

- Red-winged Blackbird. *Wilson Bull.* 86(4): 450-460.
- , & G. TWIEST. 1970. Growth rates and sex ratios of Red-winged Blackbird nestlings. *Wilson Bull.* 82: 294-303.
- , & ———. 1971. Growth and calculation of age for Red-winged Blackbird nestlings. *Bird-Banding* 42: 1-17.
- KLOMP, H. 1970. The determination of clutch size in birds. A review. *Ardea* 58: 1-124.
- OLSON, J. M. 1990. Physiological and biochemical aspects of the development of endothermy in an altricial bird, the Red-winged Blackbird. Ph.D. dissertation, Ann Arbor, Univ. Michigan.
- RICKLEFS, R. E. 1984. The optimization of growth rate in altricial birds. *Ecology* 65(5): 1602-1616.
- ROBERTSON, R. J. 1972. Optimal niche space of the Red-winged Blackbird (*Agelaius phoeniceus*). I. Nesting success in marsh and upland habitat. *Can. J. Zool.* 50: 247-263.
- . 1973. Optimal niche space of the Red-winged Blackbird (*Agelaius phoeniceus*). III. Growth rate and food of nestlings in marsh and upland habitat. *Wilson Bull.* 85(2): 209-222.
- SMITH, M. 1943. Size of breeding populations in relation to egg laying and reproductive success in the eastern Red-wing (*Agelaius phoeniceus*). *Ecology* 24: 183-207.
- WEBB, D. R., & J. R. KING. 1983. An analysis of the heat budgets of the eggs and nest of the White-crowned Sparrow (*Zonotrichia leucophrys*) in relation to parental attentiveness. *Physiol. Zool.* 56: 493-505.
- WILLIAMS, J. F. 1940. The sex ratio in nestling eastern red-wings. *Wilson Bull.* 52: 267-277.
- YOUNG, H. 1963. Age specific mortality in the eggs and nestlings of blackbirds. *Auk* 80: 145-155.

Received 8 August 1990, accepted 27 December 1990.

Nutritional and Energetic Implications for Raptors Consuming Starving Prey

REBECCA L. TAYLOR,¹ STANLEY A. TEMPLE,¹ AND DAVID M. BIRD²

¹Department of Wildlife Ecology, University of Wisconsin, Madison, Wisconsin 53706 USA, and

²Macdonald Raptor Research Centre, 21,111 Lakeshore Road, Ste. Anne de Bellevue, Quebec H9X 1C0, Canada

Starvation is often a factor that predisposes individuals to being killed by predators. Although starving individuals are weakened and easier to capture, they are also a less nutritious meal. The body of a starving animal has a greatly reduced lipid content and an increased water content and hence a lower overall caloric value than the body of a well-nourished individual.

When preying on starving individuals, predators should be forced to increase their food consumption to maintain body weight by killing more individuals than they would when preying on well-nourished individuals. This prediction is based on the fact that starving individuals provide fewer calories per gram of body weight than well-nourished individuals. We tested this prediction by feeding captive American Kestrels (*Falco sparverius*) diets that duplicated the energy and nutritional content of well-nourished and starving rodents.

General trends in the gross body composition of starving mammals include a severe reduction in lipid content and an increase in water content (Morgulis 1923). Based on fresh body weight, adult rodents fed *ad libitum* in the laboratory contain (mean \pm SE) 14.5 \pm 3.9% lipid, 61.9 \pm 3.5% water, 18.5 \pm 1.8% protein, and 3.6 \pm 0.3% ash (Morgulis 1923, Chanutin 1931, Elkington and Widdowson 1959, Bailey et al. 1960,

Hayward 1965, Fedyk 1974, Sawicka-Kapusta 1974). Rodents starved until death or a 40% loss of body weight contain 2.2 \pm 0.8% lipid, 71.1 \pm 3.9% water, 20.1 \pm 1.2% protein, and 3.6 \pm 0.9% ash (Terroine et al. 1922, Morgulis 1923, Elkington and Widdowson 1959, Rock and Williams 1979).

