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Roost Selection and Roosting Behavior of Male Common Nighthawks

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ABSTRACT.—Many studies to date have documented clear energetic costs and benefits of avian roost selection. Male Common Nighthawks (*Chordeiles minor*) spend at least half of each day during the summer on a day-roost. Therefore selection of roost-sites likely has implications for survival and long-term fitness. Our objective was to identify characteristics of day-roosts used by male Common Nighthawks in Cypress Hills Provincial Park, Saskatchewan, Canada. We measured features of roost trees and monitored behavior of roosting birds. Nighthawks preferred trees situated on north facing slopes surrounded by trees with significantly lower canopy height compared to randomly measured trees. Roost trees were taller than random trees and occurred in less dense patches of forest. Birds always roosted parallel to branches and adopted a motionless posture. There was a non-significant trend for birds to roost on branches facing east. Birds typically roosted in a direction pointing away from the sun and away from the roost tree trunk. Roost trees emerging from the canopy may provide landmarks for birds as they search for suitable day-roosts, whereas a low tree density surrounding roost trees likely reduces flight costs associated with maneuvering. Our results suggest that roosts chosen by male nighthawks may provide selective benefits in terms of microclimate, energetics and predator avoidance, but further studies are needed to determine which is the most important.

INTRODUCTION

For nocturnal animals that seek shelter during the day, day-roost selection is likely to be an important determinant of individual fitness (Kerth *et al.*, 2001). Any energetic cost associated with choosing a potential roost will reduce energy available for reproduction, resource defence and social activities, thus directly influencing individual fitness (Walsberg, 1986). Selection of a roost site can be influenced by factors including inter- and intraspecific competition, predation, ectoparasitism and microclimate (Körtner and Geiser, 1999; Kerth *et al.*, 2001). For crepuscular caprimulgid birds, camouflage at roosts should be important because these birds rely upon cryptic plumage to avoid detection by predators (Holyoak, 2001) and do not depend on conspecifics to spot predators due to their solitary roosting strategy (Krams, 2001). Roosts must also provide a suitable microclimate (Hayward and Garton, 1984) where heat loss can be minimized during periods of cold weather or maximized during warm weather (Körtner and Geiser, 1999). For torpor users, such as nighthawks and birds of the family Caprimulgidae, a suitable roost microclimate may be especially important (Fletcher *et al.*, *in press*; Holyoak, 2001). When choosing a roost, presumably individuals must weigh the importance of these factors to optimize thermal, energetic and predator avoidance benefits.

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Data collected between 1966 and 2002 as part of the North American Breeding Bird Survey indicate that Common Nighthawk (*Chordeiles minor*; hereafter nighthawk) populations are declining in the United States and Canada (including Saskatchewan; Sauer *et al.*, 2003). Reasons for this decline are poorly understood and loss of day-roosting habitat is one potential explanation. More than 50% of the daily time budget of male nighthawks is spent at day-roosts (Poulin *et al.*, 1996). It is, therefore, reasonable to expect that day-roosts are important resources for males. To date, no study has directly quantified roost requirements of Common Nighthawks. Published information consists of anecdotal reports of nighthawk day-roost characteristics, with most literature addressing characteristics of roosts on gravel roofs of human-made structures (*e.g.*, Armstrong, 1965; Brigham, 1989). Reports concerning natural roost sites suggest that nighthawks typically roost in trees and adopt a posture parallel to live and dead branches of a diameter similar to their body width (Bowles, 1921; van Rossem, 1945; Sutherland, 1963). Holyoak (2001) described the day-roost behavior of all caprimulgids as being similar with the adoption of a motionless prone posture.

In light of our poor understanding of nighthawk roosting behavior, coupled with the likelihood that the choice of day-roosts is important, we evaluated roost characteristics of these birds. Our objectives were to quantify day-roost characteristics of male nighthawks at four spatial scales: (1) location, (2) 12 m radius tree plot, (3) roost tree and (4) roost branch scale and to report information about the behavior of roosting birds during the day.

MATERIALS AND METHODS

Study area.—The study was conducted in the West Block of Cypress Hills Provincial Park, Saskatchewan, Canada (49°34'N and 109°53'W) between 8 June and 29 August 2001. The area is dominated by fescue prairie and interspersed with forests of white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta*), trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*). We expected that all four tree species would provide sites for day roosts. Female nighthawks in the Cypress Hills nest on the ground in the open prairie (Poulin *et al.*, 1996).

