Behaviour of Greenfinches *Carduelis chloris* at a communal roost

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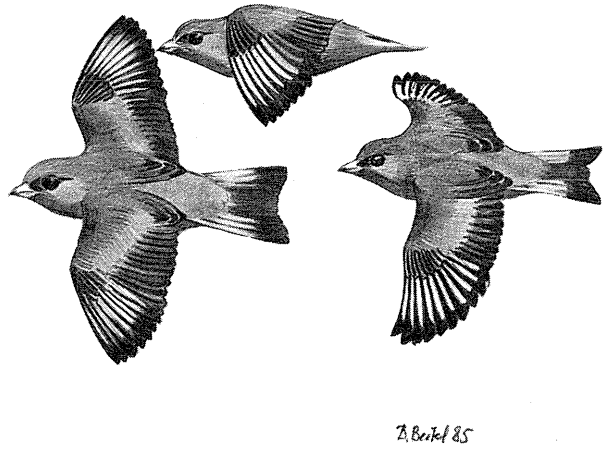

(Med et dansk resumé: Adfærd af Grønirisker på en overnatningsplads)

Introduction

Avian communal roosting has received considerable interest recently. Birds are thought to roost communally primarily for one of the following reasons, (1) to improve thermoregulation (Tast & Rassi 1973), (2) to reduce predation risks (Lack 1968), or (3) to exchange knowledge of food locations (Ward 1965, Ward & Zahavi 1973). Alternatively, (4) all birds may not be in the roost for the same reason: The dominant individuals might be there for reason (2), others for reason (3) (Weatherhead 1983).

Tests of these hypotheses are few. Hypothesis (1) has not been confirmed (Gyllin et al. 1977, Yom-Tov et al. 1977). Hypothesis (3) has gained some experimental support (Loman & Tamm 1980, de Groot 1980), but the results are not conclusive.

In this paper I evaluate the possibility of exchange of food information among Greenfinches *Carduelis chloris* at a winter roost.

Roost site

The roost was located in dense evergreen ivy *Hedera helix* on walls of multi-storeyed buildings in Århus (56°9'N,10°12'E). The bushes used for roosting were 35-60 cm thick, with long branches reaching 75 cm from the wall.

Methods

The roost was probably established during spring 1982 and came into use in the autumn from about 20 November onwards. Between 24 November 1982 and 13 March 1983 I watched the finches leave the roost on 56 mornings and enter it on 54 evenings. The observations were made from a balcony 6 m above the ground and about 20 m from the roost site. The finches did not take any notice of me at this distance.

In the morning, I started observations about 30 min or more before sunrise. I recorded the size and heading (N, NW, W, ..., NE) of flocks leaving the roost or the nearby post-roost gathering. The flocks could be followed about 200 m towards directions between S and NE, about 25 m towards N and about 15 m towards NW-SW. The intervals between flocks were sufficient (> 5 s) to permit af clear distinction between successive flocks. I finished the observations 5 min after the last flock had left (judged by the absence of finch calls and rattling of leaves).

During the evenings, I was unable to record data in a standardized manner because the finches behaved much more variably. I concentrated on recording the arrival of the first birds to the pre-roost gathering, the first birds entering the roost, and the last birds doing so. Ap-

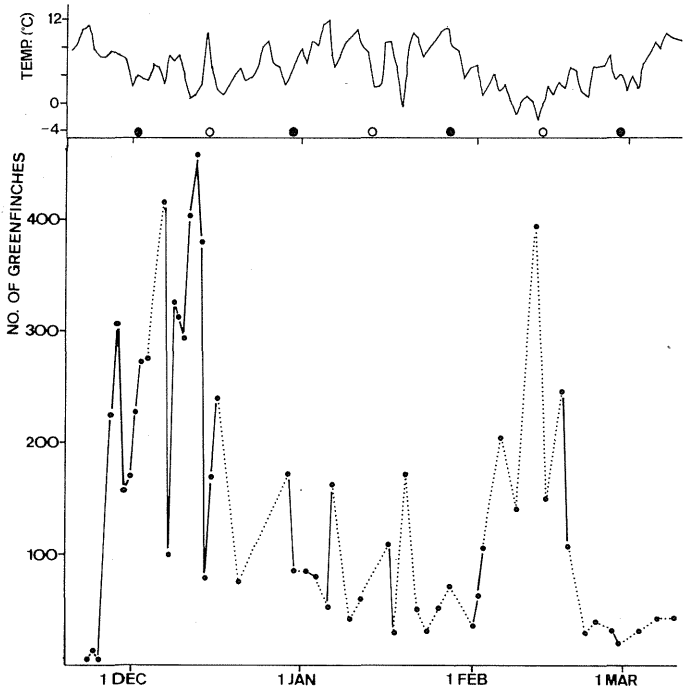

Fig. 1. Numbers of roosting Greenfinches in relation to lunar phases and maximum temperature. Stippled lines join counts more than one day apart.
Antallet af overnattende Grønirisker i forhold til månens faser og maksimum-temperaturen. De stiplede linier viser, at der er mere end én dag mellem tællingerne.

parent disagreement in some sample sizes is due to the fact that I occasionally missed certain events.

