

Influence of temperature and other factors on the daily roosting times of black-billed magpies

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On 102 occasions from September 1984 to April 1985, the time of morning departure and evening arrival of a population of black-billed magpies (*Pica pica*) was recorded at a winter roost near Edmonton, central Alberta. The goal was to determine whether an effect of cold on daily roosting time could be observed and distinguished from that of other environmental factors. Multiple linear regression analysis on the data revealed that, all other things being equal, magpies left the roost later relative to sunrise, and returned to it earlier relative to sunset on colder days, and also (i) on longer days, (ii) on darker, cloudier days, (iii) in the second half of winter, when compared with the first half, and (iv) when fewer birds were using the roost. These results held true only before the occurrence of overt territorial behaviour in March, which coincided with a notable shift towards earlier departures and later arrivals. The larger amount of time spent in the roost by magpies when it was cold may be related to an increased predisposition to inactivity induced by cold temperatures, or to possible microclimatological advantages offered by the roost. The amplitude of this temperature effect may, however, be dependent on the birds' level of hunger. Indeed, the effect of temperature on roosting times was much weaker in the case of departure, i.e., after a long night of food deprivation, than it was in the case of arrival.

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De septembre 1984 à avril 1985, des observations furent effectuées à un dortoir de pies bavardes (*Pica pica*) situé près d'Edmonton, Alberta, dans le but de déterminer si la température ambiante pouvait influencer de manière distincte les temps de départ et d'arrivée des pies fréquentant ce site. Une analyse de régression multiple, conduite sur 102 temps de départ et 102 temps d'arrivée, a montré que les pies retardaient leur départ le matin (par rapport au lever du soleil) et accéléraient leur retour en fin d'après-midi (par rapport au coucher du soleil) lorsqu'il faisait froid, de même que (i) lorsque les journées étaient longues, (ii) lorsque le couvert nuageux réduisait l'intensité lumineuse, (iii) lors de la deuxième moitié de l'hiver, en comparaison avec la première moitié, et (iv) lorsque peu d'oiseaux utilisaient le dortoir. Ces résultats ne sont valides que pour la période (septembre-février) pendant laquelle les pies ne défendaient pas leurs territoires. En mars et avril, les départs au dortoir se firent soudainement plus tôt, et les retours plus tard. Le fait que les pies aient passé plus de temps à l'intérieur du dortoir par temps froid peut s'expliquer par leur tendance à demeurer généralement inactives quand il fait très froid, et par la présence possible de conditions microclimatologiques favorables à l'intérieur du dortoir. L'amplitude de cet effet du froid peut cependant diminuer si les oiseaux sont affamés. L'effet de la température sur les temps de départ et d'arrivée au dortoir fut en effet beaucoup moins accentué dans le cas des départs, après une longue nuit sans nourriture, que dans le cas des arrivées.

Introduction

Periods of sleep or general inactivity follow the rules of endogenous, light-entrained rhythmicity in birds (Gwinner 1975). The daily regularity of crepuscular roosting flights exhibited by many birds species is probably the most easily witnessed expression of such a rhythmicity (see Wynne-Edwards 1962, pp. 283–297, for a review). The exact timing of these roosting flights relative to sunrise and sunset may, however, vary from day to day. This variation in daily roosting times is not random but rather seems to occur in response to concurrent variations in physical conditions of the environment. This is evidenced by the correlation that is often found, for many bird species, between daily roosting time and various environmental factors.

The crepuscular level of light intensity, as influenced by cloud cover, is certainly the most extensively studied parameter in this regard. Many studies (e.g., Dunnnett and Hinde 1953; Haase 1963; Hein and Haugen 1966; Davis and Lussenhop 1970; Raveling et al. 1972; Swingland 1976; Hubalek 1978 and references therein) have shown that birds leave their roost later in the morning and (or) return to it earlier in the evening on cloudy, dark days than on clear, bright days. The effect of another

light-related factor, day length, is also well known. Most birds tend to depart earlier and arrive later at the roost on short days than on long days (e.g., Brown 1946; Martin and Haugen 1960; Schreiber 1967; Brodie 1980; but see Raveling et al. 1972). Less is known, however, about the effect of environmental factors not directly related to light. Yet under certain circumstances, such factors could become important. One of these factors is temperature, which is known to affect the general behaviour of birds living under harsh winter conditions (Terres 1982, pp. 95–96).

