observer were presented to sparrows. When the feeder was adjacent to the perching site and far from the observer, the pioneers chirruped less frequently and were more likely to forage alone than when the feeder was in the other three positions. There were differences in the scanning behaviour of sparrows at these sites, suggesting that they were responding to different risks of predation. Furthermore, the chirrup rates of pioneer sparrows in this study and a previous study were found to be negatively correlated with maximum daily temperature. This is consistent with the hypothesis that energy requirements may affect the flock establishment decisions of sparrows, and that the benefits of foraging in flocks may be greater at lower temperatures.

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## Introduction

The foraging behaviour of animals often reflects a trade-off between several conflicting demands. Two of the most commonly discussed are foraging efficiency and risk of predation, although the degree of conflict may also depend on the energy

requirements of the animal. These conflicts may occur because of the attributes of resource patches, or as a consequence of the animal's foraging technique. In the former case, animals may need to choose between patches of differing quality and predation risk (e.g. Sih 1980; Grubb and Greenwald 1982; Cerri and Fraser 1983; Edwards 1983; Werner et al. 1983; Schneider 1984; Lima et al. 1985). Alternatively, the conflict may arise through the incompatibility of various activities, such as feeding and scanning for predators (see Caraco 1979a; Lendrem 1983). Here, animals are assumed to behave in a way that maximises survival by trading-off between maximising feeding rate and minimising risk of predation (e.g. Milinski and Heller 1978; Martindale 1982; Dill and Fraser 1984). Empirical studies of animal's foraging behaviour have demonstrated that they are capable of balancing conflicting demands, although the precise nature of the 'trade-off' has often proved difficult to quantify, primarily because the variables (such as feeding efficiency and predation risk) are not commensurable (but see McNamara and Houston 1986).

Foraging in groups may provide one mechanism for helping to solve the conflict between predation risk and foraging efficiency. Animals that forage in groups are able to reduce the risk of predation by either increasing the probability of detecting a predator, or reducing the predators' hunting ability, or both (see Bertram 1978; Pulliam and Caraco 1984 for review). However, foraging in groups may also increase aggressive interactions (Caraco 1979b; Elgar 1987) and the risk of competition for access to the food. An animal that joins a group may be able to forage in an area of higher predation risk, but it also bears the cost of having to share the food with others. Some studies have shown that the predator vigilance behaviour of birds increases with risk of predation (e.g. Lendrem 1983) but also decreases with group size (e.g.

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Caraco 1979b; Elgar and Catterall 1981). Thus, an animal may be able to compensate for high predation risk in its time budget by foraging in a group.

The relationship between foraging in groups and the trade-off between foraging efficiency and risk of predation can be evaluated by observing the decisions of birds that attempt to establish foraging flocks. When a solitary, 'pioneer' house sparrow (*Passer domesticus*) arrives near a food source, it often gives chirrup calls from a perch before foraging in a nearby food patch. In an earlier study, I demonstrated experimentally that these chirrup calls usually attract other sparrows, and a pioneer sparrow that arrives at a food source is more likely to forage if it is subsequently joined by other sparrows (Elgar 1986). The time for the pioneer to be joined by other sparrows is inversely related to its chirrup rate (Elgar 1986), and so chirruping and the pioneer's subsequent foraging activities give some indication of its decision to attempt to establish a foraging flock.

It is therefore possible to examine the effects of predation risk on a sparrow's decision to establish a foraging flock by presenting sparrows with feeding sites of different risks of predation, and then observing their chirruping and foraging behaviour. Sparrows at sites of low predation risk should have low chirrup rates and forage alone, whereas sparrows at sites of higher risk should chirrup more rapidly and wait to be joined before foraging.

It seems reasonable to assume that the risk of predation increases with distance from a safe perch and with proximity to a potential predator, since in both cases the chance for the individual to escape is reduced. One way of evaluating the assumption that the potential risk of predation varies at each site is to record the sparrows' scanning behaviour. Barnard (1980) and Caraco et al. (1980a) found that the scanning rate of sparrows and juncos increased with distance from cover, and Lendrem (1983) showed that the vigilance behaviour of tits was related to the proximity of the foraging patch to the ground. Caraco et al. (1980b) found that the scanning rate of juncos increased after exposure to avian predators. Any differences in predation risk between the sites may be reflected by differences in the sparrows' scanning rates, which can then be compared with any variation in the flock establishment behaviour of pioneer sparrows.

