

# FINCH FLOCK SIZE AND RISK OF HAWK PREDATION AT A MIGRATORY STOPOVER SITE

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**ABSTRACT.**—I studied migratory flocks of finches (*Fringilla coelebs* and *F. montifringilla*) feeding during three autumn and two spring seasons at a stopover site in South Sweden. Raptors attacked flocks repeatedly, and the finches showed obvious adaptations to the risk. A total of 304 attacks were recorded, of which 270 were from European Sparrowhawks (*Accipiter nisus*). Attack frequency was significantly higher in autumn (1.9 attacks/h) than in spring (0.3 attacks/h). In autumn, finch flock size varied from 10 to 10,000. Both attack frequency and hunting success increased with flock size. The risk for an individual finch to be killed (successful attacks per hour and individual) showed no correlation with flock size. Thus predation seemed not to be the primary cause for formation of large finch flocks. Instead, patchy distribution of the preferred food presumably causes large numbers of finches to aggregate. Once aggregated at a field, the best antipredator strategy for the finches is probably to crowd into a dense flock with synchronized feeding. I estimated that ca. 10% of the finches were killed by raptors during the autumn migration. Received 28 January 1988, accepted 5 November 1988.

FLOCKING may represent a response to predation (reviews by Bertram 1978, Pulliam and Millikan 1982, Perrins and Birkhead 1983, Myers 1984, Pulliam and Caraco 1984, Barnard and Thompson 1985). There are at least three reasons why increased flock size may reduce predation: first, increased vigilance leads to an earlier detection of predators (Pulliam 1973, Powell 1974, Kenward 1978); second, the predator's hunting success is reduced because of confusion (Landeau and Terborgh 1986); and, third, the "dilution" effect by which the average probability for an individual to be killed in a successful attack is related inversely to flock size (Foster and Treherne 1981). These are all numerical advantages. A fourth factor in flocking may be the "selfish herd" effect (Hamilton 1971): each animal lowers its risk by moving closer to other individuals, thereby reducing its "domain of danger."

Flocking also has disadvantages, such as increasing the risk to be detected by the predator (Vine 1973, Treisman 1975, Taylor 1979). In addition, the prey themselves can be confused and hindered by each other when trying to escape from the predator, leading to increased hunting success with increasing flock size (Crisler 1956, Schaller 1972). Besides predation, increased foraging efficiency and patchy distribution of food may encourage flocking (Pulliam and Caraco 1984, Barnard and Thompson 1985).

Predation risk for prey individuals in flocks

of different sizes can be calculated from flock size, attack frequency, and hunting success. If the risk is spread evenly among flock members, the risk for an individual to be killed in a successful attack is  $1/n$ , where  $n$  is flock size.

Each autumn large numbers of Chaffinches (*Fringilla coelebs*) and Bramblings (*F. montifringilla*) pass through southern Sweden on their way to wintering grounds in western and central Europe (Roos 1984a). Their main passage at Falsterbo, the southwesternmost point of Sweden, occurs from late September to mid-October. Roughly the same route and timing of migration are characteristic of three potential predators: the European Sparrowhawk (*Accipiter nisus*), the Merlin (*Falco columbarius*), and the Hen Harrier (*Circus cyaneus*) (Alerstam 1978, Roos 1984a).

In southern Sweden Chaffinches and Bramblings are mainly diurnal migrants with a peak of migratory flights in the first hours after sunrise (Alerstam 1978). Radar observations reveal that they normally travel in small units of 5–30 individuals (T. Alerstam pers. comm.), but when resting and feeding, they often congregate into flocks of hundreds and thousands (Lindström and Alerstam 1986). During these stopover periods they are under heavy predation pressure from migrating raptors.

Locally, the Chaffinches and Bramblings prefer to forage in fields with spill of summer rape (*Brassica napus*) which is cultivated on only 1–

4% of arable land in southernmost Sweden (Lindström and Alerstam 1986). This food source has a patchy distribution which is one possible reason for large concentrations of finches. Another explanation is that large flocks are formed in response to high predation pressure.

