THE USE OF SOARING BY THE RED-TAILED HAWK (*BUTEO JAMAICENSIS*)

JOAN M. BALLAM[1]

Department of Zoology, University of Arkansas, Fayetteville, Arkansas 72701

ABSTRACT.—Behavioral data collected year-round in northwestern Arkansas indicated that foraging is not the exclusive function of soaring flight. Red-tailed Hawks (*Buteo jamaicensis*) spent much more time soaring than would be expected from the foraging returns of this behavior. Soaring was found to be unimportant in thermoregulation. Instead of soaring to thermoregulate, birds sought shade, were inactive, and panted during heat stress. Ptiloerection and retraction of extremities were noted during cold stress. Soaring activity contributed significantly to territorial defense, and I suggest that soaring flight is superior to flapping flight in this regard. Courtship was a prominent function of soaring during late winter. Further studies on functions of raptorial soaring should investigate exploratory behavior.
Received 20 January 1982, resubmitted 9 May 1983, accepted 15 December 1983.

FEW researchers have investigated the functional aspects of nonmigratory raptorial soaring. Pennycuick (1972) suggested that East African vultures used thermal soaring for food searching and cross-country travel. Bent (1937) and Beebe (1974) described soaring as a typical hunting behavior of the genus *Buteo*. Wakeley (1978) found that foraging alone could not account for the percentage of time the Ferruginous Hawk (*Buteo regalis*) spent in soaring activity. In the present study, I investigated the possible functions of soaring behavior in the Red-tailed Hawk (*Buteo jamaicensis*), including foraging, thermoregulation, and territorial defense. Soaring is already known to function in the courtship displays of Red-tailed Hawks (Bent 1937, Fitch et al. 1946, Conner 1974).

Optimal foraging theory suggests that an organism maximizes its caloric yield per cost ratio when searching for food (MacArthur and Pianka 1966, Royama 1970, Schoener 1971, Pulliam 1974, Emlen and Emlen 1975). According to this hypothesis, a predator using several foraging techniques should apportion its time according to the benefit-to-cost ratio for each technique. A comparison of the proportion of time Red-tailed Hawks spend in soaring activity and the foraging returns of this behavior will be used to determine whether or not foraging is a primary function of soaring.

A Red-tailed Hawk must function thermodynamically in a climate space governed by radiation, humidity, air velocity, and ambient temperature (Porter and Gates 1969, Calder and King 1974). If, as suggested by several authors (Dawson and Schmidt-Nielsen 1964, Dawson and Hudson 1970, Torre-Bueno 1978), Red-tailed Hawks can reach cooler surroundings by high-altitude soaring and eliminate heat by convection and radiation, then soaring could function in thermoregulation during heat-stress situations. Many authors (Tucker 1968, Berger et al. 1971, Bernstein 1976, Torre-Bueno 1978, Hudson and Bernstein 1981) have demonstrated that birds can eliminate heat by convection, radiation, and evaporation during flight. The relative numbers of soaring hawks observed under various combinations of weather conditions will be used to evaluate thermoregulation as a possible function of soaring.

Whether or not Red-tailed Hawks occupy home ranges or defend territories appears to vary with season and location. They have been reported as being territorial only in winter (Austing 1964), in both winter and spring in California (Fitch et al. 1946), in spring and selectively for hunting perches in winter in Michigan (Craighead and Craighead 1956), and mutually exclusive in occupation of wintering areas although not territorial in Wisconsin (Gates 1972). Observations of intraspecific interactions will determine whether or not Red-tailed Hawks in northwestern Arkansas are territorial and whether or not soaring contributes to the defense of the territories.

[1] Present address: Ralston Purina Company, Checkerboard Square-1RS, St. Louis, Missouri 63164 USA.

