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ECOLOGICAL ASPECTS OF SLEEP IN BLACK-BILLED MAGPIES

by

STEPHAN G. REEBS

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled ECOLOGICAL ASPECTS OF SLEEP IN BLACK-BILLED MAGPIES submitted by STEPHAN G. REEBS in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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Abstract

Black-billed magpies (*Pica pica*) generally sleep in groups outside their breeding season. Because large aggregations of birds may attract predators, and because winter nights often are a time of thermal stress, magpies can be expected to exhibit great care, and therefore predictable consistency, in their choice of where, when, and how to sleep. To determine whether such a choice is indeed predictable and compatible with avoidance of predation and thermal stress in this species, I conducted a 2 yr observational study of roosting in populations of magpies living in or near the City of Edmonton, Alberta.

The first evidence of communal roosting was recorded in July-August. The birds roosted in dense (10870-14910 trees/ ha) thickets of deciduous trees (mainly *Populus* spp). The roosts were used inconsistently until permanent snow cover was established (October-November). Thereafter, and until the peak (February-March) and end (March-April) of the communal roosting season, magpies regularly spent the night in dense (2200-14900 trees/ ha) stands of spruce trees (*Picea glauca*). The presence of a dense network of branches was a common feature of both deciduous and coniferous roosts; perching in dense networks of branches may represent an adaptation for avoidance of nocturnal avian predators such as great horned owls (*Bubo virginianus*). Two additional features of the coniferous roosts were extensive (>50%) overhead cover and a greater than 70% reduction of wind speed within the roosts. Extensive overhead cover is known to prevent radiative heat loss to the open sky, while reduced exposure to winds diminishes convective heat loss. The choice of conifer stands for roosting thus appears to be linked with avoidance of thermal stress.

Multiple regression analysis on the times of departure and arrival of magpies at a rural roost revealed that these birds left the roost significantly later, relative to morning civil twilight, and returned to it significantly earlier,

relative to sunset, (1) on longer days, (2) on colder days, (3) on darker, cloudier days, and (4) when fewer birds were using the roost. The most marked effects were those of daylength on both departure and arrival, temperature on arrival, and light intensity on departure. The influence of daylength suggests that the magpies were trying to counteract the effect of seasonality on their activity time, whereas the effect of temperature supports the contention that magpie roosts provide advantageous micrometeorology conditions and that the birds may react to cold by spending more time in them.

Magpies fluffed up their feathers and tucked most of the head under the scapular feathers when sleeping at night, especially in winter. In this posture, the shape of the body approximated that of a sphere, and unfeathered body parts were covered. Magpies spent more time in this posture as ambient temperature decreased, most likely a behavioural adaptation for thermoregulation. They did not react to visual stimuli while in this position, but were sensitive to surrounding noises. This is a possible adaptation to detect approaching predators more effectively in dark, densely vegetated places such as their natural roosts. In two out of three trials in an artificial roost, dominant individuals preferred to perch in a central position relative to their flockmates.

The seeking by magpies of sleeping places where predation risk and thermal stress are minimized can be seen as the appetitive phase of a "sleep instinct". Similarly, the adoption of a sleeping posture compatible with thermoregulation and the subsequent act of falling asleep can be seen as the consummatory act of such an instinct. According to new "ecological theories" on the function of sleep, the adaptive significance of this instinct is to ensure that the animals who possess it remain in a state of inconspicuous, energy-saving immobility at night.

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Table of Contents

Chapter Page

List of Tables

List of Figures

I. INTRODUCTION

Avian sleep has been, over the years, the subject of considerable research (see Goodman 1974, for a review). Most of this work, however was directed only at describing, via laboratory studies, the various physiological facets of sleep in birds. Until recently little attention had been paid to the ecological aspects associated with sleeping birds. To remedy this situation, efforts have been devoted lately to the observation of bird sleep as it occurs in the wild and to the investigation of how the sleeping behaviour of birds is influenced by environmental characteristics. As a result, it was shown that ecological factors such as weather conditions, risk of predation, and presence of conspecifics influence where, when, and how birds sleep in nature (see notably Swingland 1976,1977; Balda et al. 1977; Gyllin et al. 1977, Amlaner and McFarland 1981; Lendrem 1983b, 1984; Ball et al. 1984). These findings point to a precise organization of avian sleep in space and time, and to the importance of considering ecological factors in any attempt to explain such organization (Amlaner and Ball 1983).

The consistency shown by many bird species in always choosing the same type of sleeping site, and the long distances over which they often move in order to reach such suitable sites, illustrate the precise spatial organization of avian sleep. Examples of such precision include Andean hummingbirds (*Oreotrochiles estella*) regularly sleeping in caves, sometimes travelling distances of up to 120 km to reach them (Pearson 1953, Morse 1980); sandhill cranes (*Grus canadensis*) on their migration trip almost always spending the night in open expanses of shallow water (Lovvorn and Kirkpatrick 1981; Kessel 1984); jackdaws (*Corvus monedula*) being very reluctant to roost anywhere but in urban parks, despite heavy human persecution and the prospect of having to commute to feeding grounds 30 km away (Gyllin and Källander 1976); bald eagles (*Haliaeetus leucocephalus*) sleeping preferentially in tall defoliated trees located in areas 10-20 km away from their food sources (Keister and Anthony 1983, and references therein); and assemblages of starlings (*Sturnus vulgaris*) and blackbirds travelling more than 30 km to roost daily in various places all characterized by a good overhead cover (Brown 1946; Jumber 1956; Francis 1976; Kelty and Lustik 1977; Lyon and Caccamise 1981). The two ecological factors usually invoked to explain such sleeping site selection are avoidance of adverse weather conditions and protection from predators. Avoidance of bad weather is of direct relevance to species having to cope with harsh winter conditions (Moore 1945, Morse 1980), whereas protection from predators, although of importance to most bird species, is often invoked in discussions of communally roosting birds (Lack 1968) because of the ambiguous consequences of localized aggregations in both attracting (Zahavi 1971) and facilitating escape from (Siegfrid and Underhill 1975, Krebs and Davies 1981) potential predators.

The long travelling involved in commuting between the roosting place and the feeding grounds may represent a substantial part of a bird's time budget, especially at northern latitudes where winter days can be of short duration (Gyllin and Källander 1976). Therefore, precise timing of sleeping periods is important, as any undue delay in the morning flights from the roost could result in the loss of foraging time, whereas undue delays in the evening flights to the roost could result in the birds being overtaken by darkness before reaching their destination. Several environmental factors could determine the most appropriate moment to travel. Light intensity, for example, is known to play an important role in determining when birds enter or leave the roost (Davis and Lussenhop 1970; Krantz and Gauthreaux 1975; Hubalek 1976; Swingland 1976). Other environmental factors such as daylength (Brown 1946) and temperature (Brodsky and Weatherhead 1984) may also modify the exact timing of arrival and departure relative to sunset and sunrise. Birds roosting in winter should be most sensitive to these factors, as very low temperatures put increased energetic demands on them while reduced daylength limits their opportunities for foraging, possibly forcing them to return to the roost only at the last moment.

The sleeping behaviour (sleeping patterns and postures) of birds may be equally influenced by ecological factors. Predation pressure is one of these factors. By lowering its sensitivity to environmental stimuli during sleep, a bird exposes itself to an increased risk of predation. To counter this, birds can use adaptive strategies such as periodic awakening bouts during which they can scan their surroundings for the presence of predators (Lendrem 1983a). They can also try to occupy central positions in a communal roost where peripheral individuals act as a buffer against predation (Lendrem 1983b; Weatherhead 1983). Temperature is another important environmental parameter since it can determine which sleeping posture will be adopted by a bird for thermoregulatory purposes. This may even conflict with the need for vigilance in cases where a good thermoregulatory posture is incompatible with the visual detection of an approaching predator (for example, when the eyes are covered by the scapular feathers). Only a few studies (e.g. Lendrem 1984; Weatherhead and Hoysak 1984) have investigated the influence of predation pressure and weather conditions on the sleeping behaviour of birds. Given the points raised above, it appears particularly useful to study a species that roosts communally under a wide range of temperature conditions.

It is with these considerations in mind, namely (1) that birds ought to, and indeed seem to, exhibit great care in the choice of where, when, and how they sleep in the wild, (2) that ecological factors are likely to influence that choice, and (3) that some of these factors could, in all likelihood, be easily identified in species roosting communally under winter conditions, that I report in this thesis on the roosting behaviour of black-billed magpies (*Pica pica*) in central Alberta. The range of this corvid extends from Alaska to central California and western Texas (Linsdale 1937) and, as far as is known, the species is non-migratory. Black-billed magpies are thus present in Edmonton and its surroundings in winter. They are known to roost communally, although most reports are somewhat anecdotal (e.g. Linsdale 1937; Ward 1952; Gyllin and Källander 1977; Mugaas and King 1981). Where not strongly persecuted by man, they are approachable and easily observed. Moreover, good documentation exists on their behaviour (e.g. Goodwin 1952; Baeyens 1979, 1981; Vines 1981; Buitron 1983,1984), ecology (e.g. Holyoak 1974; Bock and Lepthien

1975; Goodwin 1976; Loman 1980; Tatner 1982a,b), and physiology (e.g. Mugaas and King 1981; Hayworth and Weathers 1984). The goal of my research was to add to the knowledge of the biology of this species by finding where, when, and how magpies roost in winter, determining how predictable such actions are, and identifying the ecological factors that could be influencing these actions in a proximal (causal) and/or ultimate (evolutionary) way.

This thesis is divided into three papers. The first (Chapter II) addresses the question of where magpies roost, and also gives a general account of the magpie's roosting behaviour. It is based on observations and measurements made at six roosting sites located in the city of Edmonton. The results comprise quantitative data on the habitat features of the roosts and on the seasonal fluctuations in numbers of roosting magpies, along with a qualitative description of the pre-roosting and post-roosting behaviour of the birds. The paper also discusses how both avoidance of adverse weather conditions and protection from predators can account for the nature of the habitat selected by magpies for roosting.

The second paper (Chapter III) is concerned with the question of when magpies roost. It deals with the timing of magpies' roosting flights in relation to weather and light conditions. It is based on observations made at a large, easily-monitored roosting site located in a rural area near Ellerslie, about 7 km south of the City of Edmonton. This paper emphasizes energetic stress as one of the main factors affecting the timing of roosting flights.

The third paper (Chapter IV) deals with the question of how magpies sleep, or more precisely the way in which a magpie's behaviour during the night relates to weather, the bird's position within the roost, and its dominance status. As it is practically impossible to observe magpies at night in the wild without disturbing them, this part of the study was carried out in an outdoor aviary near Ellerslie, using a blind with a one-way window and infrared vision equipment. The results are discussed mainly with reference to thermal stress and predator avoidance.

A short concluding discussion to the thesis (Chapter V) emphasizes the ultimate (evolutionary) way in which ecological factors may influence the sleeping behaviour of magpies, as it reviews the results of the previous chapters in the light of the few "ecological theories" (e.g. Allison and van Twyver 1970; Meddis 1975, 1977) put forward to explain the function of sleep in animals.

An extensive body of literature exists on avian communal roosting (see Allen and Young 1982, for an excellent annotated bibliography) and over the years a vocabulary specific to the description of roosting behaviour has been developed. The meaning of some words, however, is not always consistent among publications. Throughout this thesis, the terms "roosting" and "communal roosting" are used interchangeably, and are meant to describe situations in which five birds (the modal size of a winter flock of magpies) or more spend the night in close proximity, i.e. within about 100 m of each other (after Baeyens 1981). The term "roost" is used to designate the parcel of habitat where an aggregation of birds sleep, and not the aggregation itself. Finally, a "roosting site" is to be understood as a broader area over which a group of birds gather and perform pre-roosting activities before splitting up and descending to one or several roosts encompassed by the area.

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II. ROOSTING BEHAVIOUR AND CHARACTERISTICS OF ROOSTING SITES OF BLACK-BILLED MAGPIES IN EDMONTON, ALBERTA

INTRODUCTION

Despite the persecution this species regularly suffers at the hands of man, the black-billed magpie (*Pica pica*) has long been recognized as an opportunistic beneficiary of human settlement (Linsdale 1937, Salt and Salt 1976). Its presence around human habitations seems to have been limited at first to rural farming areas (see Kalmbach 1927). Over the last few decades however, increasing numbers of magpies have also established themselves in urban environments, in both Europe (Tatner 1982a,b) and North America. Today, the magpie is present year-round in many urban parks and suburban residential areas, where it finds appropriate nesting trees in summer, and an abundance of food sources resulting from human activity (e.g. garbage, bird feeders) that help it survive, particularly in winter.

Habitat requirements of the magpie also include suitable roosting cover. Rural populations of magpies have been reported to roost communally in dense thickets of young trees or scrub (Goodwin 1976) but little is known of the sites used by urban individuals for roosting. The behaviour of magpies at the roost is also poorly documented. Knowing the characteristics of a bird's roosting behaviour may help us infer the selective pressures it faces during the night (Balda et al. 1977), some of which may prompt responses that are applicable only in urban areas (see for example Gyllin et al. 1977).

In an attempt to learn more about the roosting behaviour of the black-billed magpie in an urban environment, I conducted an observational study at six roosting sites located in central Edmonton, Alberta, over a period of two years. This paper reports on these observations, giving a description of the seasonal use of the roosting sites, the habitat characteristics of the roosts, and the general behaviour of magpies at these sites.

STUDY AREA AND METHODS

Edmonton (113°30'W, 53°30'N) is a city of about 660000 inhabitants. It receives on average 314.4 mm of rain and 132.1 cm of snow annually. Average daily minimum and maximum temperatures are -19°C and -10°C in January, and 12°C and 23°C in July. Sub-freezing night temperatures occur regularly from October to April. Day duration (sunrise-sunset) decreases from a maximum of 17.0 h in June to a minimum of 7.5 h in December.

In Edmonton, magpies are found mostly near the North Saskatchewan River which crosses the city from southwest to northeast. The adjacent river valley is 1.0-1.5 km wide, 50 m deep, and consists mainly of steep wooded slopes and flat open spaces. White spruce (*Picea glauca*) and quaking aspen (*Populus tremuloides*) are the main tree species in the valley. Some balsam poplar (*Populus balsamifera*) and paper birch (*Betula papyrifera*) are also present. The main shrub species are hazelnut (*Corylus cornuta*), chokecherry (*Prunus virginiana*), pincherry (*Prunus pensylvanica*), thinleaf alder (*Alnus tenuifolia*), and wild rose (*Rosa acicularis*).

I restricted my study to the south side of the river between Whitemud Creek and Mill Creek (Fig. II-1). From November 1983 to April 1985 I followed magpies from their daytime ranges to their roosting sites, herein defined as the general areas where the birds gathered and performed various activities before going to roost. Six sites were found and studied: two (Mill and Whitemud) were on the slopes of the ravines at Mill and Whitemud Creeks, two (Mayfair and Strathcona) were on the slopes of the river valley itself, and two (Windsor and Grandview) were in or at the edge of residential areas (Fig. II-1). I witnessed the behaviour of the magpies as they arrived at these sites in the evening and departed from them in the morning on numerous occasions throughout the study. I also made late evening visits (12) to the roost at Grandview in the fall of 1984, and at Strathcona (12) in the winters of 1983-84 and 1984-85. Finally, I conducted morning counts of the departing magpies about once a week in the winters of 1983-84 and 1984-85 at Mill Creek, Windsor, and Mayfair, and in the fall of 1984 at Mill Creek and

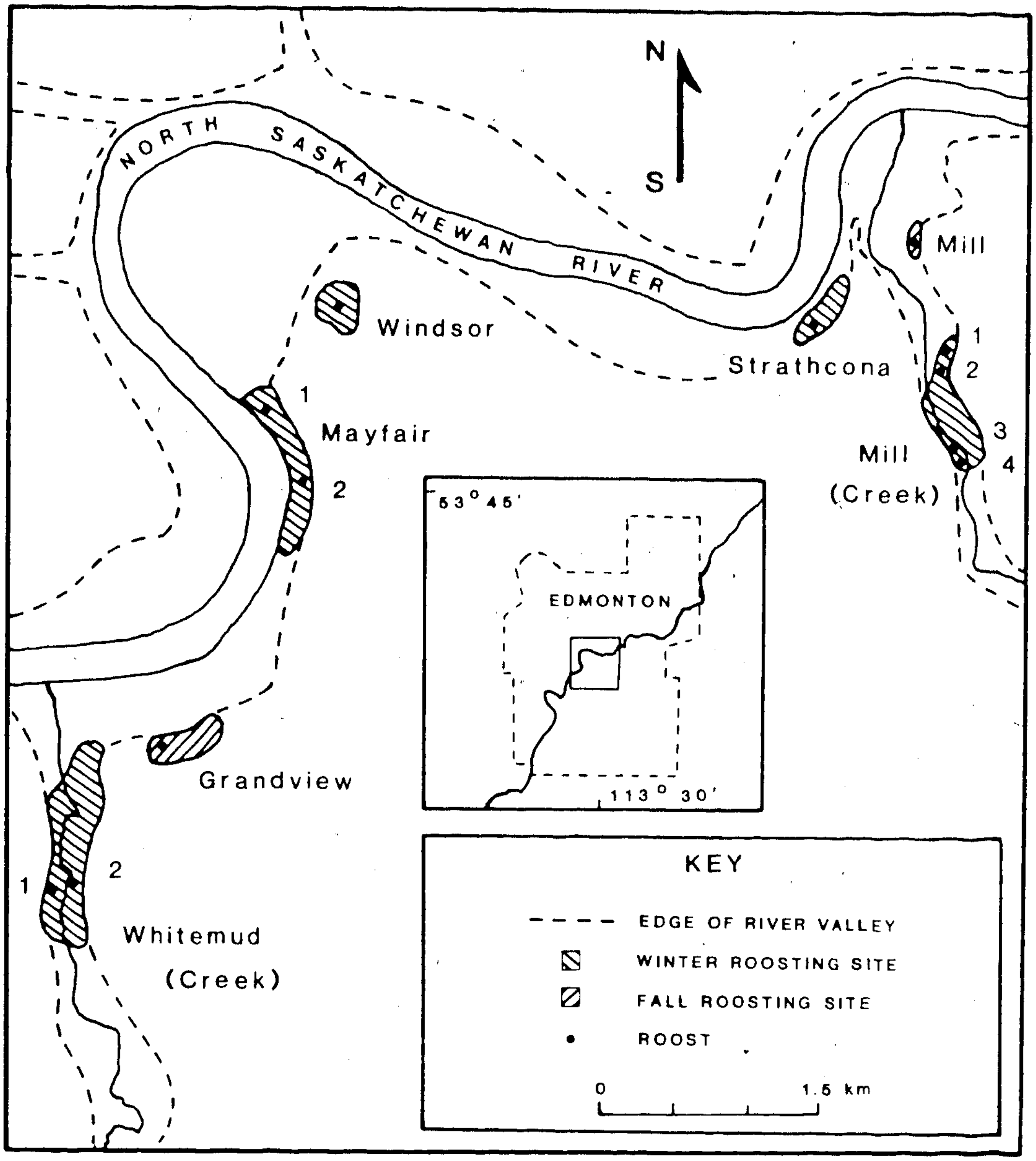

FIG. II-1: Location of the study area and the magpie roosting sites in central Edmonton, Alberta.

