WEATHER-DEPENDENT FORAGING SUCCESS AND SIBLING AGGRESSION IN RED-TAILED HAWKS IN CENTRAL WASHINGTON

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Lack (1966, 1968) and others have reviewed evidence indicating that most birds have evolved clutch sizes and related breeding behaviors which permit adults to maximize their genetic contribution to future generations. In many cases, this enhancement is equivalent to (or indistinguishable from) rearing the largest brood(s) of healthy young possible in each breeding season (Ricklefs 1977). However, data on the behavior and breeding biology of many large predatory birds seem inconsistent with such a view. For example, while Lack and others suggested that food availability ultimately limits the reproductive success of large predatory birds, the evidence for food limitation of brood size in these birds is scanty (Brown 1976). Here I report on weather-dependent delivery of prey by Red-tailed Hawks (*Buteo jamaicensis*) to unfledged young and on sibling aggression at a nest in central Washington. These observations are consistent with the hypothesis that food availability affects the number of healthy young the parents are capable of rearing.

METHODS

I observed a Red-tailed Hawk nest that was half-way up a cliff face on the Yakima River 32 km north of Yakima in Kittitas County, Washington. I used a 20× telescope (from a distance of 100 m) on 4, 9, 11, 18, 29 and 30 May, and on 3 and 4 June 1978. Every 15 min, using methods detailed in Stinson (1978), I recorded cloud cover, sunniness, wind speeds, precipitation, and wet-bulb and dry-bulb temperatures. Temperatures at 04:00 were taken from the U.S. National Weather Service's monthly summary of local climatological data at Yakima, Washington (U.S. National Oceanic and Atmospheric Administration 1978).

Four multivariate regressions were performed with the following dependent variables: (1) average rate (prey items/h) at which prey were brought to the nest in each 4-h period of the day, or observed fraction thereof (05:00–09:00, 09:00–13:00, 13:00–17:00, and 17:00–21:00); (2) dummy variable "event of prey delivery" indicating whether or not prey was delivered during each observed period of the day; (3) percent time (arcsin transformed) during which the male was perched near the nest in each observed period; and (4) percent time (arcsin transformed) during which the female was perched near the nest in each observed period. Stepwise regression procedure was used to derive the best regression with the following independent variables: number of young in the nest; average age of the young; maximum and minimum wind speeds recorded each 4-h period; average dry-bulb tempera-

ture each period; average relative humidity each period; average sunniness each period; average cloudiness each period; average rate at which precipitation occurred; dummy variables indicating each 4-h period; and a dummy variable "04:00 temperature" indicating whether the temperature at 04:00 was greater or less than 15.4°C.

Multivariate regressions were calculated with programs in the *Statistical Package for the Social Sciences* (Nie et al. 1975). In all stepwise procedures, the best regression was selected as that with the smallest residual sum of squares where all included variables were significant at the 0.05 level (determined by partial *F*-test, Draper and Smith 1967; they also discuss use of dummy variables).

RESULTS

The ranges, means, and standard deviations for the 18 variables included in the multivariate regressions (N = 23) were as follows: (1) rate at which prey were brought to nest (items/h), 0.0–1.0, 0.24 ± 0.30; (2) percent time male perched near nest (arcsin transformed), 0.0–1.98, 0.15 ± 0.42; (3) percent time female perched near nest (arcsin transformed), 0.0–90.0, 17.28 ± 17.88; (4) event of prey delivery (dummy variable), 0.0–1.0, 0.52 ± 0.51; (5) number of young in nest, 1.0–2.0, 1.43 ± 0.51; (6) average age of young in nest (days), 7.0–39.0, 23.48 ± 12.30; (7) maximum wind speed (m/s), 31.3–169.9, 85.92 ± 41.93; (8) minimum wind speed (m/s), 0.0–58.1, 13.81 ± 15.96; (9) average difference between maximum and minimum wind speeds (m/s), 24.6–82.7, 46.05 ± 18.55; (10) average dry-bulb temperature (°C), 7.4–35.0, 18.78 ± 7.34; (11) average relative humidity (%), 17.3–72.9, 42.66 ± 16.90; (12) average sunniness (%), 0.0–100.0, 69.7 ± 28.7; (13) average cloudiness (%), 0.0–99.0, 37.6 ± 35.8; (14) average rate of precipitation (mm/0.25 h), 0.0–1.3, 0.17 ± 0.39; (15) period 05:00–09:00 (dummy variable), 0.0–1.0, 0.17 ± 0.39; (16) period 09:00–13:00 (dummy variable), 0.0–1.0, 0.26 ± 0.45; (17) period 13:00–17:00 (dummy variable), 0.0–1.0, 0.26 ± 0.45; and (18) 04:00 temperature (dummy variable), 0.0–1.0, 0.17 ± 0.39.