To cope with cold, birds can conceivably alter their total activity time in two different ways (Morse 1980, p. 156), and each one of these two strategies can in turn affect the timing of the roosting flights. On one hand, during cold weather birds may decide to increase their foraging effort to compensate for increased energetic demands set by thermoregulatory expenditures (see Brooks 1968; Pohl 1971), a strategy that would result in early departures and late arrivals at the roost. On the other hand, birds may choose to diminish energy expenditures by remaining inactive in the roost for longer periods of time when it is cold, in which case the effect on roosting time would be reversed. Field observations seem to support this latter hypothesis. Late departures, early arrivals, and general inactivity at the roost under low temperatures have been reported in a number of studies (Jumber 1956; Raveling et al. 1972; Kessel

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1976; Pitts 1976; Brodsky and Weatherhead 1984). Unfortunately, however, some of these studies failed to separate the effect of temperature from that of concurrent changes in cloud cover and wind conditions, while others reported on birds that appeared to rely exclusively on food regularly supplied for them by people, a somewhat unnatural situation. Whether the effect of temperature would persist under more natural conditions is not well known.

In the winter of 1984–1985, I conducted a study on the influence of various environmental factors on the daily roosting times of a rural population of black-billed magpies (*Pica pica*) near Edmonton, Alberta. Although magpies often forage near human habitations in winter, they are often persecuted, not fed, by people, especially in rural areas (Linsdale 1937). They roost communally throughout the winter, a period during which temperatures in central Alberta are highly variable, sometimes passing from 0°C to –30°C within a few days. The results of my study can thus be used to determine whether an effect of temperature on roosting time can still be observed and quantitatively distinguished from that of other environmental factors in a population of birds not deliberately fed by man. These results are presented here.

Methods

The roost chosen for the study was a dense, natural stand of white spruce (*Picea glauca*) located on the slopes of a small tributary to Whitemud Creek, about 7 km south of Edmonton (Reebs 1985). In the winter of 1984–1985, the roost was used by 46–192 magpies (Fig. 1). These birds foraged around farms and nearby residential areas. Analysis of regurgitated pellets found at the roost indicated that the magpies fed mostly on grain, berries, voles, and garbage (Reebs and Boag 1986). All foraging grounds were east of the roost, and all roosting flights passed over open fields. As a consequence, every flying bird could be seen and counted from a single vantage point near the roost.

From 15 September to 6 April, I observed 102 morning departures and 102 evening arrivals at this roosting site. I usually arrived at the observation site (an open field near the roost) 30 min before the first signs of flight activity, and left 30 min after the last signs of flight activity. Fieldwork at the observation site included (i) recording the number of magpies leaving or arriving at the roost during each minute of the observation period, (ii) measuring air temperature ($\pm 0.5^\circ\text{C}$) at the onset of the observation period with a Taylor pocket thermometer, (iii) estimating cloud cover to the nearest 10%, and (iv) measuring light intensity at about 10-min intervals with a Gossen Tri-Lux lightmeter. The sensor of this lightmeter is a flat disk that provides only directional measurements of light intensity. The reading is thus dependent on the direction in which the probe is pointed. To obtain an estimate of the amount of light coming from the whole sky, I used the mean of two readings, one with the disk facing the zenith, and one with the disk angled at 45° relative to the horizontal, towards the sun's azimuth (i.e., the direction of the point on the horizon apparently lying directly below the sun). I compared, under various conditions of cloud cover and temperature, this index of light intensity with the reading of a Protomatic lightmeter equipped with a hemispherical probe (diffuser) that caught incoming light rays from all parts of the sky. I obtained Pearson's correlation coefficients of 0.989 for morning measurements ($n = 70$) and 0.953 for evening measurements ($n = 82$) between these two variables. Thus, my index of light intensity appears to be a good estimate of the amount of light coming from the sky. With all the measurements taken throughout a given observation period, it was possible to establish a light profile from which the values of light intensity at any moment of this observation period could be estimated by interpolation.