Grandview.

The magpies did not spend the night distributed uniformly throughout the roosting sites. Instead they occupied one or several well-delimited small parcels of habitat located within the sites. These "roosts" were dense deciduous thickets in the fall and stands of spruce trees in winter. I conducted habitat analyses at all the roosts I found (two fall roosts and nine winter roosts). The measured topographical features were horizontal surface area, slope inclination and exposure, and altitudinal position (top, middle, or bottom third) along the slope. The rest of the habitat analysis procedure differed according to the nature of the roosts.

In the deciduous thickets, only tree density, height, and DBH were measured. I used the point-centered quarter method (Cottam and Curtis 1956) to estimate tree density, using a total of 21 sampling points along seven equidistant parallel transects (three points at 10 m intervals on each transect line). Only trees over 2 m high were considered. The four trees measured at each sampling point were used to estimate mean tree DBH and height.

More attention was given to the conifer stands, as all trees present in the stand and higher than 2 m were counted and measured for height and DBH. Tree density was calculated by dividing the total number of trees by the horizontal surface area. The number of lateral branches longer than 15 cm in the bottom 6 m was noted for each tree. I also recorded the number of trees present within 1 m of each measured tree. The lower boundary of the living canopy was estimated by averaging, for all trees, the height of the lowest 1 m interval that had at least five branches bearing needles. Percentage of coniferous canopy cover was estimated visually (in classes 0-10%, 10-20%, etc.). Many spruce trees had abundant droppings on their branches and on the ground around the trunk. These trees were assumed to be the ones used by magpies for roosting. When measuring such a "roost tree", I recorded the height of the highest branch bearing droppings, and noted the directional distribution of droppings and branches around the trunk. These parameters were used to infer the positions occupied by the birds in the roost trees.

At both fall and winter roosts, slopes and tree heights were measured with the aid of an Abney level, and all measurements of direction were made with a compass. Wind speed was measured at a height of 3 m with the aid of a portable hand-held vane anemometer (Negretti and Zambra Inc.). Continuous recordings of temperature were made simultaneously inside and outside one of the roosts in Whitemud Creek (see below) using three Wilheim Lambrecht hygrothermographs, each one positioned at a height of 3 m against the bole of a spruce tree.

RESULTS

Seasonal roosting activity

In 1984 the first signs of communal roosting activity following the breeding season occurred at Grandview in early July. At that time the young magpies were 5-7 weeks old and were still moving in family groups of 4-6 birds. Many of these groups gathered at dusk, in preparation for spending the night together in a dense thicket of young aspen located on a flat expanse of terrain between residential homes and the edge of the river valley. At this time, many crows (*Corvus brachyrhynchos*) were also using the same thicket as a roosting place (the number of crows present at the roost increased steadily from 12 on 18 July to more than 300 on 1 October, the date on which they all evacuated the roost for what appeared to be the onset of their fall migration). The number of magpies using this roost from July to October fluctuated between 0 and 116 (Fig. II-2B). I often saw magpies spending the night in small clumps of trees outside the roosting site. Such groups of birds may have been alternating between roosting in the thicket and spending the night by themselves outside it. This may explain in part the fluctuations in the number of roosting birds.

The fall roost at Mill Creek was a dense thicket of paper birch, balsam poplar, and various shrubs. It was located on the west-facing slope of the creek ravine. As at Grandview, the number of roosting magpies varied

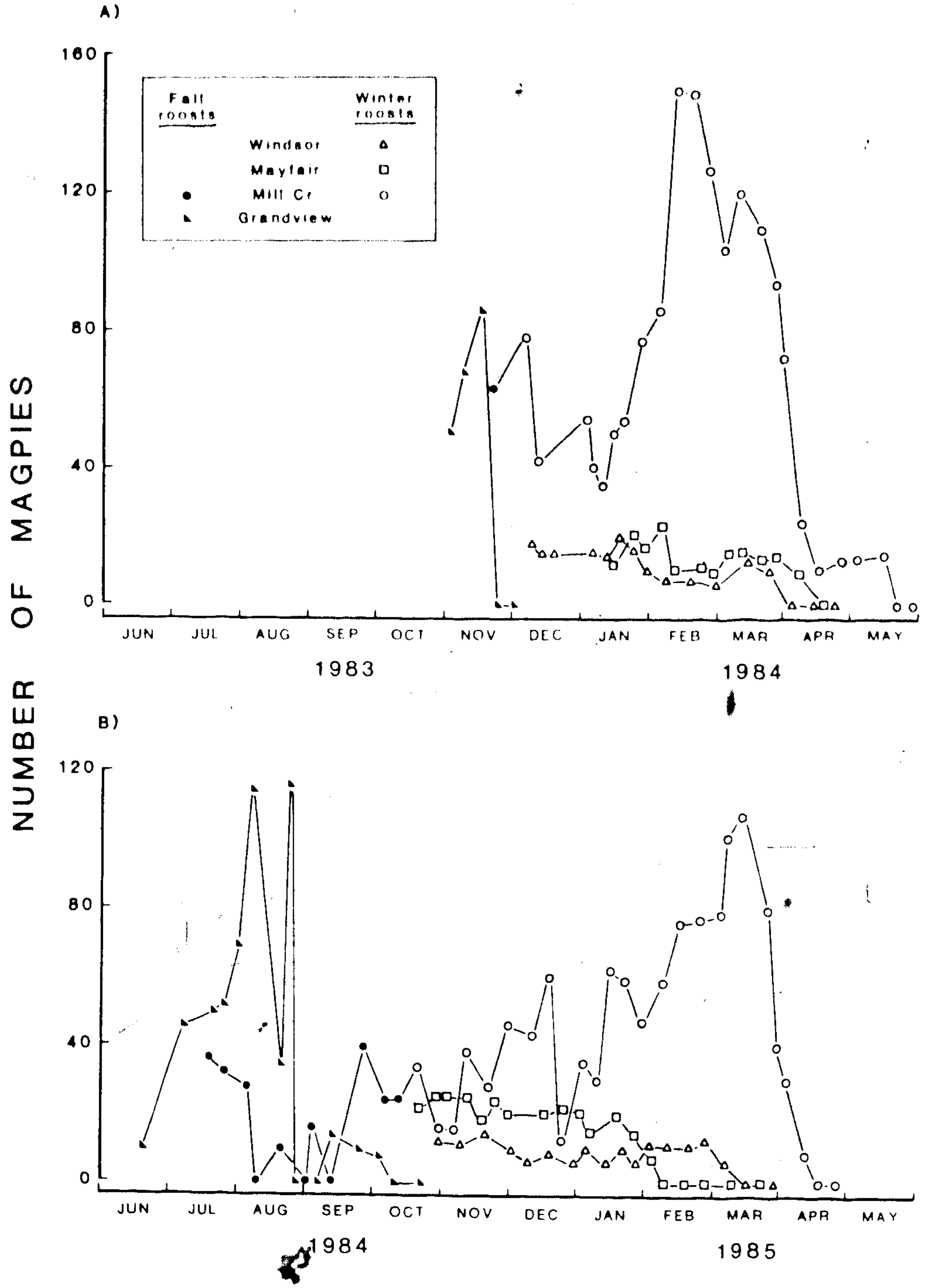

FIG. II-2: Number of magpies at four roosting sites in Edmonton, Alberta, from November 1983 to April 1985.

considerably from week to week throughout the fall (Fig. II-2B) but never exceeded 40. Many magpies were observed spending the night in small groups of 2-5 individuals elsewhere along the creek ravine. No crows were observed roosting in that ravine.

These two roosts were first found at the onset of winter the previous year (more precisely during the first week of November, 1983). At the time, 50-86 magpies were present at each site (Fig. II-2A). All trees were then leafless. Only after a snowfall that, on 20 November, left a permanent snow cover on the ground, did the magpies abandon the two fall roosts in favour of coniferous roosts. In 1984, permanent snow cover came exceptionally early (16 October) coinciding with the end of leaffall and the movement of magpies to the coniferous winter roosts. In both years, the establishment of a permanent snow cover was accompanied by a decrease of about 5°C in night temperatures (the nightly lows varied between 0 and -5°C before the snowstorm, and between -5 and -13°C during the first few days following it).

The roosting populations at the winter sites were either small and stable to slightly decreasing in numerical size (Windsor and Mayfair, Fig. II-2, A and B), or large and generally increasing in size (Mill Creek, Fig. II-2, A and B). Most birds at Windsor moved in and out of the roost in twos, suggesting paired adults as the main occupants. At Mill Creek and Mayfair, most birds were moving in flocks, and, since both adults and juveniles may be present in flocks at a roosting site, no inference can be drawn concerning the age structure of the roosting population at these sites. Differences in adult and juvenile body characteristics are minimal (Scharf 1985) and do not enable differentiation in the field unless the birds are captured.

The data from Mill Creek suggest two annual peaks in the number of roosting magpies (Fig. II-2, A and B). The first appeared to occur in December of both years. The reality of this "winter" peak, however, is questionable because of the relatively small numbers of birds involved and the absence of regular counts in the early part of the 1983-84 winter. Yet, since a winter peak was clearly observable at a roost site located outside of the city

(Chapter III), I believe the phenomenon to be real and widespread. A second peak was recorded in February of 1984 and March of 1985, involving maxima of 150 and 108 magpies respectively. In both years, this "spring" peak was followed in late March-early April by a steady decline in numbers using the roost site. Magpies in Edmonton initiate laying during the last two weeks of April (Hochachka 1985), by which time almost all winter roosting sites were empty. The only exception occurred at Mill Creek in 1984, where a small flock of 15 individuals (possibly non-breeding yearlings) kept on using one of the roosts until mid-May (Fig. II-2A).

Communal roosting does not appear to be an obligatory activity, as I have seen magpies, in both fall and winter, spending the night singly or in pairs, away from regular roosting sites. Those magpies were perching in dense clumps of aspen or spruce outside the river valley, and may have been adults roosting on their usual breeding territories (C. Scharf, pers. comm.).

Magpies can also abandon one roost for another when repeatedly disturbed. This happened at the Strathcona site where my nocturnal visits to a roost on several occasions in December of 1983 resulted in its total desertion by magpies for the rest of the season.

Habitat features at the roosts

Tree density at the fall roosts in Grandview and Mill Creek was estimated at 14511 and 10873 trees/ha respectively. The trees averaged 6.1 and 5.1 m high, and 5.9 and 5.2 cm DBH at the same respective sites. Few trees were taller than 8 m.

The conifer stands used by magpies in winter (Tables II-1 and II-2, Fig. II-3) consisted of tall (average height = 10.5 m) and slim (average DBH = 10.2 cm) spruce trees whose crowns intermeshed to provide a good overhead cover. Presumably because of this cover, the lower half of these trees was totally defoliated, leaving an extensive array of dead branches on which the birds could perch (Fig. II-3). Some deciduous trees and small spruce snags were also present in the roosts but did not appear to be used by magpies

TABLE II-1: Topographic and vegetative features of nine winter roosts used by magpies in Edmonton, Alberta.

ROOST	SLOPE			AREA	TREE/0.1 ha		COVER	
	inclination	facing[1]	roost altitude	(m^2)	total	living spruce	%	height[2] (m)
Whitemud 1	39°	45°	middle	140	1490	900	85	4.1
Whitemud 2	28°	290°	middle	138	1280	510	75	7.4
Mayfair 1	0°	(216°)	bottom	139	470	260	55	5.5
Mayfair 2	25°	232°	top	291	360	270	55	6.4
Strathcona	20°	325°	top	244	480	330	65	4.3
Mill 1	16°	264°	middle	169	330	240	75	5.4
Mill 2	21°	288°	middle	239	300	250	65	7.3
Mill 3	30°	44°	bottom	540	220	180	75	6.3
Mill 4	28°	52°	bottom	158	430	300	75	5.2

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[1] 0°=north, 90°=east, 180°=south, 270°=west.

[2] Lower boundary of living canopy.

TABLE II-2: Characteristics (means ± 1 S.D.) of roost and non-roost trees (living spruce only) at nine winter roosts used by magpies in Edmonton, Alberta.

ROOST	DBH (cm)		HEIGHT (m)		T1M[1]		BRANCHES[2]		HHBD[3]		n	
	roost	non roost	roost	non roost	roost	non roost	roost	non roost	roost	non roost	roost	non roost
Whitemud 1	7.42 ±2.75	6.30 ±3.82	8.06 ±1.81	6.49 ±2.71	5.1 ±2.1	4.3 ±2.2	89.0 ±15.5	[illegible] ±16.6	4.06 ±0.90	–	59	67
Whitemud 2	10.75 ±4.17	11.84 ±5.86	12.06 ±3.37	12.43 ±4.40	4.7 ±2.3	4.7 ±2.3	87.4 ±22.1	80.5 ±21.8	5.33 ±1.02	–	30	40
Mayfair 1	11.86 ±3.22	10.20 ±3.42	11.00 ±2.49	9.40 ±3.52	1.6 ±0.6	1.2 ±1.3	88.1 ±21.0	83.0 ±26.7	4.63 ±0.74	–	11	25
Mayfair 2	9.93 ±3.85	11.48 ±5.63	10.56 ±3.19	11.50 ±4.59	2.0 ±1.4	1.4 ±1.4	57.7 ±15.2	55.7 ±15.1	5.63 ±0.86	–	20	59
Strathcona	11.58 ±4.65	10.75 ±4.20	8.80 ±2.49	8.21 ±2.95	1.1 ±0.9	1.4 ±1.0	71.4 ±19.7	54.1 ±15.0	4.58 ±0.76	–	26	55
Mill 1	13.46 ±5.26	12.63 ±5.69	11.45 ±3.21	10.82 ±4.08	0.7 ±0.9	1.0 ±1.1	77.4 ±17.1	73.5 ±15.3	5.86 ±1.20	–	25	16
Mill 2	12.20 ±4.78	13.58 ±6.09	12.43 ±4.17	12.91 ±4.88	0.7 ±0.8	0.6 ±0.6	60.1 ±16.0	61.1 ±18.7	7.22 ±1.41	–	46	18
Mill 3	15.58 ±6.17	13.03 ±7.41	13.72 ±4.27	11.32 ±5.64	0.7 ±0.8	0.6 ±0.6	72.1 ±21.3	68.7 ±19.2	7.04 ±1.44	–	46	50
Mill 4	11.57 ±6.77	10.18 ±8.60	9.99 ±3.75	8.62 ±5.59	2.1 ±1.2	1.5 ±1.0	80.0 ±17.2	83.1 ±11.6	5.25 ±1.41	–	14	33
mean[4]	11.43	10.61	10.93	9.79	2.3	2.2	75.4	69.9	5.63			

[1] T1M= number of trees within 1 m of measured tree.
[2] BRANCHES= number of branches in the lowest 6 m.
[3] HHBD= height of highest branch bearing droppings (m).
[4] Pooled data.

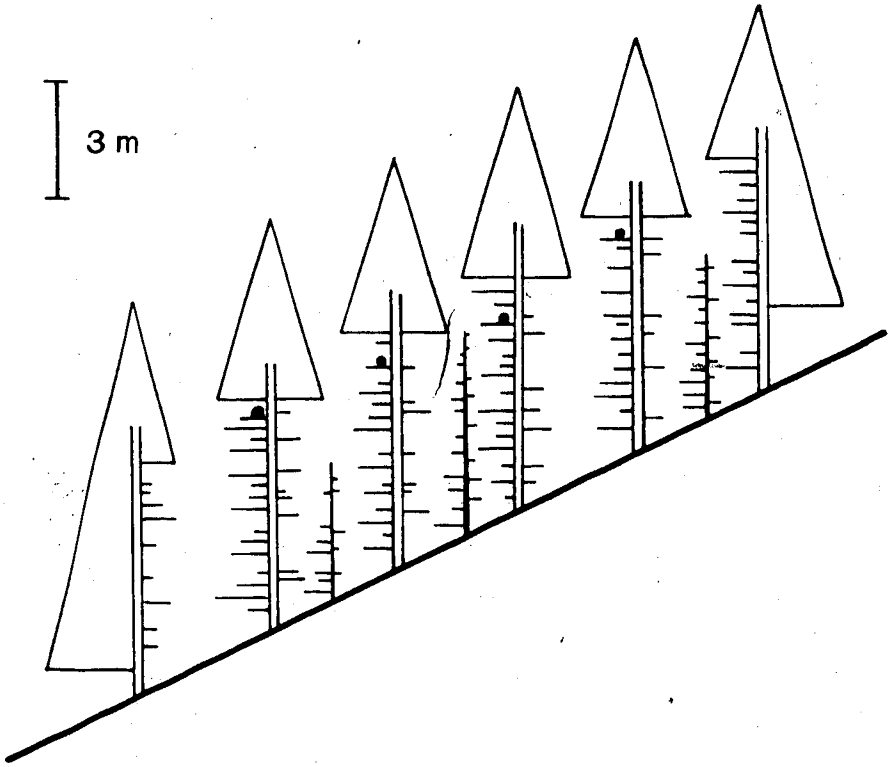

FIG. II-3: Schematized structure of the coniferous stands used by magpies for roosting in the North Saskatchewan River Valley in Edmonton. Black dots show the locations where roosting birds were most likely to be found.

for perching, as no droppings were found on or below them. Total tree density varied from 2200 to 14900 trees/ha but was mostly within the 3000-5000 trees/ha range. Living spruce trees composed an average of 67.2% of the total. With the exceptions of Whitemud 1 and Windsor (see below), all the roosts were similar in general appearance, and had trees of comparable average height and DBH. They were characterized by a canopy cover greater than 50% and by a dense network of bare branches amid which the magpies could perch.

