Influence of temperature and other factors on the daily roosting times of Mourning Doves in winter

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From November 1992 to February 1993, observations were made during 30 departures and 30 arrivals at a Mourning Dove (*Zenaida macroura*) roost in Moncton, New Brunswick, Canada. Our objective was to identify the effect of cold on the timing of roosting flights in this species, a recent addition to the local wintering fauna. The effect of other environmental factors was taken into account by including them, along with temperature, in a multiple regression analysis. Doves left the roost later relative to sunrise (*i*) on longer days, (*ii*) on cloudy mornings, (*iii*) when fewer birds were using the roosts, (*iv*) on colder mornings, and (*v*) when winds were high. They returned to the roost later relative to sunset (*i*) on colder evenings and (*ii*) in clear weather. Late arrivals on colder days represent an unusual finding. Anatomical and behavioural considerations suggest that Mourning Doves cannot reduce heat loss as substantially as other species; therefore, late arrivals on cold evenings may reflect the more important role of energy gain through extended foraging required to survive the long winter night.

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De novembre 1992 à février 1993, 30 observations de départs et d'arrivées ont été effectuées à un dortoir de Tourterelles tristes (*Zenaida macroura*) à Moncton, Nouveau-Brunswick, Canada. L'objectif était de déterminer si le froid avance ou retarde le moment du départ et de l'arrivée chez cette espèce qui a commencé, depuis peu, à passer l'hiver au Canada. L'effet d'autres variables environnementales a aussi été mesuré en incluant ces dernières dans une analyse de régression multiple. Les tourterelles ont retardé leur départ par rapport au lever du soleil (*i*) lors de journées longues, (*ii*) lors de matins ennuagés, (*iii*) quand moins d'oiseaux étaient présents au dortoir, (*iv*) quand il faisait plus froid et (*v*) par grands vents. Elles ont retardé leur arrivée par rapport au coucher du soleil (*i*) quand il faisait plus froid et (*ii*) lors d'après-midis sans nuages. L'arrivée tardive lors de temps froids, rarement observée chez d'autres espèces, s'explique peut-être chez la tourterelle par un besoin de consommer plus de nourriture en vue de pouvoir générer plus de chaleur pour compenser la déperdition calorifique occassionnée par un manque d'adaptation anatomique et comportementale.

Introduction

Low temperatures impose an energetic stress on endothermic animals. To maintain a stable body temperature in a cold environment, endotherms must increase heat production and (or) minimize heat loss. These two strategies can have opposite effects on the general activity of animals. In species where food cannot be stored on a long-term basis, increased heat production requires increased food intake and, therefore, increased foraging time. On the other hand, minimizing heat loss often requires the adoption of particular body postures and the occupation of protected sites that are more or less incompatible with activity in general and foraging in particular (see Morse 1980, p. 156, for a more complete discussion).

Most studies of the influence of cold on activity levels have been done on birds, probably because birds are relatively easy to observe at feeding sites, and also because their daily activity time can easily be determined from their conspicuous roosting flights. Thus, wintering birds have been shown to decrease activity levels and daily activity time when colder weather prevails (e.g., Jumber 1956; Raveling et al. 1972; Kessel 1976; Pitts 1976; Zammuto and Franks 1981; Brodsky and Weatherhead 1985; Reebs 1986). This indicates that, under such conditions, wintering birds save more energy by remaining inactive than they would gain by actively foraging. There are, however, some interesting exceptions. Snow buntings (*Plectrophenax nivalis*) and redpolls (*Carduelis* spp.), which overwinter at high latitudes, extend their daily activity time well into the night during periods of extreme cold (Morse 1956; Brooks 1968). This suggests that the benefits of inactivity during cold days hold only insofar as the minimum energy resources necessary to survive the upcoming night can first be gathered, and this may take more time when the minimum energy level required is raised owing to long nights and colder weather.

In the present study, we determined the effect of cold on the daily activity time of another bird species that could represent an exception to the general pattern described above. The Mourning Dove (*Zenaida macroura*) has only recently extended its wintering range into Canada (Alison 1976; Armstrong and Noakes 1983). Some aspects of the Mourning Dove's anatomy (e.g., thin foot papillae) and behaviour (e.g., a sleep posture in which the bill is not buried under the scapular feathers) are not compatible with efficient heat-loss reduction (see Thompson 1950; Hennessy and van Camp 1963; Alison 1976; Armstrong and Noakes 1983). We therefore hypothesized that energy gain is comparatively more important as a strategy for coping with cold in this species, and that this would translate into longer activity times under cold conditions. Because doves roost communally and have conspicuous roosting flights, we tested our hypothesis by determining the influence of ambiant temperatures on the timing of morning and evening roosting flights. We predicted that low temperatures would advance departure times in the morning and delay arrival times in the evening.