Capture methods.—We caught male and female birds on gravel roads where they are known to roost after dusk foraging bouts (Poulin *et al.*, 1998). Nighthawks were disoriented with spotlights and captured with long-handled nets. Birds were sexed using distinct dimorphic color patterns on the throat and tail (Poulin *et al.*, 1996). We measured mass using an electronic balance (± 0.1 g) and attached a numbered aluminium leg band to each captured bird. Radio transmitters (3.9 g model PD-2T, Holohil Systems Ltd., Carp, ON, Canada) weighing less than 5% of each bird's body mass (average male nighthawk body mass = 82.7 g; Aldridge and Brigham, 1988), were affixed using a 'backpack' style harness described by Brigham (1992).

Study design.—Simply documenting characteristics of used roost trees does not allow for an explicit statement of how these roost trees differ from available but unused trees. To make valid statements about roost selection by nighthawks, we compared roost trees to random, presumably available, but unused, trees. The criteria and statistical analyses for this study design are presented below.

Roost site characteristics.—We identified roost sites by tracking six individual males who carried transmitters. Once roost trees were located (a tracking session), we searched trees with binoculars to locate the roosting nighthawk. We did not attempt to identify roosts used by females since they were nesting during the study period. Once a roosting nighthawk was

located, we recorded the position of the roost tree with a Global Positioning System (GPS; Garmin 12XL, Olathe, KS) and left the area to minimize disturbance to the bird. At the conclusion of the study, we measured parameters of roosts at the scale of the tree and tree plot (*see below*) for both roosts and random sites. We chose random trees for comparison with roost trees by walking in a randomly determined orientation for a random distance between 25–50 m from the roost tree. We used a minimum distance of 25 m to ensure that we were far enough away from the roost tree to ensure independent measurements of tree density and a maximum value of 50 m to ensure that we stayed within the same forest stand. The nearest tree to this location with a diameter at breast height (DBH) ≥ 9.5 cm (about the smallest DBH for a roost tree), regardless of species, was chosen as the random tree. Slope aspect on which the roost was located, distance to place of capture and distance between roosts of the same individual were measured at the location scale. Slope aspect was measured using a compass and distances to place of capture and between roosts of the same individual were calculated using UTM coordinates. Because roost and random trees typically occurred on slopes oriented in the same direction, we did not compare slope aspect between roost and random trees.

To assess habitat complexity (trees/m²) around the roost and random trees, we established 12 m radius circular plots (~ 0.045 ha) surrounding each focal roost or random tree. Within each plot we counted all trees of DBH > 9.5 cm. We selected 9.5 cm DBH as a minimum tree size because trees less than this DBH were always shorter than the height of roost trees and, thus, likely had little impact on the degree of forest clutter encountered by nighthawks. Percentage canopy cover was visually estimated within the 12 m radius plots using mean values of two independent estimates. Canopy height was calculated as the mean height of two trees representative of the canopy surrounding the focal tree.

We measured three variables that have been associated with roost trees of forest dwelling bats and nocturnal birds (Barrows, 1981; Brigham *et al.*, 1998; Churchill *et al.*, 2000). Specifically, we measured: tree species, DBH and tree height. All height variables were measured using a clinometer (Suunto Instruments, Helsinki, Finland, model #PM-5/360 PC).

Branch variables included: branch status (dead or alive), branch height, compass orientation of the section of branch on which the bird was roosting relative to the tree trunk and branch width where the bird was roosting. Branch width was calculated as the mean of two independent estimates made from directly beneath the roost branch.

Finally, on each tracking day we recorded two aspects of roosting behavior of male nighthawks: orientation of the bird's head relative to the roost tree trunk and whether the bird was roosting parallel or perpendicular to the roost branch.