Magpies generally left the roost in the morning during the 45 min that preceded sunrise. The birds tended to leave the roost together, and typical departures involved large flocks (usually 30–60 individuals per

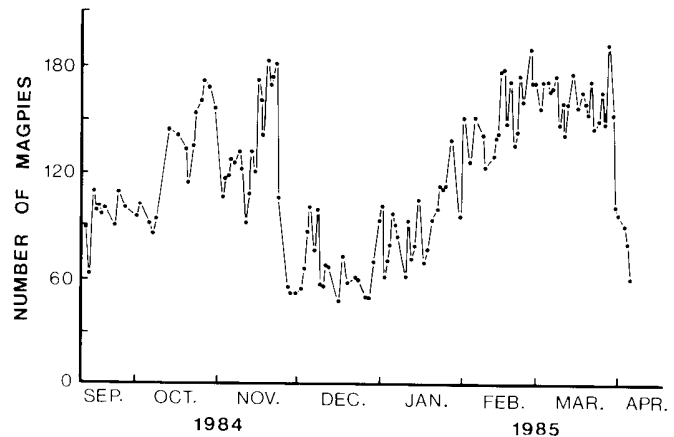


FIG. 1. Number of magpies counted at the roost from September 1984 to April 1985.

flock) followed by smaller, straggling groups (Reebs 1985). Total duration of departure was, on average, 16.4 min (range, 1–28 min). Knowing how many birds left the roost during each minute of the observation period, it was possible to calculate the mean time of departure. The number of minutes between this mean time of departure and the time of sunrise provided a standardized measure of how early (or late) the magpies left the roost each day. It represented the dependent variable used in the regression analysis on departure times.

Magpies usually returned to the roost during the hour preceding sunset. The birds' arrival was more gradual than their morning departure (Reebs 1985). Arrival involved smaller flocks (seldom more than 35 individuals per flock) and spanned, on average, 48.5 min (range, 11–84 min). The number of minutes between the mean time of arrival and the time of sunset represented the dependent variable to be used in the regression analysis on arrival times.

Other studies (e.g., Swingland 1976; Brodsky and Weatherhead 1984) have used median time (50% of the birds gone or arrived) instead of mean time to express times of departure or arrival. In the present study, mean and median times were highly correlated with each other for both departure (Pearson's $r = 0.967$, $n = 102$, $P < 0.001$) and arrival (Pearson's $r = 0.974$, $n = 102$, $P < 0.001$). The use of median instead of mean time in the calculations was tried and it led to results essentially similar to those given here.

The environmental factors (independent variables) I considered for analysis were temperature at the onset of the observation period ($^\circ\text{C}$), day length (sunrise to sunset) (h), rate of daylength change (an indicator of the seasons) (min/d), mean wind speed during the observation period (km/h), wind direction (from 1 = birds flying straight against headwinds, to 4 = birds flying straight along tailwinds), and crepuscular level of light intensity (lx). Daily values of light intensity 18 min before sunrise and 24 min before sunset were used for the analysis of departure and arrival data, respectively. They provided a standardized measure of how "dark" (cloudy) each morning or evening was. Those times were chosen because they represented the mean time of departure and arrival for the complete study. Another independent variable, the number of magpies counted at the roost, was also used. This variable differs from the other ones in that it represents a biotic rather than abiotic factor of the environment. Nevertheless, because it was not constant throughout the study (Fig. 1), it was included in the analysis (Lehner 1979). While small fluctuations in roosting numbers may be due to counting error, reasons for the larger fluctuations are unknown. Such fluctuations may reflect occasional solitary roosting (Reebs 1985) or movement to other roosts, although no such roosts could be found within at least 5 km of the study site. "Number of magpies counted at the roost" did not significantly correlate with any of the environmental parameters measured in this study.

