PRUETT-JONES, S. G., M. A. PRUETT-JONES, AND R. L. KNIGHT. 1980. The White-tailed Kite in North and Middle America: current status and recent population changes. Am. Birds 34:682–688.

WAKIMOTO, R. M. 1987. The Catalina eddy and its effect on pollution over southern California. Monthly Weather Review 115:837–855.

WHITE, G. C., D. R. ANDERSON, K. P. BURNHAM, AND D. L. OTIS. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, Los Alamos, NM.

WRIGHT, B. A. 1978. The ecology of the White-tailed Kite in San Diego County. M.Sc.thesis, San Diego State Univ., San Diego, CA.

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DIURNAL BEHAVIOR OF THE SPOTTED OWL IN WASHINGTON[1]

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Although the Spotted Owl (*Strix occidentalis*) is primarily nocturnal, it does forage occasionally during the day (Miller 1974, Forsman 1975, Forsman et al. 1984, Laymon 1988). The extent of diurnal foraging is not known, but Miller (1974) and Laymon (1988) suggested that spotted owls with fledged young frequently foraged during the day. Forsman (1975) suggested a more limited role for diurnal foraging, arguing that it was a largely opportunistic response to prey observed near daytime roosts. We investigated the amount and types of diurnal activity engaged in by Spotted Owls, including differences in diurnal activity based on reproductive status.

STUDY AREA AND METHODS

The study was conducted on the Cle Elum Ranger District of the Wenatchee National Forest, on the east slope of the Cascades Mountains in Washington. To quantify diurnal activity we conducted 96.6 hours of continuous diurnal observation on 15 Spotted Owls (seven males, eight females) that were marked with radio-transmitters. All owls were paired, and five of the eight pairs had young. Time spent observing nesting and non-nesting individuals was 57.6 and 39 hours, respectively. Owls were located during the day by homing in on their radio-transmitters with a radio receiver and hand-held directional antenna.

Once an owl was located, we sat quietly and observed the owl from a distance of 25–50 m. The owls were extremely tame and paid little attention to us once we stopped moving. After waiting 10–15 min for the owl to become accustomed to being watched, the observer began a 2-hr observation period, recording the time whenever the owl switched from one behavior type to another. Each interval between the time when an activity type began and ended was categorized as a single behavioral episode. The duration of behavioral episodes was rounded up to the nearest minute for analysis. The 2-hour observation period was strictly followed except in two cases when it became too dark to see.

Where possible, data were subdivided by sex, reproductive status, and time of day, to evaluate the relationship of these variables to the type and amount of diurnal activity. Time of day intervals examined were: 08:47–12:00, 12:01–15:00, 15:01–18:00, 18:01–20:10 PST. Observation schedules were arranged so that each owl was observed for an approximately equal number of 2-hour periods, and so that proportion of observations in each time interval were similar for nesting and non-nesting birds. All observations were conducted between 23 May and 5 September 1989.

We recorded four different behavior types (roosting, foraging, movement, and social interaction). The "roosting" category included a variety of resting and maintenance behaviors, including roosting with the eyes closed or open, preening, hopping from branch to branch within a roost tree, defecating, and consuming stored prey. The "foraging" category included two subcategories: (1) actual attempts at prey capture, and (2) visual searching behavior in which owls appeared to be looking for or observing prey. The "movement" category included any flight in which an owl actually left the roost tree and moved to a new location. The "social interaction" category included periods of vocalization or allopreening.

Methods used to assess diurnal activity included: (1) a Markov chain analysis of behavioral transition frequencies (Raphael 1990), (2) an empirical comparison of the proportion of time spent in different behavior types, and (3) a comparison of distances moved per hour.

The Markov chain analysis was used to compensate

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TABLE 1. One-step transition frequencies for behavioral changes of nesting and non-nesting Spotted Owls observed on the east slope of the Cascade Range Mountains, Washington.