Statistical analysis.—To assess which roost characteristics nighthawks selected, we used logistic regression coupled with Akaike Information Criterion (AIC) analysis as a model selection tool. We considered each roost tree as an independent sampling unit, although the same individual may have used more than one roost. If a roost was repeatedly used by the same individual we only entered that roost once in our analysis. A correlation analysis using Pearson's r was used to remove highly correlated pairs of variables from the initial model (*i.e.*, those variables with $r > 0.70$ or $r < -0.70$). No tree variables met this exclusion—tree height, canopy height—criterion so DBH, percentage ground slope and canopy closure, tree height canopy height, and tree density were entered into a logistic regression analysis. Hosmer and Lemeshow (1989) suggest that a stringent α level (*e.g.*, 0.05 and 0.10) for entry and removal of variables from logistic regression models may exclude biologically significant variables. After the initial logistic regression analysis on the full model we removed all variables with $P > 0.35$ (*i.e.*, all variables were removed after the first step of the logistic

TABLE 1.—Mean, standard deviation, range and logistic regression P-values of six variables for the 14 roosts used by birds and 14 random sites. Asterisks denote inclusion of the variable into the global model for AIC_c analysis ($P < 0.35$)

	DBH	% Ground slope	Tree Height	Canopy Height	% Canopy Cover	Tree Density
Roosts						
Mean	0.39	13.9	19.91	11.53	61	0.057
SD	0.07	10.8	3.57	3.09	17	0.031
Range	0.30–0.53	0–27.8	14.2–25.3	3.84–21.39	20–85	0.013–0.126
Random						
Mean	0.34	14.4	17.3	15.35	73	0.066
SD	0.08	11.4	3.86	3.65	20	0.027
Range	0.18–0.47	0–22.2	9.09–25.63	10.01–21.64	33–94	0.04–0.124
P-value	0.765	0.502	0.138*	0.056*	0.210*	0.114*

regression analysis). Assuming non-independence when there is in fact dependence may bias standard errors low, and thus increase the probability of Type I error. Our use of a relatively high P-value to remove variables should have eliminated this problem. DBH and percentage ground slope were excluded based on this preliminary analysis, leaving roost tree height, percentage canopy cover, canopy height and tree density, which we defined as the global model for use in the AIC analysis (Table 1). All subsets (15 possible models plus a constant only model) of this global model were then evaluated using AIC_c—a version of AIC corrected for small sample sizes (Anderson *et al.*, 2000). Models with the lowest AIC_c number and highest Akaike weights were considered to best distinguish roost from random trees (Anderson *et al.*, 2000). Our use of AIC analysis and not a strict null hypothesis testing procedure reduced the likelihood of committing Type I errors due to potential non-independence of our sampling units. Model averaging using Akaike weights was used to estimate parameter values for variables deemed important in AIC analysis. We used Rayleigh's test for circular uniformity ($\alpha = 0.05$) to determine if nighthawk roost and slope aspects were uniformly distributed (Zar, 1999). A simple binomial test was used to determine if nighthawks faced away from the trunk of the tree with probability different from 0.5 ($\alpha = 0.05$). All values are reported as means \pm sd.

RESULTS

In total, we located 14 different roost sites used by 6 males and paired these roosts with 14 random trees. Individual nighthawks were observed using these roosts on 32 occasions during 42 tracking sessions with each male using on average 2.3 roosts over the course of the study. Due to the cryptic nature of nighthawks, we were unable to find birds at roost trees on 10 occasions. Nighthawks used the same roosts over multiple tracking sessions (range 1–5 sessions consecutively). Of 14 roost sites, 6 were in lodgepole pine and trembling aspen and 1 each in balsam poplar and white spruce. Roosts occurred on slopes oriented in a northerly direction (mean slope aspect = $26^\circ \pm 64^\circ$, $R = 5.90$, $P < 0.05$). Different roosts used by the same individual were on average 1015.8 ± 1116.8 m ($N = 14$) apart. Day-roosts were 2548.2 m \pm 1998.8 m (range 125–5900 m) from where capture occurred.

From AIC_c calculations using the subsets of the global model based on logistic regression results (Table 1), four models were within 1 AIC_c unit of each other and best distinguished roost from random sites (Table 2). Canopy height (model averaged $B = -0.412$, model averaged $SE = 0.167$) appeared in all four of the top models, and as a single variable model

TABLE 2.—All subsets of the global model used for AIC analysis. Models that best distinguished male nighthawk roosts from random sites have the lowest AIC_c, lowest Δi and highest Akaike weight (w_i). Models less than 2 AIC units away from the most parsimonious model are considered competing models