The times of sunrise and sunset used in all calculations were obtained from the Weather Office of the Canadian Atmospheric Environment Service in Edmonton. Data on wind speed and direction were taken

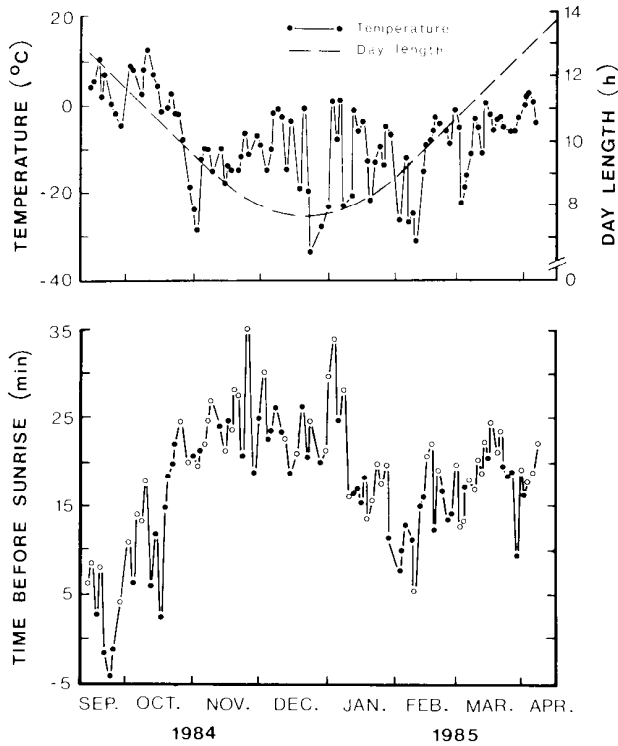


FIG. 2. Variation in day length, morning temperature, and mean time of departure of black-billed magpies from the winter roost throughout the study. Solid dots in the lower graph represent cloudy mornings (cloud cover >50%), while open dots represent clear mornings (cloud cover <50%).

from the records of the University of Alberta Meteorological Station, located 1.5 km east of the roost. All other variables were measured in the field, as described above.

I used the Statistical Package for the Social Sciences (SPSS[®]; Norusis 1983) for the analysis. The procedure was a stepwise multiple linear regression, which can be used to obtain a list of dependent variables that significantly contribute to a reduction of the unexplained error variance of a dependent variable, and to get an idea of the relative contribution of each variable in such a reduction (Sokal and Rohlf 1981; see also Zar 1974 and Norusis 1983 for more details on this statistical procedure). Entry and removal criteria were 0.05 and 0.10, respectively. Analysis of the residuals showed that the assumptions of linearity, homogeneity of variance, and normality were met. Problems of multicollinearity among the independent variables did not arise. No transformations of the variables were necessary.

Results

Variations in environmental parameters

The ranges in values covered by some of the independent variables throughout the study were as follows: temperature, -34 to 12°C (morning) and -28 to 20°C (evening); day length, 7.50 to 13.15 h; rate of day-length change, -4.5 to 4.5 min/d; wind speed, 1 to 22 km/h (morning) and 1 to 28 km/h (evening); and light intensity, 0.34 to 9.99 lx (18 min before sunrise) and 28 to 748 lx (24 min before sunset).

Departure

Figure 2 shows the variation in departure times observed throughout the study, along with the concurrent variations in temperature, day length, and general conditions of light intensity (cloud cover). As expected, the magpies left the roost earlier during the short days of winter (November, December, and January) than during the longer days of September,

TABLE 1. Summary table of the stepwise multiple regression analysis on departure time for (A) the complete set of data ($n = 102$), and (B) the truncated set of data ($n = 82$) (see text for reasons on truncation)

	Variable	R^2 change	Partial correlation coefficient	P
(A)	Day length	0.2460	-0.587	<0.001
	Light intensity	0.0745	0.349	<0.001
	Day-length change	0.0492	0.269	0.007
		0.3697		
(B)	Day length	0.5329	-0.849	<0.001
	Light intensity	0.1098	0.598	<0.001
	No. of magpies	0.0414	0.432	<0.001
	Day-length change	0.0352	-0.363	0.001
	Temperature	0.0342	0.349	0.002
		0.7535		

