

WATER ECONOMY OF NESTLING SWAINSON'S HAWKS¹

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Abstract. Six major components of the water budget of nestling Swainson's Hawks (*Buteo swainsoni*) were quantified to assess the influence of heat stress and dietary composition on water balance. Rates of food consumption, energy utilization, excrement and pellet production, and growth were measured in food trials. Rates of evaporative water loss and CO₂ production were measured gravimetrically at 25, 35, 42, and 30°C (plus direct sunlight) with an open flow system. The inverse relationship between body fat content (or energy density) and body water content in small mammalian prey has: (1) a dramatic effect on the magnitude of preformed water consumption, (2) a lesser effect on excretory water loss, and (3) a negligible effect on metabolic water production. The consequence of these relationships is that nutrient composition of the prey has a significant influence on the status of nestling water balance. Low fat diets should supply nestlings with a surplus of water, whereas high fat diets would not provide enough water to meet the minimum water needs of the rapidly growing nestlings. Water incorporated into new body tissue and water loss in excrement and pellets increased to a peak when nestlings were about 3 weeks old, an age when their rates of growth and food consumption were near maximal levels. Rates of preformed water consumption also reached peak levels during this period of maximal food consumption. Metabolic water was 10-19% of the total water input and was generated by nestling metabolic rates considerably higher than predicted by allometry for adult falconiform birds. Basal rates of evaporative water loss of 700-g nestlings at 25°C were 75% higher than rates predicted by allometry for equally large adult birds. The largest nestlings (782-935 g) had evaporation rates at 25°C nearly three times the rates predicted by allometry.

Key words: *Water balance; water budget; body temperature; energy metabolism; food consumption; evaporative water loss; nest microclimate.*

INTRODUCTION

Nestling altricial birds in hot environments, or confined in nests exposed to direct sunlight, may face extreme thermal and water balance problems (Mertens 1977) similar to those of desert animals (Dawson and Schmidt-Nielsen 1964). These nestlings may be physically unable to avoid thermally stressful situations. They rely heavily on increased respiratory water loss to combat hyperthermia and, in most species, the only source of water is food provided by the parents. This describes the situation for nestlings of many diurnal raptors; their relatively prolonged nestling periods (4-8 weeks) make them an interesting group to study in this respect.

Several lines of evidence suggest that heat stress and constraints in maintaining water balance may be important factors in shaping the nesting biology of raptors. Natural mortality of the nest-

lings from overheating has been reported by several workers (Fitch et al. 1946, Nelson 1969, deVries 1973, Beecham and Kochert 1975). Fyfe and Olendorff (1976) caution investigators, who disturb nesting birds, about the dangers of nestling heat prostration when adults are prevented from shading their young during hot times of the day. Although nestling Red-tailed Hawks (*Buteo jamaicensis*) and Swainson's Hawks (*B. swainsoni*) rapidly develop the ability to maintain elevated, but stable, body temperatures during heat stress (Kirkley 1982), the adult hawks continue to shade their young throughout most of the 38- to 46-day nestling period (Fitzner 1978, Kirkley 1982). This shading behavior does not appear to serve the immediate function of preventing death from hyperthermia, but it could instead act to protect nestlings from progressive dehydration (termed the long-term risk of hyperthermia by Mertens [1977]).

The general observation that raptors can be maintained in captivity on a diet of fresh meat without drinking water promotes an assumption

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that water shortage is not likely to be a problem for adult raptors (Bartholomew and Cade 1957). Shapiro and Weathers (1981) found that American Kestrels (*Falco sparverius*), deprived of food and water for 79 hr, lost 17–20% of their initial body mass, but showed no lasting ill effects when rehydrated on a diet of Gatorade and chicken. Tomback and Murphy (1981, p. 92) proposed that food deprivation in nestling Ferruginous Hawks (*B. regalis*) adversely affects thermoregulatory ability and they predicted that “the combined effects of inadequate food provisions and high temperature may cause much nestling mortality in years when prey populations are low.”