We created a low-lipid diet that approximated the composition of starving rodents using 1-day-old laboratory rats (*Rattus norvegicus*) as the basic ingredient. Neonatal rats are naturally as low in lipid and high in water as starving, adult rodents. A high-lipid diet that approximated the composition of well-nourished rodents consisted of chopped, adult laboratory mice (*Mus musculus*). The lower legs, tails, jaws, and skin of the mice were removed so that the diet would be as digestible as the low-lipid diet. A moderate-lipid diet, intermediate between the two previous diets, was a combination of skinned, chopped adult mice and neonatal rats. When we prepared batches of the three diets, beef fat, casein, and bone meal were sometimes added to adjust lipid, protein, and ash to constant levels.

We analyzed the lipid content, protein content, water content, ash content, and energy content of each diet. Samples of each diet were dried to a constant weight at 50°C and then ground into a homogenized powder. Samples were extracted in anhydrous diethyl

TABLE 1. Body weight (g) and food (g), with caloric intake (kcal) in parentheses, of 3 groups of American Kestrels during phases 1 and 2 of the experiment. Values ($\bar{x} \pm SE$) are expressed per bird, per day.

Group	Phase 1			Phase 2		
	Diet	Body weight	Food (caloric intake)	Diet	Body weight	Food (caloric intake)
1	High lipid	108.1 \pm 0.90	16.5 \pm 0.17 (30.2 \pm 0.31)	High lipid	108.6 \pm 0.89	18.7 \pm 0.24 (34.2 \pm 0.44)
2	High lipid	107.2 \pm 1.1	16.4 \pm 0.24 (30.0 \pm 0.44)	Moderate lipid	107.2 \pm 1.0	25.2 \pm 0.32 (36.0 \pm 0.46)
3	High lipid	111.9 \pm 1.1	16.4 \pm 0.22 (30.0 \pm 0.40)	Low lipid	112.7 \pm 1.0	38.9 \pm 0.65 (39.3 \pm 0.66)

ether for 48 h with a side-arm reflux extractor. Ether-extractable fat was calculated based upon weight loss. Ash content was determined by weighing the remains of samples that had been incinerated for 6 h in a muffle furnace at 600°C. Organic Nitrogen was determined by the micro-Kjeldahl technique (Bradstreet 1965) and multiplied by a factor of 6.25 to obtain protein content. Caloric content was calculated assuming Atwater's factors of 9 kcal/g of lipid and 4 kcal/g of protein (Morey 1936).

The high-lipid diet averaged 12.5% lipid, 65.2% water, 17.6% protein, 3.2% ash, and 1.83 kcal/g. The moderate-lipid diet averaged 7.7% lipid, 69.5% water, 18.4% protein, 3.3% ash and 1.43 kcal/g. The low-lipid diet averaged 3.1% lipid, 74.7% water, 18.3% protein, 3.0% ash, and 1.01 kcal/g. However, because not all of the casein added to the low-lipid diet was eaten by the birds (because of its consistency), these birds ingested slightly less protein.

The amount of food that each kestrel consumed was regulated carefully throughout the study to keep the bird's body weight as stable as possible. Water was supplied *ad libitum*. The body weight and food consumption of each bird was measured daily to 0.1 g.

Of 30 captive American Kestrels used in the experiment, 5 males and 5 females were assigned to each of the three diets. Before beginning the experiment, we restricted each bird's food intake to reduce its fat stores and make its body condition similar to the body condition of a wild raptor. Based on a subjective measure of subcutaneous fat deposits at the end of this preliminary phase, we assigned the fattest and thinnest birds evenly to the three groups. The remaining birds were assigned randomly.

The actual experiment consisted of two phases. In phase 1, all three groups were fed the high-lipid diet for 8 days. This established that birds in the three groups had the same energetic requirements. In phase 2, each group was fed one of the three diets for 9 days, and differences in food intake were compared.