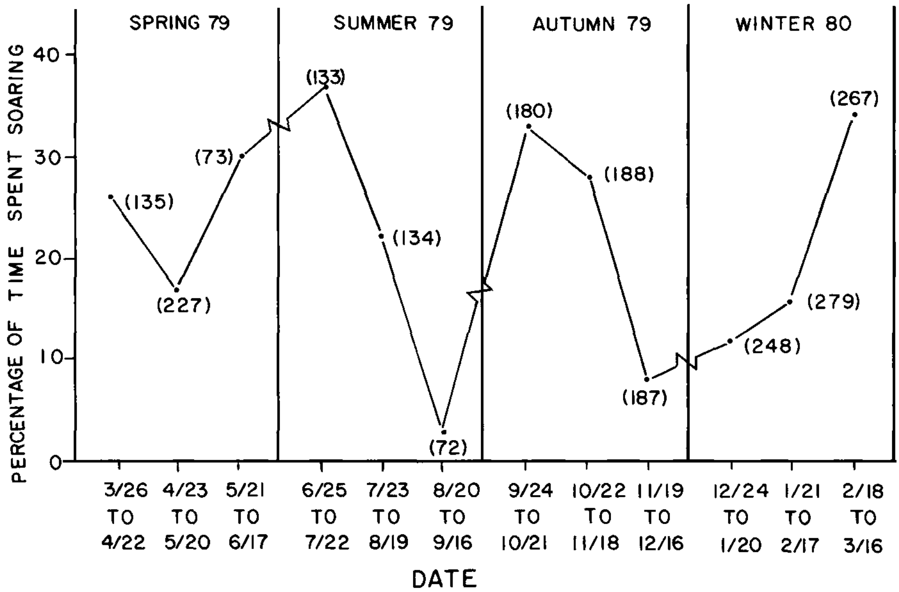

Fig. 1. Seasonal soaring activity in Red-tailed Hawks (numbers in parentheses are numbers of observations).

Study Area and Methods

The study area was located in Benton and Washington counties, Arkansas and included a mixture of oak-hickory forest, grazing land, cultivated fields, and old-field habitat. Field observations were made under as great a range of weather conditions as possible from March 1979 through March 1980. Additional fieldwork was conducted during July and August 1980.

The following variables were recorded at each hawk observation: general activity (perched, soaring, or flapping flight); age (adult or immature); solar illumination (foot candles), recorded with a Photovolt illuminometer; ambient temperature (°C) and relative humidity (%), both measured with a sling psychrometer; and wind velocity (miles/h), taken with a Dwyer wind meter. When recognizable by plumage and size differences, the identity of individual subjects was also recorded.

I observed each hawk for up to 2 h, during which time I recorded general activity at 10-min intervals and environmental factors at 20-min intervals. All foraging attempts, successful forages, territorial encounters, and inter- and intraspecific interactions were recorded. At the end of each observation period another hawk was located for observation. During each season, I collected data on as many different hawks as possible. The results of all statistical analyses are reported at the 0.05 level of significance.

Results

Time budget.—The percentage of time Red-tailed Hawks spent soaring was not significantly different between seasons (ANOVA). The hawks spent 21% of daylight time soaring during winter, 20% during spring, 24% during summer, and 22% during autumn. By subdividing each season into three 28-day periods, I found that there was considerable variation in the time spent soaring (Fig. 1). All observation points in Fig. 1 separated by greater than 8% are significantly different (Duncan's multiple range test). Fluctuations in the time spent soaring will be discussed in the following sections.

Courtship and migration.—The peak of courtship activity occurred from 6 February to 6 March when 55% of the 60 soaring hawks engaged in this activity. It was frequent through 14 March and then declined to occasional occurrences through September. The increase in relative numbers of soaring hawks from 18 February through 16 March (Fig. 1) can be largely attributed to courtship behavior. The increase in soaring activity from 24 September to 21 October and 18 February to 16 March (Fig. 1) can be partially accounted for by migration.

Foraging.—The 630 observed hunting at-

TABLE 1. Outcome of all observed foraging attempts grouped by hunting method over all seasons.

Hunting method	Percentage of time	Number of strikes: Total	Successful	Unsuccessful	Unknown success	Percentage successful[a]
Perch	72	512	90	386	36	18.9
Flap	6	61	4	47	10	7.8
Soar	22	57	3	47	7	6.0
Total	100	630	97	480	53	16.8

[a] Strikes of unknown success were omitted from the calculation of percentage successful.

tempts were divided into four hunting methods that depended upon the position of the hawk when starting a strike. They included hunting from a perch, the ground, flapping flight, and soaring flight. Because of the low occurrences of hunting attempts from the ground ($n = 6$) and their energetic similarity to perched hunting (both being sit-and-wait techniques), the two were grouped for analysis.