The relationship between ambient temperature and variation in flock size is not well understood. Dark-eyed juncos (Caraco 1979b) formed larger flocks but house sparrows (Barnard 1981) formed

smaller flocks at lower temperatures. Caraco (1979b) suggested that the larger flock size at lower temperatures was a consequence of reduced aggression, possibly because the birds require a higher food intake rate in order to compensate for the greater energy demands (see also Pulliam et al. 1974). However, the fighting rate of sparrows was negatively correlated with temperature, which suggests that fighting in sparrows was associated with high feeding priority. Barnard (1981) ascribes these discrepancies to differences in both the range of temperatures experienced by the two species, and the nature of the food sources. Analysis of the flock establishment decisions of sparrows may help to resolve the issue. If the costs of flocking are greater for sparrows foraging at lower temperatures, as Barnard (1981) suggests, then pioneer sparrows that discover a food source may be less likely to attempt to attract other sparrows at lower temperatures.

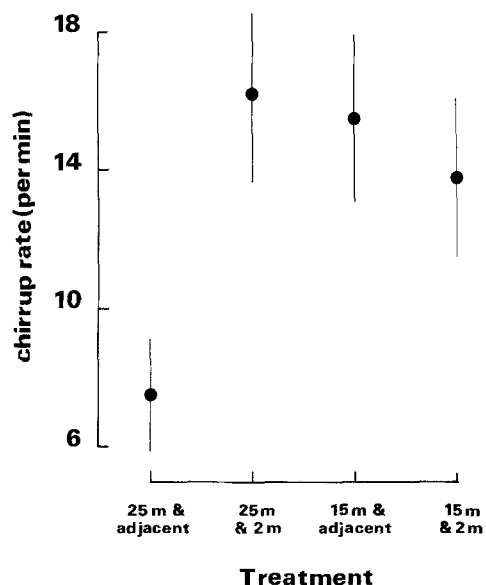
## Methods

I observed house sparrows foraging at an artificial feeder (1 m by 1 m grids) on the roof of the Department of Zoology building, Downing Street, Cambridge during the winter months of 1984 and 1985. There is a parapet along one length of the roof of the building, and pioneer sparrows usually alight on this parapet before foraging at the feeder on the roof floor (Elgar 1986). When alarmed, the sparrows fly back up to the parapet (Elgar et al. 1986), suggesting that in this context the parapet can be regarded as a safer place than the roof floor.

The feeder was placed at four different positions in terms of proximity to the parapet and observer (15 m and 25 m from the observer, adjacent and 2 m from the parapet). The positions were intended to reflect different risks of predation; proximity to the parapet was assumed to be safer because the sparrows always flew up to the parapet when alarmed, and proximity to the observer was assumed to increase risk of predation because sparrows apparently regard humans as predators. The feeder position was changed on a random basis both during and between days. About 250 ml of seed was placed in the feeder and was frequently replenished in order to maintain a constant high seed density. This seed density minimised aggressive interactions among flockmates (Elgar 1987).

The following behaviour of solitary 'pioneer' sparrows (Elgar 1986) that first arrived on the parapet was recorded: (1) the time from when the pioneer first landed on the parapet to when it either left, was joined by other sparrows, or began foraging in the feeder; (2) the total number of chirrup calls heard during this time; and (3) the sex of the pioneer.

The scanning behaviour of sparrows was observed for birds foraging in each feeder position. I selected randomly a sparrow that was foraging in the feeder, and recorded onto a continuously running cassette-recorder, the number of scans (Elgar et al. 1984) it made during a foraging bout, and the flock size as it changed. An individual's foraging bout lasted from when I began recording its behaviour until it flew back up to the parapet. The data were then transcribed using an event-recorder that yielded scanning rates for sparrows of known flock sizes. Scanning rates of birds foraging for less than 3 s were omitted from the data analysis.