On 15 April 1978, I located the nest and observed both adults taking shifts incubating. A single chick was visible beside the incubating female on 31 April. Two chicks, estimated to be six and eight days old

TABLE 1. Mean percentage of time male and female Red-tailed Hawks with unfledged young were perched at or near the nest, and mean rate of prey delivery (prey/h) by both adults to unfledged young, in each period of the day.

Period of day	Mean percent time perched near nest		Mean prey delivery rate (prey/h)
	Male	Female	
05:00–09:00	0.0 ± 0.0 (4)[a]	50.6 ± 34.7 (4)	0.0 ± 0.0 (4)
09:00–13:00	0.8 ± 1.3 (6)	2.3 ± 3.5 (6)	0.3 ± 0.4 (6)
13:00–17:00	0.3 ± 0.3 (6)	26.6 ± 40.5 (6)	0.3 ± 0.2 (6)
17:00–21:00	0.0 ± 0.0 (7)	43.8 ± 35.5 (7)	0.3 ± 0.3 (7)
Unweighted mean[b]	0.3 ± 0.7 (23)	29.7 ± 30.7 (23)	0.3 ± 0.3 (23)
Weighted mean[c]	0.3 ± 0.4	30.8 ± 21.5	0.2 ± 0.2

[a] Mean ± SD (no. periods observed).
[b] Sum of observed percentages or rates divided by 23.
[c] Sum of mean percentages or rates divided by 4.

(based on photographs in Fitch et al. 1946), were present on 4 May. One chick disappeared between 11 and 18 May, and the other chick apparently fledged successfully shortly after 4 June. No Red-tailed Hawks were seen near the nest on 14 June.

From 4 May through 4 June, I spent 82.25 h watching the pair of Red-tailed Hawks with unfledged young, and recorded weather as described above. The male and female spent 0.3% and 29.7%, respectively, of the observed daylight hours perched at or near the nest (Table 1). The percent time (arcsin transformed) during which the male was perched near the nest in each observed period had a significant regression coefficient only with the dummy variable for the period 09:00–13:00 ($P < 0.044$; regression coefficient $\beta \pm SE = 0.007 \pm 0.003$). The percent time (arcsin transformed) during which the female was perched near the nest in each observed period had a significant regression coefficient only with the dummy variable for the period 09:00–13:00 ($P < 0.039$, $\beta \pm SE = -0.45 \pm 0.20$). The male spent significantly more, and the female significantly less, time at the nest in the period 09:00–13:00 than in the other 4-h periods.

Both adults brought prey to the nest, and because they may have transferred some prey away from the nest, I do not distinguish between prey delivered by the male and that delivered by the female in the following analysis. However, the male delivered 7 of the 10 prey items seen brought to the nest between 4 and 19 May, while the female delivered 8 of the 11 prey items seen brought to the nest between 20 May and 4 June. The observed mean rate of prey delivery was 0.26 items/h (21 prey items delivered in 82.25 h). Snakes (mainly racers *Coluber constrictor* and gopher snakes *Pituophis melanoleucus*) made up 76% of the prey delivered to the nest; four small rodents and a Common Crow (*Corvus bra-*

chyrhynchos) comprised the remainder. Snake and mammal lengths were estimated to range from 40 to 100 cm (mean = 75 cm) and 15 to 20 cm (mean = 19 cm), respectively. I estimate mean snake biomass to be 140 g (based on living specimens weighed at the University of Washington), mean mammal biomass to be 200 g (Burt and Grossenheider 1976), and the crow biomass to be 400 g (Johnston and Williamson 1960). The weighted mean biomass of prey brought to the nest is 164 g/item. The weighted mean rate of prey delivery is about 0.2 items/h (Table 1). Assuming 16 h of daylight each day, I estimate that an average of about 520 g of prey was delivered to the nest each day. The event of prey delivery during each 4-h period had a significant regression coefficient with the average dry-bulb temperature each period ($P < 0.003$; $\beta \pm SE = 0.06 \pm 0.02$) and the dummy variable "04:00 temperature" ($P < 0.003$; $\beta \pm SE = -1.0 \pm 0.3$, multiple correlation coefficient = 0.66; Fig. 1). However, none of the variables examined had a significant regression coefficient with the rate at which adults brought prey to the nest.