Success ratios of the different foraging techniques were significantly different. Hunting from flapping flight and soaring flight had significantly lower success rates than hunting from a perch (Table 1: Duncan's multiple range test). The use of different hunting methods was not related to the number of strikes obtained by each method. The number of strikes obtained from flapping flight and soaring flight were very similar, although soaring flight occurred 3.7 times more often (Table 1).

The cost of each hunting technique was estimated from existing measurements of metabolic rate in nonpasserine species. The resting metabolic rate ranges from 1.7 to 3.7 times basal metabolic rate (BMR) (Pearson 1950, Wolf and Hainsworth 1971, Baudinette and Schmidt-Nielsen 1974). For hawks that are hunting from a perch, the average value of 2.6 times BMR must be expanded to account for the energy bursts of hunting attempts. For this analysis, an estimate of 3.0 times BMR is used as the cost of hunting from a perch. The best estimate of metabolic rate in soaring birds is 1.3–2.4 times the cost of perching (Baudinette and Schmidt-Nielsen 1974, Kanwisher et al. 1978). Because the estimate of hunting from a perch was 3.0 times BMR, the cost of soaring can be approximated as 1.85 (mean estimate of soaring metabolic rate) times 3.0, or 5.55 times BMR. The metabolic rate of flapping flight, independent of size or flight behavior, may be 9–14 times BMR (Hainsworth and Wolf 1969, Tucker 1972, Berger and Hart 1972, Bernstein et al. 1973, Torre-Bueno and Larochelle 1978). Because Red-tailed Hawks glide approximately 10% of the time that they are engaged in flapping flight, the average estimate of 11.5 times BMR will be reduced to 10.9 times BMR. This value is calculated as 10% of the cost of soaring plus 90% of the cost of flapping flight.

To arrive at a benefit-to-cost ratio for each foraging technique, an assumption of equal caloric returns for successful attempts from each method was made. This assumption is only weakly supported by the field observations, because less than 35% of the prey items could be identified. From the perched position, 73% of the identifiable prey were small mammals, 16% were birds, 7% were reptiles, and 4% were invertebrates. From flapping flight, the only identified prey was a small mammal and from soaring flight one small mammal and one Northern Bobwhite (*Colinus virginianus*) were recognized. The benefit-to-cost ratios were calculated by dividing the percentage of successful attempts by the cost index for each foraging technique. The ratios were 6.3 for perched, 0.72 for flapping flight, and 1.08 for soaring flight. These ratios were then compared with the amount of time spent at each hunting method. Figure 2 indicates that the amount of time spent hunting from a perch and from flapping flight are similar in proportion to their success-to-cost ratios. The amount of time spent in soaring activity is much greater in proportion to its success-to-cost ratio. This suggests that, although soaring contributes to foraging, it should also serve some other purpose.

Thermoregulation.—The most severe heat conditions occurred during the final 3 weeks of August 1979. Ambient temperature reached 35°C, solar illumination ranged to 4,200 foot

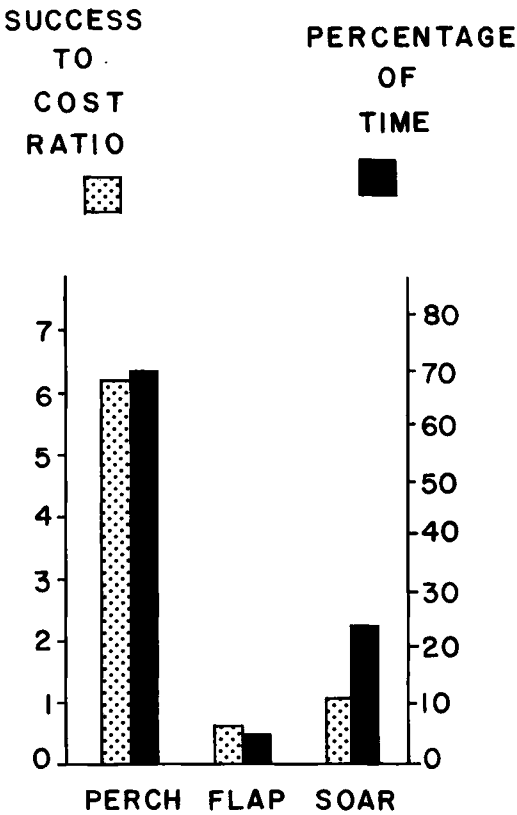

Fig. 2. A comparison of the estimated success-to-cost ratio for each hunting method and the percentage of time that method was used.