**Fig. 1.** The chirrup rate (per min) of pioneer sparrows for each experimental design. Feeders were positioned either adjacent or 2 m from the parapet, and 15 m or 25 m from the observer. There was significant variation in chirrup rate across feeder positions ( $F_{3,145} = 2.64$ ,  $P < 0.02$ )

## Results

### *Flock establishment at different feeding sites*

The chirruping behaviour of the pioneer sparrows was influenced by the position of the feeder (Fig. 1). There was significant variation in the chirrup rate across feeders, although this was entirely due to the less rapid chirrup rate of pioneers presented with the feeder 25 m from the observer and adjacent to the parapet (Fig. 1). After excluding data from this feeder position, there was no significant variation between the chirrup rates of pioneers and feeder position ( $F_{2,107} = 0.26$ ,  $P > 0.1$ ). The mean chirrup rate of pioneers presented with the feeder 25 m from the observer and adjacent to the parapet was significantly lower than the pooled mean chirrup rate of pioneers at the other

three feeders (pooled mean = 15.1 chirrup/min,  $SD = 14.7$ ,  $n = 110$ ,  $t_s = 2.91$ ,  $144$  *df*,  $P < 0.01$ ).

There was no relationship between the pioneer's chirruping rate and its sex for all four treatments ( $F_{1,145} = 2.71$ ,  $P > 0.1$ ), consistent with previous studies of sparrow chirruping behaviour (Elgar 1986) and indicating that in this study, chirruping was not related to mate attraction. The time for the pioneer to be joined was negatively correlated with its chirrup rate ( $r_s = -0.27$ ,  $P < 0.05$ ,  $n = 40$ ), consistent with previous observations (see Elgar 1986).

The pioneer sparrow's decision to forage on the roof floor was influenced by both the position of the feeder and the presence of other sparrows (Table 1). When the feeder was 25 m from the observer and adjacent to the parapet, pioneers were equally likely to forage whether they had been joined or not. However, pioneers were more likely to forage if they had been joined when the feeder was either closer to the observer, or further from the parapet. The proportion of pioneers that were joined did not alter between treatments ( $\chi^2 = 4.86$ ,  $3$  *df*,  $P > 0.1$ ,  $n = 146$ ).

The relationship between temperature and an individual's flock establishment decisions was examined by comparing the pioneers' chirrup rates with records of maximum daily temperatures from the Botanic Garden in Cambridge (1 km away from the Zoology Building). Drawing on data from the present study and a previous study (Elgar 1986), I generated a sample of 164 'pioneers' that gave at least one chirrup call while waiting on the parapet. The data set only included those experimental treatments ("bird seed" and "breadcrumbs" in Elgar (1986); feeder positions other than "25 m from the observer and adjacent to the parapet" in this study) where the pioneers attempted to establish foraging flocks (i.e. the pioneers waited to be joined before foraging).

There was a negative correlation between the pioneers' chirrup rate and the maximum tempera-

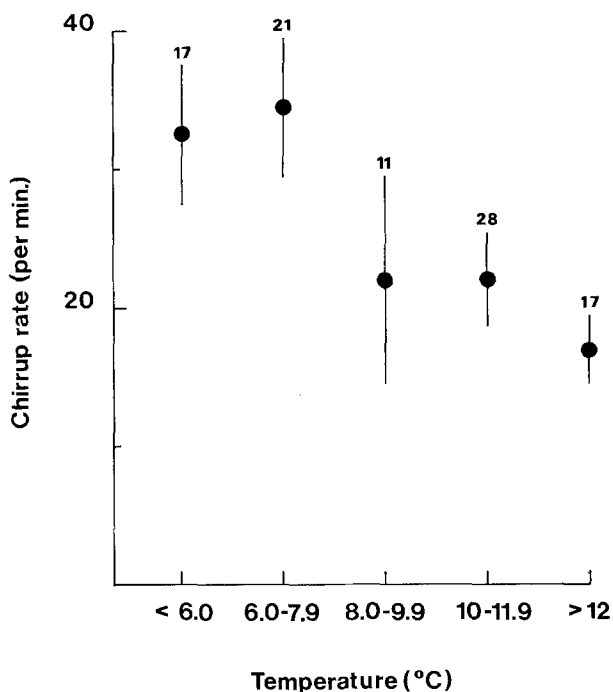
**Table 1.** The relationship between whether a pioneer sparrow was joined and whether it subsequently foraged, for sparrows presented with feeders at different distances from the observer and the parapet

	15 m from observer				25 m from observer			
	Adjacent to parapet		2 metres from parapet		Adjacent to parapet		2 metres from parapet	
	<i>Foraged?</i>		<i>Foraged?</i>		<i>Foraged?</i>		<i>Foraged?</i>	
	Yes	No	Yes	No	Yes	No	Yes	No
<i>Joined?</i>								
Yes	10	8	12	7	6	6	6	5
No	2	16	2	17	10	14	5	20
Fisher's Exact Probability	<0.001		<0.001		0.451		0.044	