Variations in both food consumption and body weight were analyzed by a two-factor (group and phase) analysis of variance. Differences in food consumption between phases 1 and 2 in the control group (Group 1) were analyzed by a Student's *t*-test.

Throughout the experiment, individual birds stayed within $\pm 3.5\%$ of their mean body weight, and the interaction between phase and group in the body weight analysis was not significant ($F = 0.09$; $df = 2, 497$; $P > 0.9$) (Table 1). Food and caloric intake during the experiment are summarized (Table 1). Variations in food consumption were explained by a highly significant interaction between phase and group ($F = 423.82$; $df = 2, 497$; $P < 0.0001$). Comparing food consumption rates between phase 1 and 2, we found that birds on the high-lipid diet increased their mean consumption by 13%, birds on the moderate-lipid diet increased their mean consumption by 53%, and birds on the low-lipid diet increased their mean consumption by 137%.

All three groups, including controls, showed increased food consumption from phase 1 to phase 2. The increase in the control group was significant ($t = 3.878$, $df = 18$, $P < 0.001$). This increase in Group 1 and at least a portion of the increases in Groups 2 and 3 were due to temperature fluctuations in the barn where the birds were housed. The mean daily high temperature during phase 2 was ca. 5°C lower than during phase 1. The temperature difference presumably affected the behavior of all birds, and their energetic needs. During phase 1, birds sat with their feathers sleeked, and they often panted after being handled. In phase 2, birds sat with their feathers fluffed, and they did not pant. We believe that energetic needs for thermoregulation increased for all three groups.

The prey populations from which predators capture their food contain an assortment of individuals in a wide variety of body conditions. For instance, Caldwell and Connell (1968) found individuals in a wild population of old-field mice (*Peromyscus polionotus*), with body lipids from 3–13.7% of fresh weight. Because they are easier to capture, starving individuals often make up a disproportionate part of a predator's diet (Temple 1987). Our results indicate that a predator's total food consumption and the concomitant kill rates will vary greatly depending on the lipid content of the prey it catches.

Preying on starving individuals necessitates a compensatory increase in the amount of food consumed.

In phase 2, kestrels in Group 1 (control group) ate 19 g of well-nourished mice, or approximately one healthy mouse per day, to maintain body weight. Kestrels feeding on starving mice (Group 3) consumed 39 g/day to maintain body weight. With 19 g as a reference, and considering that an adult vertebrate nearing death from starvation may have catabolized approximately 40% of its body weight (Jackson 1925), we suggest a starving mouse might weigh only 11 g. To obtain 39 g of starving 11-g mice, a kestrel would have to capture 3 or 4 mice per day. The kill rate of a kestrel eating starving mice would have to be triple or quadruple the kill rate of one eating well-nourished mice.

Predators that prey on cyclic prey species are known to cycle with their prey, but to lag behind in both numbers and predation rates (Keith 1963). Thus it is often food shortage and starvation that initiate the decline of the prey, whereas predator populations and predation rates do not peak until after the prey have begun to starve and decline. At this point in the cycle, heavy predation is due, in part, to numerical and functional responses of predators, but may also be caused by an increased kill rate associated with the consumption of starving prey. Raptors will select for substandard prey items. For instance, in a cyclic snowshoe hare (*Lepus americanus*) population in the second year of decline, Keith et al. (1984) found that in a population that averaged 13% starving individuals, 63% of the hares captured by Northern Goshawks (*Accipiter gentilis*) and Great Horned Owls (*Bubo virginianus*) were starving. Especially if substandard prey items are selected, each of the many predators present during the decline of its prey may have to greatly increase its kill rate. This could contribute to the extremely steep rate of the decline found in cyclic prey populations.

