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## Weather-dependent Kleptoparasitism and Aggression in a Raptor Guild

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Weather is known to affect various aspects of the foraging behavior of birds, including hunting success, rates of energy intake, foraging mode, and microhabitat selection (e.g. Schnell 1968, Grubb 1977, Alatalo 1982, Dugan 1982, Petit 1989). The effect of weather on social behavior, however, has received much less attention. Here, we report the effect of snowfall on kleptoparasitic and aggressive behaviors in a raptor guild. We also discuss changes in raptor abundance and hunting behavior following snowfall.

Our study was conducted in 1.5 km<sup>2</sup> of agricultural land west of the Boundary Bay Airport in Delta, British Columbia, Canada. The site was 70% old field, 20% plowed field, and 10% short grass. We observed raptors for 37 h during daylight on six days from 4 to 27 February 1990. Following a snowfall on 14 February, the fields at our study area were covered with 14 cm of snow until 20 February. During this period, we observed raptor activities for 22 h on 17, 18, and 19 February. To examine raptor behaviors in the absence of snow, we analyzed 15 h of observations on 4, 11, and 27 February (before snowfall and after snow melt). On each day of observation, we recorded the maximum number of individuals of each raptor species seen on the study area, the number and success of prey capture attempts per species, the number and success of kleptoparasitism attempts per species, and the number of nonkleptoparasitic aggressive interactions per species (for detailed descriptions of observational methods, see Temeles 1987, 1990). The number of individuals per raptor species and/or the number of hours of observation varied for each day of study. Consequently, we examined the rates of behaviors per individual per hour for each species, rather than counts, unless otherwise noted. To avoid inflating sample sizes by making comparisons between either numbers of observations or numbers of individuals, we compared the mean rates of behaviors for the three days snow was present with the mean rates of behaviors for the three days snow was absent (means are presented along with standard errors). All statistical procedures were performed using Minitab statistical packages (Ryan et al. 1985).

The composition of the raptor guild varied in the

presence and absence of snow cover. Prior to snowfall and subsequent to snow melt, only Bald Eagles (*Haliaeetus leucocephalus*), Rough-legged Hawks (*Buteo lagopus*), and Northern Harriers (*Circus cyaneus*) were seen on the study area. However, when snow was present, Short-eared Owls (*Asio flammeus*) also were observed during daylight hours. Numbers of raptors on the study area tended to be higher when snow was present than when it was absent (Fig. 1). In part, this resulted from increased counts due to increased diurnal activities of owls when snow was present, but numbers of Rough-legged Hawks and Northern Harriers also increased.

Hunting activity of Northern Harriers was affected by snow cover (Table 1). Although harriers made no more capture attempts when snow was absent than when it was present (Table 1;  $t = 1.85$ ,  $df = 3$ ,  $P = 0.16$ ; log-transformed data), their hunting success (number of successful captures/number of attempts) was higher with snow cover than without (Table 1;  $t = -4.71$ ,  $df = 2$ ,  $P = 0.04$ ;  $\log[y + 1]$  transformed data). Consequently, the harriers' rates of prey intake were higher in the presence of snow cover (Table 1;  $t = -3.71$ ,  $df = 3$ ,  $P = 0.034$ ;  $\log[y + 1]$  transformed data). Short-eared Owls made significantly more capture attempts ( $\bar{x} = 1.29 \pm 0.09$  attempts individual<sup>-1</sup> h<sup>-1</sup>;  $t = -5.81$ ,  $n = 89$  attempts,  $P = 0.01$ ) and had higher rates of prey intake ( $\bar{x} = 0.41 \pm 0.07$  prey individual<sup>-1</sup> h<sup>-1</sup>;  $t = -3.09$ ,  $n = 27$  prey,  $P = 0.05$ ; log-transformed data) than harriers (see Table 1), but did not differ from harriers in hunting success ( $\bar{x} = 0.32 \pm 0.05$  captures attempt<sup>-1</sup> day<sup>-1</sup>;  $t = 1.39$ ,  $df = 2$ ,  $P = 0.30$ ). The numbers of prey capture attempts by Bald Eagles ( $n = 1$ ) and Rough-legged Hawks ( $n = 3$ ) were too small for statistical comparisons. All prey captured by the four raptor species were Townsend's voles (*Microtus townsendii*).