**Table 2.** Regression analysis of scanning rates on the inverse flock size for sparrows foraging in feeders at different distances from the parapet (adjacent and 2 m) and the observer (15 m and 25 m). The sample size refers to the number of foraging bouts

Feeder position	<i>n</i>	<i>r</i> <sup>2</sup>	<i>F</i>	Slope	Elevation
15 and 2 metres	109	0.270	8.42**	0.288	0.469
15 and adjacent	80	0.284	6.85*	0.250	0.442
25 and 2 metres	57	0.497	18.02**	0.491	0.275
25 and adjacent	94	0.234	5.32*	0.294	0.309

\* *P* < 0.025      \*\* *P* < 0.005



**Fig. 2.** The relationship between the chirruping rate of pioneer sparrows that vocalised and the maximum daily temperature (°C). Data drawn from the chirrup rates of pioneers that attempted to establish foraging flocks in this study and in Elgar (1986) (see text for details). The chirrup rate was negatively correlated with maximum daily temperature ( $r_s = -0.182$ ,  $P < 0.01$ ,  $n = 164$ )

ture on the day that it chirruped (Fig. 2). Although there was a confounding effect of temperature and experimental design (not all the experiments took place during the same winter), the relationship between temperature and chirrup rate still held after controlling for experimental design ( $F_{3,163} = 4.72$ ,  $P < 0.005$ ).

*Scanning behaviour at different feeder positions*

The scanning rate of individuals significantly decreased with increased flock size for all feeder position (Table 2). Analysis of covariance (Snedecor and Cochran 1967) revealed that there was signifi-

**Table 3.** Analysis of covariance of the regression curves of log transformed scanning rates ( $\log_{10} [\text{scan rate} + 1]$ ) on inverse flock size for sparrows foraging in feeders at different distances from the observer and the parapet (see Table 2). *F*-values are given, with degrees of freedom in parentheses

	<i>Feeder Position</i>		
	15 m and adjacent	15 m and 2 m	25 m and 2 m
<i>Feeder Position</i>			
15 m and 2 m:			
Slope	0.07 (1,185)		
Elevation	0.93 (1,186)		
25 m and 2 m:			
Slope	2.65 (1,133)	1.73 (1,162)	
Elevation	2.27 (1,134)	5.43* (1,163)	
25 m and adjacent:			
Slope	0.07 (1,170)	0.01 (1,199)	1.18 (1,147)
Elevation	5.55* (1,171)	11.10** (1,200)	0.66 (1,148)

\* *P* < 0.025      \*\* *P* < 0.005

cant variation between sites in the elevations of these curves, but no significant variation in the slopes.

The scanning rate of individuals was not affected by proximity to the parapet (Table 3). When the feeders were 15 m or 25 m from the observer, there was no significant difference between the slope and elevation of the curve of scanning rate on flock size for sparrows foraging adjacent and 2 m from the parapet.

Sparrows foraging 15 m from the observer scanned more rapidly than those foraging 25 m away. Comparison of the slope and elevation of the curves of sparrows foraging either adjacent or

2 m from the parapet but at different distances from the observer revealed that the elevation (but not the slope) was significantly higher for sparrows foraging 25 m from the observer (Table 3). Thus, for all flock sizes, the sparrows were uniformly increasing their scanning rate when they were closer to the observer. The increase in scanning rates between the feeders near and far from the observer ranged from 15% when the feeder was adjacent to the parapet, to 25% when the feeder was 2 m from the parapet.

### Discussion

The results of this study indicate that solitary sparrows can resolve the conflict between foraging and predation risk, by recruiting other sparrows and foraging in a flock. The pioneer sparrow's decision to establish a foraging flock was influenced by the proximity of the feeder to either the parapet or the observer. Pioneers presented with the feeder 25 m from the observer and adjacent to the parapet foraged whether they had been joined or not. However, if the feeder was placed closer to the observer or further from the parapet, pioneers chirruped more rapidly and rarely foraged alone. Assuming that the different sites did reflect different predation risks, the results suggest that sparrows are able to exploit food resources in localities with higher risks of predation by establishing a flock.