The first exception, Whitemud 1, was a stand of younger and smaller conifers (Table II-2). This roost, however, still displayed the characteristics mentioned above, as the degree of canopy cover and of tree density proved to be the highest of all the roosts (Table II-1). Dead branches were also very abundant in the lower part of this roost (Table II-2). The second exception, Windsor, was a roost located in a residential area. No extensive coniferous stands were present there, but the area included many spruce hedge rows (22 clumps or rows of three trees or more in a 4.03 ha area). The magpies roosted within these hedge rows. Good cover and an intricate network of branches could be found within the hedge rows, as a dense growth of needles was born by the topmost branches and by the outer third of the lower branches, leaving the innermost part of the trees with numerous bare, branching limbs.

I compared roost trees (living spruce bearing droppings) and non-roost trees (living spruce not bearing droppings) within the roost. The comparison included DBH, height, the number of neighbouring trees within 1 m, and the number of branches born by the lowest 6 m of the trunk (Table II-2). For all four parameters and in all roosts, the distribution of the values for the two populations were largely overlapping. In the majority of roosts however, the mean number of neighbouring trees (6 of 9 roosts, $P=.25$, one-sided Sign test) and the mean number of branches born in the lowest 6 m (7 of 9 roosts, $P=.09$, one-sided Sign test) was higher in the population of roost trees than in that of non-roost trees, suggesting that magpies may prefer the densest part of a roost, and those trees with the greatest number of branches.

The magpies occupied those parts of the roost trees with the longest and most numerous branches. Droppings were found only on the side of the trunk where the branches were the longest and the most numerous, never on the other sides. Thus, the distribution of droppings (roosting birds) around the trunk was not exactly proportional to the quantity of perches but rather was a function of perch quality. This latter attribute may have been either the density of surrounding branches, or their orientation, as the longest and most numerous branches were almost always on the downslope side of the trees (probably a result of the greater illumination received from the direction in which the slope was exposed). Figure II-3 schematizes the structure of the winter roosts and indicates the most common location of the roosting magpies.

Except at Windsor, all winter roosts were located within the river valley or its tributary creeks. These are the only places in the city where dense conifer stands can be found. Such a location has implications for the microclimatology of the roosts, especially in terms of temperature and exposure to the wind. As in many other river valleys, temperatures tend to be colder and winds tend to be weaker in the valley of the North Saskatchewan River than in the rest of the city above it (Klassen 1962; Paterson and Hage 1979). Strong inversions commonly occur at night, which means that temperatures are often 2-6 °C higher near the top of the slopes than near the bottom. Based on this alone, one would expect birds to roost preferentially at the top of slopes. Yet, seven of the nine winter roosts in my study area were not found in such a location. Because of their patchy distribution, coniferous stands were not always available at all altitudes on the slopes, and this may have limited the birds' choice. At one site however (Whitemud 2), a coniferous stand extended from top to bottom, yet the roost in it was not located at the top of the slope but rather in the middle. Twenty days of continuous temperature recording at this site in February 1984 showed that the birds would indeed have done better, in terms of exposure to warmer temperatures, by roosting higher on the slope (Table II-3). The difference in night temperature between the location of the roost at mid-slope and the higher area, however, amounted to only 1.3°C. Furthermore, in terms of exposure to wind, roosting higher on the slope would have been disadvantageous, as the top area did not afford as much shelter from strong winds as the lower positions (Table II-4). By roosting in the river valley, and more precisely at mid-slope, magpies seem to have been compromising between greatly reduced exposure to the winds and a somewhat increased exposure to cold temperatures.

All the winter roosts were located on slopes facing either eastward or westward. The north-facing slopes seemed to be avoided in my study area, although such slopes were occupied by roosting magpies in other places along the river valley (pers. observ.). The south-facing slopes were also avoided by roosting magpies, probably because such slopes are devoid of conifers in the river valley.

Behaviour of the magpies at the roosts

Magpies went to the roosting sites during the hour preceding sunset, flying very close to house roofs and tree tops on windy days, and as high as 30-40 m in fine weather. Their arrival was gradual although large flocks were sometimes involved (Fig. II-4A). The first birds to arrive at the site usually perched in conspicuous places such as tall dead trees or the top of tall spruce trees, where they were joined by the new arrivals. Vocalizations were infrequent and occurred mainly upon the arrival of the largest flocks. The perching birds limited their activities to occasional movements from branch to branch and to preening. Sometimes the whole group would descend to the ground and forage for a few minutes, or take off in response to a disturbance and circle a few times over the roosting site before returning to it. Notable exceptions to this quiet type of assembly took place on mild days at Mill Creek and Whitemud Creek (as well as at another large roosting site outside the city). All birds would then fly around the site or move about noisily at the top of trees, sometimes chasing one another in bursts of social

TABLE II-3: Average temperature (°C), 4-24 February 1984, at three different altitudes on the west-facing slope of Whitemud Creek, Edmonton.

Altitude above sea level (m)	Position in slope	Time (MST)			
		0800	1400	2000	0200
664	top	-5.4	2.7	-1.6	-4.3
649	middle[1]	-6.6	0.1	-3.4	-5.6
635	bottom	-8.4	1.3	-3.3	-6.6

[1] Location of a magpie roost

TABLE II-4: Wind speed at three different altitudes on a west-facing slope that was entirely covered by a coniferous stand in Whitemud Creek, Edmonton. The speed is expressed as a percentage of the wind speed that was recorded concurrently in an open field above.

Altitude above sea level (m)	Position in slope	Wind direction and speed (km/h) in the open		
		SE 24.4	NE 26.1	NW 19.4
664	top	28.7%	22.6%	33.0%
649	middle[1]	9.8%	8.4%	26.8%
635	bottom	4.9%	5.0%	29.9%

[1] Location of a magpie roost

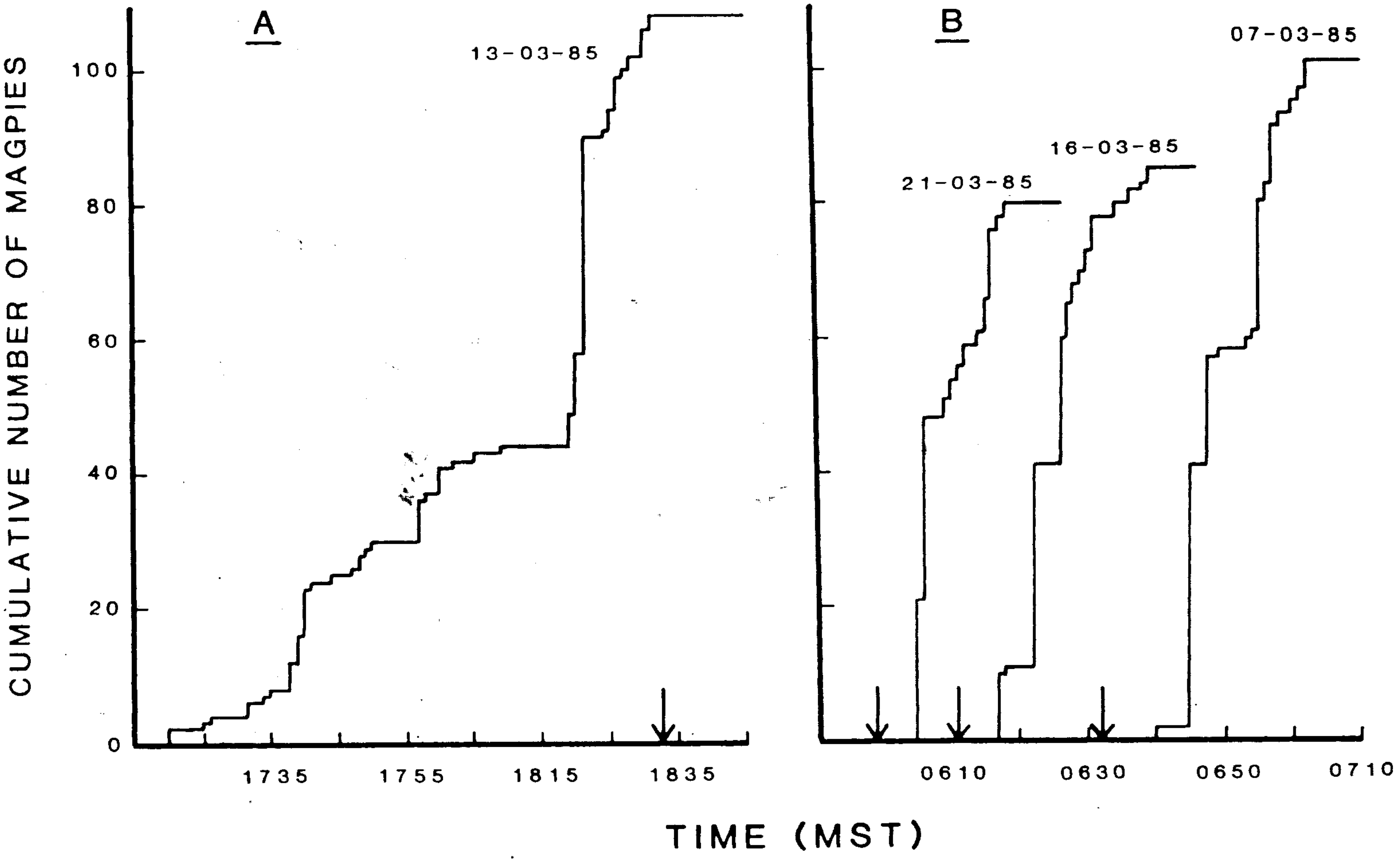

FIG. II-4: One example of arrival (A) and three examples of departure (B) of black-billed magpies at a roosting site in Mill Creek, Edmonton. Arrows indicate time of sunset in A, and times of morning civil twilight in B.

activity, a phenomenon that has also been reported for European magpies (Ward 1952). The onset of this group display would often be sudden, last for up to about 20 min, and usually end at sunset. I always witnessed it in the evenings, most frequently in the spring or on the first days of mild weather that followed long spells of cold temperatures.

At sunset, the group split up and each sub-group descended to the roosts. There, the magpies leisurely moved from branch to branch, in silence. Perching birds appeared not to allow other individuals to roost in the tree they were occupying, or even in the neighbouring trees. Likewise I never saw magpies huddling, even on evenings when the temperature was as low as -23°C. In contrast I did observe some aggressive interactions in which a magpie would chase away another conspecific that had landed in a tree next to the one occupied by the aggressor. Such behaviour resulted in a clear horizontal component in the spatial distribution of roosting magpies. Although roosting height may vary among individuals from 3 to 8 m in a given roost on a given night, the fact that the magpies tended to spread out over the roost and that no more than one individual occupied a given tree ensured that the dispersion of roosting birds was roughly uniform in a horizontal plane. Inter-individual distances (to nearest neigbour) varied between 5 and 50 m.

All activity ceased by civil twilight (sun 6° below horizon), that is 34-43 min after sunset. At that time, the magpies I could see were always on branches 0.5-1.5 cm in diameter, usually preening, scratching, stretching, and fluffing up their feathers in preparation for (or in response to?) the colder temperatures of the night. In the conifers they were usually next to the trunk, and often at the level of the lowest branches bearing needles, that is, immediately below the canopy. This latter observation is confirmed by the correlation among roosts between the mean height of the highest branch bearing droppings and the canopy height (Spearman's *rho* = 0.7, n = 9, $P<0.05$, Tables II-1 and II-2).

The birds apparently did not change place during the night, as any individual seen during the evening was invariably found in the same spot the next morning. Also, the same perch would often be used repeatedly over successive nights (presumably by the same individual), as witnessed by a few direct observations and by the very conspicuous accumulation of droppings on some lower branches.

Magpies appear to be light sleepers (Chapter IV) and are wary at night. Most remained motionless but alert when I approached them as silently as possible. If I touched their roost trees however, or turned on a flashlight, or made sudden noises and movements, all would take off precipitously and attempt to flee between the trees, hitting the branches of many of them. They also often gave one or two alarm calls (see Buitron 1984) while fleeing.

Before leaving the roosting site in the morning, magpies usually gathered again in dead trees or at the top of tall spruce trees. Departure occurred after civil twilight time, during the 45 min preceding sunrise. This activity was always shorter in duration and more synchronized than arrival, involving large flocks followed by a few smaller flocks and straggling pairs (Fig. II-4B). The birds vocalized frequently, especially when the first ones took to the air.

DISCUSSION

Seasonal use of the roosting sites

Dense thickets of deciduous trees have been reported as the magpie's preferred habitat for roosting (Goodwin 1976). The magpies in my study roosted in such thickets in the fall, even remaining in one of them after leaffall, but they switched to conifers after a marked drop in temperature and the establishment of snow cover. This seems to indicate that the presence of overhead and/or vertical cover matters to the birds only when winter conditions prevail. The use of coniferous stands as a roosting place by magpies has been observed only in winter and in northern populations (Gyllin and Källander 1977, Mugaas and King 1981) and thus appears to be an adaptation to cold (see below).

The changes in the numbers of roosting birds showed a general increase at the most populous roost throughout the winter. The cause of an assumed small peak in December is unclear but may be related to as yet unknown parameters of the magpies' ecology in Edmonton, such as the time of brood break-up and dispersal, or winter movements of birds from one feeding ground to another or from one roost to another.

The spring peak, on the other hand, may reflect a resurgence of social activity before the onset of the breeding season. At that time of the year, unpaired individuals are presumably seeking mates; they may become attracted to the largest roosting sites because of the high number of birds present there, and because of the noisy displays of social activity which may play a role in the mate-finding process and which take place at these sites on mild days. The role of communal roosting in the facilitation of pair-bond formation has already been suggested for a number of other bird species (Gurr 1968, Allen and Young 1982).

Such a mechanism could drain the smallest roosts of their unpaired individuals in favour of the largest ones. This mechanism could thus explain why, concurrent with the numerical increase at one of the sites monitored in this study (Mill Creek), the two other smaller roosting sites (Mayfair and Windsor) were slowly depleted of their occupants, and why this loss in numbers appeared less accentuated in the one roost (Windsor) where most of the magpies were apparently already paired (Fig. II-2). Other hypotheses, however, can account for the dynamics in numbers of birds at small and large roosting sites (Ward and Zahavi 1973; Weatherhead 1983) and thus the validity of the explanation expressed here must await further data on the timing and mechanisms of pair formation in magpies.

Selection of a roosting site

Winter nights at northern latitudes present adverse conditions for most bird species. The colder temperatures often impose energetic stress (Morse 1980), while darkness forces relative immobility on the birds and hinders visual detection of nocturnal predators. Birds may thus be expected to choose roosting sites on the basis of the degree of protection it offers them against bad weather and predators. Does the nature of the roosts found in this study reflect such considerations?

Three characteristics of the magpie winter roosts found in this study are (1) the reduction in wind speed afforded by the dense coniferous stands and their location on the slopes of a valley, (2) the presence of a good (>50%) overhead cover, and (3) the eastward or westward exposition of the slopes. The need to prevent convective heat loss underlies the importance of choosing a site well protected from the wind. Mugaas and King (1981) calculated that, at -20°C, a magpie could reduce its metabolic demands by as much as 8.3% by opting to spend the night in a dense fir grove where wind speed would be reduced from 14.4 km/h to 1.44 km/h. I observed similar levels of wind speed reduction in the present study, and given the colder temperatures often experienced in Edmonton throughout the winter, the benefits magpies obtained by roosting in sheltered places in the river valley could have been even more substantial. The preference for wind-protected roosts was mentioned by Goodwin (1976) as a characteristic of the magpie.

Good overhead cover prevents radiative heat loss to a clear sky (Morse 1980). Magpies selected roosts where this cover was greater than 50%, and the degree of exposure to the sky was probably further minimized by the position of the birds immediately below the tree crown. There may be other reasons, however, for roosting high in a tree, for example the need to observe conspecifics and/or movements of avian predators within the roost.

Magpies also avoided north-facing slopes, at least in the study site. Because of the lack of exposure to the sun, temperatures on these slopes are notably colder than on east- or west-facing slopes, especially at the end of the day when magpies go to roost.

Three additional strategies that the birds could have used to save energy at night were not observed. First, magpies did not consistently roost near the rim of the valley despite the warmer temperatures occurring there. This was probably due to the wind velocity being generally higher near the rim, although it is also possible that the magpies "sampled" temperatures at the different altitudes at a moment when the difference between them was too low to be detected by the birds, that is, immediately before going to roost at the end of the day. Second, magpies did not huddle. Corvids are protective of their personal space (Goodwin 1976), and given the advantages already gained from the characteristics of the roosts and the magpie's relatively large body size (Hayworth and Weathers 1984), it is possible that the need to huddle simply was not strong enough to overcome the motivation to stay apart. Finally, magpies did not roost on the ledges of buildings near warm air updrafts, a strategy that some urban populations of roosting jackdaws (*Corvus monedula*) and starlings (*Sturnus vulgaris*) have adopted (Kalmbach 1932; Davis 1955; Tast and Rassi 1973).

Although northern goshawks (*Accipiter gentilis*) have been known to prey on magpies leaving the roost (Goodwin 1976), nobody has ever reported a case of predation in a roost at night. However, given the opportunity, great horned owls (*Bubo virginianus*) would probably be able to kill magpies (see Buitron 1984), and the possibility of their being a constant source of danger at night must be considered. On three occasions, I observed great horned owls present at dusk at two of the roosting sites. The tendency to perch in the midst of a dense network of dead branches and twigs may represent the magpie's defence against such a flying predator, as it may prove difficult for an owl to approach a sleeping magpie without noisily breaking some thin branches, thereby alerting the wary sleeper. The year-round preference of black-billed magpies for very dense stands of trees or scrub appears in all references to roosting in this species (Linsdale 1937; Ward 1952; Gyllin and Källander 1977; Mugaas and King 1981). Such a preference was also found in the present study, and was further illustrated by the birds' tendency to perch in the densest part of trees located in the densest parts of the roosts.

