



## DO PARTIAL AND REGULAR MIGRANTS DIFFER IN THEIR RESPONSES TO WEATHER?

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**ABSTRACT.**—Partial migration is often considered a transitory stage between migration and residency, and whether partial migrants take weather conditions into account during migration is largely unknown. To assess whether partial migrants differ from regular migrants in their responses to weather, we compared the migratory intensity of a partial migrant, the Blue Tit (*Cyanistes caeruleus*), with more regular migrants in relation to weather at a migratory passage site in southern Sweden (Falsterbo) during the years 1993–2002. The regular migrants in the study were Linnet (*Carduelis cannabina*), Common Chaffinch (*Fringilla coelebs*), Brambling (*F. montifringilla*), and European Robin (*Erithacus rubecula*). The Blue Tit differed from the regular migrants mainly in showing a striking negative correlation between migratory activity and cloud cover. Also, weather had the highest explanatory power for migratory intensity in the Blue Tit. This suggests that the Blue Tit is more sensitive to weather conditions on migration than the regular migrants and that it preferably awaits days with wholly or partly clear skies before migrating past Falsterbo. As a consequence, Blue Tits usually restrict their migratory flights to the safest occasions, with relatively calm weather, good visibility, and all orientation cues (solar as well as magnetic) available. Received 29 April 2004, accepted 20 August 2005.

**Key words:** Blue Tit, *Cyanistes caeruleus*, evolution of migration, partial migration, timing of migration.

### ¿Difieren los Migrantes Parciales y Regulares en sus Respuestas al Clima?

**RESUMEN.**—Comúnmente se considera que la migración parcial es una etapa transitoria entre la migración y la residencia, y se desconoce en gran medida si los migrantes parciales tienen en cuenta las condiciones climáticas durante la migración. Para evaluar si los migrantes parciales difieren de los migrantes regulares en sus respuestas al clima, comparamos la intensidad migratoria de un migrante parcial, *Cyanistes caeruleus*, con la de migrantes más regulares con relación al clima de un sitio de paso migratorio en el sur de Suecia (Falsterbo) durante los años 1993–2002. Los migrantes regulares de este estudio fueron *Carduelis cannabina*, *Fringilla coelebs*, *F. montifringilla* y *Erithacus rubecula*. *C. cannabina* se diferenció de los migrantes regulares principalmente por mostrar una correlación marcadamente negativa entre la actividad migratoria y la cobertura de nubes. Además, el clima tuvo el máximo poder explicativo para la intensidad migratoria en *C. cannabina*. Esto sugiere que *C. cannabina* es más sensible a las condiciones del clima durante la migración que los migrantes regulares y que preferentemente aguarda los días con cielo total o parcialmente despejado antes de migrar a través de Falsterbo. Como consecuencia, *C. cannabina* usualmente se limita a realizar sus vuelos migratorios bajo las condiciones más seguras, con tiempo relativamente calmo, buena visibilidad y con todas las señales de orientación disponibles (tanto solares como magnéticas).

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FROM AN EVOLUTIONARY perspective, it may be somewhat tricky for a sedentary bird species to become migratory. Success as a migrant requires expression of several genetic components (Dingle 1996). Because migration is energetically costly, migrants must store fuel before migration. They must be able to determine timing, distance, and direction of migration (Helbig 1996, Berthold 2001), as well as to orient themselves and navigate. Furthermore, migrants must be able to respond to atmospheric conditions by timing their departures so as to avoid traveling in unfavorable or dangerous weather (Alerstam 1978; Richardson 1978, 1990; Kerlinger and Moore 1989) and to reduce migration costs by taking advantage of favorable weather. Migrants are often observed flying in tailwinds (Gauthreaux and Able 1970), which reduces the energy costs and duration of their trip and, thus, their exposure to predators and other dangers encountered on the way (Alerstam 1978; Richardson 1978, 1990). Precipitation, another important weather factor, is commonly associated with low migratory intensity (Alerstam 1978, Åkesson et al. 2001, Dänhardt and Lindström 2001). It has been suggested that precipitation increases the costs of migration by chilling migrants and increasing their mass (Alerstam 1978, Richardson 1978). Poor visibility is also known to affect migratory intensity negatively, though some species are observed migrating beneath, above, or even in clouds (Richardson 1990).