Roosting times, however, are not influenced only by temperature. Sunrise and sunset times, day length (or night length), light intensity (cloud cover), wind speed (wind-chill

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factor) and the number of birds using the roost have all been shown to influence daily roosting times (e.g., Reebs 1986 and references therein). We controlled for the effect of sunrise and sunset time by always measuring morning departure time relative to sunrise time, and evening arrival time relative to sunset time. We accounted for the other variables by including them, along with temperature, in a multiple regression analysis of the variation observed in roosting times. We conducted our study in Moncton, New Brunswick, a place where Mourning Doves are now abundant (Erskine 1992) and where ambient temperature in winter can vary from a few degrees above 0 to −30°C.

Materials and methods

The roost we studied was located on the campus of the Université de Moncton and consisted of three white spruce (*Picea glauca*) and three Norway spruce (*P. abies*). The position of the roost in relation to surrounding buildings protected it from the dominant west winds but left it somewhat exposed to east winds. Doves left the roost in the morning in small groups (no more than four birds at a time) and headed immediately towards the closest residential areas. Their departure could easily be observed from a spot 75 m east of the roost. They arrived back at the roost in late afternoon in groups of various sizes (1–30 birds), flying over a nearby soccer field that was used as the evening observation site. The morning observation site, closer to the roost, could not be used in the evening, because doves often moved from tree to tree before settling down for the night, making it impossible to distinguish between arriving and tree-switching individuals. Conversely, the evening observation site could not be used in the morning, because of the low light levels when doves left the roost, which forced us to make observations from closer to the roost.

From 24 November 1992 to 11 February 1993, 30 departures from the roost and 30 arrivals at the roost were observed. Observation days were chosen to maximize the variation in environmental factors within our data set. The observer arrived at the site a minimum of 15 min before the first bird was sighted and left 15 min after having counted the last bird. Fieldwork at the observation site included (*i*) counting the number of Mourning Doves departing from or arriving at the roost during each minute of the observation period, (*ii*) measuring air temperature with a hand-held thermometer 10 min after arrival on site, (*iii*) estimating the percentage of cloud cover to the nearest 10%, and (*iv*) measuring incident light intensity at intervals of 5 min with a Gossen Lunasix 3 light meter. Light intensity was obtained by pointing the light meter towards the zenith. The light meter's hemispheric diffusing cap was left on, and thus readings were of light coming from the whole sky.

For each day, the median time of departure or arrival could be determined from the minute-by-minute count. The number of minutes separating sunrise time from the median time of departure, and sunset time from the median time of arrival, was used as the dependent variable in the morning and evening analyses, respectively. Negative values corresponded to departures or arrivals that preceded sunrise or sunset. Hereafter, we shall continue to use the terms "departure time" and "arrival time" with the understanding that they refer to the number of minutes separating median departure time from sunrise and median arrival time from sunset, respectively. Sunrise and sunset times were obtained from the Weather Office of the Canadian Atmospheric Environment Service at the Moncton Airport, 8.5 km east of the roost.

As independent variables we used air temperature (as measured on site, in degrees centrigrade), day length (from sunrise to sunset, in hours), mean wind speed during the observation period (obtained from the Moncton Airport, in metres per second), cloud cover during the observation period (percent), and light intensity (as measured on site, in lux) 20 min before sunrise and at sunset. These times, arbitrarily chosen at the beginning of the study, allowed us to compare

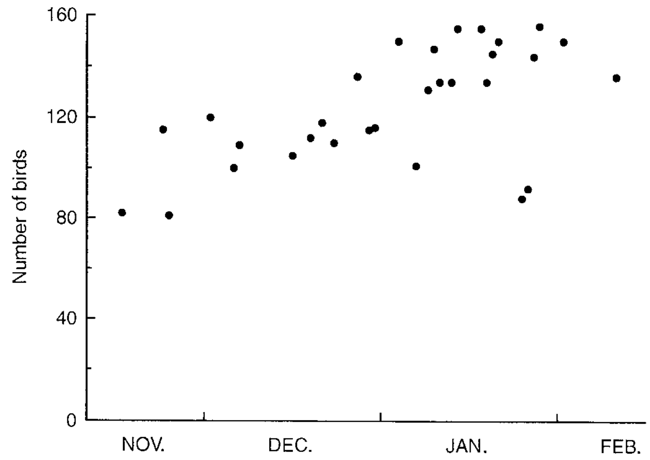

FIG. 1. Number of Mourning Doves counted at the roost from November 1992 to February 1993.

the level of "darkness" of each day, while standardizing for sun height relative to the horizon. The light intensity values were obtained by interpolation from the measurements taken on site. An additional variable, "number of birds," differed from the other variables in that it represented a biotic rather than an abiotic factor of the environment, but because this variable did not remain constant throughout the study (Fig. 1), it was included in the analysis (see Lehner 1979).