On 4, 9, and 11 May, I spent 32.1 h watching the nest and its two unfledged young. On 4 May, when the chicks were about six and eight days old, they frequently would extend their necks and push against each other. I observed pecking only rarely. The female would generally alternate feeding the two young. On 9 and 11 May, interactions between the two chicks were more violent. During feedings, one chick planted itself in front of the female and pecked at its sibling whenever it approached. Because the young Red-tailed Hawks were not easily distinguished, I cannot say that the same chick always dominated the other during feeding. However, my impression was that the slightly larger chick was usually the dominant chick. Only occasionally did the
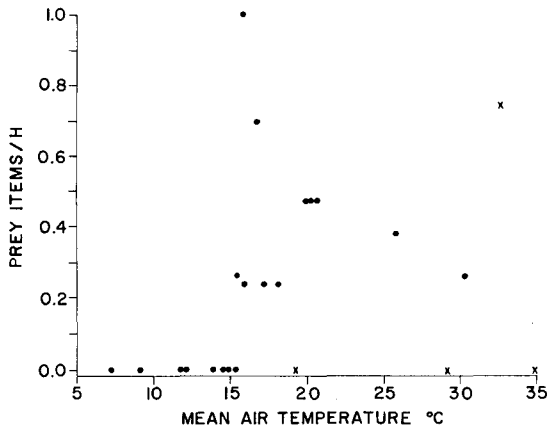
FIGURE 1. Prey delivery by adult Red-tailed Hawks in relation to mean air temperature during each observed 4-h period (or fraction thereof). Circles represent data from 4-h periods in days preceded by cool nights (temperature at 04:00 less than 15.4°C), and crosses represent data from 4-h periods in days preceded by warm nights (temperature at 04:00 higher than 15.4°C).

female feed the subordinate and frequently pecked chick. The chicks fought more frequently when the female was present than when she was absent. On 18 May, only one chick was in the nest.

DISCUSSION

The Red-tailed Hawks I observed fed their young primarily snakes. The delivery of these prey to the nest depended highly on air temperature. When mean air temperature during a 4-h period was below about 15.4°C, no prey were brought to the nest (Fig. 1). At higher temperatures, delivery of prey items was regular but did not increase with rising temperatures (Fig. 1). A switch in the behavior of the snakes from inactivity to activity as mean air temperature rose above about 15.4°C was probably responsible for the temperature-dependent prey delivery by the hawks.

Shortly before the chick fledged, when nocturnal temperatures were warm enough that snakes may have been active throughout the night, prey delivery was significantly reduced during 4-h periods in days preceded by warm nights (Fig. 1). There are two likely explanations for this finding. First, when weather conditions permit, snakes may confine their activity to night. Such a shift from diurnal to nocturnal activity with the advent of summer occurs in the southwestern speckled rattlesnake (*Crotalus mitchelli*; Moore 1978) and in some gopher snake populations (Mosauer 1935,

Klauber 1939). Indeed, Huey and Slatkin (1976) suggested for other reptiles that predation restricted to certain times could be sufficient to cause avoidance of those times even if activity was physiologically possible. Second, snakes simply may be less active in the summer. Reduced levels of above-ground diurnal activity (with no increase in nocturnal activity) during summer months have been reported for the racer (Brown 1973, cited by Parker 1974) and for other gopher snake populations (Fautin 1946, Parker 1974). The reduced level of diurnal activity after warm nights cannot be attributed to snakes avoiding intolerably hot diurnal temperatures, because the diurnal temperatures in question were often within the range of diurnal temperatures (preceded by cool nights) when snakes were active (Fig. 1). Apparently, snakes in central Washington are available as prey for breeding Red-tailed Hawks primarily in late spring when nocturnal temperatures are too cool but diurnal temperatures are warm enough for snakes to be active.

Obviously, the rate of prey delivery to the nest depends not only on prey availability but also on the amount of time the adults devote to hunting. Female Red-tailed Hawks do relatively little hunting for their unfledged young (Beebe 1974). In my study, the female spent about 30% of the observed daylight hours perched at the nest throughout the nesting period. Certain factors, notably the need to guard the young from potential predators, may limit the time available to the parents for hunting. Great Horned Owls (*Bubo virginianus*) and other predators take Red-tailed Hawk nestlings (Craighead and Craighead 1956, Luttich et al. 1971, Gates 1972, McInvaille and Keith 1974, Johnson 1975, Wiley 1975). There is selective advantage in reducing the risk of predation by having an adult remain at the nest, despite the reduction in rate of prey delivery that this guarding necessitates. Because of the predation potentially suffered by nestling Red-tailed Hawks, the female's relative inactivity is not inconsistent with either the hypothesis that food availability affects the number of healthy offspring the adults can rear or the hypothesis that brood size reflects the largest number of offspring which usually can be reared.