The adaptiveness of communal roosting in magpies

The mechanism that underlies the nocturnal gathering of some communally roosting species may be the same that prompts these birds to form groups at any other time during the day (Goodwin 1976). This mechanism could be a very general one by which social birds would seek the company of conspecifics whenever they are frightened or under stress. Goodwin (1976) has pointed out how corvids, like men and other social animals, seem to feel most in need of company whenever they are ill at ease or slightly afraid, and that they, like many other diurnal birds, seem to find the approaching darkness frightening indeed (as witnessed under captivity conditions by the sudden restlessness displayed at dusk by otherwise calm birds). That some individuals can sometimes be seen not to roost communally, as in the present study, does not necessarily contradict the idea if it can be shown that the individuals involved are adults perching on their territory, a place with which they are familiar and in which they presumably feel secure. If such a mechanism is indeed operating, then the benefits of communal roosting can be as diverse, effective, and non-exclusive as the general benefits of flocking, and the selective pressures that maintain communal roosting may not be easily dissociated from those which maintain flocking and general gregariousness.

Feeling "ill at ease" can mean being thermally stressed. Being in a group is then adaptive if individuals can maintain body contact in clusters or if some of them can follow knowledgeable birds to sites of more suitable microclimate. Thermal stress is, as already emphasized, likely to occur at night, particularly in winter. Magpies in the present study did not huddle, however, and the whole idea that some of them may be following others to good roosting sites is difficult to test. Moreover, the explanation cannot apply to fall roosting, as magpies do not appear to be thermally stressed during that season, at least not before they move to conifer stands.

Feeling "ill at ease" can also mean feeling threatened by predators. Being in a group when threatened by predators is likely to be adaptive because of factors such as increased total vigilance, dilution effect, or predator confusion

(Krebs and Davies 1981). Night is likely to be a period when diurnal birds feel vulnerable, as they can hardly see and move in the dark. The extent to which this applies to the magpies observed in this study remains, however, uncertain until more information can be obtained on the frequency of nocturnal attacks by owls or other predators on these corvids.

Finally, "ill at ease" can mean being hungry. Being in a group when hungry can be adaptive if the rate of food discovery becomes disproportionately enhanced relative to the rate of food consumption when birds join with each other, or if other individuals' food can be stolen or shared. Although birds may not be hungry at dusk, they may know by experience that they will be so at the end of the night, and thus they may gather at dusk in order to ensure their being together once dawn comes. The synchrony in departure witnessed at all roosts is consistent with the idea that magpies may strive to belong to large groups after a long night without food. Whether this synchrony results from the action of poor foragers "parasitizing" successful ones by following them to their feeding grounds (Ward and Zahavi 1973), or from individuals aggregating because of the benefits equally derived by all flock members from group foraging (Evans 1982), is an open question. Data on the foraging success of leaders and followers in a flock, as well as on the patterns of flock formation and dissociation away from the roost, would be required to adequately answer that question.

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III. FACTORS INFLUENCING THE DAILY ROOSTING TIMES OF BLACK-BILLED MAGPIES IN CENTRAL ALBERTA

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 bird species is probably the most easily witnessed expression of such a rhythmicity (see Wynne-Edwards 1962:283-297, for a review). The exact timing of these roosting flights relative to sunrise and sunset may, however, vary from day to day. Indeed, several environmental factors, the levels of which often change from one day to another, can be expected either to alter a bird's perception of when the night is about to begin or to end, or to modify the balance between its need to forage and its need to be in the relative safety and comfort of the roost.

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. Dunnett and Hinde 1953, Haase 1963, Hein and Haugen 1966, Davis and Lussenhop 1970, 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 daylength is also well known; most birds tend to depart earlier and arrive later at the roost with decreasing daylength (Brown 1946, Martin and Haugen 1960, Schreiber 1967, Brodie 1980). Other, less studied factors could also influence the timing of roosting flights. Cold temperatures, for example, could result in early departures and late arrivals if the birds need to increase their foraging effort to compensate for increased energetic demands set by thermoregulatory expenditures. An opposite effect could also occur, however, if the roost is located in a sheltered place and the birds choose to diminish energy expenditures by spending more time in it. That was found by Brodsky and Weatherhead (1984), who observed late departures and early arrivals at a black duck (*Anas rubripes*) roost on cold days. The birds involved in that study could forage only during the noon hour, however, because they were feeding exclusively on grain provided at noon by a local resident. Whether the effect would persist under more natural conditions is not known.

Black-billed magpies (*Pica pica*) wintering in central Alberta are an ideal subject for a study pertaining to the influence of daylength, temperature, and other factors on roosting times. This species roosts communally from July to April (Chapter II), a period during which daylength in central Alberta varies by as much as 6 h. Winter days can be very cold (-30°C) and differences in mean temperature between successive spells of cold and mild weather can amount to as much as 30°C. Conditions of cloud cover and wind speed are also variable. Winter days can, therefore, present various combinations of daylength, temperature, light intensity, and wind conditions. In this paper, I present the results of a multiple regression analysis used to examine the influence of these parameters on the arrival and departure times of a population of magpies roosting in a rural area south of Edmonton, central Alberta.

METHODS

The roost chosen for this 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 (Fig. III-1). In the winter of 1984-85, when I conducted this study, the roost was used by 46-192 magpies (Fig. III-2). The birds foraged 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 (Fig. III-1).

From 15 September to 6 April, I observed 102 evening arrivals and 102 morning departures at this roosting site. Field work included (1) recording the number of magpies leaving or arriving at the roost during each minute of the observation period, (2) measuring ambient temperature at the onset of the observation period, (3) noting cloud cover, sun visibility, and wind conditions, and (4) measuring light intensity at about 10-min intervals with a Gossen Tri-Lux

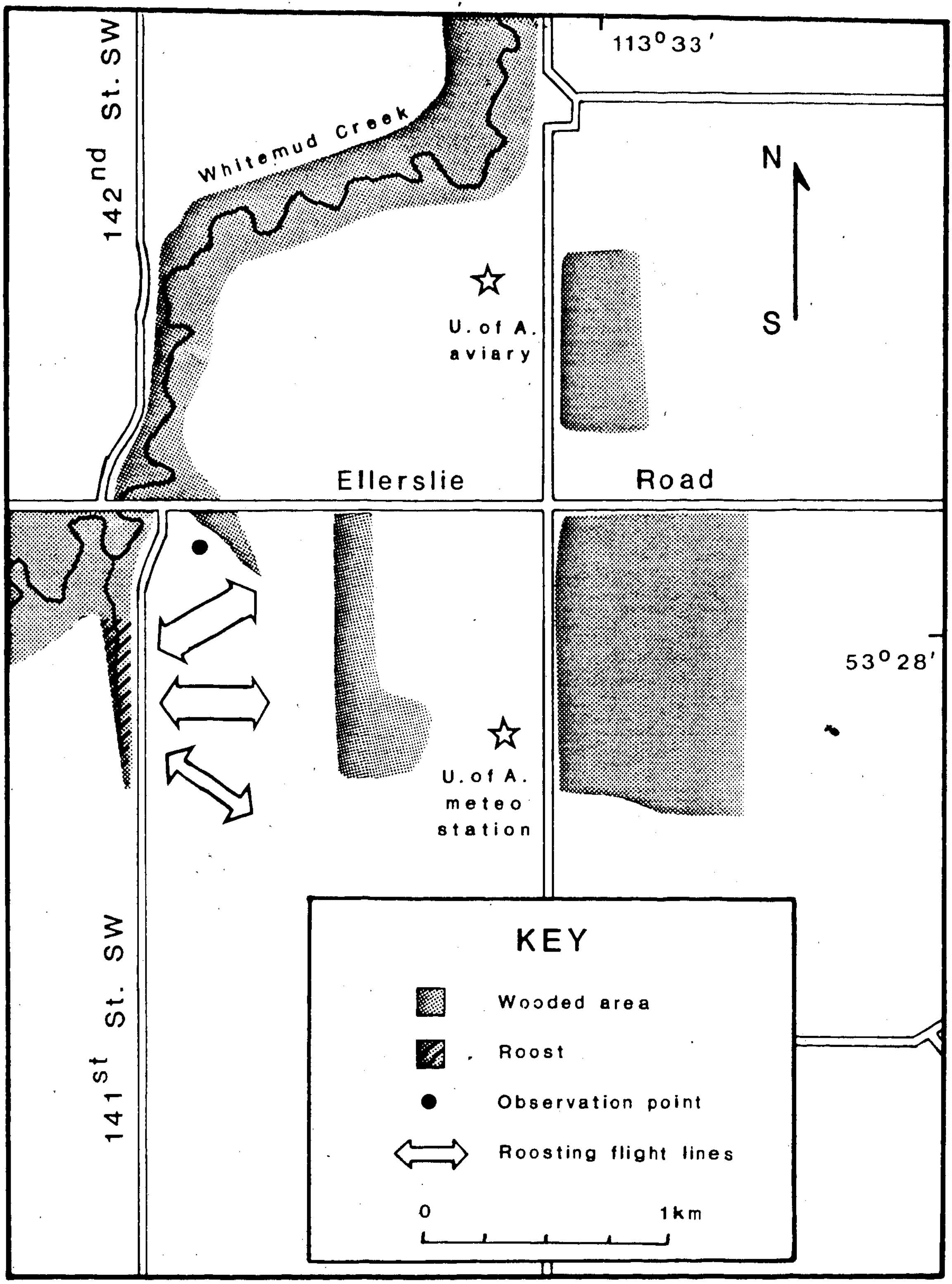

FIG. III-1: Study site and location of the winter roost at Ellerslie, 7 km south of Edmonton. Breadth of arrows indicates relative proportion of birds using the different flight lines.

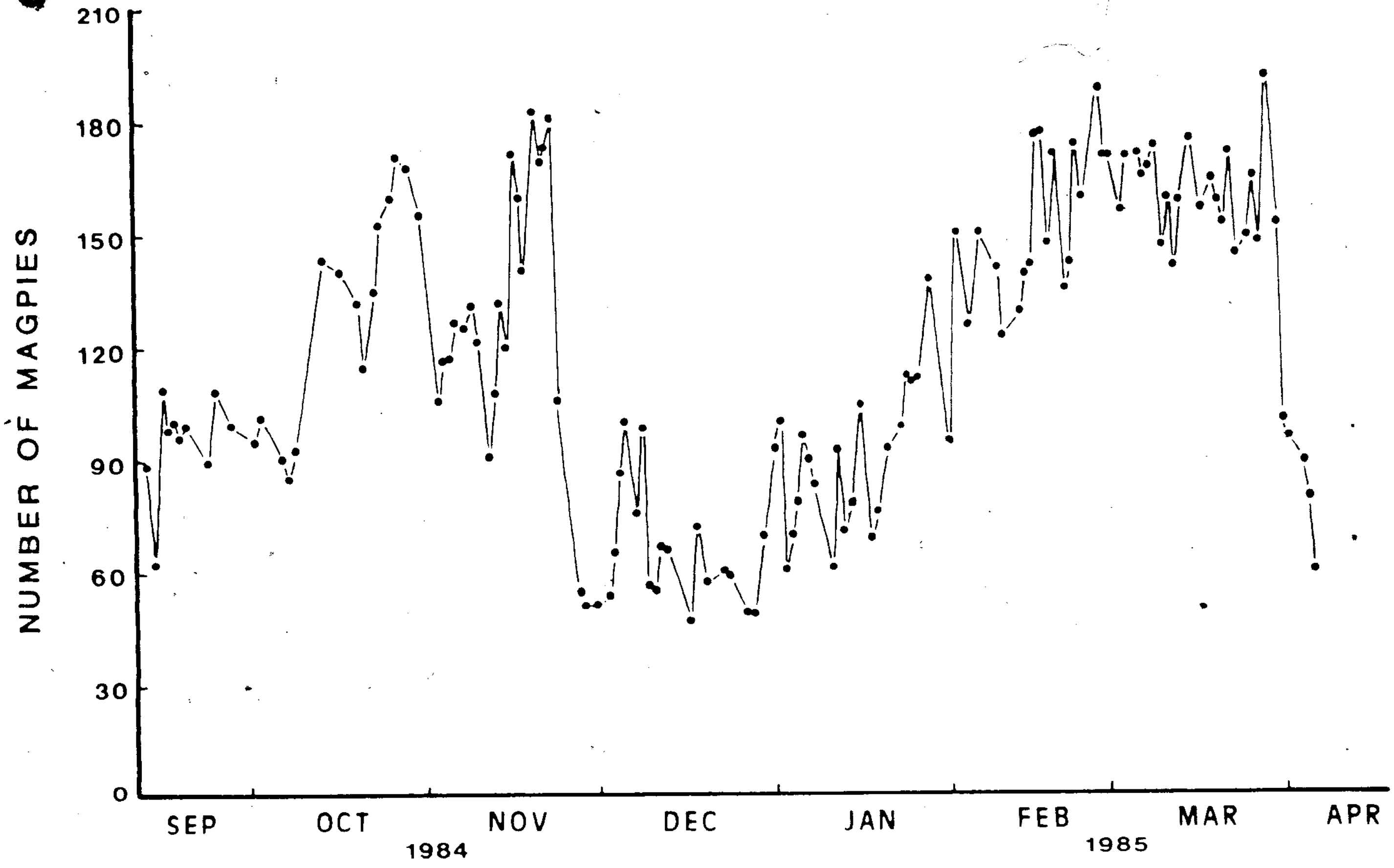

FIG. III-2: Number of magpies counted at the roost from September 1984 to April 1985.

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 current 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 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 an observation period, it was possible to establish a light profile from which the values of light intensity at any moment of the observation period could be estimated by interpolation.

Magpies left the roost in the morning (Fig. III-3) in a manner similar to that of urban individuals (see Chapter II). The dependent variable for the regression analysis was the number of minutes between the mean time of departure and the time of civil twilight (the moment at which the sun is 6° below the horizon) (Fig. III-3). This provided a standardized measure of how early (or late) the magpies left the roost each day. I chose to use civil twilight instead of sunrise as a reference point because civil twilight is when magpies start to vocalize and become active in the roost. I also chose to use mean time of departure rather than median time because departure often occurred in two distinct waves, with the first group of birds often numerically larger than the second. Median time does not take into account how late after the first wave the second group of birds left the roost. Mean time does, however, and, therefore, I judged it a better indicator of the overall time of departure (mean and median times of departure were highly correlated with

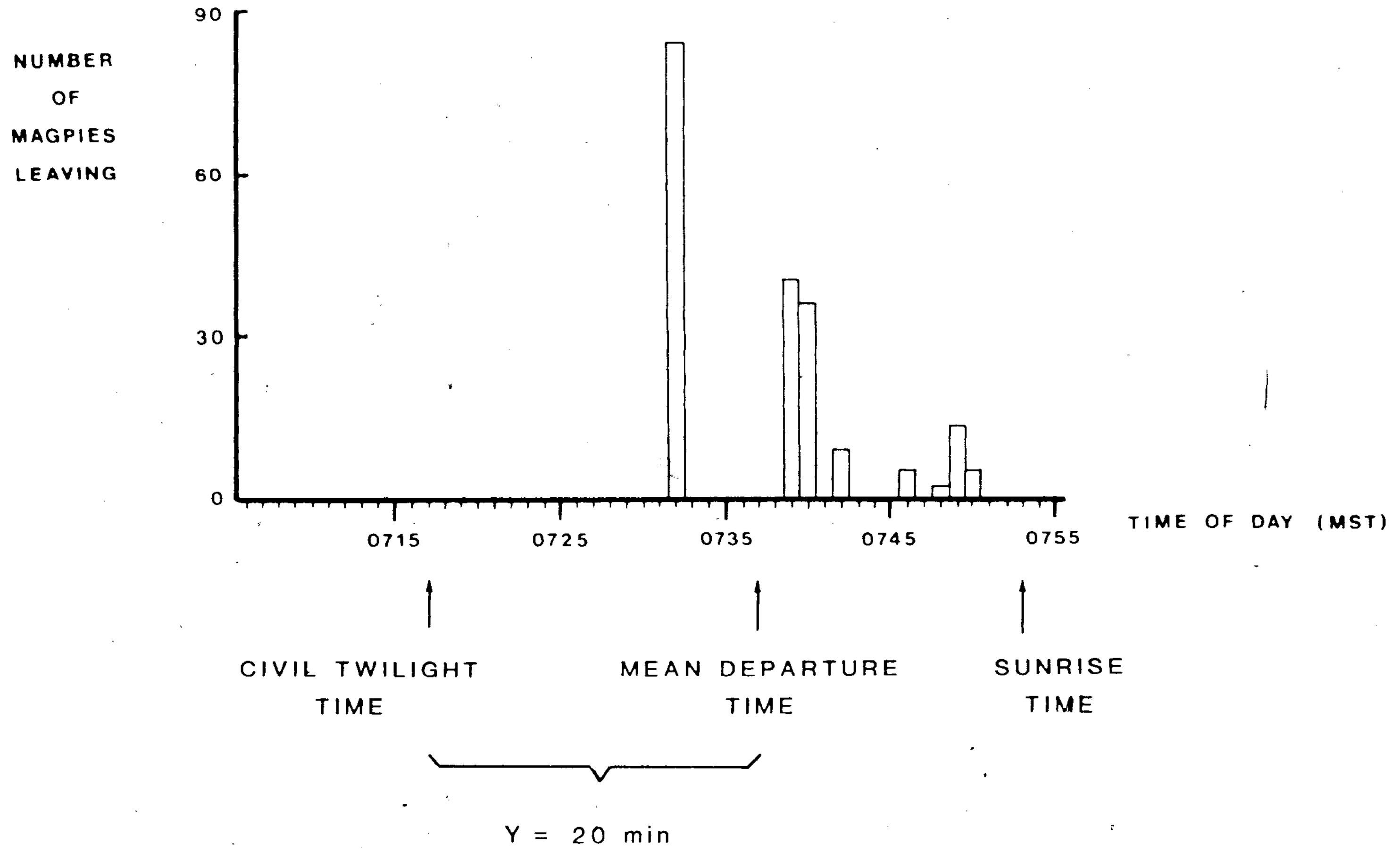

FIG. III-3: Typical pattern of departure of black-billed magpies from the winter roost (15 February). The number of minutes between civil. twilight and mean departure time (in this case, 20) is the value of the dependent variable for that day.

each other anyway (Pearson's r = 0.967) and the use of median instead of mean times in the calculations led to results essentially similar to those given in this paper).