Data were analyzed using stepwise multiple linear regression (STATISTIX 4.0, analytical software). These regressions helped determine the relative contribution of each independent variable to the variation in departure and arrival times at the roost. Because there was a significant ($p < 0.05$) correlation between light intensity and cloud cover, we did two sets of regressions. The first was done using light intensity, but not cloud cover, as one of the independent variables. In the second set, light intensity values were replaced by those of cloud cover. Comparisons between the two sets of regressions show which of these two variables best explains the variation in departure and arrival times. There was no significant correlation between any of the other independent variables.

Results

Range of variables

The following ranges were observed for the variables in our data set: departure time, 40 min before sunrise to 26 min before sunrise; arrival time, 8 min before sunset to 20 min after sunset; temperature, −18.8 to 4.5°C (morning) and −17.9 to 3.7°C (evening); light intensity, 0.8 to 15.8 lx (20 min before sunrise) and 33.8 to 757.3 lx (at sunset); cloud cover, 0/10 to 10/10 (morning or evening); wind speed, 0 to 7.2 m/s (morning) and 0 to 13.4 m/s (evening); day length, 8.62 to 10.17 h; and bird numbers, 81 to 156.

Influence of environmental factors on departure

The stepwise multiple regression using light intensity as one of the independent variables accounted for 51% of the variation in departure time, whereas that using cloud cover accounted for 77% of the variation (Table 1). The results show that departure from the roost occurred later (*i*) on long days, (*ii*) on dark or cloudy mornings, (*iii*) when fewer birds were using the roost, (*iv*) on cold mornings, and (*v*) when wind speed was high. Day length explained the largest part of the variation (Table 1). The apparent effect of cold, on the other hand, was modest, both in terms of variation explained (6.9%) and in terms of magnitude of delay (about 2 min for every drop of 10°C).

TABLE 1. Results of the stepwise multiple linear regression analyses of the departure times ($n = 30$) of Mourning Doves at their winter roost

(A) Analysis with light intensity as one of the independent variables but not cloud cover

Variation	R^2	Partial correlation coefficient	p
Day length	0.4176	0.530	<0.001
Light intensity	0.0887	−0.546	0.036
Total	0.5063		

(B) Analysis with cloud cover as one of the independent variables but not light intensity

Variable	R^2	Partial correlation coefficient	p
Day length	0.4176	0.600	0.001
Cloud cover	0.1440	0.707	<0.001
Number of birds	0.0884	−0.503	0.009
Temperature	0.0689	−0.563	0.003
Wind speed	0.0527	0.433	0.027
Total	0.7716		

NOTE: The table shows only those variables that entered the regression ($p < 0.05$).

TABLE 2. Results of the stepwise multiple linear regression analyses of the arrival times ($n = 30$) of Mourning Doves at their winter roost

(A) Analysis with light intensity as one of the independent variables but not cloud cover

Variable	R^2	Partial correlation coefficient	p
Day length	0.5170	0.684	<0.001
Temperature	0.1064	−0.314	0.010
Total	0.6234		

(B) Analysis with cloud cover as one of the independent variables but not light intensity

Variable	R^2	Partial correlation coefficient	p
Temperature	0.3209	−0.329	<0.001
Cloud cover	0.1364	−0.504	0.002
Total	0.4573		

NOTE: The table shows only those variables that entered the regression ($p < 0.05$).

Influence of environmental factors on arrival

The stepwise multiple regression using light intensity accounted for 62% of the variation in arrival time, whereas that using cloud cover accounted for 46% of the variation (Table 2). Our results show that arrival at the roost occurred later (*i*) on clear evenings and (*ii*) on cold evenings. The other independent variables did not enter the regression (at $p < 0.05$). Light intensity accounted for the largest part of the variation in arrival time. Temperature also had an important effect: it was the most important factor in the regression using cloud cover and the second most important in the regression using light intensity (Table 2). On average, arrival was 4 min later for every drop of 10°C.