We consider the water budget of nestling birds of prey to have six major components categorized under three groupings: water input, water output, and water storage. We use water storage to mean water incorporated in new body tissues as the nestling grows. Water input has two components: preformed and metabolic water. Swainson's Hawks lack access to drinking water during the 6-week nestling period. Thus, preformed water in their food and metabolic water must meet all their water requirements. Water output has three components: evaporative, pellet, and excretory water. The nestling's body surfaces, both cutaneous and respiratory, continuously lose water to the environment through evaporation. Panting suppresses heat-induced rises in body temperature by increasing the rate of evaporative cooling; consequently, panting increases the rate of water output. Some of the materials ingested by the nestling cannot be digested and are regurgitated as a moist pellet composed mainly of water and hair. Waste products from both the digestive and urinary tracts combine in the cloaca to form moist excrement.

This study examines the effects of elevated rates of evaporation during heat stress and of the body composition of prey on nestling water balance. We quantified all six major components of the nestling water budget to show the dynamic patterns of water input and water utilization throughout nestling development in the Swainson's Hawk.

MATERIALS AND METHODS

We measured components of the water budget on nestlings collected from nests in Cache Valley in northern Utah (elevation 1,340–1,524 m). We measured evaporative water loss on 13 nestlings

in 1982 and 15 nestlings in 1984. We measured the other five water budget components with food consumption trials on seven nestlings in 1981 and nine nestlings in 1983. When we removed nestlings from a nest, we left at least one nestling, so that the adults would not abandon the nest. At the end of the experiments we returned all surviving nestlings to active nests, usually to that of their parents.

FOOD CONSUMPTION TRIALS

Housing. We measured rates of food consumption, excrement production, pellet production, and body growth of nestlings in captivity for 4 weeks. To facilitate excrement and pellet collection, each nestling lived in a cubicle (28 × 40 cm) lined with plastic sheeting and fitted with an elevated floor of 12-mm mesh hardware cloth. During the first 2 weeks of captivity nestlings had access to a heat source (a carpet-covered section of stove pipe, sealed on the ends with plywood covers, and heated from within by four 75-W incandescent light bulbs). In 1981 the rearing cubicles were outdoors in a shelter which shielded nestlings from direct sunlight and rain. Ambient temperatures were monitored continuously with a shaded thermograph placed beside the rearing cages.

In 1983 nestlings were housed indoors in a walk-in environmental chamber at $25 \pm 2^\circ\text{C}$ with a photoperiod of 15L:9D (08:00–23:00). We randomly assigned the nine nestlings to two experimental groups and one control group (except that siblings were not assigned to the same group). The control nestlings remained at 25°C continuously. Nestlings in the two experimental groups were exposed daily to either 4 or 8 hr of heat stress ($35 \pm 2^\circ\text{C}$) to test the effects of prolonged heat stress on the water content of excrement. These exposures began at 12:00 for both groups and ended at 16:00 for the 4-hr group and at 20:00 for the 8-hr group.

Diet. We fed each nestling with forceps three times daily in 1981 and four times daily in 1983. Nestlings readily habituated to handling and hand feeding. The diet was ground Uinta ground squirrels (*Spermophilus armatus*) prepared by grinding entire, gutted carcasses of a large number of squirrels en masse. The mixture of finely ground meat, hair, and bones was sealed in plastic bags and stored frozen until the day of use. Packages of food were thawed as needed and small weighed

samples were refrozen for later analysis. The meat to be fed to nestlings was placed in individually marked plastic canisters which were then weighed before and after each feeding to determine, by difference, the fresh wet weight (WW) of food consumed.

Materials sampled. Four consecutive feeding trials, each 7 days in length, were conducted on each nestling. We assumed the food consumed by a nestling during a trial had the same composition as the pooled food samples collected during that period. Excrement production of each nestling during each trial was determined by weighing the excrement which accumulated on the plastic lining of each cubicle. New plastic lining was applied at the beginning of each 7-day trial. Contaminants in the excrement (i.e., feather sheath fragments, hair pellet fragments, etc.) were removed before final weighing of the oven-dried excrement.