The aggressive behavior of the two chicks described above is apparently the first report of sibling aggression in nestling Red-tailed Hawks. Ingram (1959) cited Criddle (1917) as evidence that Red-tailed Hawks

are cannabalistic. However, Criddle (1917) commented that only one of six nests fledged more than one chick and that dead chicks in the other nests "presented no indication of violence, but seemed to show that, in all probability, death was due to starvation." Criddle's observations do not imply either cannibalism or scavenging by Red-tailed Hawks. I prefer to follow Mc-Nicholl (1977) in distinguishing between "scavenging" (i.e., the ingestion of a previously dead item, including conspecifics dead from other causes) and "cannibalism" (i.e., killing and eating a conspecific), rather than lumping the two instances under "cannibalism" as Ingram (1959) has done. Scavenging of dead nestlings by Red-tailed Hawks was reported by Hagar (1957).

The brood reduction often associated with sibling aggression in other raptors is thought to increase the surviving chicks' probability of attaining breeding age by increasing each survivor's share of food delivered to the nest (Lack 1966, Newton 1977, Stinson 1979). The relatively low rate of food delivery seen here is consistent with this food-limitation hypothesis. McInvaille and Keith (1974) reported that Red-tailed Hawks brought an average of 710 g of prey daily to broods of two young, and an average of only 410 g daily to single chicks. Over a 5-year period, adults were found to bring an average of 340 to 570 g of prey daily to each nestling (McInvaille and Keith 1974). The estimated daily delivery of 520 g of prey in my study is within this range of biomass delivered per chick, and is well below the average of 710 g apparently required for the maintenance and growth of two nestlings. Also in agreement with the hypothesis that sibling aggression is a response to low food availability is the observation by Fitch et al. (1946) of adult Red-tailed Hawks removing uneaten (and consequently spoiled) prey remains from the nest; they did not observe any sibling aggression. Adults were never seen removing prey from the nest in my study, again consistent with the food-limitation hypothesis.

If the weather-dependent prey delivery reported here is typical of Red-tailed Hawks in this region, the survival of second (and third) nestlings in a given season will be related to weather conditions in that season. However, if females cannot predict the nestling-period weather at the time of egg laying, clutch sizes may correspond to a relatively large brood size optimal during years with favorable weather. Sibling aggression probably acts to reduce the brood to a size commensurate with the weather-limited prey delivery when nestling-period weather is unfavorable.

LITERATURE CITED

BEEBE, F. L. 1974. Field studies of the Falconiformes of British Columbia. B.C. Prov. Mus. Occas. Pap. No. 17.
BROWN, L. 1976. British birds of prey. Collins, London.
BROWN, W. S. 1973. Ecology of the racer, *Coluber constrictor mormon* (Serpentes, Colubridae), in a cold temperate desert in northern Utah. Ph.D. diss., Univ. of Utah, Salt Lake City.
BURT, W. H., AND R. P. GROSSENHEIDER. 1976. A field guide to the mammals. Houghton Mifflin, Boston.
CRAIGHEAD, J. J., AND F. C. CRAIGHEAD, JR. 1956. Hawks, owls, and wildlife. Stackpole, Harrisburg.
CRIDDLE, N. 1917. The Red-tailed Hawk in Manitoba. Ottawa Nat. 31:74–76.
DRAPER, N. R., AND H. SMITH. 1967. Applied regression analysis. Wiley, New York.
FAUTIN, R. W. 1946. Biotic communities of the northern desert shrub biome in western Utah. Ecol. Monogr. 16:251–310.
FITCH, H. S., F. SWENSON, AND D. F. TILLOTSON. 1946. Behavior and food habits of the Red-tailed Hawk. Condor 48:205–237.
GATES, J. M. 1972. Red-tailed Hawk populations and ecology in east-central Wisconsin. Wilson Bull. 84:421–433.
HAGAR, D. C., JR. 1957. Nesting populations of Red-tailed Hawks and Horned Owls in central New York State. Wilson Bull. 69:263–272.
HUEY, R. B., AND M. SLATKIN. 1976. Costs and benefits of lizard thermoregulation. Q. Rev. Biol. 51:363–384.
INGRAM, C. 1959. The importance of juvenile cannabalism in the breeding biology of certain birds of prey. Auk 76:218–226.
JOHNSON, S. J. 1975. Productivity of the Red-tailed Hawk in southwestern Montana. Auk 92:732–736.
JOHNSTON, D. W., AND F. S. L. WILLIAMSON. 1960. Heart weights of North American crows and ravens. Wilson Bull. 72:248–252.
KLAUBER, L. M. 1939. Studies of reptile life in the arid southwest. Bull. Zool. Soc. San Diego 14:1–64.
LACK, D. 1966. Population studies of birds. Clarendon Press, Oxford.
LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.
LUTTICH, S. N., L. B. KEITH, AND J. D. STEPHENSON. 1971. Population dynamics of the Red-tailed Hawk (*Buteo jamaicensis*) at Rochester, Alberta. Auk 88:75–87.
MCINVAILLE, W. B., JR., AND L. B. KEITH. 1974. Predator-prey relations and breeding biology of the Great Horned Owl and Red-tailed Hawk in central Alberta. Can. Field-Nat. 88:1–20.