Partial migration, in which only a fraction of a population—often subdominant individuals such as juveniles and females—is migratory (e.g. in the Blue Tit [*Cyanistes caeruleus*; Smith and Nilsson 1987]), is often considered a transitional stage between residency and regular migration. Do partial migrants—in which the individual's readiness to depart on migration is conditional—respond to weather in the same way as regular migrants, which are adapted to perform annual migratory journeys throughout their lifetimes?

The Blue Tit is a common species, occurring year-round in forested habitats over large parts of Europe. However, in the northern part of its range (i.e. Scandinavia), the Blue Tit is a partial migrant and frequently appears both in ringing statistics and visual observations at Falsterbo, on the southwestern tip of Sweden (Heldbjerg and Karlsson 1997). In terms of its weather response during autumn migration, Lindskog and Roos (1980) found that the Blue Tit preferred to

migrate in winds from the southwest (i.e. head winds)—which, they argued, was attributable to poor flight ability and, therefore, an adaptation to avoid wind drift over the sea.

Our aim here is to investigate the behavior of Blue Tits in comparison with regular migrants migrating during the same period, with respect to the relationship between weather and migratory intensity. Our main hypothesis is that partial and regular migrants differ in their responses to weather, which can be expected if partial migration represents a transitional evolutionary stage between residency and migration. Such differences might arise because adaptations to migration have not been perfected in partial migrants, which are therefore constrained in their migratory ability. Furthermore, partial migrants have to deal with more complex selection pressures, because they also need adaptations for residency.

If partial and regular migrants differ in relation to weather, partial migrants may be constrained in the ability to travel under variable and difficult conditions, or in the ability to select the most favorable weather for migration. Hence, we will first test our hypothesis about the existence of differences in weather response between partial and regular migrants. If such differences are found, we will evaluate whether they indicate that Blue Tits differ from regular migrants mainly in their ability to choose the most favorable conditions for their migratory flights or in their ability to continue migration under difficult conditions (e.g. under an overcast sky, lacking solar orientation cues; in strong winds that cause problems of wind drift and compensation; or in poor visibility, which reduces the potential use of landmarks; etc.). The first case may be inferred if partial migrants show smaller variation than regular migrants in migratory intensity between days with different weather conditions and if weather accounts for less of the variation in migratory intensity among partial than among regular migrants. The second case may apply if partial migrants tend to travel under specific weather conditions and if weather explains more of the daily variation in daily migratory intensity than in regular migrants.

#### METHODS

The study was done using the visual observation counts and daily ringing records of

migrating birds at Falsterbo, in southwestern Sweden, for 10 years, 1993–2002. Selected study species from the visual observation material, apart from the Blue Tit, were Linnet (*Carduelis cannabina*), Common Chaffinch (*Fringilla coelebs*), and Brambling (*F. montifringilla*); Common Chaffinches and Bramblings regularly travel in mixed flocks and cannot be counted separately). From the ringing material, we selected European Robin (*Erithacus rubecula*) and the combined captures of Common Chaffinch and Brambling as representing regular migrants. In southerly parts of their breeding ranges, the European Robin and Common Chaffinch are partial migrants, though they are generally not considered as such in Sweden. The regular migrants in Falsterbo are mainly obligate migratory populations from Scandinavia and more northeasterly areas. The Brambling, for instance, breeds exclusively in the mountain ranges in northernmost Scandinavia. Therefore, we do not think that the improbable and minimal occurrence of partially migratory populations among our regular migrants will affect the aims of the present study. These regular migrants are all common, short- to medium-distance, small passerine migrants, occurring at Falsterbo during approximately the same period as the Blue Tit and thus exposed to the same variation in daily weather conditions (for median dates, see Table 1). Like the Blue Tit, the Linnet, Common Chaffinch, and Brambling are diurnal migrants, whereas the European Robin is a nocturnal migrant.