The kestrels in our study did not have the energetic expenses associated with free-flying raptors that must capture and handle their prey. These expenditures would increase food consumption and kill rates. Even if a predator feeding on starving prey could catch enough individuals to satisfy its energetic demands, it might not be able to eat enough to meet its caloric needs before reaching satiation. Birds in our study could eat the caloric equivalent of four starving mice each day. However, they were not fed the fur and other indigestible materials that a wild raptor consumes and stores until expelled as a daily pellet (Welty and Baptista 1988). It would be difficult for a wild kestrel to actually eat and store the undigested parts of four mice in a day. This predicament was observed also in humans. Preble (1908: 201) noted, "When Indians are living mainly on rabbits [snowshoe hares during a cyclic crash], they call it 'starving,' though they may be eating bounteously of the meat every two or three hours, and it is said that if nothing else is obtainable, they gradually grow weaker on this diet."

We thank William A. deGraw, Scott R. Derrickson, and an anonymous reviewer for helpful suggestions on the manuscript. Taylor also thanks all of the graduate students who have given their constant encouragement and advice. Kevin Strang, Bruce Basson, and Patricia McConnell were of particular help.

LITERATURE CITED

- BAILEY, C. B., W. D. KITTS, & A. J. WOOD. 1960. Changes in the gross chemical composition of the mouse during growth in relation to the assessment of physiological age. *Can. J. Anim. Sci.* 40: 143-155.
- BRADSTREET, R. B. 1965. The Kjeldahl method for organic Nitrogen. New York, Academic Press.
- CALDWELL, L. D., & C. E. CONNELL. 1968. A precis on energetics of the old-field mouse. *Ecology* 49: 542-548.
- CHANUTIN, A. 1931. The influence of growth on a number of constituents of the white rat. *J. Biol. Chem.* 93: 39-47.
- ELKINGTON, J. R., & E. M. WIDDOWSON. 1959. Effect of chronic undernutrition on body composition in the rat. *Metab. Clin. Exp.* 8: 404-417.
- FEDYK, A. 1974. Gross body composition in postnatal development of the bank vole. I. Growth under laboratory conditions. *Acta Theriol.* 19: 381-401.
- HAYWARD, J. S. 1965. The gross body composition of six geographic races of *Peromyscus*. *Can. J. Zool.* 43: 297-308.
- JACKSON, C. M. 1925. The effects of inanition and malnutrition upon growth and structure. Philadelphia, P. Blakiston's Sons & Co.
- KEITH, L. B. 1963. *Wildlife's ten-year cycle*. Madison, Univ. Wisconsin Press.
- , J. R. CARY, O. J. RONGSTAD, & M. C. BRITTINGHAM. 1984. Demography and ecology of a declining snowshoe hare population. *Wildl. Monogr.* No. 90.
- MOREY, N. B. 1936. An analysis and comparison of different methods of calculating the energy value of different diets. *Nutr. Abstr. Rev.* 6: 1-12.
- MORGULIS, S. 1923. *Fasting and undernutrition: a biological and sociological study of inanition*. New York, E. P. Dutton & Co.
- PREBLE, E. A. 1908. A biological investigation of the Athabaska-Mackenzie region. *North American Fauna*, No. 27. Washington, D.C. Government Printing Office.
- ROCK, P., & O. WILLIAMS. 1979. Changes in lipid content of the montane vole. *Acta Theriol.* 24: 237-247.
- SAWICKA-KAPUSTA, K. 1974. Changes in the gross body composition and energy value of the bank voles during their postnatal development. *Acta Theriol.* 19: 27-54.
- TEMPLE, S. A. 1987. Do predators always capture sub-

standard individuals disproportionately from prey populations? *Ecology* 68: 669-674.

TERROINE, E., E. BRECKMANN, & A. FEURBACH. 1922. Identité de composition des organismes de même espèce lors de la mort par inanition. *Comptes Rendus Acad. Sci. (Paris)* 175: 1112-1114.

WELTY, J. C., & L. BAPTISTA. 1988. *The life of birds*. New York, Saunders Coll. Publ.