The costs of establishing a flock, in terms of competition, were constant between the feeder positions, because there were no differences in either seed density, or availability (see Elgar 1987). It would be interesting to examine how the interaction between risk of predation, and competition for food influences individuals' flock establishment decisions, since sparrows do not attempt to establish flocks when the resources are not divisible (Elgar 1986). Their decisions may depend upon their social status: Schneider (1984) demonstrated that differences in the patch utilisation of white throated sparrows reflected differences in dominance. Dominant white throated sparrows foraged closer to cover than subordinates who were unable to gain access to the preferred sites.

The scanning behaviour of sparrows did not significantly alter with distance from the parapet, at either distances from the observer, which contrasts with previous studies of avian scanning behaviour (Barnard 1980; Caraco et al. 1980a). However, proximity to the observer influenced a sparrow's scanning rate; individuals foraging closer to the observer scanned at an uniformly higher rate for all flock sizes. Sparrows are charac-

teristically wary of humans, and the increased scanning rate observed for sparrows foraging closer to the human observer probably reflects an increase in their perception of danger (see also Caraco et al. 1980b).

The pattern of sparrows' scanning behaviour did not completely correspond with flock establishment decisions. The sparrows' scanning rates reflected the pioneers' foraging decisions when the feeder was placed at different distances from the observer, but not when the feeders were placed at different distances from the parapet. There are several possible explanations. For example, the parapet may not necessarily be a safe place and therefore the scanning rates would not be expected to change at any distance from the parapet. However, sparrows always flew up to the parapet when alarmed (Elgar et al. 1986), and rarely foraged alone when the feeder was far from the observer but 2 m from the parapet. Secondly, scanning rates may not alter linearly with risk of predation; although 2 metres from the parapet may have been far enough to affect the pioneers' foraging decisions, it was not far enough to elicit an increase in the sparrows' scanning rate. In Barnard's (1980) study, the sparrows were observed between 0.5 m and 8 m from cover. Similarly, in Caraco et al.'s (1980a) study of juncos, the distance from cover ranged between 0.5 m and 6 m.

Since pioneers that chirrup more rapidly are joined more quickly, the negative correlation between chirruping and temperature suggest that sparrows are more likely to establish foraging flocks during colder weather. This result is consistent with the idea that flocking is most advantageous when there is a high risk of starvation (e.g. Pulliam et al. 1974), but contrasts with Barnard's (1981) observation that smaller flocks are found at lower temperatures.

Previous studies that have examined the relationship between patch choice and the trade-off between foraging efficiency and predation risk have generally found that animals prefer to forage in areas of low predation risk and low quality than in areas of high predation risk and high quality (e.g. mammals, Edwards 1983; Lima et al. 1985; birds, Grubb and Greenwald 1982; Schneider 1984; fish, Werner et al. 1983; insects, Sih 1980). The sparrows in this study have apparently demonstrated a similar preference. In the three feeder positions where the sparrows established flocks, 85% ( $n=62$ ) of the pioneers that were not joined left the feeder without foraging presumably in order to forage elsewhere, compared with 58% ( $n=24$ ) of the pioneers presented with the feeder 24 m from

the observer and adjacent to the wall ( $\chi^2=7.42$ ,  $P<0.01$ ; see Table 1). This result is consistent with Grubb and Greenwald's (1982) experiments that showed that sparrows preferred to forage closer to cover (although their result may have been simply because the travel time from a resting place to the feeder was shorter).

It is possible that the sparrows' decisions were based on the way they expected to allocate their foraging time to certain activities. Rather than foraging alone in a patch where risk of predation is high and hence scanning rates may be higher (e.g. Lendrem 1983), the pioneers may have attempted to attract other sparrows in order to reduce the time required for predator surveillance, thus allowing more time to be spent in other activities (see Elgar et al. 1986). Similarly, in colder weather sparrows that forage in a flock could spend less time in predator surveillance, and hence more time pecking for food. However, there may be energetic costs to chirruping, and the additional time a pioneer spends waiting to be joined by others represents a cost in terms of time that could otherwise have been spent foraging. Clearly, analysis of the time budgets of animals that forage in groups needs to take into consideration the time allocated to attracting other group members.

Several comparative studies have illustrated the influence of predation risk on flocking behaviour. Willis (1972) suggests that birds do not generally flock in Hawaii, where there are few predators, and Pulliam (1973) noted that flocking was apparently less common in habitats where there was less predation. The results of this study suggest a possible mechanism for this pattern of group foraging; where risk of predation is low, individuals do not attempt to establish foraging groups, perhaps because the costs of waiting to be joined and the potential competition between individuals exceed the benefits of foraging in a group.