Visual observations of migrating birds were conducted daily from 1 August to 20 November each year by one or two observers located at the southwestern tip of the Falsterbo Peninsula. Observations began at dawn and lasted 8 h. Observations from 1993 to 2000 were carried out by Gunnar Roos, and those from 2001 to 2002 by Nils Kjellén.

Migratory birds are mist netted daily from 21 July to 10 November in Falsterbo lighthouse garden by Falsterbo Bird Observatory. Depending on weather and wind conditions,  $\leq 21$  mist nets are used. The nets are opened at dawn and are closed, at the earliest, 6 h later, or until  $<10$  birds are captured during an hour. Between 75% and 80% of migrating Blue Tits are captured within the first 6 h (Heldbjerg and Karlsson 1997). Mist nets are emptied every half hour, and more often in damp weather.

Wind and weather conditions are recorded by the Swedish Meteorological and Hydrological Institute (SMHI) at the weather station in Falsterbo lighthouse garden. For wind direction and speed, barometric pressure, temperature, visibility, cloud cover, and humidity, observations are recorded every 3 h. Cloud cover was recorded on a scale of 0–8 units, where 0 is clear and 8 overcast. For the present study, the weather recordings at 1000 hours were used in all analyses. Precipitation is recorded during 12-h intervals, from 0600 to 1800 hours and from 1800 to 0600 hours. The diurnal record of precipitation was used for the present study. Because of the problem of treating circular and continuous data in the same analysis, wind direction, measured in degrees, was transformed into a category variable reflecting the four quadrants: northeast, southeast, southwest, and northwest winds.

We treated and analyzed visual observations and ringing separately, because they represent different aspects of migratory activity. Birds captured for ringing have interrupted their migration, in contrast to birds recorded by visual observations, which are seen migrating past the study area. For the two species, where comparisons of the two recording methods are possible, the correlation was not consistent (Blue Tit:  $r = 0.72$ ,  $P < 0.001$ ; Common Chaffinch–Brambling:  $r = -0.05$ ,  $P = 0.5$ ), which indicates that the two data sets represent somewhat different aspects of migration.

We are aware that neither the visual observations nor the capture data from our study site fully reflect the true variation in migratory intensity. Visual observations will be biased toward low-altitude flights along coastlines (Alerstam 1978), whereas “captures” are birds that have temporarily interrupted their migratory flights to land in the lighthouse garden. Still, these general biases are the same for the different species, so that interspecific differences in weather relationships revealed by a comparative analysis are expected to reflect fundamental differences in departure activity in relation to weather, in addition to possible differential weather effects on flight and landing behavior.

Daily numbers of birds recorded in the visual observations (observation counts) and captured in the lighthouse garden (captures) were analyzed in relation to weather data using EXCEL

TABLE 1. Average annual number of migrating birds, median date, and duration of migration period for observed and captured birds, respectively, of each species in the study based on annual data (1993–2002). Average migration period was tested with an ANOVA (Tukey HSD). Different superscript letters indicate significant differences ( $P < 0.05$ ) between species.