The patterns of arrival at the roost in the evening (Fig. III-4) were also similar to those observed in the City of Edmonton (Chapter II). The number of minutes between mean arrival time and sunset time represented the dependent variable to be used in the regression analysis (Fig. III-4). It assumed a positive value when the mean arrival time preceded sunset (100 of 102 observations) and a negative value otherwise. I chose to use mean time of arrival rather than median time for reasons of consistency with the departure data (see above). Mean and median times of arrival were correlated with each other (Pearson's r=0.974) and the use of median instead of mean times in the calculations once again led to results essentially similar to those given here.

The environmental factors (independent variables) I considered for analysis were civil daylength (morning civil twilight to evening civil twilight) (h), rate of daylength change (min/d), temperature at the onset of the observation period (°C), 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), number of magpies counted at the roost, and light intensity (lux). Values of light intensity 20 min after morning civil twilight and 24 min before sunset were used for the analysis of departure and arrival data respectively. Those times were chosen because they represented the mean time of departure and arrival for the complete study.

Times of sunrise, sunset, morning and evening civil twilight, as well as data on daylength and the rate of daylength change, were obtained from the Weather Office of the Canadian Atmospheric Environment Service in Edmonton. Data on wind speed and direction were taken 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. "Number of roosting magpies" differs from the other variables in that it represents a biotic rather than an abiotic factor of the environment. Nevertheless, because it was not constant

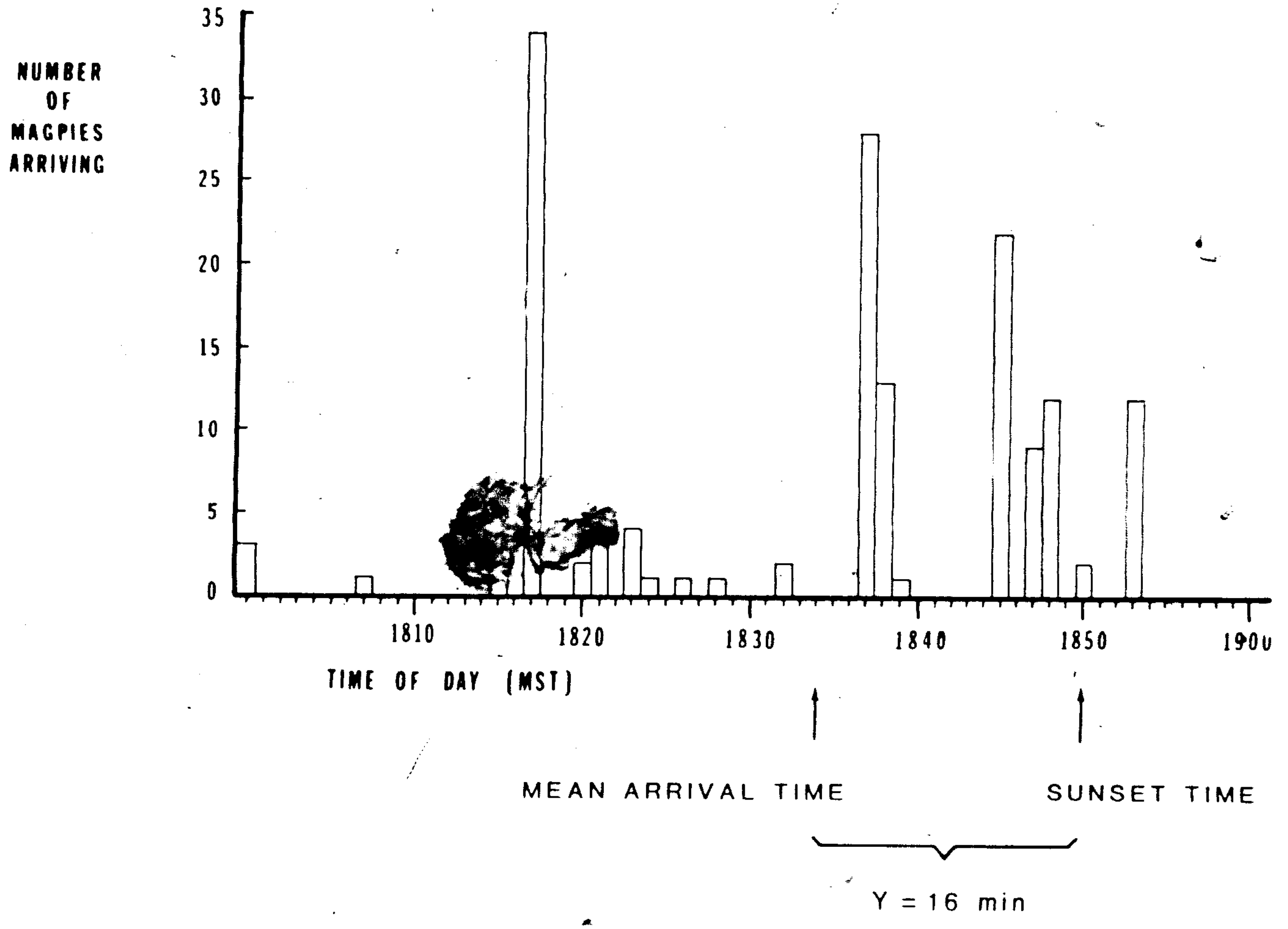

FIG. III-4: Typical pattern of arrival of black-billed magpies at the winter roost (25 March). The number of minutes between mean arrival time and sunset time (in this case, 16) is the value of the dependent variable for that day.

throughout the study (Fig. III-2), it was included in the analysis (Lehner 1979).

I used the Statistical Package for the Social Sciences (SPSSx; Norusis 1983) for the analysis. The procedure was a stepwise multiple regression, with 0.05 as the entry criterion and 0.1 as the removal criterion. All assumptions of the model were met, and 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: daylength, 8.92 to 14.35 h; rate of daylength change, -4.5 to 4.5 min/d; temperature, -34 to 12°C (morning) and -28 to 20°C (evening); and light intensity, 0.34 to 9.99 lux (20 min after morning civil twilight) and 28 to 748 lux (24 min before sunset).

Departure

Figure III-5 shows the variation in departure times observed throughout the study, along with the concurrent variations in temperature and daylength. As expected, magpies left the roost earlier during the short days of winter (November, December, and January) than during the longer days of September, 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 daylengths. Magpies in central Alberta start to actively defend breeding territories in late February-early March (pers. observ.), 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 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). Because I

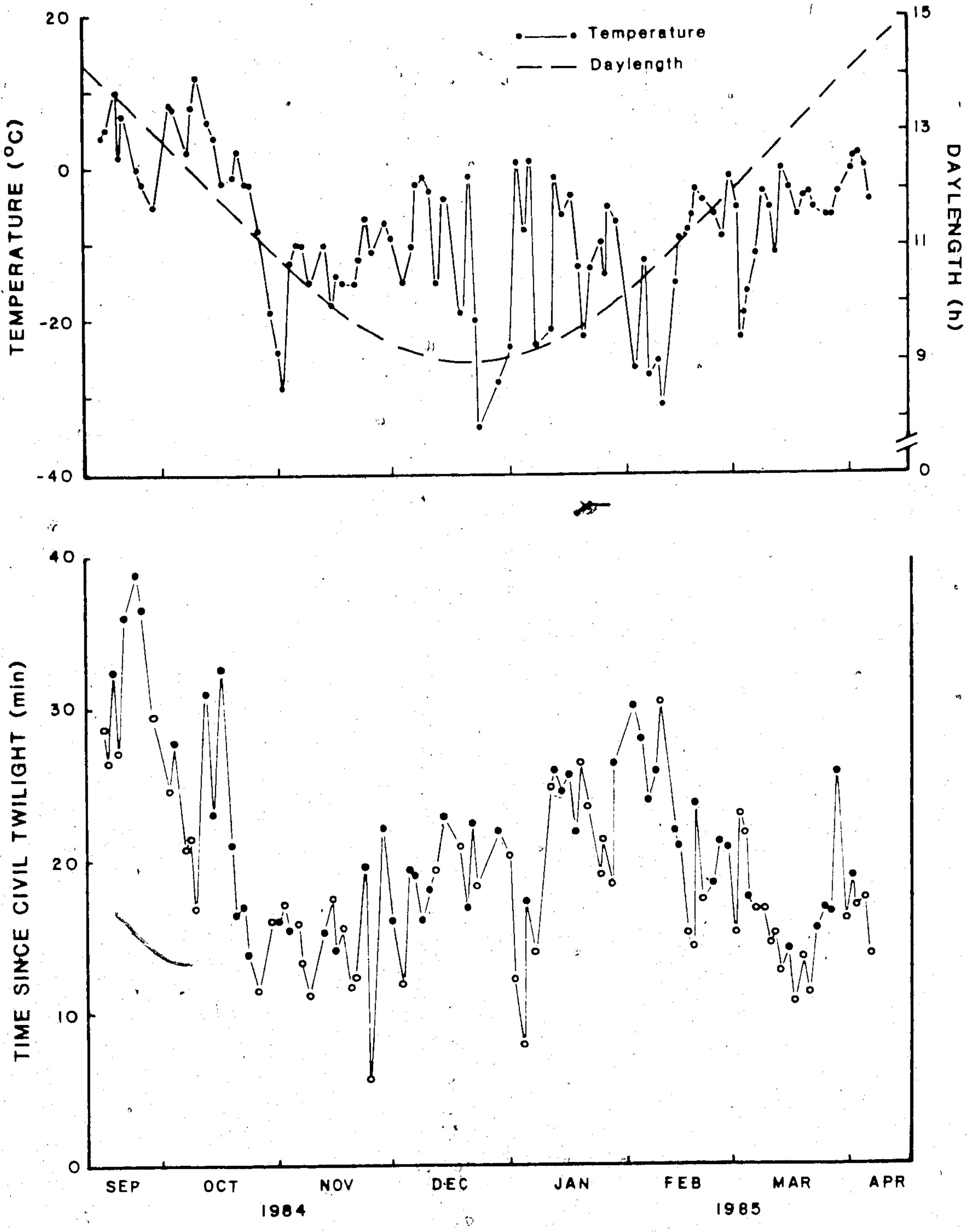

FIG. III-5: Variation in daylength, morning temperature, and mean time of departure of black-billed magpies from the winter roost throughout the study. Solid dots in the lower graph represent cloudy mornings (cloud cover > 50%), while open dots represent clear mornings (cloud cover < 50%).

had no 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 complete set. Although I present the results of both analyses in Table III-1, I focus my attention on the results yielded by the truncated set of data only.

The multiple regression analysis explained 60% of the variance in departure time (Table III-1). Daylength and light intensity contributed two thirds of that total, whereas the number of magpies using the roost, rate of daylength 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 (1) on long days, (2) on dark, cloudy days, (3) when few birds were using the roost, (4) in the fall, when days were getting shorter, and (5) on cold days.

Starting in mid-October, magpies generally left the roost as soon as levels of light intensity reached 1-5 (often 1-3) lux (Fig. III-6), possibly the minimum illumination under which they could fly safely and navigate. Because a given level of illumination is always reached later on a cloudy day than on a clear day, magpies left the roost relatively late on cloudy days. In September and early October, magpies did not leave the roost at fixed levels of illumination (Fig. III-6). During these months, they were leaving the roost later, but also at lower light intensities, on cloudy mornings than on clear mornings. I expected the same phenomenon to repeat itself in March and April, when daylength was similar to that of September and early-October, but that did not occur; magpies still left the roost at 1-5 lux. This, as explained above, was probably caused by the onset of territorial behaviour prompting relatively early departures. Excluding these months and assuming that magpies leave their roost as soon as a certain threshold in light intensity is reached, figure III-6 shows that the sensitivity of magpies to light intensity in the morning is low but

TABLE III-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.

	Step	Variable	R^2 change	Partial corr. coeff.	P
A)	1	Light intensity	.0796	-.404	.004
	2	Daylength	.0614	.361	.009
	3	Rate of daylength change	.0628	.220	.007
	4	No. of magpies	.0383	-.219	.029
			.2421		
B)	1	Daylength	.2523	.749	.000
	2	Light intensity	.1623	-.596	.000
	3	No. of magpies	.0783	-.508	.001
	4	Rate of daylength change	.0674	-.326	.001
	5	Temperature	.0435	-.315	.006
			.6038		

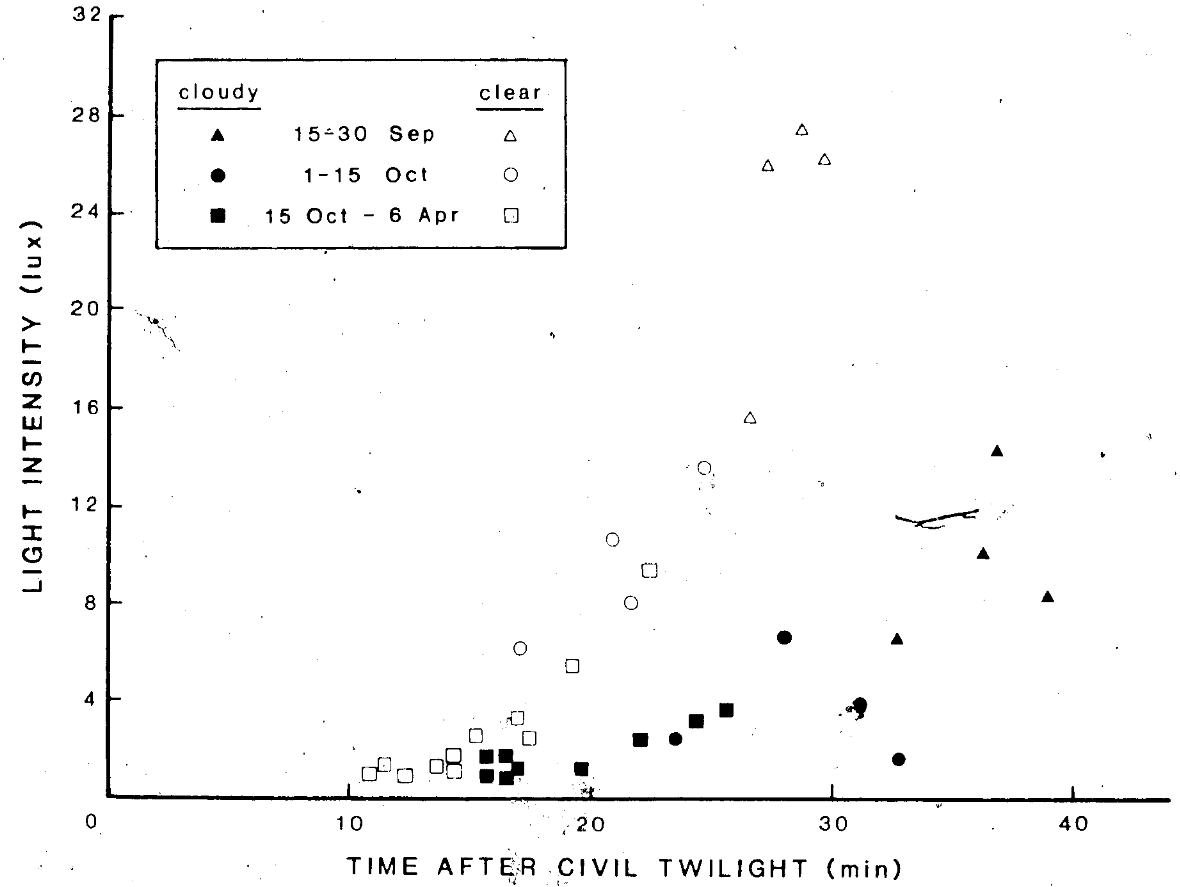

FIG. III-6: Light intensity at each mean time of departure recorded from 15 September through 15 October, and at 20 randomly-selected mean times of departure recorded thereafter (15 October to 6 April). During this latter period, 87% (75/86) of all departures occurred no later than 26 min after civil twilight *and* at light intensities not exceeding 5 lux. Ten of the 11 exceptions occurred on cold (<-17°C) mornings.

increasing throughout dawn after relatively short nights (September) but becomes increasingly higher and constant throughout dawn as the duration of the night increases (early October, November to February).

Arrival

Figure III-7 shows that the general variation in arrival times loosely parallels that of daylength 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 usual based on daylength 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 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 III-2), but will concentrate only on the results given by the latter.

The regression explained 75% of the variance in arrival times (Table III-2). The five variables involved were the same ones that had been found to influence departure. Daylength and temperature (as opposed to daylength and light intensity for departure) were the most important predictors of arrival time, contributing two thirds of the total variance explained. According to the signs of the partial correlation coefficients, magpies tended to arrive at the roost relatively early (1) on long days, (2) on cold days, (3) in the spring, when days were getting longer, (4) on dark, cloudy days, and (5) when few birds were using the roost.

Except for the rate of daylength change, the conditions causing early arrivals were the same ones that caused late departures, so that it can be said that magpies spent relatively more time in the roost (1) on long days, (2) on cold days, (3) on dark, cloudy days, and (4) when few birds were using the roost.