The results are reported as mean ± one standard error.

The Danish Meteorological Institute provided the weather data which were collected at Viby, about 6 km SSW of the roost.

Results

Changes in roost size

The number of Greenfinches roosting varied between 4 and 462 birds and roost size was rarely constant for more than two or three days (Fig. 1). Number of roosting finches was significantly and negatively correlated with maximum temperature (partial r=-0.38, $P<0.01$) and wind force (partial r=-0.36, $P<0.01$, n=51 mornings) but not with minimum temperature, visibility or snow cover (multiple regression analysis of roost size against the weather variables for the day the birds joined the roost). The roost size did not depend in any obvious way on the moon phase (Fig. 1); a dependence might be expected if the birds joined the roost to reduce nocturnal predation risks (Fleming 1981).

Departure pattern

The Greenfinches began to leave the roost on average 20 ± 1.4 min before sunrise (n=55). The interval between the departure of the first flock and sunrise correlated significantly and negatively with the interval between the date and winter solstice (21 Dec.; r=-0.52, $P<0.001$). Thus, the first flock left early relative to sunrise when the days were short.

On 17 of 53 mornings between 1 and 77% of the birds leaving the roost joined post-roost gatherings in trees about 20 m from the roost. Eleven percent of all birds (n=6349) joined the post-roost gatherings. Usually the birds leaving the roost early did not join the gatherings. The interval between the departure of the first flock and the post-roost gathering averaged 9 ± 1.9 min (n=17), and 23 ± 7.1% of the birds in the roost had left by then. A significant tendency for a larger fraction of the birds to join the gatherings was observed in larger roosts (Fig. 2). Sixty-three percent of the birds (n=729) left the post-roost gatherings in flocks consisting entirely of birds from the gatherings. The rest joined birds leaving the roost directly. The size of the flocks leaving the post-roost gatherings without joining birds departing directly from the roost was 3.76 ± 0.34 birds (n=127) which

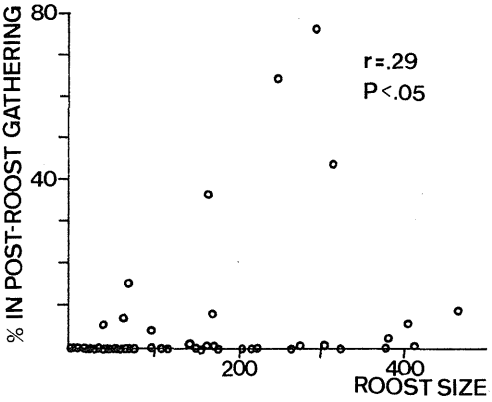

Fig. 2. Fraction of Greenfinches joining post-roost gatherings in relation to roost size.
Andelen af Grønirisker (y-akse), som deltager i fællessamling efter overnatningen, i forhold til antallet af overnattende Grønirisker (x-akse).

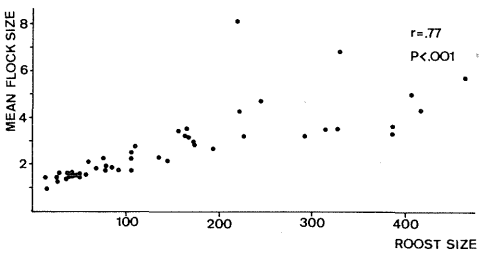

Fig. 3. Mean departure flock size of Greenfinches in relation to roost size.
Gennemsnitlig flokstørrelse ved udflyvningen (y-akse) i forhold til antallet af overnattende Grønirisker (x-akse).

was significantly smaller (t=4.6, P<0.001) than the size of the mixed flocks consisting of birds from the gatherings and the roost (6.47 ± 0.49 birds, n=72).