All regurgitated pellets were collected in tared plastic bags. The freshness of each pellet was noted (i.e., fresh pellets were observed being regurgitated; semifresh pellets were known to be no more than 20 min old). We opportunistically intercepted fresh samples of ejected excrement with tared plastic bags. Excrement samples and pellets were weighed fresh (WW) then oven-dried to constant dry weight (DW) to determine the water content. All pellets produced by a nestling during a food trial were combined, shredded to remove shotgun pellet fragments or stones, and mixed prior to taking a subsample for energy analysis.

PREY AND NESTLING CARCASS COLLECTION

In the field, prey items were noted during all nest visits. Representative, fresh samples of each prey type were collected, weighed (WW), and stored frozen for later analysis. Swainson's Hawk nestlings which died in the laboratory or were obtained freshly dead from the field were also weighed and stored frozen. Prey items and nestling carcasses were analyzed for water, fat, and energy content.

MATERIALS ANALYSES

Analyses of food, excrement, pellets, prey items, and nestling carcasses involved drying each of the items in an oven at 60°C for 5–10 days until weight was constant (DW). Water content of each

item was the difference between its fresh weight and dry weight (WW – DW). Dried materials were ground to a fine powder in a Wiley mill (20 mesh/inch screen) and samples were compacted with a Parr pellet press. Energy content of pelleted materials was determined with a semi-micro bomb calorimeter (Parr Instruments Company, Model 1411) standardized with benzoic acid. Critical materials, such as the pooled samples of the squirrel diet, and samples which had unusually high or low energy values, were analyzed twice. Since these duplicate determinations were usually within 1–4% of the original value, most other samples were analyzed only once. One or two drops of mineral oil were added to the regurgitated pellet material, composed mainly of hair, to promote total combustion. We corrected for the heat of combustion of the oil.

Weight of fat in the ground squirrel diet, prey items, and nestling carcasses was determined by Soxhlet fat extraction (Bligh and Dyer 1959). After extraction, samples were dried in their filter paper thimbles at 60°C for 48 hr; fat content was determined from the difference between initial and final dry weights. We weighed large items such as prey samples or food canisters to the nearest 0.01 g and smaller items to the nearest 0.1 mg on Mettler analytical balances.

GROWTH MEASUREMENTS

In the laboratory, rates of nestling growth were monitored by weighing captive nestlings to the nearest gram with an Ohaus triple beam balance each morning prior to the first feeding. For comparison we monitored, at 3-day intervals, the growth rates of seven wild-reared nestlings (in three nests) in 1984 by weighing birds in the morning to the nearest gram with a Pesola spring scale. When exact hatching dates were unknown, nestling ages were estimated by comparing body weight with nestlings of known age. We obtained additional weights of wild-reared nestlings during visits to other nests in other years.

EVAPORATIVE WATER MEASUREMENTS

Evaporative water loss was measured with an open flow, indirect calorimetry system similar in principle to a system devised by Haldane (1892). Water vapor and CO₂ production were measured gravimetrically through the use of the absorbents Drierite and Ascarite, respectively.

Small nestlings requiring air flow rates less than

5 l/min were tested in a 15-l Plexiglas chamber (30.3 × 22.8 × 21.7 cm). Dynapumps at each end of the system moved air through a single sample line. Large nestlings were tested in a 137-l aluminum chamber (61 × 58 × 39 cm). Air was pulled by an air compressor through two parallel sample lines, which reduced resistance to airflow, thus allowing flow rates up to 13 l/min. Flow rates were measured with a calibrated rotameter and were controlled by fine adjustment valves. Proper adjustment of the valves maintained a balance between the rate of air entering and leaving the metabolism chamber and kept chamber air pressure close to atmospheric pressure (differences were less than 10 mm Hg as indicated by a manometer).

The interior walls and floor of the aluminum chamber were painted flat black to diminish reflection; the Plexiglas chamber was not painted. Each chamber had a clear Plexiglas lid which made an airtight seal against a silicone rubber seating coated with silicone grease. Nestlings rested upon hardware cloth which supported them above a pool of mineral oil 2–3 cm deep. Excrement produced during a trial usually fell to the bottom of the mineral oil, preventing it from losing water vapor to the chamber air.