Snow cover drastically increased the frequency of kleptoparasitism in the raptor guild. We did not observe any kleptoparasitism attempts when snow was absent but, in the presence of snow, we observed 49 kleptoparasitism attempts: 2 by Bald Eagles, 13 by Rough-legged Hawks, and 34 by Northern Harriers (also see Table 1). One Rough-legged Hawk, 23 Northern Harriers, and 25 Short-eared Owls were victims of kleptoparasitism attempts. We witnessed two raptors simultaneously attempt to rob the same victim on four occasions, and nine cases of sequential kleptoparasitism attempts: a harrier would steal a vole from an owl, and then a different harrier or a Rough-legged Hawk would attempt to steal the vole from

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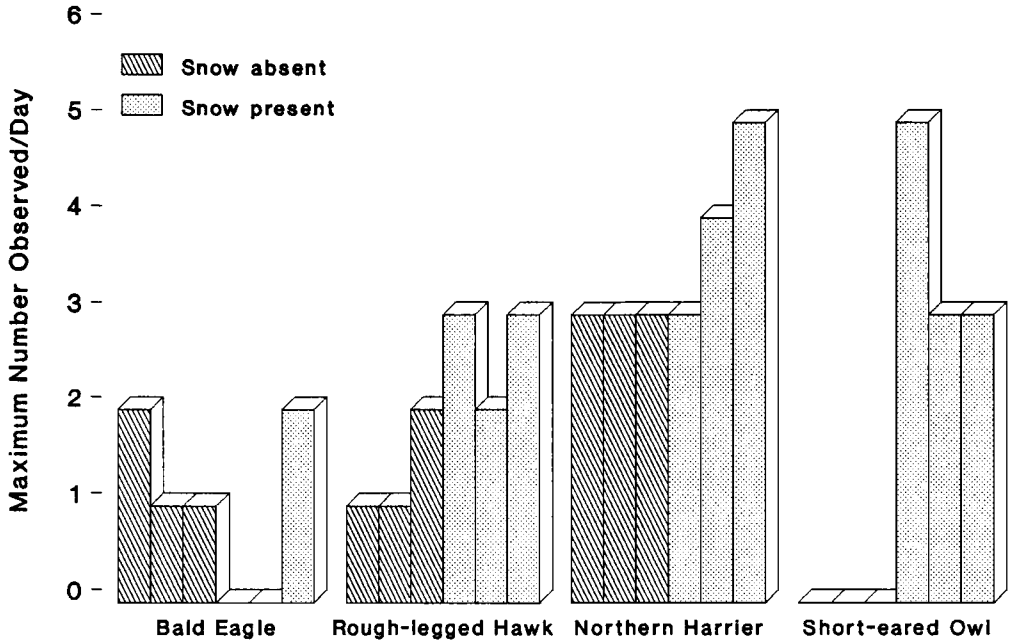


Fig. 1. Maximum numbers of individuals of four raptor species recorded on three days when snow was present and three when it was not. Missing bars indicate zeros. Numbers of Rough-legged Hawks and Short-eared Owls were significantly higher when snow was present (*t*-tests;  $P < 0.05$  for both species).

the harrier. Thirty-three of the 49 kleptoparasitism attempts recorded involved two species, and the larger species was the kleptoparasite in all of them (binomial test,  $P < 0.0001$ ). Relative to Northern Harriers, a higher proportion of kleptoparasitism attempts by Rough-legged Hawks was directed towards other species rather than their own (12 of 13 attempts by Rough-legged Hawks vs. 19 of 34 attempts by Northern Harriers;  $X^2 = 4.05$ ,  $df = 1$ ,  $P < 0.05$ ).