I analyzed the risk for an individual finch to be killed in relation to flock size and the anti-predator behavior of the finches. I also estimated the total mortality of finches caused by predation during the migration season.

#### METHODS

Mixed flocks of Chaffinches and Bramblings were studied in an area east of Lund in southernmost Sweden over three autumns (26 September to 29 October 1984, 16 September to 24 October 1985, and 15 September to 14 October 1986) and two springs (3–18 April 1985 and 24 March to 28 April 1986). The study area comprises farmland with scattered woods, with groves and shrubs surrounding the fields. The finches fed on spill seeds in the open fields (Lindström and Alerstam 1986). They used the surrounding woods and shrubs for roosting and resting between periods of foraging.

I recorded all raptor attacks against flocks of foraging finches as accurately as possible and noted date, time, attacking species, hunting behavior and success, as well as the size and activity of the attacked flock. In most cases I was alerted before an imminent attack by the behavior of the finch flock. The time until I spotted the predator varied, so I was unable to decide at what distance the finches reacted to the approaching predator. Most observations were made from a car at 10–200 m.

I divided feeding flocks into two categories: flocks in protected foraging were normally within 20 m of cover. When flushed, they flew immediately into bushes and trees surrounding the fields. Flocks in exposed foraging were far out in the open fields. When flushed, they often circled, normally for less than a minute, above the feeding place before they landed and resumed feeding activities. I counted the take-offs/min of some of the foraging flocks.

Flock sizes were estimated to the nearest 10 when under 100; to the nearest 50, up to 400; to the nearest 100, up to 2,000; and to the nearest 1,000, up to 10,000. I pooled the flocks into seven classes: five classes between 10 and 1,000 (in intervals of 200), one category between 1,100 and 2,000, and one group of the largest flocks between 3,000 and 10,000.

*Attack frequency.*—I observed finch flocks of different sizes in 60-min periods and recorded the number of raptor attacks. Flocks were often studied at the same locality on consecutive days. Because flock size often varied markedly between days (indicating a high

turnover rate of individuals), I treated observations from different days as different flocks. I included in the data only attacks recorded during the systematic 60-min observation periods.

*Hunting success.*—I used only attacks where attacking species, size and activity of the attacked flock, and hunting success were known. Thus, any individual attack could be included in the attack frequency data or in the hunting success data, or in both.

*The risk of being killed.*—The risk of predation,  $R_i$ , for an individual finch during 1 h in a flock belonging to class  $i$ , was calculated as:

$$R_i = \frac{F_i \cdot S_i}{N_i},$$

where  $F_i$  is the number of attacks/h,  $S_i$  is the proportion of successful attacks, and  $N_i$  is the mean flock size of class  $i$ .

#### RESULTS

*Flocking behavior of finches.*—Separate fields of summer rape were usually more than 500 m apart and flocks in different fields had no visual contact. There were normally only one feeding finch flock in each field and most flocks consisted of 100–1,000 birds (maximum flock size = 10,000 in both spring and autumn).

A feeding bout normally was initiated by a smaller flock perched in a treetop, often very exposed. Single birds called loudly (Elgar 1986), but these calls were usually not given in flocks of more than 5 birds. As finches joined the small flock, they slowly dropped and reached the bushes at the field's edge. During the first feeding attempts, the birds remained near cover. The flock plunged back into cover not only when attacked, but also very often when no imminent danger could be seen. After 15–30 s, they flew out again. Each time this procedure was repeated, the flock advanced farther into the field. Feeding flocks were attractive to other finches within range and flocks could grow very rapidly. Several times I saw flock size increase from ca. 50 to 500 in only a few minutes. As flocks grew, the finches often changed from protected foraging to exposed foraging. Only a few flocks larger than 600 birds were seen in protected foraging. The feeding sequence was often terminated by a raptor attack. The flock scattered into smaller groups that perched in treetops, usually in another part of the field. The rebuilding of large flocks was then repeated. Some flocks, however, particularly in exposed for-

TABLE 1. Raptor attacks against finch flocks recorded at stopover sites in southwestern Sweden.