October, and February. An unexpected feature of the pattern of departure times, however, was how early magpies left the roost in March and April; one would have expected later departures because of the longer day lengths. Magpies in central Alberta start to actively defend breeding territories in late February – early March (personal observations), and thus the early departures observed in March and April may indicate that the magpies became reluctant to leave their territories unoccupied in the spring, and attempted to spend as much time as possible on them. Unusually early singing and awakening times in spring have been noticed in a number of other species, and attributed to the influence of the breeding season (e.g., Davis 1958; Leopold and Eynon 1961; Fisler 1962; Aschoff et al. 1970; Daan and Aschoff 1975). Because I had no easy way to measure this territorial tendency in magpies, I assumed that it was negligible up to the end of February but important thereafter, and accordingly I conducted the regression analysis, not only on the complete set of data, but also on a truncated set of data that was obtained by eliminating all March and April observations from the original complete set. Although I present the results of both analyses in Table 1, I will from here on focus my attention on the results yielded by the truncated set of data only.

The multiple regression analysis explained 75% of the variance in departure time (Table 1). Day length contributed two thirds of that total, whereas light intensity, the number of magpies using the roost, rate of day-length change, and temperature were responsible for the remaining third. Wind speed and direction failed to predict departure time. The signs of the partial correlation coefficients indicate that magpies tended to leave the roost relatively late (*i*) on long days, (*ii*) on dark, cloudy mornings, (*iii*) when few birds were using the roost, (*iv*) in the second half of winter, when the rate of day-length change was positive, and (*v*) on cold mornings. Although significant, the effect of temperature was not important, as evidenced by the low partial correlation coefficient attached to this variable, and the small percentage of the variance it explained (Table 1).

Magpies generally (78 out of 102 occasions) left the roost as soon as levels of light intensity reached 1–5 (often 1–3) lx (Fig. 3), possibly the minimum illumination under which they could fly safely and navigate. Most exceptions occurred either during cold (below -19°C) weather (8 occasions) or during the first 4 weeks of observations, when nights were relatively short (13

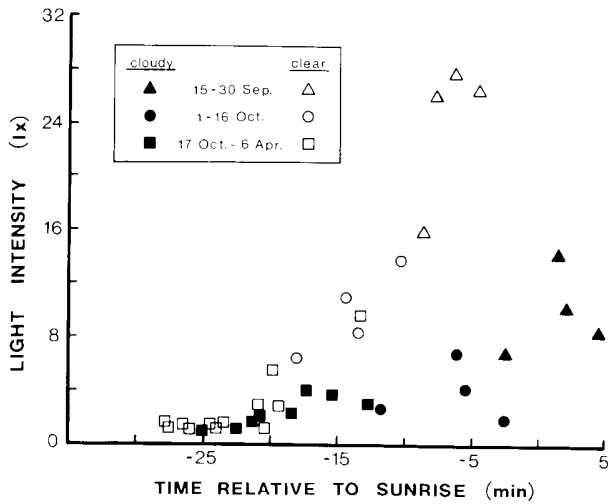


FIG. 3. Light intensity at each mean time of departure recorded from 15 September through 16 October, and at 20 randomly selected mean times of departure recorded thereafter (17 October to 6 April). During this latter period, 87% (75/86) of all departures occurred at light intensities not exceeding 5 lx. Eight of the 11 exceptions occurred on cold (below -19°C) mornings. Negative values on the x-axis indicate time before sunrise, positive values indicate time after sunrise.