Discussion

How was cold correlated with roosting times, and what does that tell us about the Mourning Dove's strategies to cope with cold? To generate answers to this question, it is necessary to consider dawn and dusk separately, as low temperature was not similarly correlated with activity at both times. In other studies, where the effect of cold was studied on both departure and arrival times, cold was always correlated with late departures and early arrivals (a decrease of activity at both ends of the day; see Zammuto and Franks 1981; Reebs 1986; Warkentin 1986). For Mourning Doves, cold did lead to late departures, but also led to late rather than early arrivals.

Later departures in the cold may reflect the adoption of a "heat loss minimizing" strategy in the first few minutes of the morning. Doves may be hesitant to leave advantageous microclimate conditions inside the roost. Although we did not measure conditions within the branches of the conifers, it seems likely that their dense structure offered substantial protection against winds and prevented exposure to the open sky. Another more intriguing possibility to explain delays in departure is related to a possible reduction in body temperature during cold nights. Ivacic and Labisky (1973) have reported that, in the two doves they tested, body temperature decreased by 2–4°C at night (at an ambiant temperature varying between −10 and −18°C), when the birds had been well fed, and by 5–10°C after a 24-h starvation period. It would be interesting to determine whether the nocturnal reduction in body temperature is greater in colder weather, and if so, whether it would then take more time for the birds to raise body temperature back to normal before becoming active again in the morning.

Late departures in the morning may also reflect successful foraging during the previous evening. If doves are successful at "stocking up for the night" (see below), then some of these reserves may still be available in the morning, allowing doves to slightly decrease their activity levels and foraging activity in the cold, at that time. Confirming this hypothesis will require precise measurements of food consumption and body reserves at different times of the day and at different temperatures.

Later arrivals at the roost in cold weather are suggestive of such an "energy-gathering" strategy in doves. The birds may need to spend more time feeding in the evening to gather the energy reserves necessary to survive the colder night, and thus they return later to the roost. Reserves can be gathered in the form of seeds stored in the crop and stomach. Armstrong and Noakes (1981) have reported fuller crops in doves wintering in Ontario than in doves wintering in New Mexico. For our study, it may be argued that a delay of only 4 min for every drop of 10°C does not represent a significant increase in food-intake opportunity, but one must remember that food is easy to find (in all likelihood, doves use bird feeders set up in residential areas) and that this species is renowned for its capacity to ingest food at a rapid rate (Terres 1982). For a bird that is at the northern limit of its wintering range, 4 min may very well make a difference.

Wind speed was included in the analysis to see whether wind chill had an effect. Wind speed did not correlate with arrival time and it explained only a small percentage of the variation in departure time. A low regression coefficient (0.007) indicated that departures were delayed only when wind speed was quite high. It is possible that daytime-foraging areas offered enough protection that the effect of wind speed was negligible. Similar results and conclusions have been reached in other studies (e.g., Reebs 1986; Warkentin 1986).

The effects of day length and light intensity (or cloud cover) were important (more than those of temperature) and were similar to those found in previous studies (e.g., Dunnett and Hinde 1953; Haase 1963; Hein and Haugen 1966; Davis and Lussenhop 1970; Raveling et al. 1972; Swingland 1976; Hubalek 1978; Reebs 1986). They shall not be discussed further here (for more details see Aschoff et al. 1970; Daan and Aschoff 1975). Nevertheless we should mention that light intensity was a better predictor of arrival time than was cloud cover, probably reflecting the greater precision of light-meter measurements and the fact that "cloud cover" does not differentiate between various cloud types and positions that can affect light intensity. In the morning, both light intensity and cloud cover were poor predictors of departure time, probably because the doves left the roost well before sunrise, when light intensity was low and did not vary much from day to day.

These early departure times of the Mourning Dove, irrespective of the variation correlated with environmental factors, are interesting when compared with those of the black-billed magpie (*Pica pica*), a species with slightly greater body mass that also winters in Canada. In Edmonton, magpies face colder and shorter days and have less reliable food sources than do doves in Moncton and yet they leave the roost later than doves and return to it earlier (by about 15 min on average (see Reebs 1986)). This may reflect the need for doves to forage more in order to counter high thermoregulatory expenditures that are exacerbated by poorer anatomical and behavioural adaptations to cold. It would be interesting to compare the roosting times of Mourning Doves wintering in Canada with those of other species of similar mass or with other dove populations that winter farther south. Comparing the metabolic rates of these different species or populations under various conditions of food availability would yield complementary information.

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