Harriers attempted kleptoparasitism as frequently as they attempted to capture prey when snow was present and were as successful at kleptoparasitism as they were at prey capture (Table 1). As a result, the rate of prey intake of harriers via kleptoparasitism did not differ significantly from the rate of prey intake

from hunting (Table 1). However, the harriers' success at kleptoparasitism and rates of prey intake via kleptoparasitism when snow was present were significantly higher than their capture success and rates of prey intake from hunting when snow was absent (success,  $t = 7.26$ ,  $df = 2$ ,  $P = 0.018$  untransformed data; rate of intake,  $t = 4.07$ ,  $df = 2$ ,  $P = 0.05$ ;  $\log[y + 1]$  transformed data). Rough-legged Hawks and Bald Eagles made too few hunting and kleptoparasitism attempts to permit similar comparisons.

Overall, the frequency of nonkleptoparasitic aggressive interactions was higher when snow was present (Table 2). We observed 56 aggressive acts (primarily chases, escorts, and stoops; for descriptions of aggressive behaviors, see Bildstein and Collopy 1985,

TABLE 1. Effect of snow cover on rates (number individual<sup>-1</sup> h<sup>-1</sup>) and success (number of successes/number of attempts) of foraging and kleptoparasitic behaviors of Northern Harriers. Values are means and standard errors calculated from observations on three days when snow was present and three when it was not. Number of times a behavior was observed is in parentheses.

Variable	Snow	
	Present	Absent
Prey capture attempts	0.40 ± 0.12 (28)	1.18 ± 0.51 (44)
Capture success	0.49 ± 0.11 (12)	0.02 ± 0.02 (1)
Prey intake (hunting)	0.17 ± 0.04 (12)	0.02 ± 0.02 (1)
Kleptoparasitism attempts	0.43 ± 0.05 (34)	0.00 (0)
Kleptoparasitism success	0.51 ± 0.06 (17)	—
Prey intake (kleptoparasitism)	0.22 ± 0.05 (17)	—

TABLE 2. Effect of snow cover on frequency of aggressive acts (number individual<sup>-1</sup> h<sup>-1</sup>) of all raptor species in guild, Northern Harriers, and Rough-legged Hawks ( $\bar{x} \pm SE$  calculated as in Table 1). Number of times an aggressive act was observed is in parentheses.

	Snow	
	Present	Absent
All raptors	0.24 $\pm$ 0.03 (49)	0.10 $\pm$ 0.04 (7)
Northern Harriers	0.34 $\pm$ 0.03 (27)	0.17 $\pm$ 0.07 (6)
Rough-legged Hawks	0.08 $\pm$ 0.04 (5)	0.00 (0)

Temeles 1990): 1 by a Bald Eagle, 5 by Rough-legged Hawks, 33 by Northern Harriers, and 17 by Short-eared Owls. The majority (40 of 56) of aggressive interactions involved two individuals of the same species; however, of the 16 interactions involving two species, the aggressor was the smaller species in all cases (binomial test,  $P < 0.001$ ). Relatively, intraspecific aggression was more frequent among Northern Harriers (24 of 27 interactions) than among Short-eared Owls (6 of 17 interactions;  $X^2 = 11.45$ ,  $df = 1$ ,  $P < 0.001$ ). Although the frequency of aggressive interactions in the raptor guild increased when snow was present, this increase apparently resulted from the presence of Short-eared Owls, because rates of aggression of both Northern Harriers and Rough-legged Hawks did not differ significantly in the presence and absence of snow (Table 2;  $t$ -tests,  $P > 0.15$  for both species).

When snow was present, raptors dramatically increased their use of kleptoparasitism relative to their use of hunting. Brockmann and Barnard (1979) noted that both food shortage and a large concentration of hosts may favor the use of kleptoparasitism. Several investigators have observed kleptoparasitic behavior when food was scarce and rates of prey intake from hunting (or scavenging) were low (e.g. Stalmaster and Gessaman 1984, Hansen 1986, Knight and Skagen 1988, Temeles 1990), although kleptoparasitism also may occur when food is abundant (e.g. Stalmaster and Gessaman 1984, Hansen 1986, Knight and Skagen 1988). In addition, Ens et al. (1990) noted an increase in the frequency of kleptoparasitism relative to hunting when flooding reduced the size of a local feeding site and as a result Eurasian Curlews (*Numenius arquata*) were restricted to foraging within a smaller area.