The duration of the departure of all flocks varied between 15 and 54 min (35 ± 1.2 min, n=53). It was significantly correlated with roost size (r=0.40, P<0.01). Departure flock size (from the roost or the post-roost gathering) ranged from 1 to 51 birds with an average of 2.69 ± 0.10 birds (n=2364). Forty-eight percent of the flocks leaving was single birds, 19% consisted of two birds, 9% of three birds, 6% of four birds, 4% of five birds, 3% of six birds, and 11% of more than six birds. Daily average flock size varied between 1.0 and 8.1 birds, and both the daily average flock size (Fig. 3) and the number of departing flocks (r=0.85, P<0.001, n=49) increased with roost size. The average bird left the roost or the post-roost gatherings together with 5.45 companions.

Flocks tended to leave the roost temporally more clumped in larger roosts as indicated by a significant correlation between the variance: mean ratio of the number of flocks leaving per three-minute interval and the total number of flocks leaving each morning (r=0.69, P<0.001, n=49). The choice of a three-minute interval was arbitrary, but running the analysis with two other intervals gave the same result. The variance:mean ratio was larger than one in each of the analyses indicating that departures were temporally clumped.

Two of the eight departure directions predominated: 40 ± 2.3% of the flocks leaving the roost each day headed W and 26 ± 1.4% flew N. The third most common departure direction was NE (10 ± 0.1%). The distribution of departure directions changed abruptly from day to day (Fig. 4). To analyse the diversity of the departure directions, I followed Fleming (1981) in using the magnitude $e^{H'}$ as an index of the diversity of departure directions; $H' = -\Sigma p_i \ln p_i$ is the Shannon index, with p_i representing the proportion of flocks departing in the *i*th direction. Values of $e^{H'}$ were not correlated with the number of flocks leaving the roost each morning (r=0.10, P>0.4, n=49).

If some Greenfinches roost communally to follow others to their feeding areas, we might expect flocks to depart in the same direction as the previous flock (Fleming 1981). To examine this, I compared the distribution of the differences in the departure directions of successive flocks with a distribution computed from the observed distribution of departure directions assuming a statistically independent choice of

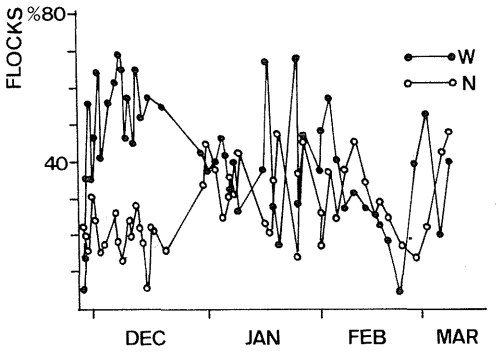

Fig. 4. Fraction of Greenfinch flocks leaving towards the two major departure directions.
Andelen af Grønirisk-flokke (y-akse), som flyver i hver af de to hyppigste udflyvningsretninger vest (W) og nord (N).

Tab. 1. Flight direction of leaving flocks compared to that of the previous flock, all cases and cases where the previous flock was large (≥ 10 birds). The expected frequencies are calculated from the observed distribution of departure directions, assuming independence between flocks.
Udflyvningsretninger for flokke sammenlignet med retningen for den foregående flok, alle observationer henholdsvis de tilfælde, hvor den foregående flok var stor (≥ 10 fugle). De forventede tal er beregnet ved hjælp af den observerede fordeling af udflyvningsretninger under antagelse af uafhængighed mellem flokkene.

	Departure direction in relation to direction of previous flock *Udflyvningsretning i forhold til retning af foregående flok*		
	Same *Samme*	Different *Anderledes*	χ^2
All flocks *Alle flokke*			
Observed *Observeret*	662 (30.9%)	1477 (69.1%)	0.32, NS
Expected *Forventet*	716 (30.4%)	1640 (69.6%)	
Large flocks *Store flokke*			
Observed *Observeret*	63 (47.0%)	71 (53.0%)	16.1, P<0.001
Expected *Forventet*	42 (31.3%)	92 (68.7%)	

departure direction by successive flocks. The distribution of departure directions changed from day to day (Fig. 4), so I ran the analysis for each day and pooled the results. Tab. 1 shows that successive flocks did not depart in the same direction more often than expected by chance. However, large flocks might have a higher probability of holding birds with knowledge about food, so I made a separate analysis of flocks leaving after large flocks. Tab. 1 shows that flocks departing after large flocks headed in the same direction more often than expected by chance.

If larger flocks are more likely to include birds with knowledge about food, we might also expect other flocks to depart shortly after large flocks. It is possible to test the negation: Periods when no flocks left the roost are expected more often after smaller flocks. The result is as predicted (Fig. 5).