McNicholl, M. K. 1977. Usage of the terms "cannibalism" and "scavenging" in ecological literature. Can. Field-Nat. 91:416.

Moore, R. G. 1978. Seasonal and daily activity patterns and thermoregulation in the southwestern speckled rattlesnake (*Crotalus mitchelli pyrrhus*) and the Colorado desert sidewinder (*Crotalus cerastes laterorepens*). Copeia 1978:439–442.

Mosauer, W. 1935. The reptiles of a sand dune area and its surroundings in the Colorado desert, California: a study in habitat preference. Ecology 16:13–27.

Newton, I. 1977. Breeding strategies in birds of prey. Living Bird 16:51–82.

Nie, N. H., C. H. Hall, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. SPSS statistical package for the social sciences. Second ed. McGraw-Hill, New York.

Parker, W. S. 1974. Comparative ecology of two colubrid snakes, *Masticophis t. taeniatus* (Hallowell) and *Pituophis melanoleucus deserticola* Stejneger, in northern Utah. Ph.D. diss., Univ. of Utah, Salt Lake City.

Ricklefs, R. E. 1977. On the evolution of reproductive strategies in birds: reproductive effort. Am. Nat. 111:453–478.

Stinson, C. H. 1978. The influence of environmental conditions on aspects of the time budgets of breeding ospreys. Oecologia 36:127–139.

Stinson, C. H. 1979. On the selective advantage of fratricide in raptors. Evolution 33:1219–1225.

U.S. National Oceanic and Atmospheric Administration. 1979. Local climatological data, May–June 1978, Yakima, Washington. National Climatic Center, Asheville, North Carolina.

Wiley, J. W. 1975. The nesting and reproductive success of Red-tailed Hawks and Red-shouldered Hawks in Orange County, California, 1973. Condor 77:133–139.

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RECENT PUBLICATIONS

Allan Brooks: Artist Naturalist.—Hamilton M. Laing. 1979. Special Publication No. 3, British Columbia Provincial Museum, Victoria. 249 p. $16.00 cloth, $10.00 paper. Allan Brooks (1869–1946) is remembered today chiefly as the artist of innumerable plates of birds or mammals that enriched books and *National Geographic* articles a few decades ago. This biography of him has been written by a longtime friend, neighbor, and birding companion. Much of the story is told in passages from Brooks's journals and letters. Laing provides explanations, commentary, and anecdotes while keeping himself in the background. The book is illustrated with photographs, many of Brooks's sketches, and eight color paintings which show the development of his technique. It makes a valuable contribution to the histories of North American ornithology and of bird art.

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Arctic Summer: Birds in North Norway.—Richard Vaughan. 1979. Anthony Nelson, Shrewsbury, England. 152 p. £6.25. Available: Buteo Books, P.O. Box 481, Vermillion, SD 57069. The Varanger Peninsula at the top of Norway (lat. 70°30′) is the northernmost place in the world to which one can drive all the way, a great asset for the study of arctic nature. The author's experiences and observations there during a five-week visit one summer are the content of this book. It is a personal account of the birds he saw and photographed, without any pretense of research. There are many fine photographs in color and monochrome, but the latter have suffered in reproduction. A book to be enjoyed by others who have watched arctic birds.

Population Ecology of Raptors.—Ian Newton. 1979. Buteo Books, Vermillion, SD. 399 p. $35.00. This book is concerned with all aspects of population regulation in falconiform birds, with their social behavior, dispersion, numbers, movements, breeding, mortality, and conservation, and the effects on them of pesticides and pollutants. It draws together a great deal of recent worldwide research in a well-written and stimulating manner. Illustrated with many fine photographs and with attractive drawings by Jim Gammie. Bibliography, 68 (!) tables, and index. Authoritative and important for those who investigate and admire raptors, and relevant to population studies of other birds.