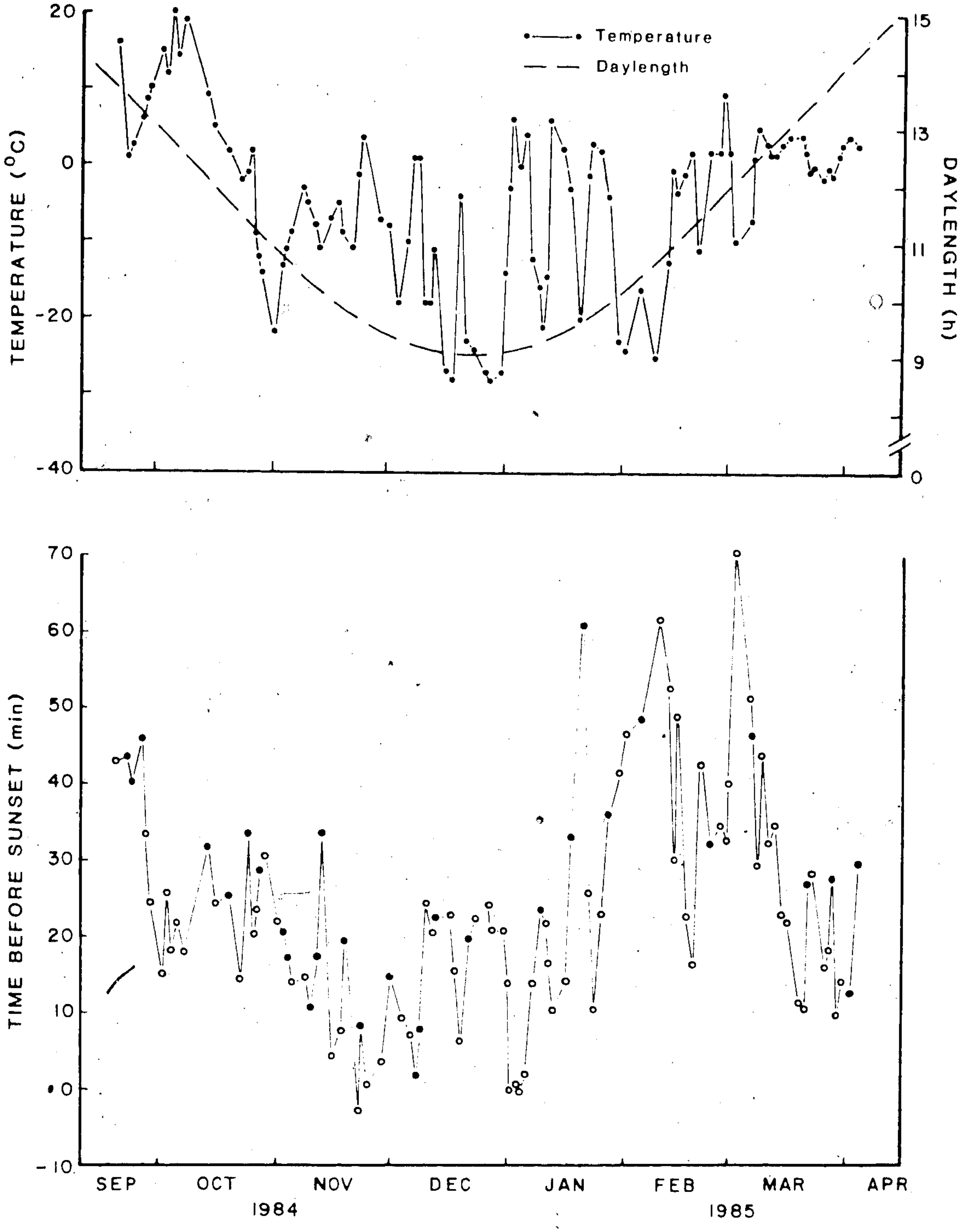

FIG. III-7: Variation in daylength, evening temperature, and mean time of arrival of black-billed magpies at the winter roost thr...ghout the study. Solid dots in the lower graph represent cloudy evenings (clo... cover > 50%), while open dots represent clear evenings (cloud cover < 50...

TABLE III-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).

	Step	Variable	R^2 change	Partial corr. coeff.	P
A)	1	Daylength	.1091	.506	.001
	2	Temperature	.1581	-.421	.000
			.2672		
B)	1	Daylength	.2273	.846	.000
	2	Temperature	.2913	-.719	.000
	3	Rate of daylength change	.1742	.680	.000
	4	Light intensity	.0361	-.334	.002
	5	No. of magpies	.0167	-.248	.028
			.7457		

DISCUSSION

Effect of daylength

In winter, magpies are faced with relatively harsh conditions. insects, their normal summer diet (Kalmbach 1927) are absent, snow cover limits access to vegetal food sources such as grain and other seeds, and cold temperatures cause increased energy expenditures for thermoregulatory processes (Hayworth and Weathers 1984). Reduced daylength exacerbates these problems: it reduces the time available for foraging (day) while extending the time during which the birds must endure continuous lack of food and the coldest temperatures of the 24-h period (night). Daylength was found to be the prime factor affecting the roosting times of the magpie in this study (this variable had the largest partial correlation coefficients in the analyses on both departure and arrival time (Tables III-1 and III-2)). Magpies left the roost early and returned to it late on the shortest days of the study, thus appearing to try to counteract the seasonal effect of daylength on their activity time. This shift in roosting times on short winter days has also been noted in a number of other species (see references in introduction).

It seems likely that the birds were trying to increase their activity time because of a need to increase their foraging opportunities. I observed that, when given food at dusk, magpies went to the roost with large boluses of food stored in their sublingual pouch, an indication that they had the intention and potential to process this food during the ensuing hours. Storage of food in the sublingual pouch is one way to compensate for a short foraging time when night comes, but when the food is not readily available, to return to the roost later and forage longer may be the only other solution. Dunnet and Hinde (1953) have shown that food availability can influence in that way the time at which great tits (*Parus major*) go to the roost in winter.

The magpies could not completely counteract the effect of shortening daylength on their activity time. The latter, if measured as the total time between departure from the roost in the morning and arrival at the roost the following afternoon declined, on average, from 12.0 h in September to 7.8 h in December. Yet it seems that magpies could have added to their activity time by returning to the roost later than they did, even in the middle of winter. The mean time of arrival never occurred more than 3 min after sunset, i.e. at least 20 min before levels of light intensity similar to those at which the magpies left the roost in the morning would have been reached. That diurnal birds generally return to the roost at higher levels of light intensity than those at which they leave it in the morning has also been noted in a number of other studies (e.g. Seibert 1951, Dunnett and Hinde 1953, Swingland 1976). Perhaps birds would incur high costs if overtaken by darkness away from the roost, hence the need for a 'security time margin' in returning to the roost.

Effect of temperature

For a given daylength, magpies tended to depart from the roost later and return to it earlier on cold days than on mild days. This finding parallels that of Brodsky and Weatherhead (1984) in wintering black ducks. It gives support to the contention that magpie roosts offer advantageous conditions of microclimate to their occupants (see Chapter II). It also indicates that magpies do not increase their activity time in response to cold, and may actually decrease it, at least under the conditions of my study. I often observed magpies to spend extended periods of time inactive in trees, perching with their feathers greatly fluffed up, during the days when temperature approached -30°C. Increased inactivity as a response to very low (<30°C) temperatures has also been observed in the spotted nutcracker (*Nucifraga caryocatactes*) by Andreev (1977), who calculated that such inactivity resulted in daily energy requirements much lower than what would be expected on theoretical grounds for a passerine of similar size active at these temperatures.

The reduction in activity by magpies at cold temperatures is unlikely to be caused by a change in food availability: magpies feed mostly on grain, berries, and garbage in winter at my study site (Reebs and Boag, unpublished data), and the availability of these food items seems unlikely to be greatly affected by temperature. The effect of cold on roosting times could nevertheless be modified by the birds' level of hunger. The effect of cold was less pronounced on departure time than on arrival time (temperature had a partial correlation coefficient, of only -0.315 for departure versus -0.719 for arrival). Magpies presumably were very hungry in the morning, following a long night, and their increased motivation to get food might have overcome part of their reluctance to leave the roost in the cold.

Effect of factors related to light

The magpies also tended to spend more time in the roost on cloudy days, but, in general, arrival time was less affected by light intensity than departure time was. Although light intensity at dawn was the second most important variable in predicting departure time, with a partial correlation coefficient of -0.596, illumination at dusk was only the fourth in importance in predicting arrival time, with a coefficient of -0.334. At dusk, light intensity is not the only parameter on which magpies may cue in to determine when the day is about to end. The position of the sun can also be used (such an alternative is not available to the birds in the morning to determine when the day will begin, as magpies always left the roost before sunrise). On most days of this study, the sun was entirely or partly visible above the western horizon, even when various cloud conditions above meant that different readings of light intensity were obtained. If magpies use the position of the sun on all but completely overcast days, then light intensity may become a poor predictor of arrival time when clear days are included in the analysis. Indeed, when the regression analysis is run using only data from days when the sun was either constantly or even temporarily visible during the hour preceding sunset (n=62), light intensity fails to enter the equation (final P-value = .175) (Table III-3), an indication that, on such days, magpies do not rely on light intensity (at least as I measured it) to determine when the day is about to end. On the other hand, if only days when the sun was totally and always obscured in the afternoon (n=20) are considered, then light intensity becomes a significant predictor of

TABLE III-3 Summary table of the stepwise multiple regression analysis on arrival time (truncated set of data) for days when the sun was (A) at least temporarily visible (n=62), or (B) never visible (n=20), during the hour preceding sunset.

	Step	Variable	R^2 change	Partial corr. coeff.	P
A)	1	Daylength	.2013	.866	.000
	2	Temperature	.3305	-.761	.000
	3	Rate of daylength change	.2349	.734	.000
	4	No. of magpies	.0176	-.275	.035
			.7843		
B)	1	Daylength	.3309	.869	.008
	2	Temperature	.2135	-.668	.012
	3	Rate of daylength change	.1266	.683	.025
	4	Light intensity	.0871	-.5[illegible]	.035
			.7581		

arrival time (Table III-3), with a partial correlation coefficient even larger than the one obtained with the complete set of data (Table III-2).

A parameter closely related to light intensity that could also influence arrival time is the total amount of solar radiation received during the day. In a study on the roosting behaviour of brown-headed cowbirds (*Molothrus ater*), Krantz and Gauthreaux (1975) found a correlation between total daily solar radiation and the time at which the first bird entered the roost. First entry occurred later when total solar radiation had been high. This finding was in accordance with Aschoff's (1960) rule, which states that diurnal species become more active during longer activity periods under increasing levels of light intensity. One problem with solar radiation however, is that it generally shows strong correlation with dusk levels of illumination, so that the respective effect of these two parameters can hardly be distinguished in the field. Inspection of Krantz and Gauthreaux's (1975) figure 1 indicates that days with a high total solar radiation also had high levels of illumination at dusk, so that it is difficult to determine which of these two factors (if not sun visibility) was responsible for the late arrivals observed on those days.

Effect of the number of magpies present at the roost

Departure occurred slightly earlier and arrival slightly later than usual when more magpies were using the roost. One possible explanation hinges upon the assumption that the number of birds present at a roost is proportional to the number of birds present on the foraging grounds, and that large numbers of birds on a foraging ground result in increased competition and decreased individual foraging success (see Swingland 1975). Arriving early on the foraging ground, and departing from it late, may represent the magpie's way of coping with competition. If such a strategy was adopted by a sufficiently large proportion of the roosting population when competition at the foraging grounds is high, then large numbers of roosting birds could become correlated with early departures and late arrivals at the roost.

Effect of the seasons (rate of daylength change)

The rate of daylength change is the only variable for which the sign of the partial correlation coefficient for arrival differs from that of departure. This makes interpretation of the results difficult. The rate of daylength change is an indicator of the seasons (with negative values for fall, near-zero values for winter, and positive values for spring). Some seasonal effects may thus have been responsible for the significance attached to this variable in the analysis. One example of such a seasonal effect is the occurrence of extensive displays of social activity at the roost on mild spring afternoons (pers. observ., Chapter II). These displays may have a role to play in mate-finding (Ward 1952) and unpaired individuals may become more eager to go to the roost to take part in them. Although this hypothesis can account for the early arrivals observed in early spring (before March and April) it does not make any predictions regarding the spring pattern of departures, as no particular social activity was observed in the morning. Possible causes for the early departures of spring relative to fall remain unknown.

Effect of wind

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, 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 0.218, indicating that, as expected, magpies tended to go to the roost somewhat early on very windy days. That a similar effect did not occur in the morning is not surprising since cold itself had a lesser effect on departure than on arrival.

Wind direction, in the way I measured it, was also included in the analysis based on the presumption that headwinds could slow the magpies down in their roosting flights. This variable, however, never approached significance in the analysis. Wind direction did, nevertheless, affect the way in which magpies flew, especially the height at which they returned to the roost. On days with strong headwinds (westerly winds), I always observed the birds to fly low (only 1-3 m above the ground), whereas on days with tailwinds (easterly winds), or no wind, they flew at a more normal height of 20-30 m.

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IV. SLEEPING POSTURES AND NOCTURNAL BEHAVIOUR OF BLACK-BILLED MAGPIES

INTRODUCTION

In a recent review article on avian sleep, Amlaner and Ball (1983) listed the different sleeping postures that are adopted by birds in the wild. Only a few postures have been noted, and the difference between them resided mainly in the position of the bird's head. Most birds were reported to sleep with their head either drooped between the shoulders (bill pointing forward) or turned around and lying on the back (bill usually, but not always, tucked under the scapular feathers). A reported characteristic of the sleeping behaviour of many birds, while in either one of these postures, was their ability to open and close their eyes alternately at various rates during a sleep bout (a behaviour called "blinking" by Amlaner and McFarland (1981) and 'peeking' by Lendrem (1983)).

Many of the studies reviewed by Amlaner and Ball (1983) reported on observations made only during daylight or twilight hours, or at night by means that did not prevent observer disturbance. Prolonged, unobstrusive studies of birds sleeping at night in natural or even semi-natural conditions are still few. Yet, only studies of this kind can reveal whether birds modify their sleeping postures and general night behaviour in response to varying environmental conditions, thus providing clues about the adaptive value of these postures and behaviour.

In an attempt to provide such a study, I used infra-red vision equipment to observe black-billed magpies (*Pica pica*) sleeping in an outdoor aviary. The conditions at the aviary approximated those found in the wild (see Chapter II) in that the birds were exposed to natural light-dark cycles and ambient temperatures, were provided with overhead cover and perches of appropriate dimension, and slept in the company of conspecifics. This paper gives a description of the sleeping postures adopted by magpies, and reports on the influence of nightlength, temperature, and individual dominance status on the nocturnal behaviour of these birds.

METHODS

The outdoor aviary used in this study (Fig. IV-1) was located in a rural area 7 km south of the City of Edmonton, Alberta. It consisted of a 10.0 x 3.6 x 1.9 m wire mesh enclosure (flight cage) adjacent to a 1.8 x 3.6 x 2.3 m observation hut. A one-way glass window allowed unobstrusive observation of the birds in the flight cage from the hut. A linear arrangement of five perches was installed in a north-south direction 2.4 m away from the hut. Each perch consisted of a 3.8 x 3.8 cm post mounted with a 'roost' dowel 1.76 m high, and an "access' dowel 1.5 m high. Each dowel was 1 cm in diameter, 20 cm long, and could accommodate only two perching birds. A row of four posts 6 cm apart was present on both sides of each perch to provide some protection from the wind and to endow the perches with a certain degree of physical, yet not visual, separation from each other. The wire mesh directly above the line of perches was covered with planks to provide protection from rain, snow, and exposure to the open skies. An unpainted wooden plank, 23 cm wide, ran across the enclosure 10 cm behind the perches, providing an appropriate background against which the black and white magpies could be seen easily.

Three infra-red lamps were hung from the ceiling of the flight cage along the hut wall. Each lamp consisted of a 60 W light bulb set up in a lightproof cardboard box that had a Wratten gel infra-red filter (Kodak #87C) mounted on the side facing the perches. Under normal conditions, these filters are very sensitive to heat which does not permit prolonged use of the lamps. This problem was reduced in my study by the sub-freezing temperatures under which I carried out most of my observations.

Three trials were made, each one involving three magpies. Each set of three magpies was captured near the aviary with a baited funnel trap (Alsager et al. 1972), a few days prior to the onset of their respective trial. Upon capture, each bird was weighed to the nearest 0.5 g, and marked with a

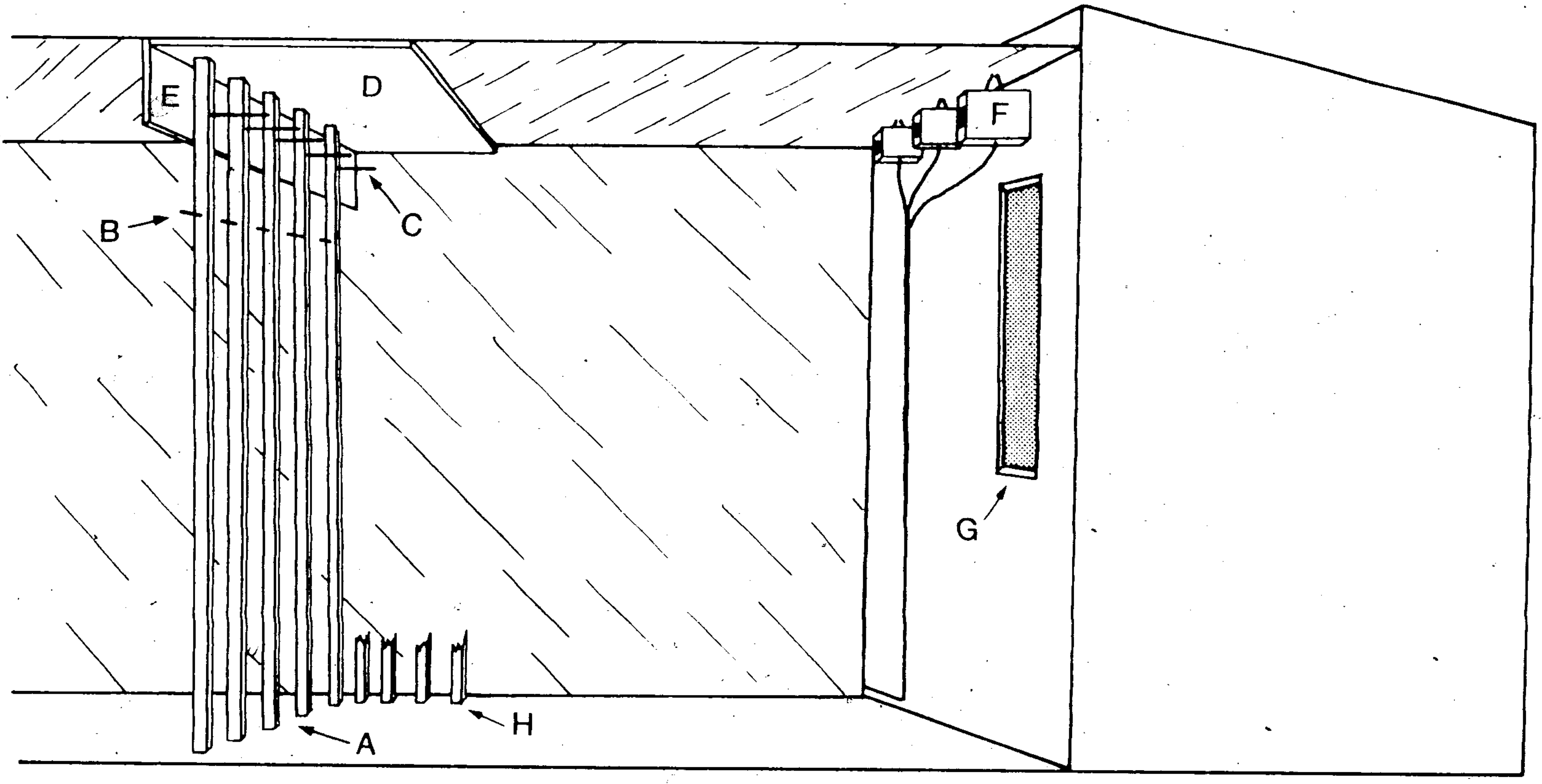

FIG. IV-1: Aviary set-up. (A) Row of five perches in a north-south direction, (B) access dowel, (C) roost dowel, (D) overhead cover, (E) backdrop plank, (F) infra-red lamp, (G) one-way glass window. Between each perch, as well as at both extremities of the row of perches, stood one row of four posts in a east-west direction (H). These were omitted from this figure for clarity.

distinctive pattern of black hair dye on its white belly feathers to allow recognition at night under infra-red illumination. The magpies were then given at least seven days to habituate to the pen conditions.