Breeding status	t − 1	Behavior at time t				Row totals
		R[1]	F	S	M	
Non-nesting	R	445	22	13	11	491
	F	20	1	0	1	22
	S	12	0	0	2	14
	M	12	0	1	0	13
Nesting	R	761	66	38	34	1,398
	F	62	6	0	7	75
	S	39	0	0	11	50
	M	35	4	12	4	55
Markov steady-state probability of a behavior						
Non-nesting		0.90	0.04	0.03	0.03	
Nesting		0.83	0.07	0.05	0.05	

[1] R = roosting, F = foraging or predation, S = social behavior, M = movement.

for potential lack of independence with sequentially recorded data. Our Markov analysis assumed a one-step, stationary process in which a bird's behavior at time t depended only on its behavior at time t − 1, and the transition probabilities did not change over time. Markov steady-state vectors were calculated using program MARKPROB (Douglas Call, pers. comm.). Markov steady-state vectors indicate the probability that, over the long run, an owl will be found exhibiting a particular behavior. Chi-square tests were used to compare transition matrices of breeding and non-breeding birds.

Straight-line movements associated with each 2-hr observation period were summed and converted to an hourly rate. The overall average was the average of the hourly rates for the individual observation periods.

RESULTS

Forty-nine observation periods were completed between 23 May and 5 September 1989. Comparison of marginal row totals of behavioral transition frequencies (Table 1) indicated a significant difference in behavior of nesting and non-nesting birds ($\chi^2 = 17.39$, 3 df, $P = 0.001$). The most obvious difference was that nesting birds spent less time roosting ($\chi^2 = 26.48$, 3 df, $P < 0.001$) and more time in active types of behavior (foraging, socializing, moving) ($\chi^2 = 12.56$, 3 df, $P = 0.006$, Table 1).

On an hourly basis, nesting birds spent an average of 4.55 min (SE = 0.71) socializing, 4.16 min (SE = 0.68) foraging, and 2.19 min (SE = 0.41) moving about. In comparison, non-nesting birds spent an average of 1.19 min (SE = 0.45) socializing, 2.15 min (SE = 0.60) foraging, and 1.08 min (SE = 0.42) moving per hour. Comparison of the mean number of minutes spent per hour in active types of behavior (foraging, socializing, moving) per owl also indicated that nesting owls were significantly more active during the day than non-nesting individuals ($F = 4.10$, 1 df, $P = 0.05$).

The proportion of time spent in roosting versus active behaviors differed significantly depending on time of day, with owls becoming more active after 18:00 hours ($\chi^2 = 87.30$, 3 df, $P < 0.001$, Table 2). The proportion of time spent in roosting versus active behaviors did not differ between males and females ($\chi^2 = 0.09$, 1 df, $P = 0.76$).

The total number of minutes in Table 2 summed to 101.5 hrs, which was more than the total hours (96.6) spent observing owls. This was due to rounding up to the nearest minute when recording the duration of individual behaviors. While this resulted in a slight overestimate of the sample size, it should not have appreciably effected the analysis, since all types of behavior were assessed in the same way.

Of 97 observations of foraging, 88 (91%) were cases in which owls appeared to be visually observing or searching for prey, and nine (9%) were cases in which owls attempted to capture prey. Of the nine attempts at prey capture, eight were by nesting birds and eight were launched from the tree in which the owl was initially found roosting. The exception was a case in which an owl flew about 20 m to a different tree before attacking. Of nine capture attempts, two (22.2%) were successful. Prey captured were a chipmunk (*Tamias* spp.) and an unidentified small animal. Intended prey could be identified in four of the nine capture attempts. All four were chipmunks.

On average, nesting owls made 0.12 attempts to capture prey 0.12 per/hr (SE = 0.06) and non-nesting owls made 0.02 attempts to capture prey 0.02 per/hr (SE = 0.03). Multiplying the hourly rate of capture attempts by 12 (the average number of daylight hours/day, ex-

TABLE 2. Relationship between time of day and activity of Spotted Owls in Washington, expressed as the proportion of the total number of minutes spent in different activity types.