	Observation counts			Captures		
	Blue Tit	Linnet	Common Chaffinch–Brambling	Blue Tit	European Robin	Common Chaffinch–Brambling
Number of migrating birds						
Average	30,608	14,701	519,461	3,171	2,176	220
Standard deviation	37,600	6,578	391,283	3,098	821	90
Maximum	120,005	27,823	1,490,542	9,957	3,230	367
Minimum	275	6,067	115,248	138	683	111
Median date of migration						
Median	7 October	5 October	7 October	8 October	26 September	3 October
Standard deviation	5	8	9	9	11	16
Maximum	11 October	12 October	16 October	16 October	1 October	10 October
Minimum	29 September	30 September	28 September	2 October	21 September	18 September
Migration period (in days)						
Average	10.9 <sup>a</sup>	24.1 <sup>b</sup>	19.7 <sup>b</sup>	22.5 <sup>a</sup>	36.0 <sup>b</sup>	44.1 <sup>b</sup>
Standard deviation	4.8	5.5	11.3	8.7	7.5	11.6
Maximum	19	30	36	39	49	65
Minimum	7	13	6	10	25	29

2002 (Microsoft, Redmond, Washington) and SPSS, version 11.0 (SPSS, Chicago, Illinois). In the visual observations, one year of Blue Tit migration (1998) had to be excluded because of negligible numbers of passing migrants. Both univariate and multivariate general linear models were used for assessing the absolute and combined importance, respectively, of the weather variables. The dependent variable, daily migratory intensity, was expressed as proportions of the annual total, to correct for the annual variation in total numbers and to facilitate comparisons between species. The annual duration of the migratory period (number of days) was defined as the 80% window of the total migration in each season. Excluding the initial and final 10% of the annual total of each species reduced the effect of extremely early and late migrants in our analyses.

#### RESULTS

The average annual number of recorded birds and timing of migration of the selected species during the period 1993–2002 are presented in Table 1. The species migrated during approximately the same period, with median dates of migration occurring within the week of 3–8 October, with the exception of European Robins, which had a median date of 26 September (Table 1). Blue Tit migration lasted for a significantly shorter period than the other species' migrations, both for visual observations (analysis of variance [ANOVA]:  $F = 7.26$ ,  $df = 2$  and  $26$ ,  $P = 0.003$ ) and for captures (ANOVA:  $F = 13.43$ ,  $df = 2$  and  $27$ ,  $P < 0.001$ ).

Compared with the other species, Blue Tits have a low proportion of days with moderate migration during the migration period. Instead, they have a high proportion of days with little or no migration as well as a higher proportion of days with intense migration than the regular migrants (Fig. 1A, B). Thus, a large proportion of Blue Tits migrate during specific days (Fig. 1C, D). By contrast, the largest cumulative number of individuals of the other species tended to be associated with days of intermediate migratory activity.

The species varied in how weather variables affected migratory intensity (Table 2). According to univariate analyses, Blue Tit migration showed a significant variation with wind speed, but not with wind direction. By contrast, when

combined in multivariate analyses, wind direction and speed had a large effect on all species, except for Common Chaffinch–Brambling in the ringing material, which are captured independently of all weather factors (Table 3). As for the other weather variables, cloud cover seemed to affect Blue Tit migration to a large extent. The migratory intensity of Blue Tits declined sharply with increasing cloud cover according to both visual observations and captures, though the decline was not as steep for captures as for visual observations (Fig. 2). The migratory intensity of European Robins also declined with increasing cloud cover; however, the decline was more gradual. Remaining species seem to migrate independently of this weather factor. In the data set based on visual observations, visibility also explained part of the total variation in migratory intensity in all species. In this interspecific comparison, Blue Tits showed the highest overall dependence on weather, as indicated by the fact that weather explained the largest part of the variation in migratory intensity of all species in both methods of recording migration (Table 3).

#### DISCUSSION

In conclusion, we found Blue Tits to have a shorter migratory period than the regular migrants in our study. Furthermore, migration of Blue Tits was more concentrated to peak days, compared with that of regular migrants. Blue Tits consequently had higher proportions of days with little or no migratory activity, and the days with intense migration were of greater numerical importance for them than for regular migrants, most of which migrated on days of intermediate migratory intensity. We also found a striking negative correlation with cloud cover for Blue Tits alone, apart from correlations with wind speed. Finally, weather explained a higher proportion of variation in migratory intensity in Blue Tits than in the other species.