On 30 of the following days, I observed the magpies as they settled down on the perches at dusk, and during the subsequent hour. I noted the number of aggressive interactions and the identity of the individuals involved. These interactions all consisted of displacement of one bird by another, and their outcome was used to establish the dominance status of each individual. Each day, I also noted the final position taken by the three magpies in the linear arrangement of perches. Throughout the duration of the trial, the magpies had free access to an ample supply of snow, grit, and bite-size dog food pellets (Wayne pet food).

On 11 of the 30 days, I conducted night observations of the magpies' behaviour with the aid of an infra-red visionscope (FJW Industries) equipped with a 200 mm Nikon telephoto lens. I used *ad libitum* sampling (see Lehner 1979) throughout the first 4 h following sunset to obtain a general description of the nocturnal behaviour of the birds. I also used an additional 20 scan samples (see Lehner 1979) at 6-min intervals during the third and fourth hour following sunset, to obtain an estimate of the frequency at which each bird could be found in a given sleep postures (see below). The state of each bird was characterized by the position of the head, the state of the eyes, and the direction the bird was facing. The infra-red lights were switched on and off as needed for the *ad libitum* sampling conducted during the first 1.5 h following sunset. They remained continually on thereafter. I found no indication that the magpies behaviour was affected by the infra-red illumination.

The three trials were conducted during winter and spring, as this is when magpies roost communally in the wild, and have to face large variations in ambient temperatures and nightlength in central Alberta. The first trial was conducted between 1 December 1984 and 11 January 1985 and involved three juvenile females, the second, between 27 January and 5 March 1985, with a mixed-sex flock of two juvenile females and one juvenile male, and the third, between 23 March and 2 May 1985, with three adult males. Sex and age were determined by measurements of external body parts (Scharf 1985). Data on temperature, wind direction, and wind speed were taken from the records of the University of Alberta Meteorological Station, which was located 2 km south of the aviary site. Late evening temperature ranged between -30 and 2°C, -25 and 7°C, and 1 and 14°C for the first, second, and third trial respectively. Civil nightlength (evening civil twilight to morning civil twilight) varied between 15.1 and 14.7 h, 14.1 and 11.8 h, and 10.4 and 7.6 h for the same respective trials.

In addition to the results of these winter trials, I obtained qualitative observations of the magpie's nocturnal behaviour by conducting preliminary work at the aviary in the summer of 1984, and indoors in the summer of 1985. These observations are included where appropriate in the descriptive part of the results below.

RESULTS

Dominance hierarchies

All dominance hierarchies were linear. No reversals were observed. In the second trial, the male was dominant over the two females. In each trial except the first one, the heaviest individual was the dominant one. The second heaviest bird was dominant in the all-female flock, the heaviest one being relegated to second rank. In general, these observations are consistent with those of Scharf (1985).

Nocturnal behaviour and sleeping postures

I subjectively divided the magpies' behaviour following sunset in four phases. These are, in the order in which they occur chronologically during the night: the "settling" phase, the "eyes open" phase, the "eyes blinking" phase, and the "bill under scapulars" or BUS (Amlaner and Ball 1983) phase.

In the "settling" phase, the magpies selected and settled down on specific roost dowels, during the half-hour following sunset. Once on the perches, the birds engaged in comfort behaviours such as scratching, preening, stretching, and bill-wiping. They also frequently pecked at the dowels. I never observed the birds to huddle, as all three magpies always occupied different perches on a given night. This general behaviour was similar to that of wild individuals (see Chapter II).

The magpies did not always occupy the same perches every night (Table IV-1). Only four birds used specific perches more often than expected by chance (Table IV-1) and the pattern of "preference" did not always repeat itself from one trial to another. A more consistent pattern emerges, however, when an individual's position is considered relative to that of its flockmates (Table IV-2). In the last two trials, the dominant (alpha) individual occupied a central position relative to the other two birds more often than would be expected by chance, whereas the beta bird tended to be the southernmost one, and the omega individual tended to be the northernmost one.

The magpies initiated the "eyes open" phase by squatting on their respective dowels, shaking and fluffing up their feathers, and eventually becoming immobile. In this position, the head was slightly drooped between the shoulders and the bill was pointing either directly forward or somewhat sideways. In winter, the greatly fluffed up belly feathers covered the tarsus and toes as well as the dowel upon which the bird sat. In summer, the belly feathers were only slightly fluffed up, and it was clearly visible that the birds were often sitting on only one leg, the other one being retracted close to the body. Except for occasional defecation, reorientation of the bill, and reversal of direction faced on the perch (mainly when strong winds shifted directions), I did not observe any particular activity once the magpies had taken this state of immobility. Their eyes remained continually open however, and thus the birds appeared not to be sleeping.

The "eyes blinking" phase occurred later in the night, when magpies began to alternately close and open their eyes. In general, bouts of eye

TABLE IV-1: Number of nights each magpie occupied a given perch during a 30-nights trial. The most dominant bird was assigned rank 1. The northernmost perch was assigned number 1.

TRIAL	MAGPIE'S DOMINANCE RANK	PERCH					P[1]
		1	2	3	4	5	
1	1	3	5	12	6	4	0.09(NS)
	2	3	9	9	8	1	0.06(NS)
	3	6	8	5	8	3	>0.1(NS)
2	1	0	14	12	2	2	<0.001
	2	2	4	3	9	12	<0.02
	3	9	7	4	4	6	>0.1(NS)
3	1	3	10	8	5	4	>0.1(NS)
	2	5	0	3	5	17	<0.001
	3	11	7	4	0	8	<0.02

---

[1] Based on a X^2 test for goodness of fit, with 6 as the expected value for all perches, and 0.05 as the level of significance.

TABLE IV-2 Number of nights each magpie was the northernmost, central, or southernmost of the three birds during a 30-nights trial. The most dominant individual was assigned rank 1.

TRIAL	MAGPIE'S DOMINANCE RANK	POSITION RELATIVE TO FLOCKMATES			P[1]
		north	middle	south	
1	1	8	8	14	>0.1(NS)
	2	9	14	7	>0.1(NS)
	3	13	8	9	>0.1(NS)
2	1	7	20	3	<0.001
	2	5	8	17	<0.03
	3	18	2	10	<0.005
3	1	7	19	4	<0.005
	2	5	7	18	<0.01
	3	18	4	8	<0.01

[1] Based on a X^2 test for goodness of fit, with 10 as the expected value for all positions, and 0.05 as the level of significance.

opening or eye closure lasted 1-35 s. During the eye closure bouts, the pale grey eyelid of the magpie could easily be seen against the black background of the head feathers. This "eyes blinking" stage never lasted more than 3 min and consequently I did not always witness it.

In the BUS phase, the magpies, with a shaking motion of the head, tucked the bill under the scapular feathers. They always closed their eyes just prior to the tucking movement. In winter, the scapular and back feathers were greatly fluffed up, thereby covering not only the bill but also most of the head, including the eyes, as well as part of the wings. The shape of the magpies in this position approximated that of a ball (Fig. IV-2). On warm (12-20°C) summer nights, or inside at room temperature, the back and scapular feathers were only slightly elevated, and covered less of the head and wings. The eyes still appeared obscured by feathers when a bird was observed from the side or from the back, but one was often visible when seen at an angle from the front. It was, nonetheless, continually closed.

Unless disturbed, the magpies remained in the BUS posture, once they had adopted it, throughout the rest of the night in summer, and throughout the rest of the observation period in winter. Shining a light beam for a prolonged time directly at the magpies when in the BUS posture did not elicit any response from them, in either summer or winter, although the same stimulus greatly alarmed them when their eyes were open. This lack of reaction probably indicates that the eyes remained closed under the scapulars, or, if not always closed, that the covering feathers completely obscured the bird's vision. On the other hand, sudden noises, such as the knocking of my fingers on the one-way glass window, often prompted the magpies to expose their heads instantaneously, and to keep their eyes open for some time before resuming the BUS posture. This sensitivity to noises became somewhat diminished as the night progressed. Only louder or more sustained noises would alert the birds once they had spent more than about an hour with their bill under the scapulars. Overall, however, magpies remained sensitive to any new noise of moderately low intensity (a gentle clap of the hands, for example) and to me

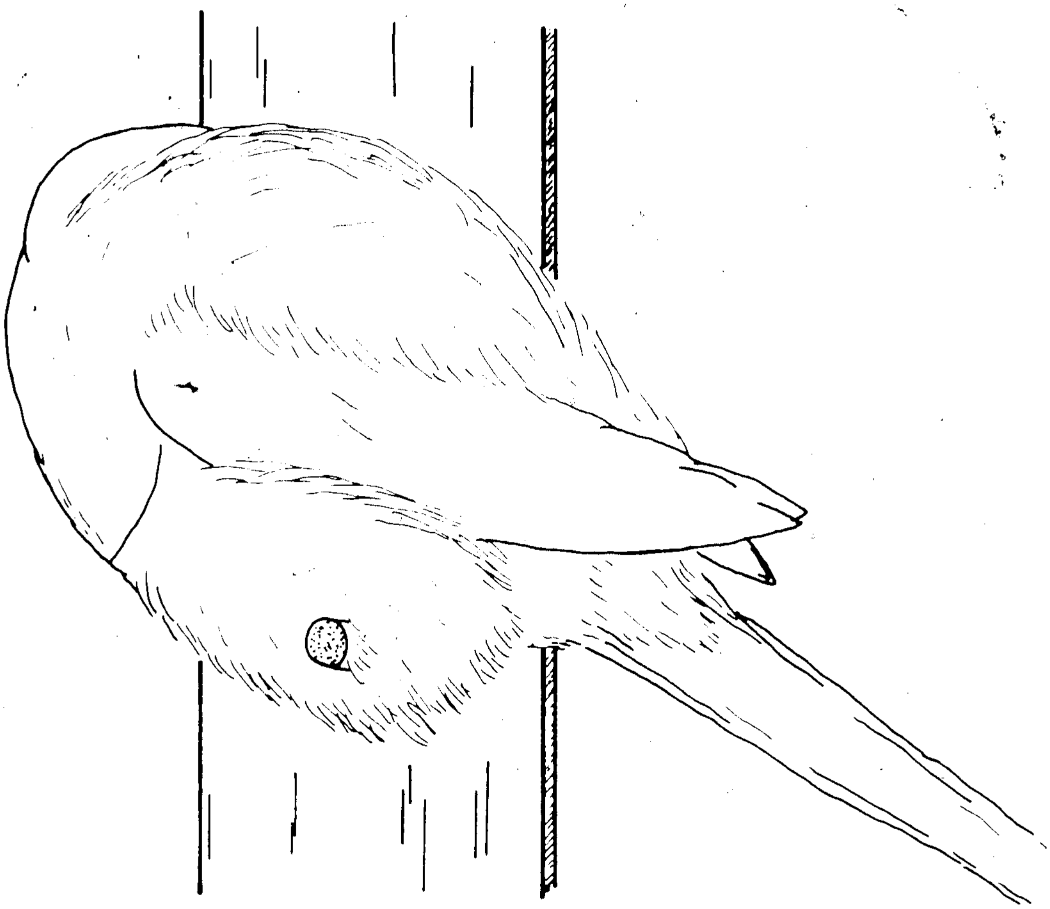

FIG. IV-2: Sleeping posture of black-billed magpies on cold winter nights.

they appeared to be light sleepers.

Once during each of the first two trials a great horned owl (*Bubo virginianus*) landed on the observation hut while I was conducting night observations. The magpies reacted by first adopting an alert position, sitting horizontally on the dowels with their neck elongated and their feathers sleeked. Then, presumably in reaction to a movement by the owl, one or two magpies gave an alarm call, and all magpies took off and flew frantically from one side of the flight cage to the other. After I flushed the owl, the magpies settled on the ground and remained there until morning. They presumably could not see the perches in the dark. Overall, this reaction to a potential predator was similar to that of wild individuals reacting to my presence in their natural roost (see Chapter II).

I observed some signs of sleeping activity during the day. From time to time, a magpie would come to rest on the ground or on a dowel, fluffing up its feathers, drooping its head between the shoulders, and starting to blink. On the coldest days, the resting magpies often tucked their head under the scapulars. The eyes were then obscured by feathers but, unlike the nocturnal situation, the birds regularly exposed the head, at intervals varying from a few seconds to several minutes. I view this diurnal resting activity as an equivalent of the blinking stage that precedes the permanent adoption of the BUS posture in the nocturnal situation.

Factors influencing nocturnal behaviour

Except for the "eyes blinking" stage which was always very short, the duration of each of the previously mentioned phases depended on nightlength and temperature. On the short (5.5 h) nights of summer, the magpies often went directly from the "settling" phase to the BUS phase. Unless disturbed, they remained in the BUS posture until the next morning. On the longer (average of 9.0 h) nights of the third trial, magpies generally assumed the BUS posture only during the second hour following sunset, and were found in that position in many of the scan samples I made in the third and fourth hour of the night (Fig. IV-3). The magpies behaviour in the early parts of the still longer (average of 13.3 h) nights of December, January, and February (first and second trial) depended on ambient temperature (Fig. IV-3). On the coldest (-20 to -30°C) nights of the first two trials, the magpies settled down very early on the perches (4-18 min after sunset) and most of them almost immediately put their head beneath the scapulars. Seldom did they expose their heads during the ensuing hours. When they did, it was only for a few minutes at a time. On the mildest (-10 to 1°C) nights, however, they would settle down later (15-28 min after sunset) and often wait with the eyes open until sometime during the third, fourth, or even fifth hour of the night before entering the blinking stage and finally taking the BUS position. When disturbed by a noise, they would expose their heads and remain alert, sometimes for more than 30 min.

At least seven of the nine birds involved in this study spent, on average, more time with their eyes exposed and open when they were in a peripheral rather than central position relative to their flockmates (Table IV-3). This may indicate that the magpies felt more vulnerable in the peripheral positions than in the central positions, and compensated by sleeping less (probably being more vigilant). This difference was never significant, however, possibly because of the small sample sizes and large variances (resulting from the overriding effect of temperature) associated with each mean value of time spent with the eyes open at the various positions.