Model	AIC _c	Δi	w_i
Canopy height	30.8	0	0.224
Tree Height, Canopy Height, Tree Density	31.0	0.259	0.196
Tree Height, Canopy Height	31.6	0.774	0.152
Canopy Height, Tree Density	31.8	1.012	0.135
Tree Height, % Canopy Cover, Canopy Height, Tree Density	32.4	1.601	0.100
% Canopy Cover, Canopy Height, Tree Density	33.0	2.247	0.073
% Canopy Cover, Canopy Height	33.1	2.362	0.068
Tree Height, % Canopy Cover, Canopy Height	34.3	3.506	0.038
% Canopy Cover, Tree Density	39.4	8.578	0.003
Tree Height, % Canopy Cover, Tree Density	39.8	9.043	0.002
Tree Height	40.0	9.266	0.002
% Canopy Cover	40.2	9.39	0.002
Tree Height, % Canopy Cover	40.5	9.768	0.001
Constant only model	40.8	10.20	0.001
Tree Height, Tree Density	41.5	10.768	0.001
Tree Density	42.5	11.690	0.001

had the lowest AIC_c number and highest Akaike weight, suggesting it was the most important feature distinguishing roost trees from random trees (Table 2). One or both of tree density (model averaged $B = -22.14$, model averaged $SE = 15.10$) and roost tree height (model averaged $B = 0.138$, model averaged $SE = 0.095$) appeared in all four models and, therefore, both of these variables were also important for distinguishing between roost and random trees (Table 2).

When birds returned to a tree that had been used before, they always roosted on the same branch and in the same location along the branch. Both dead and live branches were each used 7 times. Mean branch orientation was due east ($104^\circ \pm 84^\circ$), but this did not differ significantly from a uniform circular distribution ($R = 4.69$, $P = 0.21$).

Nighthawks roosted motionless and parallel to branches 100% of the time and faced away from the trunk of the tree 78.1% of the time (binomial test, $N = 32$, $P = 0.002$). Nighthawks used branches that were 0.10 ± 0.02 m in diameter and 12 ± 3 m high, which was 61% of mean roost tree height and approximately equal to canopy height.

DISCUSSION

Quantifying roost tree requirements will allow for an assessment of the impact of habitat loss due to forestry or agricultural processes on natural roosting sites of nighthawks and will aid in the management and protection of this species. Declining populations of this particular species indicate the need for further study and quantification of vital resources such as roost sites.

Location characteristics.—Nighthawks roosted in trees found on north facing slopes despite no qualitative difference in abundance of potential roost trees between north and south facing slopes. Roosting close to night-roosting sites cannot explain this pattern because we found that individuals traveled up to 6 km between day and night roosting sites. Thus, they selected roost trees from among a large pool of potential trees throughout the study area.

Barrows (1981) found that Spotted Owls (*Strix occidentalis*) also used roost trees on north facing slopes and argued that selection of such roosts provided an overall cooler microclimate compared to roosts on south facing slopes. This may be especially important in the Cypress Hills where afternoon temperatures routinely reach temperatures that exceed the upper critical temperature of nighthawks (approximately 35° C; Lasiewski and Dawson, 1964). While a comparative study between north and south facing slope temperatures would allow for an explicit description of roost macroclimate, we hypothesize that these nighthawks roosted in sites on north facing slopes because they are cool relative to sites with a southern exposure.

Roost tree and tree plot characteristics.—The most important factor distinguishing roost trees was a low canopy height within a 12 m radius of the roost tree. Tree height was also an important factor that emerged from AICc analysis of our logistic regression model. Low canopy height was also important for roost selection by Northern Saw-whet Owls (*Aegolius acadicus*; Churchill *et al.*, 2000). Emergent tall trees in a familiar area could provide landmarks for individuals returning from dawn foraging bouts flying above the canopy, as has been suggested for tree roosting bats (Vonhof, 1995; Vonhof and Barclay, 1996). Temperate bats and nighthawks are similar in their ecology and behavior, suggesting that their roost requirements may be similar as well. Studies of roost selection by bats have documented the importance of a low canopy height coupled with a high roost tree height and this trend also appeared in our models. Big-brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) both roost in cavities found in tall trees with low clutter from surrounding trees (Vonhof, 1995; Vonhof and Barclay, 1996). The ability to remember and re-use beneficial roosts day after day based on locations of landmark trees could reduce energetic costs of searching for quality day roosts and could explain the apparent loyalty of nighthawks to specific roost sites or patches of forest.