We suggest that both food shortage and a large concentration of hosts may have been responsible for the increased frequency of kleptoparasitism when snow was present, although of the two, the availability of an easy-to-kleptoparasitize host may have been more important. Although essentially crepuscular, Short-eared Owls will hunt in daylight in order to meet their energetic demands (Clark and Ward 1974), which might explain why we observed them hunting during the day only in the presence of snow. As shown here, rates of prey capture of owls were considerably higher than rates of prey capture of the other raptor species in the guild. Even though rates

of prey intake via hunting for some of the raptor species (e.g. harriers) increased when snow was present, the increased encounter rates with a smaller, easy-to-kleptoparasitize host (owls) carrying prey may have favored the use of kleptoparasitism as a foraging strategy. In contrast, the lack of kleptoparasitism observed when snow was absent may not have resulted as much from high prey availability favoring the use of hunting as from a low frequency of prey capture (and, hence, fewer potential hosts carrying prey) and the unavailability of a potential host (e.g. owls; for a related discussion, see Bildstein 1987).

Similarly, rates of nonkleptoparasitic aggressive interactions increased when snow covered the ground. This increase in aggression may have been due in part to an increase in the number of competitors for prey items on the study area and to short-term changes in prey availability. In addition, some of the increase in aggression may have been in response to the increased frequency of kleptoparasitism. Both Bildstein (1987) and Temeles (1990) observed that larger raptor species tended to kleptoparasitize smaller raptor species and that smaller species defended against larger potential kleptoparasites by attempting to evict them from their foraging areas using aggressive behaviors. Our observations that Short-eared Owls, which were both the smallest members of the guild and the most frequently kleptoparasitized, responded aggressively only toward larger raptor species are consistent with the explanation that owls acted aggressively to deter kleptoparasitism. The similarity of our observations in British Columbia to those made in south-central Ohio (Bildstein 1987) and in northern California (Temeles 1990) suggests that kleptoparasitism of smaller species and aggression against larger species may be a general phenomenon in wintering raptor guilds. Finally, the number of potential kleptoparasites (i.e. Northern Harriers, Rough-legged Hawks) increased on the study area during the period when snow was present, and intraspecific aggression was observed frequently in these species (especially among harriers). This raises the intriguing possibility that in addition to competing among themselves for food items, individuals of these two species may have been competing for opportunities to kleptoparasitize smaller owls.

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## Pterylography of Birds-of-paradise and the Systematic Position of Macgregor's Bird-of-paradise (*Macgregoria pulchra*)

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Macgregor's Bird-of-paradise (*Macgregoria pulchra*) is a poorly known species that occurs higher in the mountains of New Guinea than any other member of its family (Gilliard 1969, Cooper and Forshaw 1977). *Macgregoria* was originally discovered in 1896 and observations on its breeding behavior were first made by Rand (1940), who located the species in 1933 and 1938. More recently, Beehler (1983, 1991) visited its habitat on several occasions and reported on the species' behavior and ecology. As far as is known, *Macgregoria* habitat is cloud forest and subalpine *Dacrycarpus* (*Podocarpus*) forest at the edge of alpine grasslands between 2,800 and 4,000 m. Although the species appears to be sedentary, relatively easy to observe, and fairly common in *Dacrycarpus* groves when

the trees are fruiting, the high mountains where *Macgregoria* lives are difficult of access and the birds disappear to unknown habitat when *Dacrycarpus* is not fruiting (Beehler 1991).

Because the species is little studied and rare in collections, knowledge of the morphology of *Macgregoria* is limited. When Bock (1963) published a study of the Paradisaeidae based on skull morphology and jaw musculature, no specimen of *Macgregoria* then existed in alcohol; Bock's only material for that genus was a skull taken from a study skin. He found that, within the family, *Macgregoria* was the only genus that did not clearly fall into either the large subfamily of typical birds-of-paradise (Paradisaeinae) or the small group (Cnemophilinae) that Bock proposed for *Cne-*