*Length of the migratory period.*—The migratory period of Blue Tits at Falsterbo was shorter and less variable than that of regular migrants. Little variation in the timing of Blue Tit migration was also observed by Winkler (1974) at Col de Bretolet, and he concluded that the migration pattern resembled that of a regular migrant. The comparatively short and synchronized migratory period of Blue Tits may arise as a consequence of limited recruitment areas for



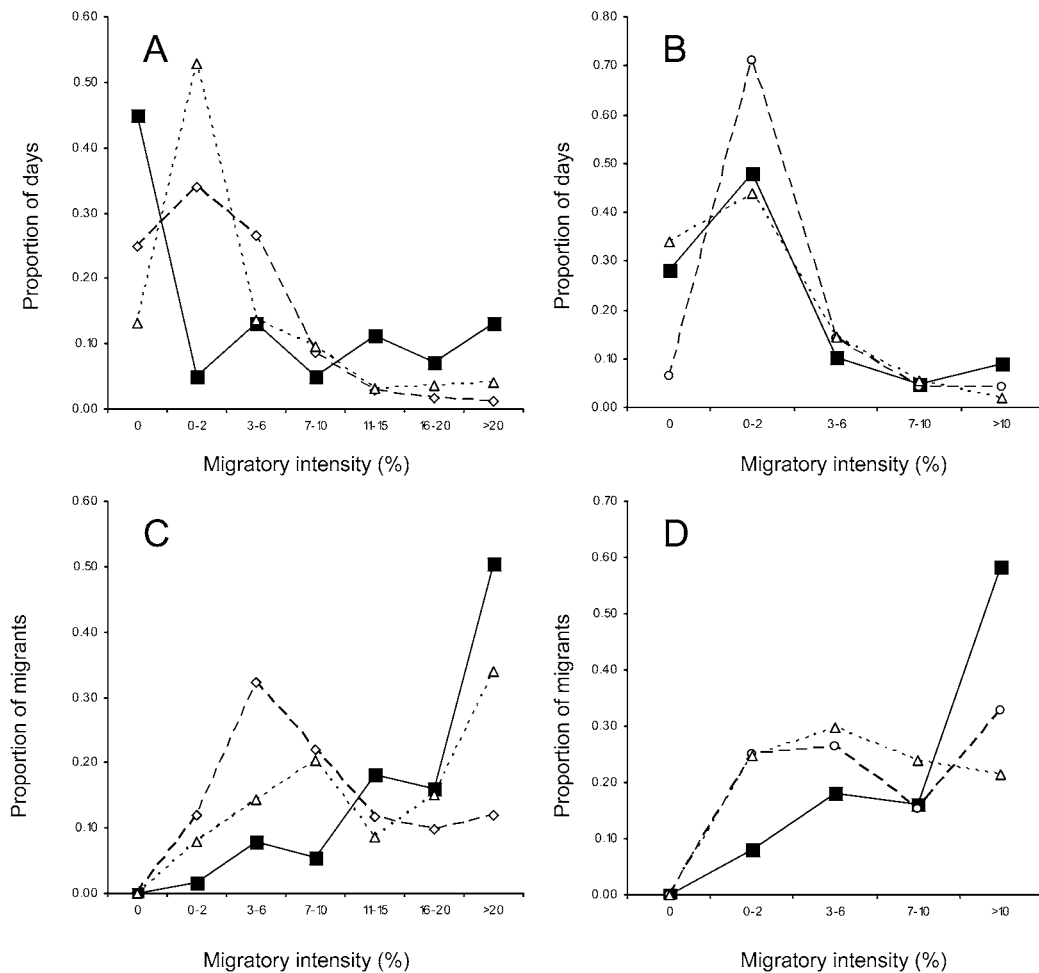


FIG. 1. Proportion of days with different migratory intensities of each species (A and B) and the proportion of all migrants migrating during days with different migratory intensities (C and D). (A) and (C) refer to migratory intensity according to visual observations, and (B) and (D) to migratory intensity reflected by captures. Data for Blue Tit are shown by filled squares, for Common Chaffinch-Brambling by open triangles (dotted lines), for Linnet (only A and C) by open diamonds (broken lines), and for European Robin (only B and D) by open circles.