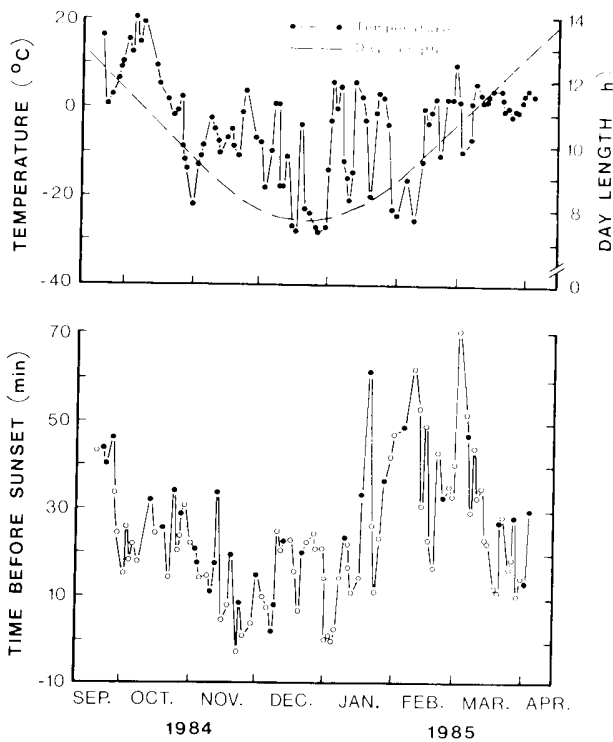


FIG. 4. Variation in day length, evening temperature, and mean time of arrival of black-billed magpies at the winter roost throughout the study. Solid dots in the lower graph represent cloudy evenings (cloud cover $>50\%$), while open dots represent clear evenings (cloud cover $<50\%$).

occasions). In all cases, magpies left the roost at higher light intensities. This is probably related to the delaying effect of low temperatures and long day lengths on departure time. Note, however, that additional delaying caused by heavy cloud cover did not necessarily translate into higher levels of light intensity at departures. During the first four weeks of observation, for

TABLE 2. Summary table of the stepwise multiple regression analysis on arrival time for (A) the complete set of data ($n = 102$), and (B) the truncated set of data ($n = 80$) (see text for reasons on truncation)

	Variable	R^2 change	Partial correlation coefficient	P
(A)	Temperature	0.1659	-0.433	<0.001
	Day length	0.1159	0.520	<0.001
		0.2818		
(B)	Temperature	0.2971	-0.724	<0.001
	Day length	0.2342	0.850	<0.001
	Day-length change	0.1652	0.677	0.001
	Light intensity	0.0356	-0.333	0.003
	No. of magpies	0.0189	-0.266	0.019
		0.7510		

example, magpies left later but also at lower light intensities under heavy cloud cover than under clear skies (Fig. 3).

Arrival

Figure 4 shows that the general variation in arrival times loosely parallels that of day length until early March. Up to that time, magpies, as expected, tended to arrive late on short days. In March and April, however, they arrived later than expected based on day length alone. Again, this may have been due to the onset of strong territorial behaviour in the spring, which prompted the birds to remain on their territories away from the roost for as long as possible. As before, I used both the complete set of data and a truncated one (in which March and April observations were excluded) for the regression analysis (Table 2). From here on, I will concentrate only on the results yielded by the truncated set.

The regression explained 75% of the variance in arrival times (Table 2). The five variables involved were the same ones that had been found to influence departure. This time however, temperature was one of the most important predictors, contributing two-fifths of the total variance explained. Day length was also important, showing the highest partial correlation coefficient. According to the signs of the partial correlation coefficients, magpies tended to arrive at the roost relatively early (i) on long days, (ii) on cold afternoons, (iii) in the second half of winter, when the rate of day-length change was positive, (iv) on dark, cloudy afternoons, and (v) when few birds were using the roost.

No consistent pattern was found in the light intensities at which magpies arrived at the roost. Values of light intensity at arrival were higher and more variable (range, 24.2–1174.2 lx) than those at which magpies left the roost in the morning (see Fig. 3).

The conditions causing early arrivals were the same ones that caused late departures, so that it can be said that, at least until the breeding season, magpies spent relatively more time in the roost on long days, in cold weather, on dark and cloudy days, in the second half of winter, and when few birds were using the roost.

Discussion

In the present study, temperature was found to be correlated with the daily roosting times of magpies. All other things being equal, magpies tended to depart from the roost slightly later and return to it earlier on cold days than on mild days. This result

parallels that of other studies in which the same relationship was found for birds regularly fed by people (Kessel 1976; Brodsky and Weatherhead 1984). It indicates that, in the conditions of my study, magpies did not try to improve their foraging opportunities by increasing their activity time when it was very cold.