Raptor	Attacks recorded ( <i>n</i> )	No. of attacks* used for calculating:		
		Attack frequency	Hunting success	Hunting success (%)
European Sparrowhawk ( <i>Accipiter nisus</i> )	270	181	176	8
Hen Harrier ( <i>Circus cyaneus</i> )	18	9	15	13
Merlin ( <i>Falco columbarius</i> )	13	4	9	11
Common Buzzard ( <i>Buteo buteo</i> )	2	1	2	0
Goshawk ( <i>Accipiter gentilis</i> )	1	—	1	0
Total	304	195	203	8

\* Events under "Attack frequency" were recorded during 60-min observation periods. Events under "Hunting success" were those where flock size, flock activity, and result of attack were known. A specific attack can be included in one or both of these data sets.

aging, remained intact after an attack and resumed feeding as soon as the raptor left the scene.

The flocks showed no preference for certain parts of the fields. Moreover, I distributed large amounts of summer rape (2–3 kg in 10 m<sup>2</sup>) in small areas of the fields, but these spots were not visited more often than other parts.

During feeding, flocks regularly took off for no obvious reasons. The average rate of takeoffs during feeding in autumn (0.8/min) and in spring (0.7/min) was not correlated with flock size (autumn:  $r = 0.34$ ,  $df = 12$ ,  $P > 0.05$ ; spring:  $r = -0.35$ ,  $df = 13$ ,  $P > 0.05$ ). In autumn, flocks were dense and their movements highly synchronized. In spring, flocks were looser and the movements less coordinated.

Regularly, individual birds did not flush when the rest of the flock took off. In one case this was fatal; the bird was seized by an attacking sparrowhawk. Page and Whitacre (1975) mention three occasions where such a "hesitating" bird was struck by a raptor.

Although I often was within 30–50 m of a flock when it was attacked, I only once heard an alarm call before the flock took off. Once in the air, the finches called loudly and intensively. I heard these calls only when a predator was nearby.

*Predators and hunting mode.*—I observed 304 attacks by five different raptor species (Table 1). Sparrowhawks were responsible for 89% of the registered attacks. In almost all attacks the raptor approached at high speed just above ground level. The hawk was often discovered by the finches at a distance of 50–100 m. Almost invariably the hawk failed to capture single birds separated from the main flock in subsequent

pursuit flights. Only if the flock were taken by complete surprise, did the attacks sometimes succeed. Finches were normally struck on the ground (1 case) or just above the ground (8 cases). Sometimes, however, they were struck a few meters into the air (2 cases) after a short pursuit. It was difficult to tell the victim's position in the flock, but out of 17 successful attacks, 12 victims seemed to be from the main body while 1 bird was definitely from the periphery.

*Attack frequency.*—There was a significant positive correlation between flock size and attack frequency in autumn (Fig. 1; Spearman rank-order correlation,  $r_s = 0.27$ ,  $n = 93$ ,  $P < 0.01$ ) with more than a fourfold increase in mean attack frequency between the smallest and largest flocks. There was no significant correlation between flock size and attack frequency in spring (Fig. 2; Spearman rank-order correlation,  $r_s = -0.03$ ,  $n = 48$ ,  $P > 0.1$ ).

Average attack frequency was significantly higher in autumn (1.9 attacks/h, 179 attacks in 93 h) than in spring (0.3 attacks/h, 16 attacks in 48 h;  $\chi^2 = 58.0$ ,  $P < 0.001$ ). The lower predation pressure in spring was not due to different timing of migration of predators and prey (Nilsson and Peterz 1986; pers. obs.). Because attack-frequency data from spring were rather scanty and predation pressure relatively low, I focused on the autumn migration.