Arrival pattern

The first flock of Greenfinches was spotted flying over the roost on average 54±4.8 min (n=29) before sunset. The interval between the arrival of the first flock and sunset correlated significantly with the interval between the date and winter solstice (r=0.87, P<0.001), indicating later arrival relative to sunset on shorter days. If not disturbed by Sparrowhawks *Accipiter nisus* the finches flew around in a few loose flocks (1-3 m between the birds). On the appearance of a hawk, the finches rose from the normal flight height of 10-15 m to 25-35 m and assembled in one dense flock (a few dm between the birds).

The first birds landed in tree-tops near (10-40 m) the roost 20±3.9 min (n=11) after the first flying finches had been observed. Attempts by Sparrowhawks to approach the finches caused them to take off, circle for a few minutes and land again several times each afternoon. As time passed, the finches preferred to sit in trees progressively nearer the roost and circling flocks passed lower and more frequently over the roost. The first birds entered the roost 7±1.7 min (n=44) before sunset and the last birds had settled down 12±1.0 min after sunset (n=50).

The pre-roost activities took 64±4.5 min (n=24) whether Sparrowhawks visited the roost (64±6.6 min, n=12) or not (63±6.6, n=12).

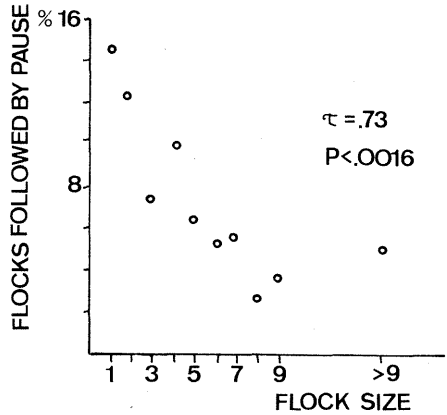

Fig. 5. Fraction of Greenfinch flocks of different sizes followed by pauses (> 1 min without any flocks departing). Kendall rank correlation coefficient τ indicated.
Andelen (y-akse) af Grønirisk-flokke af forskellig størrelse (x-akse), som efterfølges af pause (mindst 1 min., hvor ingen flyver af sted). Kendall rang korrelationskoefficienten er vist.

The duration of the pre-roost activities increased during the study ($r=0.67$, $P<0.001$, $n=24$).

Predators

Up to 3 Sparrowhawks were observed during the arrivals and the departures of the Greenfinches, with a total of 91 observations during the study. Hawks were observed more often during the arrivals (1.3 ± 0.3 obs./afternoon, $n=54$) than during departures (0.3 ± 0.2 obs./morning, $n=54$) ($t=2.87$, $P<0.01$, $n=108$). The male:female ratio was 76:6 among the hawks. Most (91%) observations were of Sparrowhawks flying as though they were hunting (low, high speed flight with many turns, making use of available shelter to approach the roost) while the rest were flying high over the roost and apparently not hunting at the moment. Six strikes after a Greenfinch were observed. Four attempts were unsuccessful, one probably so, and the outcome of one attempt could not be determined.

Discussion

The winter 1982-1983 was mild in Denmark, only rarely with maximum temperatures below zero (Fig. 1). Yet, up to 462 Greenfinches joined the study roost each night (Fig. 1), the largest numbers of birds turning up on cold, windy evenings. The principal benefit of this behaviour is unknown.

The thermoregulation hypothesis (Tast & Rassi 1973) suggest that the birds roost communally to save metabolic heat. However, Gyllin et al. (1977) and Yom-Tov et al. (1977) have independently shown, in Jackdaws *Corvus monedula* and Starlings *Sturnus vulgaris* respectively, that the energetic cost of flying to and from the roost exceeds the energetic advantage of being in it. Furthermore, birds are expected to seek warm, sheltered roost sites irrespectively of the ultimate cause of communal roosting unless such sites for some other reason. (e.g. large predation risks) is less beneficial. Proponents of this hypothesis must show either that the roost site is favourable due to the presence of the birds and not the physical characteristics of the site (Fleming 1981), or that favourable roost sites are rare.

Alternatively, birds might roost communally to reduce predation risks (Lack 1968) or to exchange information about the locations of food (Ward & Zahavi 1973). In this paper I have interpreted the observations in terms of the latter hypothesis. If Greenfinch roosts are information centres each of the following results are as predicted: More flocks than expected by chance departed in the same direction as the previous large flock (Tab. 1). The departures of small flocks were more often than the departures of large flocks followed by a period when no flocks left the roost (Fig. 5). The fraction of the birds which joined the pre-roost gatherings was significantly correlated with the size of the roost (Fig. 2). The departures were temporally clumped and the degree of clumping increased with the size of the roost.