In addition to canopy and tree height, tree density within a 12 m radius plot centered on focal trees also distinguished roost from random sites. Poulin *et al.* (1998) hypothesized that nighthawks should prefer unobstructed space for take-off, landing and flying in general because of the high aspect ratio of their wings. Although tree density may play a role in roost selection, the fact that mean roost height was approximately equal to canopy height may negate the importance of low surrounding roost clutter. Another potential benefit of roosts with a low tree density in the immediate area is exposure to wind (Barrows, 1981). A relatively open roost above the forest canopy would facilitate convective heat loss via increased air movement, thereby reducing metabolic costs due to heat stress (Barrows, 1981). This hypothesis was consistent with our finding that nighthawks select roosts on north facing slopes to potentially mitigate costs associated with heat stress.

Branch choice.—Once a bird selected a specific roost, it reused the same branch on all tracking days when it was found in that particular tree. Repeated use of the same branch suggests that branch characteristics, in addition to tree characteristics, are important for roost selection.

Orientation of roost branches did not differ from a uniform distribution, but 11 of 14 roost branches were oriented in an easterly direction. Sun exposure in the morning at such a roost would allow for passive re-warming after cool morning temperatures, while providing a shaded microhabitat in the afternoon. This may be especially important as recent evidence suggests that arousal from bouts of torpor by nighthawks may occur in the morning hours while on a day-roost (Fletcher *et al.*, *in press*). Hoary bats (*Lasiurus cinereus*), a foliage roosting bat, use roost branches oriented in a southeasterly direction (Willis, *in press*). There is no evidence to suggest that nighthawks switch roosts during the day to avoid or expose themselves to sun, as do some other avian species (Barrows, 1981). Selecting roosts with

a specific orientation may reduce the need for nighthawks to switch roosts during the day to meet changing microclimate requirements (Carrascal *et al.*, 2001). This would reduce flight costs and the likelihood of revealing roost locations to potential predators. A similar cryptic roosting strategy coupled with the similar roosting strategy of both nighthawks and hoary bats in the same area suggests convergent selection pressures for roost choice.

Roosting behavior.—Although roost orientation appears to play a role in reducing thermoregulatory costs, postural adjustments aid in reducing sun exposure and minimizing the need for movement between roost sites. Our data show that nighthawks usually face away from the trunk during afternoon hours, which is consistent with the hypothesis that males use postural adjustments to decrease body area exposed to the sun. Female nighthawks are known to adjust their body according to the sun's orientation (Weller, 1958). Weller (1958) showed that between 1300–1800 h female nighthawks typically face in an easterly direction, positioning their heads away from the sun (Weller, 1958). In summer, Spotted Owls also characteristically adjust their position while day roosting such that their back is toward the sun, thereby reducing sun exposure (Barrows, 1981). Reduction of sun exposure on the body and head by postural adjustments would be an energetically beneficial metabolic expenditure while under heat stress (Weller, 1958). Facing away from the roost tree trunk would also allow for a less obstructed view, facilitating predator vigilance (Krams, 2001).

The roosting behavior of male nighthawks may allow them to avoid being detected by predators. Adopting a parallel and motionless roosting posture likely improves camouflage from the perspective of overhead predators, reducing the probability of detection (Holyoak, 2001). To human observers, nighthawks closely resemble part of the roost branch while motionless and are difficult to detect even after a roost tree has been located by tracking radio-tagged birds. Consistent with this hypothesis, we recorded no predation on tagged birds at roost sites even though potential predators were observed in the study area.

Conclusion.—Our data suggest that nighthawks select roost sites that reduce thermoregulatory costs and reduce flight costs associated with maneuvering in cluttered forests and locating suitable roost sites on the landscape. Furthermore, their behavior at the roost site may serve to help them detect and avoid detection by predators. At the location scale, birds used sites on north facing slopes, which may result in a relatively cool roost macroclimate. At the tree and tree plot levels, selection was based on landmark trees emerging from a low uncluttered canopy. These three characteristics of roost trees could reduce flight costs associated with searching for potential roosts and maneuvering in the vicinity of roosts. At the branch scale, roosting on an easterly facing branch could facilitate warming during morning hours and heat stress avoidance in the afternoons. Postural behavior allows for concealment, while potential postural adjustments could further reduce body exposure to intense heat, while allowing the bird to maintain predator vigilance. We acknowledge that our small sample size may limit our ability to generalize about roosting patterns of male Common Nighthawks and that further replication of our study would be useful to corroborate our inferences regarding nighthawk roost selection at the tree and tree plot scale and roost use at the location and branch scales (Johnson, 2002). Clear documentation of fitness benefits or costs from roost choice is still required for this species.

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