There was no significant relationship between the size of the attacked flocks in autumn and the time of day (Kolmogorov-Smirnov test,  $D = 0.095$ ,  $P > 0.1$ ). The attack frequency varied significantly with time of day (Kolmogorov-Smirnov test,  $D = 0.153$ ,  $P < 0.05$ ) and was relatively lower in the morning. Average attack frequency between 0800 and 1300, when 77%

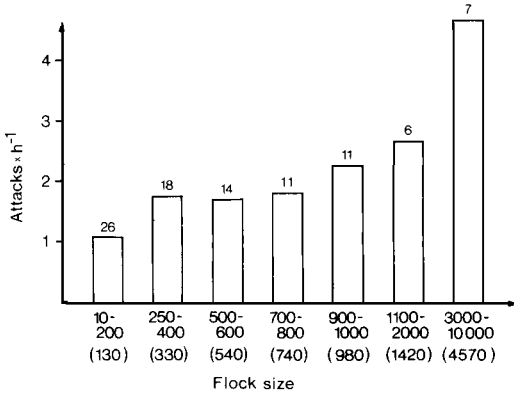


Fig. 1. Attack frequency by raptors on finch flocks of different sizes during autumns of 1984-1986 in South Sweden. Observation hours are at the top of the box; mean flock size of each class is in parentheses.

of the 60-min observation periods were conducted, was 1.8 attacks/h as compared to 2.4 attacks/h in the afternoon. Thus, the figure of average attack frequency in autumn (1.9 attacks/h) is slightly conservative.

**Hunting success.**—All raptors used a similar hunting technique and were equally successful (Table 1). Furthermore, there was no significant seasonal difference in hunting success (1 successful attack out of 20 in spring, 16 out of 188 in autumn;  $\chi^2 = 0.36, P > 0.1$ ). I pooled data for the different raptor species and from both seasons to calculate hunting success in relation to flock size (Fig. 3). There were significant differences in hunting success against different flock sizes (Kolmogorov-Smirnov test,  $D = 0.327, P < 0.05$ ), and hunting success increased with flock size (Fig. 3).

Between 26% and 41% of flocks in the smaller size classes (10-600) were attacked when in protected foraging (Fig. 3). Within this range of flock sizes, there was no significant difference in hunting success against flocks in protected foraging and exposed foraging, respectively ( $\chi^2 = 0.29, P > 0.1$ ).

**The risk of being killed.**—From attack frequency and hunting success for the different classes of flock sizes (and mean flock sizes were similar in the two data sets), I calculated the individual's risk of being killed. The number of successful attacks per hour and per individual,  $R_i$ , showed no significant relationship with flock size (Spearman rank-order correlation,  $r_s =$

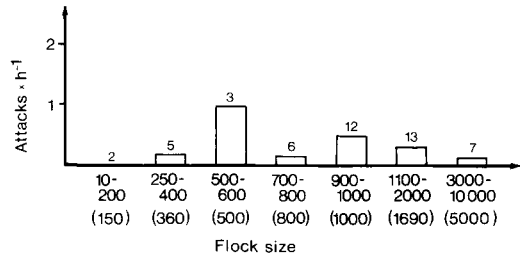


Fig. 2. Attack frequency by raptors on finch flocks of different sizes during the springs of 1984-1986 in South Sweden. Observation hours are at the top of the box; mean flock size of each class is in parentheses.

$-0.29, n = 7$  flock-size classes,  $P > 0.1$ ; Fig. 4). The risk was highest in an intermediate flock size.

**Predator-related mortality during migration.**—To calculate the proportion of finches taken during migration, I assumed that the relationship between predators and prey along the migration route was the same as in this study area. I estimated the autumn migration period of Chaffinches and Bramblings to be ca. 45 days (on the basis of banding data from *Memoranda Societatis pro Fauna et Flora Fennica 1929-1969*). Furthermore, I assumed that, on average, the finches feed and rest 10 of the 12 daylight hours, leaving 2 h/day for migration. I used the distribution of flock sizes recorded during the median observation hour each day to estimate the typical distribution of flock sizes in which finches congregate during the migratory stopover periods (Table 2).