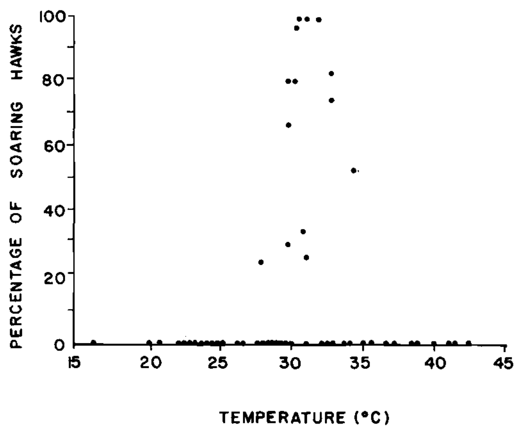

Fig. 3. Relationship between percentage of soaring hawks and mean ambient temperature during 52 3-h observation periods in the summer.

candles, relative humidity reached 75%, and wind velocity dropped to less than 2 miles/h. Although the high levels of solar illumination and ambient temperature increased thermal soaring opportunities (Ballam 1981), a marked decrease in soaring flight was noted (Fig. 1). Figure 3 indicates that the decrease in soaring activity occurred at 34°–35°C. Supplementary data from July and August 1980 are included in Fig. 3. Instead of soaring to thermoregulate, the hawks sought shade, became inactive, and panted at ambient temperatures of 27°C. Hayes (1978) states that panting maintains a stable body temperature in Red-tailed Hawks at all ambient temperatures to 34°C with zero wind and 1.1 cal$\cdot$cm$^{-2}\cdot$min^{-1} radiation load, providing no body movement occurs.

The most extreme winter conditions occurred during January 1980 when mid-day temperatures dropped to −4°C, illumination fell to 384 foot candles, wind velocity reached 20 miles/h and relative humidity reached 98%. Figure 1 indicates a drop in soaring activity at this time, which suggests that soaring does not function in thermoregulation during cold stress. Red-tailed Hawks experienced some thermal stress at temperatures below freezing, as indicated by the retraction of their legs into their feathers and by ptiloerection.

Territorial defense.—Twenty-nine intraspecific aggressive interactions were observed. Eight of these encounters were initiated by perched hawks approaching other hawks by flapping flight, and 21 were initiated by soaring hawks. Of the 21 aggressive soaring interactions, three involved adult hawks diving and supplanting perched hawks, and 18 involved attacks between two soaring hawks. Any aggressive soaring interactions that could be confused with courtship behavior were not included.

The observed aggressive interactions were concentrated during October ($n = 7$), November ($n = 7$), and December ($n = 6$), with significantly more interactions involving soaring flight than flapping flight (Binomial test). The involvement of adult and immature hawks appeared to be proportional to their ratio in the population. From September 1979 through March 1980, 12.8% of the observed hawks were immature, and, of the 29 aggressive encounters, 13.6% involved immature hawks. I suspect that resident hawks are more territorial than nonresidents, but the results are inconclusive due to the unknown residency of 41% of the aggressively interacting birds. Resident hawks were recognized by plumage characteristics and their habitual use of certain perch sites. There were 13 aggressive interactions noted between resident and nonresident birds and 4 interactions observed between nonresidents. The peak in soaring activity between 24 September and 18 November (Fig. 1) would be partially due to territorial defense.