the individuals of this species passing Falsterbo, compared with possibly more wide-ranging recruitment areas for the regular-migrant species. The origin of Blue Tits passing Falsterbo was analyzed by Heldbjerg and Karlsson (1997), who concluded that "there should be little doubt that most Blue Tits migrating at Falsterbo originate from the southern third of Sweden." Unfortunately, there are very few ringing recoveries to indicate the recruitment areas of the other species (Roos 1984). However, these recruitment areas are likely to extend also

to more distant regions in northern Scandinavia and Finland, as demonstrated by the significant proportion of Bramblings (originating from these northerly regions) among the migratory Common Chaffinches (see also Roos 1984).

An additional, and not mutually exclusive, explanation for the short and synchronized migratory period of the Blue Tit may depend on the species' specific weather response, resulting in migratory Blue Tits being inclined to leave on the first opportunities with favorable weather within the migration window (see

TABLE 2. Univariate analyses between weather variables and migratory intensities within and between species. Correlation coefficients are given except for wind direction, where one-way ANOVA was used to analyze differences in migratory intensity between four groups of wind directions. Differences in weather response between species were tested by two-way ANOVA, with  $P$ -values given for the species\*weather interaction. For  $0.05 < P < 0.010$ , significance levels are given as (\*);  $*P < 0.05$ ,  $**P < 0.01$ , and  $***P < 0.001$ .

Weather variable	Observation counts				Captures			
	Blue Tit	Linnet	Common Chaffinch-Brambling	$P^a$	Blue Tit	European Robin	Common Chaffinch-Brambling	$P^a$
Wind direction	(*)	***	***	ns	ns	**	ns	0.008
Wind speed	-0.38**	-0.07	-0.21**	<0.001	-0.32**	-0.35**	0.02	<0.001
Pressure	0.20 (*)	-0.11 (*)	-0.06	0.009	0.16*	0.22**	0.00	0.012
Temperature	-0.11	0.26**	0.27**	0.003	0.09	0.02	0.01	ns
Precipitation	-0.18 (*)	-0.02	0.02	0.082	-0.15*	-0.15*	0.02	0.022
Visibility	0.18 (*)	0.06	-0.03	0.090	0.10	0.09	-0.05	0.093
Cloud cover	-0.46**	-0.07	-0.05	<0.001	-0.23*	-0.13*	-0.06	0.029
Humidity	-0.24*	0.00	0.16*	<0.001	-0.13*	-0.06	0.03	0.084

<sup>a</sup> Difference between species.

TABLE 3. Multivariate analyses of migratory intensity in relation to weather variables. Numbers show the proportion of the total variation explained by each weather variable (only statistically significant contributions to explanatory power are included). Numbers do not add up exactly to the total explanation ( $r^2$ ) because of an imbalance in the ANOVA model (type III sum of squares was used to calculate the relative contribution of each variable to the full model).

Weather variable	Observation counts			Captures		
	Blue Tit	Linnet	Common Chaffinch–Brambling	Blue Tit	European Robin	Common Chaffinch–Brambling
Wind direction	0.10	0.14	0.12	0.03	0.04	–
Wind speed	0.15	0.04	0.08	0.09	0.11	–
Pressure	–	0.02	–	–	–	–
Temperature	–	0.04	0.03	–	–	–
Precipitation	–	–	–	–	–	–
Visibility	0.05	0.04	0.02	–	–	–
Cloud cover	0.13	–	–	0.01	–	–
Humidity	–	–	–	0.02	–	–
$r^2$	0.447	0.275	0.250	0.220	0.163	0.000
$r^2$ (with interactions)	0.447	0.347	0.293	0.247	0.190	0.013