From the risk of predation,  $R_i$ , for the seven classes of flock sizes ( $i$ ), I calculated the proportion ( $P$ ) of birds expected to be killed by predators during the entire fall migration (Table 2). The number of birds killed in each class,  $K_i$ , during an exposure time of 450 h (45 days  $\times$  10 h) at different stopover sites is

$$K_i = I_i [1 - (1 - R_i)^{450}],$$

where  $I_i$  is the number of finches present in flock sizes of class  $i$  and  $R_i$  is the predation risk encountered by a bird in class size  $i$ .  $P$  is then

$$P = \frac{\sum_{i=1}^7 K_i}{\sum_{i=1}^7 I_i}.$$

Following the assumptions outlined above,

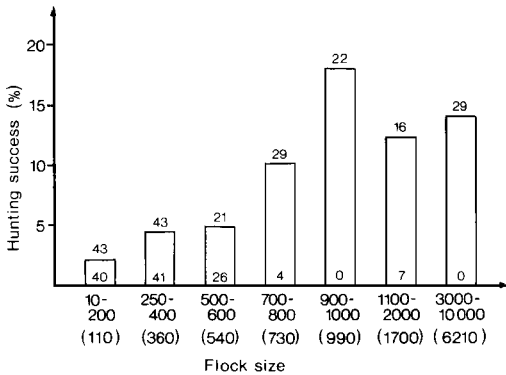


Fig. 3. Hunting success of raptors attacking finch flocks of different sizes during 1984-1986 in South Sweden. Numbers of attacks are at the top of the box; mean flock size of each class is in parentheses; numbers within box are the percentage of flocks in protected feeding (see text).

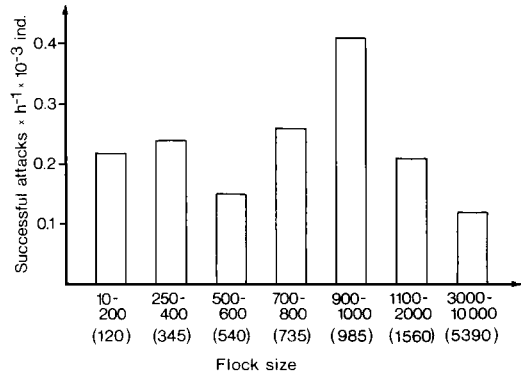


Fig. 4. The risk for a finch to be killed in different classes of flock size. Mean flock size of each class (in parentheses) was calculated as the mean of the values for attack frequency and hunting success.

about 10% ( $P = 0.094$ ) of the finches are expected to be killed during a 1.5-month period of autumn migration. It is a rough estimate and may be high because the ratio predators:prey may be unusually high in the study area, caused by a concentration of raptors because of the topography of Scandinavia. This possible bias is counterbalanced by a somewhat conservative estimate of attack frequency.

DISCUSSION

Only a few studies of predator-prey interactions have estimated attack frequency, hunting success, and risk in relation to flock size (Table 3). The results of my study differed from all of these.

*Attack frequency.*—In autumn, raptor attack

frequency increased with flock size (Fig. 1). Large flocks are easier for a predator to detect (cf. Vine 1973, Treisman 1975, Taylor 1979), which may lead to an increased attack frequency. In addition, finches in the largest flocks ( $\geq 700$ ) almost always foraged under exposed conditions.

Higher hunting success against large vs. small finch flocks (Fig. 3) ought to make large flocks the most attractive targets for the predators. The hawks can move freely between potential targets and hunting areas, and choose the most profitable flocks to attack. Page and Whitacre (1975) estimated that a Merlin directed relatively more attacks towards single birds (with a higher hunting success) than towards flocks.