Discussion

The amount of time Red-tailed Hawks spent perching and in flapping flight appeared to be related to the successful prey captures made per unit of energy expended. The hawks spent the greatest amount of time hunting by sit-and-wait techniques, and this method had the highest success-to-cost ratio. The use of each hunting method in proportion to its success-to-cost ratio would result in greater foraging efficiency than could be obtained by using each method at random. The amount of time Red-tailed Hawks devoted to soaring activity was approximately twice that predicted from the success-to-cost ratios. This suggests that, although soaring flight contributed to foraging activity, it must also serve additional functions.

Soaring was a significant contributor to the defense of territories. The concentration of aggressive interactions during October, November, and December demonstrated that wintering territories rather than home ranges were being established. The establishment of breeding territories was not evident due to the absence of aggressive interactions between nesting hawks. The reduced number of hawks present in the study area during the summer would lessen the chances of interacting and relax competition for resources. This may explain the increased tolerance between hawks during the breeding season.

Soaring flight has three possible advantages over flapping flight in territorial defense. First, a hawk can survey virtually all of its territory from the soaring position and simultaneously advertise that the territory is occupied. Second, a dive from soaring flight may be energetically less costly, and perhaps more intimidating, than flapping from tree to tree to displace perched intruders. This is particularly true as the distance between perched hawks increases. Finally, if a trespassing hawk is soaring, it can only be attacked by a hawk that is soaring above it. Therefore, soaring flight is a necessity for defending against other soaring hawks.

A marked decrease in soaring activity was noted at temperatures above 35°C, indicating that soaring is not a thermoregulatory technique during heat stress. The abundant availability of shade allowed inactivity and panting to act as adequate thermal regulators. In areas where shade is not available, as in desert environments, it is possible that soaring enables hawks to eliminate heat by convection, radiation, and evaporation. As Dawson and Schmidt-Nielsen (1964) have recognized, the use of soaring to thermoregulate would require maintaining flight with little energy expenditure and little heat production. Definitive data on the response of body temperature during soaring flight will require advanced biotelemetric monitoring of body temperature.

Once the hawk is aloft, the soaring position provides it with an energetically economical opportunity to conduct a variety of activities. The relative importance of each activity shifts with season and weather conditions. Courtship displays and migration account for much of the spring soaring activity, whereas territorial defense and southward migration occupy much of the time spent in fall soaring. Activities such as foraging and exploration occur throughout all seasons.

Further studies on the function of nonmigratory raptorial soaring should focus upon exploratory behavior. Exploring the area outside a territory would provide valuable information on alternative foraging sites, territorial boundaries of neighboring hawks, and locations of unmated hawks. Exploratory behavior could prove to be a prime function of nonmigratory soaring activity.

Acknowledgments

I thank D. A. James for his encouragement and advice throughout the study. W. Clark is gratefully acknowledged for his aid in securing grants and permits. Financial support was provided by the Arkansas Audubon Society Trust Fund, Frank M. Chapman Memorial Fund, Alexander E. Bergstrom Fund, Sigma Xi Grants-in-Aid of Research, and the Department of Zoology, University of Arkansas.

Literature Cited

Austing, G. R. 1964. The world of the Red-tailed Hawk. Philadelphia, J. B. Lippincott.

BALLAM, J. M. 1981. The use of soaring by the Red-tailed Hawk (*Buteo jamaicensis*). Unpublished M.Sc. thesis. Fayetteville, Arkansas, Univ. Arkansas.

BAUDINETTE, R. V., & K. SCHMIDT-NIELSEN. 1974. Energy cost of gliding flight in herring gulls. Nature 248: 83–84.

BEEBE, F. L. 1974. Field studies of the Falconiformes of British Columbia. British Columbia Prov. Mus. Occ. Pap. No. 17.

BENT, A. C. 1937. Life histories of North American birds of prey. U.S. Natl. Mus. Bull. 167.

BERGER, M., & J. S. HART. 1972. Die Atmung beim Kolibri *Amazilia fimbriata* wahrend des Schwirrfluges bei verschiedenen Umgebungstemperaturen [English summary]. J. Comp. Physiol. 81: 363–380.

———, ———, & O. Z. ROY. 1971. Respiratory water and heat loss of the Black Duck during flight at different ambient temperatures. Can. J. Zool. 49: 767–774.

BERNSTEIN, M. H. 1976. Ventilation and respiratory evaporation in the flying crow, *Corvus ossifragus*. Respir. Physiol. 26: 371–382.