*Acknowledgements.* I thank Tim Clutton-Brock, Nick Davies, John Endler, Dave Gibbons, Paul Harvey, Naomi Pierce and Andrew Read for their comments. I am especially grateful for the financial support of Christ's College, Cambridge.

## References

- Barnard CJ (1980) Flock feeding and time budgets in the house sparrow (*Passer domesticus* L.). *Anim Behav* 28:295–309
- Barnard CJ (1981) Factors affecting flock size mean and variance in a winter population of house sparrows. *Behaviour* 74:114–127
- Bertram BCR (1978) Living in groups: predators and prey. In: Krebs JR, Davies NB (eds) *Behavioural Ecology: an evolutionary approach*. Blackwells, Oxford, pp 64–96
- Caraco T (1979a) Time budgeting and group size: a theory. *Ecology* 60:611–617
- Caraco T (1979b) Time budgeting and group size: a test of theory. *Ecology* 60:618–627
- Caraco T, Martindale S, Pulliam HR (1980a) Avian time budgets and distance to cover. *Auk* 97:872–875
- Caraco T, Martindale S, Pulliam HR (1980b) Avian flocking in the presence of a predator. *Nature* 285:400–401
- Cerri RD, Fraser DF (1983) Predation risk in foraging minnows: balancing conflicting demands. *Am Nat* 121:552–561
- Dill LM, Fraser AHG (1984) Risk of predation and the feeding behaviour of juvenile coho salmon (*Oncorhynchus kisutch*). *Behav Ecol Sociobiol* 16:65–71
- Edwards J (1983) Diet shifts in moose due to predator avoidance. *Oecologia (Berl)* 60:185–189
- Elgar MA (1986) House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Anim Behav* 34:169–174
- Elgar MA (1987) Food intake rate and resource availability: flocking decisions in house sparrows. *Anim Behav* 35 (in press)
- Elgar MA, Catterall CP (1981) Flocking and predator surveillance in house sparrows: test of an hypothesis. *Anim Behav* 29:868–872
- Elgar MA, Burren PJ, Posen M (1984) Vigilance and perception of flock size in foraging house sparrows (*Passer domesticus* L.). *Behaviour* 90:215–223
- Elgar MA, McKay H, Woon P (1986) Scanning, pecking and alarm flights in house sparrows. *Anim Behav* 34:1892–1894
- Grubb TC, Greenwald L (1982) Sparrows and a brushpile: foraging responses to different combinations of predation risk and energy cost. *Anim Behav* 30:637–640
- Lendrem DW (1983) Predation risk and vigilance in the blue tit (*Parus caeruleus*). *Behav Ecol Sociobiol* 14:9–13
- Lima SL, Valone TJ, Caraco T (1985) Foraging-efficiency-predation-risk trade-off in the grey squirrel. *Anim Behav* 33:155–165
- Martindale S (1982) Nest defense and central place foraging: a model and experiment. *Behav Ecol Sociobiol* 10:85–89
- McNamara JM, Houston AI (1986) The common currency for behavioral decisions. *Am Nat* 127:358–378
- Milinski M, Heller R (1978) Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). *Nature* 275:642–644
- Pulliam HR (1973) Comparative feeding ecology of a tropical grassland finch (*Tiaris olivacea*). *Ecology* 54:284–299
- Pulliam HR, Caraco T (1984) Living in groups. In: Krebs JR, Davies NB (eds) *Behavioural Ecology: an evolutionary approach*, 2nd edn. Blackwells, Oxford, pp 122–147
- Pulliam HR, Anderson KA, Misztal A, Moore N (1974) Temperature dependent social behaviour in juncos. *Ibis* 116:360–364
- Schneider KJ (1984) Dominance, predation, and optimal foraging in white throated sparrow flocks. *Ecology* 65:1820–1827
- Sih A (1980) Optimal behaviour: can foragers balance two conflicting demands? *Science* 210:1041–1043
- Snedecor GW, Cochran WG (1967) *Statistical Methods*. Iowa State University Press, Ames, Iowa
- Werner EE, Gilliam JF, Hall DJ, Mittlebach GG (1983) An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548
- Willis EO (1972) Do birds flock in Hawaii, a land without predators? *Calif Birds* 3:1–8