Ward & Zahavi (1973) envisaged two different procedures used by birds leaving the roost. Either the unsuccessful individuals follow the successful ones from the roost (to food), or the unsuccessful birds will be the first to leave, departing early, but alighting or circling in flight after having gone a short distance. Then, as the successful birds depart from the roost, the unsuccessful birds follow or join them. However, the first Greenfinches arrived late to the post-roost gatherings, on average 9 min after the departure of the first flock. The reason may be that both unsuccessful and successful Greenfinches join the post-roost gatherings, the successful ones gaining from reduced predation risks in large flocks during departure or later on. Unsuccessful birds might gain from being led to food otherwise unknown to them. According to this proposal, the birds from the post-roost gatherings which follow birds departing directly from the roost are unsuccessful individuals; in flocks of both successful and unsuccessful birds departing from the post-roost gatherings the former ones depart first and the latter ones join them. This interpretation would be consistent with the two-strategies-hypothesis of Weatherhead (1983).

However, the results may also be interpreted in terms of predator avoidance (Lack 1968). For instance, following a large flock could reduce predation risks for an individual (the dilution effect), and clumped departures in large roosts could reflect intense predation during severe periods. These problems of interpretation may be widespread (Bayer 1982). A critical assessment of the predation risks hypothesis would include the predation rates on solitary and communally roosting individuals (Fleming 1981). Unfortunately, such data are

difficult to obtain because most Greenfinches roost communally in winter (Newton 1972).

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Resumé

Adfærd af Grønirisker på en overnatningsplads

I løbet af undersøgelsesperioden 24/11 1982 - 13/3 1983 svingede antallet af Grønirisker på en overnatningsplads i en tyk stedsegrøn vedbend på en husmur fra 4 til 462 individer (Fig. 1).

Grøniriskerne begyndte at flyve ud fra sovepladsen 20 min. før solopgang. Nogle af Grøniriskerne samledes i træerne lige uden for nattesædet ca 1/3 af dagene, mens fuglene de andre dage fløj direkte bort. En større procentdel af Grøniriskerne deltog i disse samlinger efter overnatning, når der var mange på sovepladsen (Fig. 2). Ca 2/3 af fuglene i disse samlinger efter overnatning slog sig sammen med andre samme sted og fløj bort i flokke på gennemsnitligt 3,8 fugle, mens resten fulgtes bort med fugle, som fløj direkte fra sovepladsen, i større flokke på gennemsnitligt 6,5 fugle. Gennemsnitsstørrelsen af flokkene og antallet af flokke, som forlod sovepladsen, var større, når der var mange på sovepladsen (Fig. 3). Flokkene forlod fortrinsvis sovepladsen i to retninger, men dette varierede meget fra dag til dag (Fig. 4). Flokke, som fløj fra sovepladsen lige efter store flokke, havde en klar tendens til at flyve i samme retning som disse, mens dette ikke var tilfældet, når alle flokke betragtes under ét (Tab. 1). Andre flokke havde også en tendens til at flyve ud lige efter større flokke, idet perioder, hvor ingen flokke fløj af sted, var sjældne efter store flokke (Fig. 5).

Udflyvningsperioden for samtlige Grønirisker varede 15-54 min. og var længere, når der var mange fugle.

Om eftermiddagen sås de første Grønirisker flyve rundt over sovepladsen gennemsnitligt 54 min. før solnedgang. Senere, efter en periode med megen flyven omkring, satte de første irisker sig i vedbenden, og de sidste havde fundet nattesæde 12 min. efter solnedgang.

I forbindelse med Grøniriskernes til- og fraflyvning fra sovepladsen sås Spurvehøge ialt 91 gange. Høgene blev observeret i gennemsnit 0,3 gang pr morgen og 1,3 gang pr eftermiddag. Trods høgenes livlige aktivitet ved sovepladsen under til- og fraflyvningen så jeg aldrig en høg fange en Grønirisk.

Hvilke fordele har de enkelte Grønirisker af at søge sammen på overnatningspladsen? Flere mulige fordele kan tænkes. Den nyeste hypotese går i korthed ud på, at fuglene på sovepladsen ikke alle er der af samme grund. De dominante individer, der er gode til at finde føde, drager ifølge hypotesen fordel af den mindskede risiko for at blive taget af et rovdyr, den enkelte fugl løber i større flokke; de ikke-dominante kommer derimod til sovepladsen for at kunne følge efter de dominante til deres gode fourageringssteder. Ingen af mine resultater strider mod denne idé, men man kan imidlertid også forestille sig, at alle Grøniriskerne overnatter kollektivt for at mindske risikoen for at ende som bytte for et rovdyr, eller at de alle benytter sovepladsen for i ugunstige perioder at få oplysninger om gode fourageringssteder.

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