Absorbents upstream from the metabolism chamber removed water vapor and CO₂. Water and CO₂ bound by the absorbents in the downstream line(s) were assumed to be entirely the products of the nestlings. Trials, using an empty metabolism chamber, had insignificant weight changes in the sample line absorbents.

After a nestling was sealed inside the chamber, air was pumped through the system for 15–60 min to equilibrate the chamber gases. We used equilibration periods which equaled or exceeded the periods required for 99% equilibration of chamber gases (Lasiewski et al. 1966). Sampling periods, measured with a stopwatch, varied from 30–60 min depending upon the time required for measurable weight changes in the downstream absorbents. Drierite downstream from the Ascarite collected water vapor generated by the Ascarite/CO₂ reaction (see Gessaman 1987, p. 296). Weight changes of the absorbents were measured to the nearest 0.1 mg and used to determine rates of CO₂ production and evaporative water loss in mg/min.

Appropriate flow rates kept relative humidities in the chambers between 19 and 31% (computed from equation 3 of Lasiewski et al. 1966).

The chambers were placed in a controlled temperature, walk-in environmental room illuminated by fluorescent lights. Three temperatures were used to provide measures of: (1) basal evaporation rates at a thermally nonstressful temperature (25°C); (2) nearly maximal evaporation rates at a temperature equal to or greater than nestling body temperature (42°C); and (3) an intermediate rate of evaporation at a temperature which caused nestlings to pant intermittently (35°C).

In a fourth thermal condition, we placed the metabolism chamber outdoors in the midday sun (11:00–13:00) and maintained chamber air temperature at 30 ± 2°C by either partially immersing the Plexiglas chamber in an ice water bath or by slowly circulating cold tap water through the double-walled water jacket of the aluminum chamber. In these outdoor experiments nestlings were heat stressed by the combined effects of solar radiation and an air temperature similar to daily high temperatures during the nesting period in northern Utah. Metabolism chamber air temperatures and nestling cloacal temperatures were measured with a calibrated thermocouple thermometer (Wescor, TH50). An epoxy-coated copper-constantan thermocouple (24 gauge) was inserted 2.5 cm into the cloaca immediately before and after each experimental period.

Food deprivation experiment. The suggestion that food deprivation may inhibit the thermoregulatory capabilities of hawk nestlings (Tomback and Murphy 1981) prompted us to run an additional set of experiments in 1984 in conjunction with the solar radiation, evaporative water loss tests mentioned above. Seven nestlings were tested under the solar radiation condition above after periods of fasting. Four of these nestlings were initially tested in a well-fed condition, then deprived of food for 24 hr before their second midday test. The other three nestlings were fasted for 14–19 hr prior to their first midday test and then another 23 hr prior to the second test on the next day. Afterwards, the fasted nestlings were fed several large meals prior to being returned to their nests in the field.

STATISTICAL ANALYSES

Where appropriate, our graphs indicate the mean, range, and the interval including one standard deviation above and below the mean. Regression lines were fitted with least squares regression

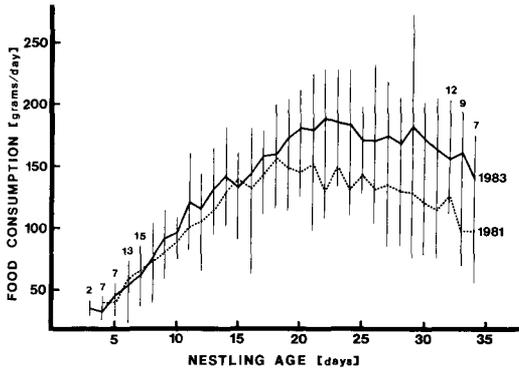


FIGURE 1. Food consumption rates of captive nestling Swainson's Hawks. Vertical lines represent the range of values at each age. The average rates for nestlings reared in a particular year are indicated by a dotted line (seven nestlings in 1981) or a solid line (nine nestlings in 1983). Sample size at each age equals 16 unless indicated otherwise above the vertical line.

techniques for the linear segments of the data scatter. Trend lines connect average values for nonlinear segments of data. Statistical comparisons of means were made using paired *t*-tests, and significance was assumed at an alpha level of 0.05 unless stated otherwise.

