

experience in parenting activities which could enhance reproductive success later in life, but the costs would be lost initial reproductive success (Selander 1964, Brown 1978). When helpers are related and when the benefit/cost ratio is large, we might expect selection to lead to greater social specialization (Brown 1978) such as adoption. However, in our observations, the adopters were mature hens; thus, there would be little reproductive experience gained since two of the four hens were successful in previous years, and three had existing broods. In contrast to the other situations, costs to the hen on the June 27, 1988 observation were low. This hen had lost here complete brood, and we had not observed reneesting following hatching of a brood. The benefit/cost ratio in this situation would have been larger. Since in the Black Hills the risks of dispersing from the family units are minimal, mates and territories are plentiful, and initial breeding success is high, the establishment of family social units and adoption should be rare (Emlen 1982).

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Diurnal foraging by Spotted Owls.—The Spotted Owl (*Strix occidentalis*) is thought to be one of the most nocturnal of North American owls (Bent, Life histories of North American birds of prey, U.S. Natl. Mus. Bull. 170, 1938). However, Miller (Miller, The book of owls, L. W. Walker, ed., Alfred Knopf, 1974) observed them foraging “. . . at all hours of the day or night . . .” while they were feeding young in Marin County, California. Forsman (Forsman et al., Distribution and biology of the Spotted Owl in Oregon, Wildl. Monogr., 1984) observed very little diurnal foraging during their studies of Spotted Owls in Oregon, concluding that

TABLE 1
DATE, TIME (PDT) AND DISTANCE FROM NEST DURING DIURNAL FORAGING BOUTS BY
BREEDING SPOTTED OWLS

Individual	Date	Time	Distance (km)
Gaddis female	7 July	1200	1.0
Gaddis male	8 July	1045	1.4
Gaddis male	11 July	1230	1.5
Gaddis male	15 July	1000	0.8
Gaddis female	15 July	1230	1.1
McCulloh male	13 July	1100	0.7
McCulloh male	30 July	1230	1.0
McCulloh male	7 August	1130	1.5
Wallace male	8 August	1300	1.4

the few diurnal foraging bouts observed were opportunistic, and they suggested that Miller's observations of diurnal foraging were most likely also opportunistic.

I collected pellets from four breeding and 13 nonbreeding pairs of Spotted Owls near Georgetown, El Dorado County, California. Prey were identified to species from pellet contents and divided into diurnal and nocturnal categories, based on their life history patterns. I attached radio transmitters to six pairs of Spotted Owls, using a backpack configuration and a teflon-tubing harness. I tracked the owls to their roosting sites using a receiver and two-element Yagi antennae. I define foraging as an active search for prey, as opposed to opportunistic foraging, which I define as taking prey if it presents itself.

During 1982, Spotted Owls captured a relatively high proportion of diurnal prey. Prey items were identified from seven pairs of owls ($N = 572$ prey items); 10% were diurnal birds and 4% were diurnal mammals. I noted that 20% of the 208 prey items from the breeding pair were diurnal, while 10% of the 364 prey items taken by the six nonbreeding pairs were diurnal. This was a statistically significant difference ($\chi^2 = 11.34$, $df = 1$, $P < 0.001$).

During 1983, I placed radio transmitters on four pairs of Spotted Owls. One, the Gaddis pair, was breeding, and the other three were not. I tracked each of these eight owls to diurnal roosts on ten occasions, approximately one week apart, during the summer. On 7 July, after the young had fledged but were still dependent, I tracked the Gaddis female to a daytime roost 1 km NW of the nest site. The female was roosting in the sunlight in a Douglas fir (*Pseudotsuga menziesii*) (Table 1). Canopy closure around the roost site was much lower than most summer roost sites. The bird was obviously foraging rather than roosting. She was alert, reacting to every sound and staring intently at a nearby incense cedar (*Libocedrus decurrens*). As I watched, she suddenly left her perch, gliding towards the cedar, plucked a long-eared chipmunk (*Eutamias quadrimaculatus*) from the trunk near a stick nest 9 m above the ground and immediately returned to the Douglas fir with her prey. She lost her grip on the chipmunk, which fell to the ground and immediately ran to the safety of a brush pile. I found the Gaddis female foraging diurnally on one other occasion and found her mate foraging diurnally on three occasions (Table 1). On 17 July, both of the Gaddis juvenals were killed by a predator. The next day, both the male and female stopped foraging diurnally and became predominantly nocturnal.

During 1984, two breeding pairs were equipped with radio transmitters. I tracked each of these four owls to diurnal roosts on ten occasions, approximately one week apart, during

the summer. The male of the McCulloh pair was observed foraging diurnally on three occasions (Table 1). During a foraging bout on 7 August he caught a Douglas squirrel (*Tamiasciurus douglasii*). The Wallace male was observed foraging diurnally once on 8 August.

All nine diurnally foraging owls were found between 1000 and 1300 PDT (Table 1). In all nine cases of the 50 visits to roosting Spotted Owls with young, the owls were alert to motion and sound and were not drowsy as I normally found them when roosting in the daytime. In addition, in all cases, the owls were at a greater distance from the nest site than normal. The mean distance was 1.2 km and the range was 0.7 to 1.5 km (Table 1). I generally found roosting owls with young within 0.1 km of the nest. During seven of these nine cases, they were at sites where they would not normally roost in the summer due to scant canopy closure. The canopy closure at these nine sites ($\bar{x} = 63.6\% \pm 10.5$ [2 SE]) was significantly lower ($P < 0.01$) than at 120 summer roosting sites ($\bar{x} = 85.8 \pm 3.9$ [2 SE]) (Laymon, The ecology of the Spotted Owl in the central Sierra Nevada, California, Ph.D. diss., Univ. of California, Berkeley, 1988).

Nonbreeding Spotted Owls that I visited 70 times during 1983 and 1984 were not observed foraging during daylight hours even though 14% of their 627 prey items were diurnal. It is likely that some of these food items were captured opportunistically and that others were captured at dawn and dusk. The breeding birds, however, based on a sample of 445 prey items captured 25% diurnal prey. This difference was statistically significant ($\chi^2 = 21.79$, $df = 1$, $P = 0.0001$). When the proportion of foraging bouts vs visits is compared for breeding (18% of 50 visits) and nonbreeding owls (0% of 70 visits) the difference is also significant ($\chi^2 = 12.07$, $df = 1$, $P < 0.001$).

Forsman and colleagues believed, based on their data from Oregon, that Spotted Owls did not forage diurnally and captured diurnal prey opportunistically. Unlike Forsman et al. (1984) and in agreement with Miller (1974), I found that Spotted Owls in the Sierra Nevada captured more diurnal prey and regularly foraged diurnally to feed their young during the first six weeks following fledging. The observations of diurnal foraging presented here must represent a small proportion of the actual diurnal foraging of these breeding birds, since each owl was tracked to a daytime roost only 10 times during the summer and was observed for an hour each time. On six occasions, out of approximately 20 visits, adult owls were seen bringing food to their young during the middle of the day.

The immediate change exhibited in foraging behavior when the young of the Gaddis pair were killed suggests that the need to provide food for the young was the stimulus that led to their diurnal foraging. It is likely that diurnal foraging is a reaction to food stress placed on the adult Spotted Owl by rearing young. It is also possible that only pairs that commit to intensive diurnal foraging are able to raise young in the disturbed environment where this study was done. Spotted Owls in less disturbed areas, with more abundant preferred nocturnal prey, might not forage diurnally during the breeding season.

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