There may be several reasons why birds spend more time in their roost at low temperatures. First, birds, like other animals, often greatly decrease their general level of activity under very cold temperature (e.g., Canada geese, *Branta canadensis*, Raveling et al., 1972; black-capped chickadees, *Parus atricapillus*, Kessel 1976; black ducks, *Anas rubripes*, Brodsky and Weatherhead 1985; magpies, personal observations). This is probably adaptive. In the spotted nutcracker (*Nucifraga caryocatactes*), increased inactivity under very cold (below -30°C) temperatures has been shown to result in daily energy requirements much lower than what would be expected on theoretical grounds for a passerine of similar size active under similar conditions (Andreev 1977). If a motivation to "rest" is involved in going to the roost and staying in it, then a general predisposition to inactivity induced by cold could conceivably lead to advanced arrivals and delayed departures at the roost. Second, the roost may present advantageous conditions of microclimate that may entice the birds to spend more time in it when temperatures are very low. I did not make any microclimatological measurements inside the roost I studied, but it was unmistakably similar to other typical magpie roosts which, in a separate study (Reebs 1985), were found to reduce wind exposure by more than 70% and exposure to the open sky by at least 50%. I believe that the roost studied here presented at least comparable advantages.

Another possibility is that cold temperatures cause a reduction in food availability, thus making foraging less profitable and prompting the birds to spend less time on the foraging grounds (i.e., more time in the roost). That particular effect of temperature would, however, appear unlikely in the present study, as it is hard to see how temperature could affect the availability of such food items as grain, berries, and garbage.

This is not to say, however, that food availability *per se*, or maybe the birds' level of hunger, cannot affect roosting time (see Dunnet and Hinde 1953; Alonso et al. 1985). In the present study, the effect of cold was found to be much less pronounced on departure times than on arrival times ("temperature" had a partial regression coefficient of only -0.163 for departure versus -0.805 for arrival). Magpies presumably were very hungry in the morning, following a long night, and their increased motivation (need?) to get food might have overcome part of their reluctance to leave the roost in the cold. This interpretation suggests that the outcome of any possible trade-off between saving energy by remaining inactive in the roost and gaining energy by foraging and eating depends not only on ambient temperature but also on a bird's level of hunger, or possibly its need to avoid starvation. It also suggests that the influence of temperature on roosting time could take place under a certain set of conditions (e.g., food readily available, birds easily meeting their food requirements) but not under others (e.g., food rare, birds always hungry).

Wind speed was included in the analysis because I expected the wind chill factor to play a role similar to that of cold. This seems, at first sight, not to be the case, since wind speed failed to enter the equation in both departure and arrival analyses. The final *P* value for wind speed was 0.2775 and 0.0569 in these respective analyses. The latter value shows that wind speed only

barely failed to become a significant predictor of arrival time. Its partial correlation coefficient for arrival was positive, indicating that, as expected, magpies tended to go to the roost somewhat early on very windy days. The portion of the variance that would have been explained by wind speed, had it entered the equation, remains very small however. Perhaps, the conditions at the foraging grounds were so that magpies could forage in protected places (such as the leeward side of buildings or wood lots), thus minimizing the effect of wind chill.

Many other variables entered the equation: day length, crepuscular level of light intensity, rate of day-length change, and number of magpies. The important effect of day length was not surprising in the light of previous studies (see Palmgren 1949, and Daan and Aschoff 1975, for discussions of the possible mechanisms underlying this effect). The effect of light intensity and the tendency for magpies to leave the roost at relatively low and fixed levels of light intensity when compared with arrival are also typical (Aschoff and Wever 1962). The correlations I found between roosting time and both the rate of day-length change and the number of roosting birds are less usual, but these two independent variables accounted for a relatively small percentage of the variance in roosting time, and the nature of their influence is open to several speculative interpretations (Reebs 1985).

The results discussed so far were based on those data obtained before breeding territories became established and defended. A notable shift towards early departures and late arrivals occurred when magpies began to show overt territorial behaviour. Active territorial defense in the spring is probably a sound indicator that levels of gonadal hormones are beginning to rise in magpies. At least one gonadal hormone, testosterone, is known to be directly responsible for increased duration of daily activity in birds (Turek and Gwinner 1982). Increased levels of gonadal hormones during the breeding season could thus account for the early departures and late arrivals exhibited by magpies at the roost in the spring. Whether both males and females, or males only, contributed to this effect is uncertain. Further studies on sex differences regarding the timing of roosting flights and the effect of gonadal hormones on the circadian system of birds would be needed to answer that question.

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