———, S. P. THOMAS, & K. SCHMIDT-NIELSEN. 1973. Power input during flight of the Fish Crow, *Corvus ossifragus*. J. Exp. Biol. 58: 401–410.

CALDER, W. A., & J. R. KING. 1974. Thermal and caloric relations of birds. Pp. 259–413 *in* Avian biology, vol. 4 (D. S. Farner and J. R. King, Eds.). New York, Academic Press.

CONNER, R. N. 1974. A note on aerial courtship of Red-tailed Hawks. Bird-Banding 45: 269.

CRAIGHEAD, J. J., & F. C. CRAIGHEAD, JR. 1956. Hawks, owls and wildlife. Harrisburg, Pennsylvania, The Stackpole Co.

DAWSON, W. R., & J. W. HUDSON. 1970. Birds. Pp. 223–310 *in* Comparative physiology of thermoregulation, vol. 1 (G. G. Whitlow, Ed.). New York, Academic Press.

———, & K. SCHMIDT-NIELSEN. 1964. Terrestrial animals in dry heat: desert birds. Handbook Physiol. Sec. 4: 481–492.

EMLEN, J. M., & M. G. R. EMLEN. 1975. Optimal choice in diet: test of a hypothesis. Amer. Natur. 109: 427–435.

FITCH, H. S., F. SWENSON, & D. F. TILLOTSON. 1946. Behavior and food habits of Red-tailed Hawks. Condor 48: 205–237.

GATES, J. M. 1972. Red-tailed Hawk populations and ecology in east-central Wisconsin. Wilson Bull. 84: 421–433.

HAINSWORTH, F. R., & L. L. WOLF. 1969. Resting, torpid, and flight metabolism of the hummingbird, *Eulampis jugularis*. Amer. Zool. 9: 1100–1101.

HAYES, S. R. 1978. The combined effects of air temperature, wind and radiation on the resting metabolism of avian raptors. Unpublished Ph.D. dissertation. Logan, Utah, Utah State Univ.

HUDSON, D. M., & M. H. BERNSTEIN. 1981. Temperature regulation and heat balance in flying White-necked Ravens, *Corvus cryptoleucus*. J. Exp. Biol. 90: 267–281.

KANWISHER, J. W., T. C. WILLIAMS, J. M. TEAL, & K. O. LAWSON, JR. 1978. Radiotelemetry of heart rates from free ranging gulls. Auk 95: 288–293.

MACARTHUR, R. H., & E. R. PIANKA. 1966. On optimal use of a patchy environment. Amer. Natur. 100: 603–609.

PEARSON, O. P. 1950. The metabolism of hummingbirds. Condor 52: 145–152.

PENNYCUICK, C. J. 1972. Soaring behavior and performance of some East African birds, observed from a motor glider. Ibis 114: 178–218.

PORTER, W. P., & D. M. GATES. 1969. Thermodynamic equilibria of animals with environment. Ecol. Monogr. 39: 227–244.

PULLIAM, H. R. 1974. On the theory of optimal diets. Amer. Natur. 108: 59–74.

ROYAMA, T. 1970. Factors governing the hunting behavior and selection of food by the Great Tit (*Parus major* L.). J. Anim. Ecol. 39: 619–668.

SCHOENER, T. W. 1971. Theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369–404.

TORRE-BUENO, J. R. 1978. Evaporative cooling and water balance during flight in birds. J. Exp. Biol. 75: 231–236.

———, & J. LAROCHELLE. 1978. The metabolic cost of flight in unrestrained birds. J. Exp. Biol. 75: 223–229.

TUCKER, V. A. 1968. Respiratory exchange and evaporative water loss in the flying Budgerigar. J. Exp. Biol. 48: 67–87.

———. 1972. Metabolism during flight in the Laughing Gull. Amer. J. Physiol. 222: 237–245.

WAKELEY, J. M. 1978. Hunting methods and factors affecting their use by Ferruginous Hawks. Condor 80: 327–333.

WOLF, L. L., & F. R. HAINSWORTH. 1971. Time and energy budgets of territorial hummingbirds. Ecology 52: 980–988.