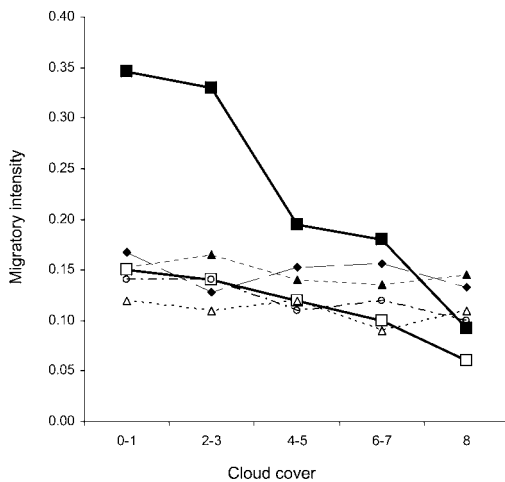


FIG. 2. Relationship between migratory intensity and cloud cover (mean migratory intensities per day and cloud cover category) for Blue Tit (squares; filled for visual observations, open for captures), European Robin (open circles, broken and dotted lines), Common Chaffinch–Brambling (triangles; filled for visual observation, open for captures, dotted lines), and Linnet (filled diamonds, broken lines).

below). Furthermore, because Blue Tits migrate the shortest distance of the species studied, they may not need as much time to prepare for migration as species migrating longer distances and can thus start migration on shorter notice.

*Degree of influence of weather on daily variation in migratory intensity.*—The peak days of migration are of great numerical importance in Blue Tits (Fig. 1). Whereas the regular migrants pass Falsterbo at a more constant rate over a longer period, Blue Tits leave during a few days with high migratory intensity (see also Lindskog and Roos 1980).

We found that weather explained more of the variation in Blue Tit migratory intensity than in that of regular migrants, irrespective of recording method and associated biases (see above). The low explanatory power of weather in the case of regular migrants may reflect a high level of adaptation to migration, assuming that regular migrants are able to migrate irrespective of most weather conditions. Blue Tits, on the other hand, seem to be more sensitive to weather conditions on their migration; they await favorable weather before migrating past Falsterbo, which results in their migrating during a few days with optimal conditions. This higher sensitivity to weather indicates that Blue Tits differ from regular migrants in their ability to continue migration under difficult weather conditions and not in their ability to select the



most favorable conditions for their migratory flights (see above). Thus, partial migrants like the Blue Tit may not have the same ability as regular migrants to continue migration in difficult weather. They are evidently more selective of specific weather factors, such as cloud cover and wind direction and speed, which are important predictors of Blue Tit migratory intensity. However, the Blue Tit probably migrates the shortest distance of the study species; perhaps it can therefore afford to wait for favorable weather before departing on migratory flights.

*Responses to different weather factors.*—Weather cues used for migratory movements seemed to differ between our study species. All species depended on wind direction (preferably migrating in headwinds; see Lindskog and Roos 1980) and speed, and to some extent also visibility (Table 3), which indeed are crucial for successful migration (Alerstam 1978, Richardson 1978), but Blue Tits depended much more on cloud cover than any of the other species (Fig. 2). This finding is supported by Lindskog and Roos (1980), who also found a negative relationship between migratory intensity of Blue Tits and cloud cover. Alerstam (1978) analyzed the daily migration counts of 15 species at Falsterbo in relation to weather. Two species were particularly strongly influenced by cloud cover (increasing cloud cover being associated with reduced migration), namely Hooded Crow (*Corvus cornix*) and Eurasian Jackdaw (*C. monedula*). As with Blue Tits, the variation in daily migratory intensity of these two species could largely be explained by weather factors ( $r^2 = 0.50$  and  $0.56$  for Hooded Crow and Eurasian Jackdaw, respectively; compare table 6 in Alerstam [1978]). It may be more than coincidental that both these species—like the Blue Tit, which was not included in Alerstam (1978)—are distinctly partial migrants in Scandinavia, in contrast to the other species, which are mainly or entirely regular migrants.