An increased attack frequency with larger finch flocks could occur if seasonal and daily fluctuations in numbers largely coincided for migrating hawks and finches. However, ac-

TABLE 2. Estimated mortality of finches due to raptor predation during the entire autumn migration.  $I_i$  is the number of finches in flocks of class  $i$  during the median observation hour each day.  $R_i$  is the number of successful attacks per hour per individual.  $K_i$  is the calculated number, and  $P_i$  the proportion, of finches killed during autumn migration (see text).

$i$ (flock sizes)	$I_i$ (number of days)	$R_i$	$K_i$	$P_i$
1 (10-200)	1,650 (11)	$0.22 \times 10^{-3}$	156	0.095
2 (250-400)	2,850 (9)	$0.24 \times 10^{-3}$	292	0.102
3 (500-600)	3,200 (6)	$0.15 \times 10^{-3}$	209	0.065
4 (700-800)	4,500 (6)	$0.26 \times 10^{-3}$	497	0.110
5 (900-1,000)	4,800 (5)	$0.42 \times 10^{-3}$	827	0.172
6 (1,100-2,000)	2,900 (2)	$0.21 \times 10^{-3}$	262	0.090
7 (3,000-10,000)	9,000 (3)	$0.12 \times 10^{-3}$	473	0.053
Total	28,900 (42)		2,716	0.094

TABLE 3. Predator-prey interactions where attack frequency (AF), hunting success (HS), and individual risk to be killed were positively (+), negatively (-), or not (0) correlated with flock size. All studies refer to solitary hunting predators.

Study	Predator	Prey	Flock sizes	Correlation with flock size		
				AF	HS	Risk
Neill and Cullen 1974	Fish	Fish	1-20		-	
Page and Whitacre 1975	Bird	Bird	1-50+	-	- + <sup>a</sup>	-
Munro and Bédard 1977	Bird	Bird	1-20			-
Kenward 1978	Bird	Bird	1-50+		-	
Ryan et al. 1981	Bat, frog, opossum	Frog	44-425	0		-
Kus 1982, 1986	Bird	Bird	1-3,000	- + <sup>b</sup>	-	-
Treherne and Foster 1982	Fish	Insect	1-150	0	-	-
Morgan and Godin 1985	Fish	Fish	1-20	-	0	-
Landeau and Terborgh 1986	Fish	Fish	1-15		-	
Trail 1987	Bird	Bird	1-61	-		
Buchanan et al. 1988	Bird	Bird	50-10,000+		0	
This study	Bird	Bird	10-10,000	+	+	0

<sup>a</sup> Hunting success was lowest against intermediate flock sizes.

<sup>b</sup> Single birds and the largest flocks were attacked to an unproportionally high degree.

ording to countings of diurnal migrants in 1973-1985 at Falsterbo (40 km southwest of the study area) the ratio of migrating finches : hawks varied more than twentyfold between different 10-day periods from 10 September to the end of October (calculated from Roos 1974; 1977a, b; 1978a, b; 1979-1983; 1984b; 1985). Moreover, Sparrowhawks had the lowest daily variation in numbers among the migrants at Falsterbo (Alerstam 1978).

Increased hunting success against larger flocks and easier detection through size and behavior of these flocks may be sufficient to explain the increased attack frequency with increasing flock size.

*Hunting success.*—There was a positive correlation between size of the attacked finch flock and raptor hunting success (Fig. 3). The advantages of early detection or confusion of the predator were obviously not important enough to suppress the success of hunting directed towards large finch flocks.

Flock members in large flocks may confuse and hinder each other during escape (Crisler 1956, Schaller 1972). When the raptor has come within striking distance of the flock without detection (the typical situation for successful attacks against finches), it is of utmost importance for all individuals to localize the predator immediately. For a finch in the middle of a flock of 1,000 or 10,000 birds, it must be difficult to see the predator. Maneuverability might also be limited. When a single bird is separated from the flock (i.e. has the possibility to move freely),

the predator seldom succeeds (Rudebeck 1950, 1951; Page and Whitacre 1975).