Received 10 May 1990, accepted 28 December 1990.

Short-term and Long-term Consequences of Predator Avoidance by Tree Swallows (*Tachycineta bicolor*)

NATHANIEL T. WHEELWRIGHT AND F. BLINN DORSEY

Department of Biology, Bowdoin College, Brunswick, Maine 04011 USA

In the presence of a potential nest predator, birds commonly respond with distraction displays or alarm calls, mobbing the predator, or avoiding the area entirely (Curio 1976). Model predators have been used to elucidate the adaptive basis of such behaviors and determine the conditions under which birds are willing to defend their nests or expose themselves to predators (references in Knight and Temple 1986, Montgomerie and Weatherhead 1988). Most of these studies, couched in the framework of life history theory, interpret the antipredator behavior of birds as a reaction to the direct threat of injury or death to themselves or to their offspring (e.g. Hoogland and Sherman 1976, Shields 1984, Curio and Regelman 1985, Brown and Hoogland 1986). Increased mortality risk is presumed to be the major fitness cost to birds when a predator is near their nest.

There may be other costs imposed by the presence of a potential predator. Nestling feeding opportunities may be missed when the presence of a predator forces parents to abandon their nests temporarily. Time or energy that could have been used for attracting mates or foraging may be diverted to antipredator behaviors (e.g. Powell 1974, Biermann and Robertson 1983, Conover 1987; cf. Martindale 1982). Predators could indirectly reduce the fitness of nesting birds if the birds' expenditure of extra energy made them more vulnerable to other sources of mortality, or if the disruption of parental care resulted in the production of offspring that were less likely to survive to reproductive age.

Dring and Dring (1984) reported a possible example of a predator indirectly decreasing the fitness of breeding birds. Ring-billed Gulls (*Larus delawarensis*) perching on Tree Swallow (*Tachycineta bicolor*) nest boxes caused the parent swallows to reduce the rate at which they fed their nestlings, which in turn apparently slowed nestling development and prolonged the nestling period by approximately 25% at one nest. Nestling growth rates in Tree Swallows are known to be related to food availability (Quinney et

al. 1986). If the response of birds to a perceived risk of predation extends the period of parental care or elevates foraging costs, and if these effects diminish the probability that parents or their offspring will survive, these frequently neglected costs of avoiding predators could have evolutionary implications.

On Kent Island, New Brunswick, Canada, Tree Swallows nest within a colony of Herring Gulls (*Larus argentatus*). The gulls perch on swallow nest boxes, which they use mostly to monitor their own nearby nests. When the opportunity arises, however, gulls seize and eat adult swallows as they leave the nest boxes or enter them to feed their nestlings (pers. obs.). Swallows respond to gulls perched on their nest boxes by mobbing them or simply staying away from the nests until the gulls leave. We report the results of an experiment to determine whether the avoidance of potential predators near their nests has any short-term effects on the growth rate of nestling Tree Swallows, and whether these effects translate into long-term costs in future reproductive success and survival (cf. De Steven 1980, Nur 1988).

The study area, the Bowdoin Scientific Station, is on Kent Island, an 80-ha island located 9 km south of Grand Manan Island in the Bay of Fundy (44°35'N, 66°46'W). Since 1935, Tree Swallows have nested in artificial nest boxes erected at 30-m intervals in a former hay field in the center of the island (Paynter 1954). At Kent Island Tree Swallows are single-brooded. The colony currently comprises approximately 100 pairs of Tree Swallows (Wheelwright et al. in press). Paynter (1954) described in detail the natural history of Kent Island Tree Swallows and Williams (1988) described their energetics during the breeding season. Almost all breeding females and their nestlings, as well as many males, have been banded with numbered aluminum bands since 1966. Kent Island also supports a large colony of Herring Gulls, which nest in the center of the island at an average density of ca. 6 pairs/ha (cf. Cannell and Maddox 1983). Each breeding season we found 10-20 bands of adult and fledg-