Time period (PST)	*n* (minutes)	Activity type			
		Roost	Forage	Social	Moving
08:47–12:00	457	0.92	0.03	0.02	0.03
12:01–15:00	1,989	0.94	0.03	0.02	0.01
15:01–18:00	2,543	0.94	0.02	0.03	0.01
18:01–21:10	1,105	0.85	0.04	0.03	0.07

cluding twilight hours) produced an average of 1.44 capture attempts/day for nesting birds and 0.24 attempts/day for non-nesting individuals. Multiplying 1.44 by 0.22 (average rate of capture success) indicated that nesting individuals might be expected to capture an average of 0.32 animals during a typical 12-hr diurnal period. For a nesting pair this number could be expected to double to 0.64 animals/day after the young fledged and both pair members began to hunt.

Average distance moved per hour during the day did not differ between nesting birds ($\bar{x}$ = 20.6 m/hr, SE = 5.06) and non-nesting birds ($\bar{x}$ = 11.5 m/hr, SE = 3.64) (t = 1.47, P = 0.15). In 23 of 47 observation periods, owls did not leave their roost trees (two periods were removed from the sample because they included the beginning of nocturnal foraging). Owls moved more than 50 m from their initial location in only five of 47 observation periods. The maximum cumulative distance moved during a single 2-hr observation period was 175 m. Of five cases where movements exceeded 50 m, three occurred in the late afternoon (after 16:00 hours PST).

DISCUSSION

Our analyses indicated that nesting Spotted Owls were more active during the day than non-nesting individuals, as suggested by Miller (1974) and Laymon (1988). However, both nesting and non-nesting owls spent most of the day roosting and rarely traveled far from their roost sites during the day.

The fact that eight of nine capture attempts were launched from trees where owls were initially found roosting, and that owls rarely moved far from their roosts to forage during the day, suggested that diurnal foraging was an opportunistic response to prey detected while owls were roosting. Laymon (1988) suggested that nesting Spotted Owls in the Sierra Nevada Mountains regularly foraged during the day when they were feeding fledged young. He based this on nine instances of diurnal foraging observed during a three-year study and on the considerable numbers of diurnal prey in the diet of owls in his study area. Although he provided little supporting data, he implied that owls were regularly leaving their roost areas to forage during the day. We can not evaluate the amount of diurnal foraging or movement from his data because he presented no information on rates of diurnal activity or distances moved during the day. However, our observations indicate that a high proportion of diurnal prey in the diet and occasional observations of diurnal foraging do not necessarily indicate extensive diurnal movements.

A potential confounding factor in this study was the possibility that the observer's presence influenced activities of potential prey, thereby causing prey to be more or less vulnerable than they would have been in the absence of the observer. We could not assess this factor. It should also be noted that our observations did not include the early morning hours, when rates of foraging behavior could possibly differ from other times of day.

Regardless of differences in diurnal activity between nesting and non-nesting birds, prey captured during the day unquestionably contributed biomass to the diet of owls that we observed. This additional biomass may be particularly important during periods when pairs are feeding young or during times of low prey abundance, as suggested by Laymon (1988) and Miller (1974).

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LITERATURE CITED

FORSMAN, E. D. 1975. A preliminary investigation of the Spotted Owl in Oregon. M.Sc.thesis, Oregon State Univ., Corvallis, OR.

FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildl. Monogr. No. 87.

LAYMON, S. A. 1988. Ecology of the Spotted Owl in the central Sierra Nevadas, California. Ph.D.diss., Univ. of California, Berkeley, CA.

MILLER, G. M. 1974. Grace M. Miller on Spotted Owls, p. 130–146. *In* L. W. Walker [ed.], The book of owls. Alfred A. Knopf, New York.

RAPHAEL, M. G. 1990. Use of Markov chains in analysis of foraging behavior. Studies in Avian Biol. 13:288–294.