Alternatively, the predator may be very good at finding and killing substandard individuals (Rudebeck 1950, 1951). If substandard individuals are distributed randomly among flocks, the absolute number of such individuals in a flock increases with flock size, as does the chance of a successful attack. However, almost all pursuit hunts after the raptor had separated a single finch from the main flock (potentially a substandard individual) were unsuccessful. Kenward (1978) reported that among Wood Pigeons (*Columba palumbus*), single birds were in poorer condition than birds in flocks.

*Flock size and predation risk.*—The risk for a finch to be killed,  $R_i$ , neither decreased nor increased consistently with increasing flock size (Fig. 4). Thus, the simple numerical advantage of being in a larger flock is balanced by the combined effect of the increased attack frequency (Fig. 1) and hunting success (Fig. 3) against larger flocks. This is in contrast to all other studies where it has been possible to estimate the individual risk of predation (Table 3).

*The formation of large finch flocks.*—I believe that the finches do not gain numerical advantage against predation when in large flocks. Thus, predation cannot be the prime factor to explain the formation of large finch flocks. When many birds are attracted to a certain field because of the food, a functional advantage concerning predation may be gained if the birds form a single

dense flock rather than feeding in smaller parties scattered over the field. Hamilton (1971) argued that, when peripheral flock members stand a higher risk of being victims than central individuals, dense flocks may form as a result of prey individuals trying to "hide" themselves among others and thereby reducing their "domain of danger." I found no evidence that birds on the periphery were the most vulnerable to attacks. More likely, advantages shared by all flock members were operating to keep the finch flocks together. Hunting success or attack frequency, or both, may be lower against dense flocks compared with the same number of scattered individuals. Dense flocks allow synchronized feeding activities and birds can minimize the total time exposed to predation in open fields. The comparatively loose spring flocks, when predation pressure was much lower than in autumn, is a further indication of a functional advantage of forming dense flocks.

Animals may flock, or increase flock density, in response to predators both on a short-term and long-term basis. Territorial Buff-breasted Sandpipers (*Tryngites subruficollis*) temporarily abandoned their territories and formed flocks when a raptor flew over (Myers 1980). Wintering Sanderlings (*Calidris alba*) were territorial in winters with no resident Merlins but normally formed flocks in winters when resident Merlins were present (Myers 1984). Turnstones (*Arenaria interpres*) formed denser flocks after sparrowhawks attacked (Whitfield 1988). Seghers (1974) found that densities of fish schools in small rivers in Trinidad were positively correlated to predator abundance.

*Predator-related mortality during migration.*—As much as 10% of the finches may be killed by raptors during autumn migration. In both Swedish and British chaffinches, adults have an average annual mortality rate of 33% (Anvén and Enemar 1957, Dobson 1987). Even if annual mortality in first-year birds is higher than this, the mortality due to predation alone during 45 days of migration clearly exceeds what should be expected from an evenly distributed annual mortality. The figure is also high in comparison with other studies on predator-related mortality. In Scotland, 15–20% of some shorebird populations were killed each winter by predators, mainly Sparrowhawks (Whitfield 1985). In California, 21% of the wintering Dunlin population were killed by raptors over 5 months (Page and Whitacre 1975). Sparrowhawks during their

nesting season killed up to 30% of juvenile tits in the surrounding forest (Perrins and Geer 1980). Tinbergen (1946) estimated that ca. 25% of the summer mortality of Chaffinches was due to Sparrowhawks and about 50% was due to all other predators. I believe that predation during migration may be of great importance for the population dynamics and the migration strategies of Chaffinches and Bramblings.

#### ACKNOWLEDGMENTS

Göte Lindvall kindly allowed me to work in his fields throughout the study. Thomas Alerstam provided advice during both fieldwork and writing. I thank John B. Dunning Jr., Henrik G. Smith, Brian A. Millsap, and Jan-Åke Nilsson for comments on an earlier version, and Gösta Lindström for improving the English. Financial support was given by the Swedish Natural Science Research Council (to T. Alerstam), the Swedish Royal Academy of Sciences, and the Gustaf Danielsson Foundation.

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