Dependence on cloud cover in partial migrants may be a specific weather reaction for this sort of migratory behavior and an indication that partial migrants have less ability to continue migration under difficult weather conditions, compared with regular migrants. One explanation, albeit speculative, could be that partial migrants primarily rely on the sun compass for their orientation (Kramer 1957, Emlen 1975). Whether magnetic orientation

mechanisms are present in these migrants is, to our knowledge, unknown (Wiltschko and Wiltschko 1995). Another possible explanation is that migratory movements are particularly risky for Blue Tits and other partial migrants, which are poorly adapted for long and sustained flights (and perhaps have small fuel reserves; see Alerstam and Lindström 1990, Kullberg et al. 1996). As a consequence, they usually restrict their migratory flights to the safest occasions, with relatively calm weather and good visibility and with all orientation cues (solar as well as magnetic) available.

In their responses to weather, Blue Tits also resemble European Robins (capture data set in Table 2), though the latter are exclusively nocturnal migrants and appear at Falsterbo lighthouse garden in the early morning, whereas Blue Tits generally appear before noon but well past sunrise (Heldbjerg and Karlsson 1997). Furthermore, European Robins are solitary migrants, whereas Blue Tits migrate in flocks. Despite these differences, both species are influenced by barometric pressure, precipitation, cloud cover, and wind speed in the univariate analyses. The resemblance may result from the method of sampling (i.e. ringing) and its associated biases. However, it is still remarkable that the Blue Tit, in its weather response, seems to resemble a nocturnal migrant more than the diurnally migrating Common Chaffinch and Brambling. Although the European Robin is well known to possess a magnetic compass (Wiltschko and Wiltschko 1972), it also uses its celestial compass on migration during extended periods, between occasions of calibration to geomagnetic directions (Wiltschko and Wiltschko 1975).

*Evolution of weather responses.*—In partial migrants, the evolution of migration and of responses to weather may differ depending on the evolutionary pathway, which may have two different starting points. First, partial migration may develop from sedentary populations that expand into regions of stronger seasonality, whereupon parts of the populations start to migrate. Partial migrants among such typically sedentary species include Blue Tits, Hooded Crows, and Eurasian Jackdaws. Furthermore, the number of migratory Blue Tits has increased at Falsterbo during the past two decades (Heldbjerg and Karlsson 1997). The selection pressures for the evolution of weather responses in such populations are entirely unknown, and

it is largely unknown to what extent sedentary birds are equipped with the necessary migratory genetics. However, one interesting case is the House Finch (*Carpodacus mexicanus*), analyzed by Able and Belthoff (1998). House Finches from sedentary western populations were introduced to eastern North America, where a partially migratory system rapidly evolved. Suppressed migratory traits, as in the House Finch, can lead to rapid evolution of migration, in contrast to evolution of migration by gene flow or mutations, which is presumably a much slower process (Pulido et al. 1996).

Finally, partial migration may also evolve in a regular migrant—for example, when expanding its breeding range into areas permitting winter survival of part of the population, or when climate change increases winter survival of resident individuals. The migratory traits must become partially suppressed in such cases, but we can expect the same type of weather response among individuals migrating in such a population as among the ancestral regular migrants. A possible outcome of the evolution from migration to partial migration could be the more rigid manner of obligate partial migrants, where individuals are either migratory or resident, regardless of environmental conditions (Terrill and Able 1988). One such species may be the Blackcap (*Sylvia atricapilla*), which has become partially or wholly sedentary in some southerly regions (Berthold 1996). The Blackcap would also make a good within-species comparison for evaluating the weather response in relation to migratory habit in future studies.

Differences in ancestral conditions and evolutionary processes could be further elucidated, if weather responses and other essential components of migration were investigated in other partial migrants.

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