RESULTS AND DISCUSSION

PREFORMED WATER INTAKE

In feeding trials, mean food consumption rates (g WW/day) of captive nestlings increased steadily during the first 3 weeks of nestling life, peaked in the 4th week, and gradually declined afterwards (Fig. 1). Olendorff (1974) reported similar trends in three species of *Buteo*, but he found food consumption was maximal during the 5th week. Food consumption rates of nestlings raised in 1981 and 1983 were similar up to 18 days of age, but later nestlings reared in 1983 consumed

significantly more food (average 17–43% more) than nestlings reared in 1981. The disparity in food consumption between years reflects the higher energy density (25–34% higher) of the squirrel meat used in food trials 3 and 4 of 1981 (Table 1), and, therefore, these nestlings needed less of the high energy food to meet their daily energy requirements.

The rates of preformed water consumption in captive nestlings changed with age in the same general pattern as food consumption rates (Fig. 1). A marked disparity in the preformed water consumption rates between years resulted from a combination of lower food consumption rates and lower water content of the high energy diet in the last two food trials of 1981 (Table 1).

Average water content of meadow voles (*Microtus* spp.), pocket gophers (*Thomomys talpoides*), and snakes (*Thamnophis* spp.) (Table 2) are similar to the 73% average water content of the food trial diet, excepting the high energy food discussed above. Five juvenile Uinta ground squirrels (average 84 g) collected from hawk nests in late May–early June had the highest mean water content and lowest mean fat and energy content of the prey types analyzed (Table 2).

METABOLIC WATER PRODUCTION

The rate of water produced in the oxidation of assimilated nutrients is estimated from the rate of energy metabolism and the proportions of proteins, fats, and carbohydrates oxidized. The computation is simplified in a carnivore, since the prey biomass contains very little carbohydrate (Subcommittee on Furbearer Nutrition 1982). The bulk of the energy is, therefore, derived from fats and proteins which produce about the same amount of water per unit of energy metabolized, i.e., 0.0270–0.0275 g H₂O/kJ for fats; 0.0270–0.0280 g H₂O/kJ for protein (Schmidt-Nielsen

TABLE 1. Composition of diet used in eight food trials.

Food trial	Year	Food packages sampled	% water content mean (SD)	% fat content of pooled samples (dry weight)	Energy content of pooled samples (kJ/g)	
					(dry weight)	(wet weight)
1	1981	12	72.8 (2.2)	21.6	21.527	5.853
2	1981	11	72.9 (1.8)	21.7	21.573	5.845
3	1981	19	68.1 (1.2)	26.0	23.485	7.494
4	1981	18	67.4 (1.7)	25.0	22.506	7.338
1	1983	15	73.3 (3.0)	12.7	21.007	5.611
2	1983	34	72.9 (1.6)	13.3	21.237	5.757
3	1983	45	73.6 (1.3)	13.3	21.702	5.728
4	1983	46	73.6 (1.7)	12.5	21.447	5.661

TABLE 2. Body composition of *Buteo* nestling carcasses and prey items.

	n	% water content \bar{x} (SD)	n	% fat content (dry weight) \bar{x} (SD)	n	Energy content (kJ/g)	
						(dry weight) \bar{x} (SD)	(wet weight) \bar{x} (SD)
Prey items							
Meadow vole (<i>Microtus</i> spp.)	20	71.9 (1.8)	5	13.6 (4.1)	5	20.13 (0.67)	5.69 (0.54)
Pocket gopher (<i>Thomomys talpoides</i>)	16	73.2 (1.6)	5	14.9 (5.9)	5	20.92 (1.76)	5.82 (0.92)
Ground squirrel (<i>Spermophilus armatus</i>)	5	78.1 (1.0)	5	10.3 (3.1)	5	19.08 (1.17)	4.18 (0.38)
Snake (<i>Thamnophis</i> spp.)	6	73.1 (2.6)					
Fresh nestling carcasses							
Swainson's Hawk	3	82.1 (2.8)	3	15.2 (5.0)	3	21.94 (0.93)	3.93 (0.71)
Red-tailed Hawk	5	82.7 (2.0)	3	14.0 (1.8)	5	21.57 (0.55)	3.75 (0.47)
Semifresh nestling carcasses							
Swainson's Hawk	8	73.9 (4.6)	6	21.4 (16.5)	7	22.5 (3.01)	5.86 (1.68)
Red-tailed Hawk	1	72.3				20.0	5.54