Individuality appeared to influence the percentage of time a bird spent in the BUS posture. In each trial, it was usually possible to identify one or two individuals that consistently spent, at all temperatures, either more or less time in the BUS posture than the other bird(s) (see Fig. IV-3). Dominance status did not appear to be linked to this characteristic (Fig. IV-3), contrary to what might have been expected based on the fact that, in two trials, dominant birds were found most often in a central position (Table IV-2). The percentage of time spent in the BUS posture could in fact be an indicator of "sleepiness", an individual trait not necessarily correlated with behavioural characteristics such as

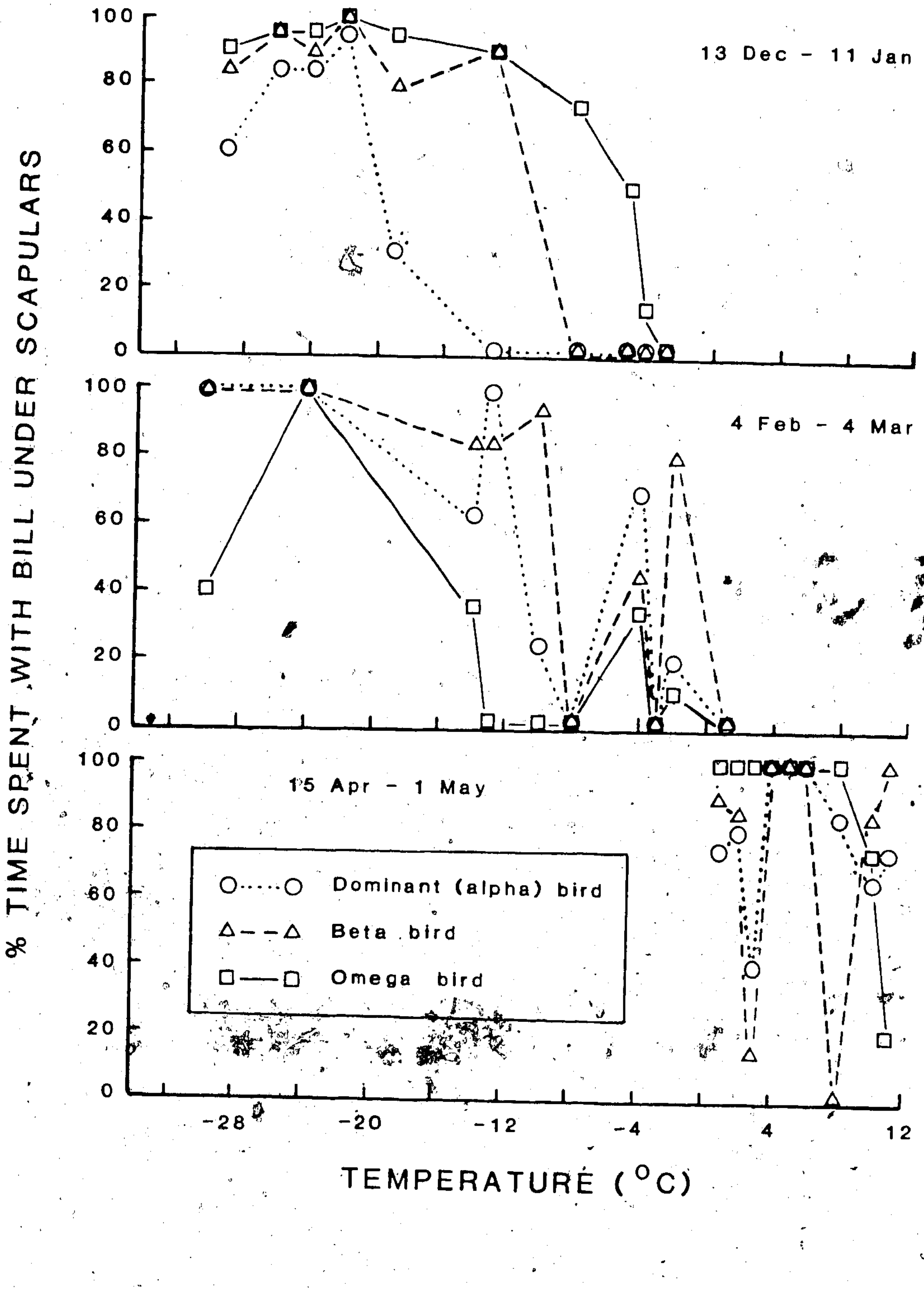

FIG. IV-3: Percentage of time spent by magpies with the bill under the scapular feathers during the third and fourth hour of nights of different temperatures. Dates indicate the earliest and latest day at which observations were made for each trial. The points at -4°C in the first trial, -14°C in the second trial, and 4°C and 2°C in the last trial are the means of two nights of observations at these temperatures.

TABLE IV-3 Mean proportion of time (with "n" in parentheses) spent by each magpie with its eyes open, at middle and peripheral positions (relative to its flockmates). The most dominant individual was assigned rank 1.

TRIAL	MAGPIE'S DOMINANCE RANK	POSITION		P[1]
		middle	peripheral	
1	1	0.57 (2)	0.69 (9)	NS
	2	0.41 (5)	0.56 (6)	NS
	3	0.40 (4)	0.30 (7)	NS
2	1	0.46 (7)	0.55 (4)	NS
	2	0.25 (4)	0.41 (7)	NS
	3	- (0)	0.73 (11)	-
3	1	0.12 (6)	0.25 (5)	NS
	2	0.00 (2)	0.25 (9)	NS
	3	0.00 (3)	0.03 (8)	NS

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[1] Based on Mann-Whitney test, with 0.05 as the level of significance.

dominance.

DISCUSSION

Position of the dominant bird in a roost

As part of a twofold hypothesis to explain the adaptiveness of communal roosting, Weatherhead (1983) suggested that dominant birds benefit from the presence of conspecifics by forcing their way into the central positions of a roost, thus surrounding themselves with subordinate individuals that unwillingly act as a buffer against predation. Evidence for relationships between dominance status and position in communal roosts comes from studies on rooks (*Corvus frugilegus*) (Swingland 1977), cowbirds (*Molothrus ater*) (Good 1979, cited in Weatherhead 1983), and red-winged blackbirds (*Agelaius phoenicus*) (Weatherhead and Hoysak 1984). In magpies, whose dispersion in a natural roost occurs along a horizontal plane (see Chapter II), one would expect a dominant individual to position itself so as to be surrounded by conspecifics on as many sides as possible.

If one agrees that support was given to this hypothesis each time a dominant bird occupied a central position relative to its flockmates in this study, then my results are only in partial agreement with the hypothesis. They seem at first to be consistent with the hypothesis since, in the last two trials, the dominant bird did occupy a central position more often than expected by chance. Yet, in the first trial, the dominant bird failed to do so. One can attempt to explain away this discrepancy by pointing out that only females were used in the first trial, and that females may rely on their mate or on their male flockmates to establish a position in the roost for all of them. This, however, appears unlikely in the light of the active role female magpies often take in the defense of, for example, the breeding territory (Baeyens 1981). Additionally, it is difficult to explain why, in the last two trials, the dominant bird roosted in a peripheral position on about one-third of the nights. I sought an answer to that question in the pattern of wind directions, based on the presumption that the dominant bird might have preferred southernmost positions when winds were blowing from the north, and northernmost positions when winds were blowing from the south. This, however, did not appear to be true because for only 9 of the 21 nights when the dominant bird was in a peripheral position in the last two trials did it occupy the position predicted according to wind direction (the same argument also fails to explain the results of the first trial, since for only 10 of 22 nights did the dominant bird occupy the correct peripheral position). As they stand, these results remain inconclusive.

Sleeping posture in magpies: the absence of blinking

In the absence of EEG recording, I use the chronological order in which the different phases of the magpies' nocturnal behaviour appeared during the night, and the definitions of Goodman (1974), to associate the "eyes open" phase with wakefulness, the "eyes blinking" phase with "dozing", and the BUS phase with sleep. I thus consider the BUS posture as the typical sleeping posture [illegible] magpies. This is in accordance with Goodwin's (1976:29) statement that "to sleep, corvids, like other passerines (...) turn the head round so that it rests on the back with the bill tucked into the scapulars" and that "the fluffed-up feathers then largely obscure the head, giving a rounded outline". That the magpies eyes appeared to be always closed in the BUS posture contradicts, however, the statement of Amlaner and Ball (1983:93) that "an important cue for all sleeping posture (in birds) appears to be whether the bird's eyelids blink". Blinking, in the present study, was observed only for short periods at night or during diurnal "dozing" bouts. It is possible that magpies open their eyes while their head is buried under the scapular feathers, but that appears unlikely since I could elicit no response to visual stimuli while in this posture, and I determined that the birds did not open their eyes in summer when the feathers were less erected.

Bouts of eye opening during sleep presumably function to visually scan the environment for danger (Amlaner and McFarland 1981, Lendrem 1983).

Magpies, in contrast, seemed to rely more on their sense of hearing to detect disturbance. This could be related to the need to cover the eyes with feathers to protect them against cold, and/or to the nature of the magpie's usual roosting sites (see Chapter II). In the wild, magpies roost in dense thickets where visibility is reduced and darkness deep. Looking around for predators may not be as efficient as listening for the noise they would make when moving through the network of branches and twigs that characterizes such habitat.

In contrast, Barbary doves (*Streptopelia risoria*) (Lendrem 1984), mallard ducks (*Anas platyrhynchos*) (Lendrem 1983), and herring gulls (*Larus argentatus*) (Amlaner and McFarland 1981), all of which have been reported to "blink" or "peek" in their sleep, roost in open places. Furthermore, two of these studies (Lendrem 1983, 1984) reported only on observations carried out during the day, when levels of illumination allowed for good visibility, or when "[illegible]zing" instead of deep sleep might have been witnessed. Magpies [illegible] when "snoozing" in the flight cage during the day, never kept [illegible]sed or covered by feathers for long periods [illegible]. They did so, however, in the darkness at night. Based on this, a[illegible] few references in the literature to non-blinking sleeping birds (Dunshea[illegible]ncaster 1941, Goodman 1974, Cooper 1979), I suggest that the pre[illegible]erance of blinking (peeking) activity in [illegible]ping birds has been suggested prematurely by Amlaner and Ball (1983), and that further studies are needed to evaluate the true significance of this behaviour in avian sleep. These studies should be carried out both in the laboratory, where the relationships between EEG a[illegible] and sleep posture or eye state can be examined, and in the field, where observations of different bird species sleeping in various environmental conditions could provide the basis for a comparative approach to the study of avian sleeping behaviour.

Sleeping posture in magpies: the need for thermoregulation

Given the numerous nights of sub-freezing temperatures occurring in central Alberta, one should expect the characteristics of the sleeping postures of birds residing year-round in Edmonton to reflect the need to minimize heat loss. The magpie s posture indeed appears to be the best one to serve such a function, with the ball-like shape of the sleeping bird minimizing the surface/volume ratio as well as the exposure of uncovered body parts (feet, bill, eyes). That magpies spent a greater proportion of their time in this posture on the coldest nights of winter is consistent with this idea. That the birds cease to cover their feet and eyes on summer nights also indicates that thermoregulatory needs can modify the characteristics of a sleeping posture. It may seem surprising, however, that magpies still tucked their bill under the scapulars when indoors at room temperature. The thermoneutral zone of the black-billed magpie extends from 21.0 to 32.5°C (Hayworth and Weathers 1984) and thus there is no need for heat conservation at 23°C. Perhaps, in the magpie at least, the BUS posture is the only one compatible with the neck muscle relaxation that commonly occurs in sleeping birds (Goodman 1974). Without the scapular feathers and folded wing to hold it in place, the bill might slide over the shoulder and the head then drop forward, placing the bird in an uncomfortable position that could hinder proper maintenance of balance on the perch. This sometimes happens to young (about 3 weeks old) magpie chicks when they put their bill on rather than beneath their partially developed back feathers while sleeping (pers. observ.).

The high proportion of time spent by magpies in the BUS posture during the long and coldest nights of winter raises questions about the extent to which sleep can be expanded to occupy a larger portion of the 24-h time budget. To sleep in the early hours of such nights seems superfluous since the magpies do not do it at milder temperatures. Are magpies always sleeping when in the BUS posture? Do magpies take the BUS posture on cold nights only to prevent heat loss, or both to prevent heat loss and to sleep? Only by making EEG recordings, or performing experiments on arousal thresholds, could these questions be answered.

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V. CONCLUDING DISCUSSION

In this study, I found black-billed magpies (*Pica pica*) to exhibit consistency in their choice of where, when, and how to sleep. I also found that environmental parameters were correlated with some aspects of the magpie's behaviour immediately before, during, and immediately after the night, and that, based on these correlations, inferences could be drawn regarding the adaptive significance of these actions. These observations can be summarized as follows.

Magpies always slept in densely wooded areas, and, within these areas, they often perched amid dense networks of branch. Avoidance of large nocturnal avian predators is a likely reason for such a choice, but its true importance cannot be assessed until more information is gathered about the vulnerability of both exposed and unexposed magpies to birds of prey. After the first heavy snowfall of the fall season, magpies were consistently found in places that, in addition to dense branch networks, offered good overhead cover and reduced exposure to winds. This is an obvious adaptation to cold (Morse 1980, Mugaas and King 1981).

Magpies almost always left the roost between morning civil twilight and sunrise, and they generally returned to it in the hour preceding sunset. Daylength, temperature, light intensity (cloud cover), and season were the best predictors of the amount of time between morning civil twilight or sunset and the departure or arrival of the birds at the roost. The role of temperature suggested that avoidance of unfavourable thermal conditions is a prime consideration, not only in the choice of where to sleep (see above), but also in the decision of how long to stay at the sleeping site. The role of daylength and season introduced the notion that the amount of time devoted to being in a roost may be a function of the amount of time that is necessary for successfully completing other activities, such as foraging and defending the breeding territory.

Magpies always slept in the same posture, which was found to minimize the exposure of unfeathered body parts, and to occur earlier in the night as temperature decreased. Thus, again, avoidance of adverse thermal conditions appeared important in determining the magpies night behaviour. The birds were also found to keep their eyes continually closed in this posture, but to be sensitive to surrounding noises, a possible adaptation against predation in dark, densely vegetated places such as their usual roosting sites.

For diurnal species of animal, night is an ecologically unprofitable, if not adverse, part of the day-night cycle. Since no activity can be economically accomplished because of failure to see in the dark, immobility may be the best behavioural strategy for survival. The advantages may be two-fold. First, by remaining motionless, an animal can render itself less visible to predators. Second, immobility can help save energy that could later be spent on activities best executed during the day. Thus, according to recent 'ecological theories', of which Meddis (1975, 1977) is the most articulate proponent, sleep evolved as a mechanism that helps maintain an inconspicuous, energy-saving state of immobility. Sleep fulfils this function by suppressing other drives and by rendering the animal less sensitive to stimuli that would otherwise elicit responses from it.

As Meddis (1975:680) wrote "It is an essential feature of the immobilization conception of sleep function that somnolence plays a secondary role to vital waking activities. Accordingly, the amount of t[illegible]t sleeping by any given species is limited by the time normally availabl[illegible] these essential activities have been completed". The early departures and late arrivals observed at a magpie roost on short days, when less than optimum time may be available for foraging, and on late spring days, when time must be devoted to territory defence (Chapter III), can be explained in this light (with the difference that the amount of time in the roost instead of the amount of time sleeping is considered). It seems likely that, in each case, magpies hastened their departure from the roost and delayed their return to it in order to devote more time to essential activities. Similarly, the early arrivals and late departures of the fall (Chapter III) can be viewed as an indication that the birds had more than enough time to complete all essential daily activities, and that the remaining spare time was best devoted to resting.

Also central to such ecological theories is the concept that sleep is an instinct, with the appropriate appetitive phase (searching for a sleeping place) and consummatory act (assuming a sleeping posture and falling asleep) (Tinbergen 1951). In the same way that the appetitive phase of reproductive behaviour, for example, implies searching for an appropriate mate, the appetitive phase of sleeping behaviour should imply searching for a sleeping place that maximizes energy conservation and minimizes predation risks (Meddis 1975). The sleeping posture should also contribute to energy conservation. These concepts seem to apply to birds in general (Amlaner and Ball 1983) as well as to magpies in particular (this study). Since all the roosting sites in this study offered conditions compatible with avoidance of both predation and inclement weather, the roosting flights of magpies to these sites can be seen as the appetitive phase of their sleeping instinct. Even the seeking of conspecifics with which to spend the night can be viewed as part of this appetitive phase if the presence of conspecifics helps a bird to feel secure at night (Chapter II). Finally the adoption of the bill under scapulars posture can be construed as the consummatory act of the sleep instinct.

If night renders a bird more vulnerable to predation, then, it seems at first paradoxical to reduce vigilance by sleeping at this time (Amlaner and Ball 1983). This applies only, however, to animals that cannot find a secure place to sleep (Allison and van Twyver 1970). A bird can afford to sleep (reduce its vigilance) for prolonged periods if the risk of predation at the sleeping site is very low. In magpie roosts, security appears to be enhanced by the density of vegetation and also, possibly, by the presence of conspecifics that give alarm calls when a predator is detected (Chapters II and IV). Because of this, a sleeping magpie at the communal roost may be as secure, if not more so, than an alert individual alone in the open in broad daylight.

Amlaner and Ball (1983) proposed that birds may use another solution to compensate for their lack of vigilance at night. They suggested that birds, occasionally throughout the night, raise their energy usage and open their eyes to look for predators. As I mentioned in Chapter IV, however, this 'peeking' habit has been found only in species sleeping in open places. The reduction in total true sleeping time in such species resembles that of ungulates living in open plains, who spend very little time sleeping (Allison and van Twyver 1970, Meddis 1975). Magpies, by contrast, sleep in secure places, and thus they do not need to expend energy on peeking (Chapter IV). They save energy by keeping their thresholds for detection of external stimuli at a low level, so that only unusual noises will arouse them. This level, presumably, has been set by natural selection so that the benefits of successfully locating true danger by sound outweighs the costs of energy wastage when the source of the disturbance turns out to be harmless, or the costs of failing to detect a silent predator.

Immobility can equally help the magpie to avoid detection by predators. Sleep appears not to be necessary, however, to achieve immobility: during the longest nights of winter magpies often spent several hours immobile yet not sleeping (Chapter IV). Thus, the argument of sleep as a way to maintain a state of inconspicuous immobility does not apply well to magpies in this study.

Sleep could nevertheless be necessary to prevent wasting energy. King (1974) reported that fasting birds sitting quietly in the dark, yet awake, use up 25% more energy than birds sleeping in the same conditions. He attributed the difference to the neuromuscular tonus and psychic activity associated with wakefulness. Sleep in birds can be further differentiated from wakefulness and drowsiness by the absence of movements, higher arousal thresholds, quantitative differences in electroencephalographic activity, and a decline in heart rate, respiration rate, and brain temperature (Goodman 1974). All these characteristics appear compatible with energy saving, but are not found in a bird that is simply immobile and awake. Energy saving is probably of substantial importance to magpies wintering in Alberta because of the relatively harsh conditions winter poses for survival (see Andreev 1977).

Many results of the present research are original because they were obtained under forbidding winter conditions (see methods in Chapter II for a summary of the climatic conditions in Edmonton). For example the selection of coniferous roosts by magpies, the influence of temperature on roosting times, and the covering of the eyes in the magpie's typical sleeping posture were all reported here but are absent from studies on roosting conducted under milder climates. Magpies wintering in England have not been recorded roosting in conifers (see for example Ward 1952). Brodie (1980) found very little influence of temperature on the roosting times of starlings (*Sturnus vulgaris*) wintering in Scotland and Balda et al. (1977) reported that pinon jays (*Gymnorhinus cyanocephalus*) roosting in northern Arizona cover their bill but not their eyes under the scapular feathers while sleeping. Thus, although my results give insight on how birds can adjust their roosting behaviour to harsh winter conditions, they do not allow generalization of the conclusions to populations living under other climatic conditions. I nevertheless believe that an ecological approach to the study of sleep can prove fruitful under a large array of environmental conditions and that additional efforts along these lines could lay the foundation for interesting comparative studies of avian sleep.

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