1964, p. 30, 40; Schmidt-Nielsen 1980, p. 163, 319).

Metabolized energy (ME) of each nestling was computed for each food trial by subtracting the energy of egested pellets (PE) and excrement (EE) from gross energy intake (GEI). ME changed with nestling age (Fig. 2), in a similar pattern both years, and peaked at age 20–25 days, as did food and water consumption.

Some of the metabolized energy of growing nestlings is stored as new body tissue rather than being oxidized to heat and metabolic water. The energy used in oxidative metabolism (Fig. 3) equals ME minus the energy stored in new body tissue (TE). We calculated TE using nestling

weight gains together with the mean water content (82.5%) and energy density (21.7 kJ/g DW) of eight fresh nestling carcasses of Swainson's and Red-tailed hawks less than 2 weeks of age (Table 2).

These rates of oxidative metabolism estimated from food consumption (ME – TE) are 22–34% higher than metabolism we estimated from CO₂ production rates (Fig. 4) measured during the EWL experiments (assuming 1 g CO₂ = 14.25 kJ and R.Q. = 0.7). This is likely due to the higher levels of activity and the greater heat increment of feeding during the week-long feeding trials.

Oxidative metabolism (ME – TE) multiplied by factor 0.0275 g H₂O/kJ equals metabolic water production which increased with age from about

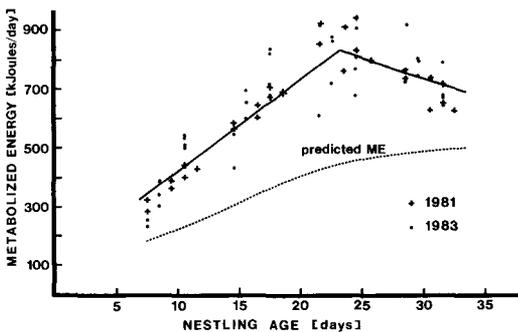


FIGURE 2. Metabolized energy (ME) of captive nestling Swainson's Hawks. Energy values are plotted at nestling ages at the midpoints of the food trials. Least squares regression of values in the first three trials yielded the relationship (metabolized energy = $31.30 [\text{age}] + 5.21$; $r = 0.91$); then the line deflects down through the average ME (723.8 kJ/day) at age 30 days. Dotted line is predicted ME for falconiform birds from Wijnandts (1984, p. 41); i.e., $\text{ME} = 9.772 W^{0.577}$ where ME is in kJ/day and W is body weight in grams.

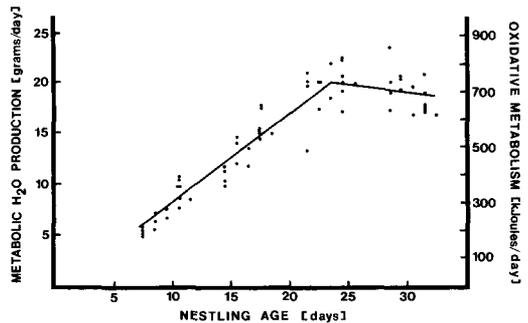


FIGURE 3. Oxidative metabolism (calculated as metabolized energy minus the energy content of new body tissue) and metabolic water production of nestling Swainson's Hawks. The regression line was determined for the first three trials (oxidative metabolism = $31.76 [\text{age}] - 23.43$; $r = 0.95$); then the line deflects down through the average values for an age of 30 days (energy [673.6 kJ/day] or water [18.5 g/day]).

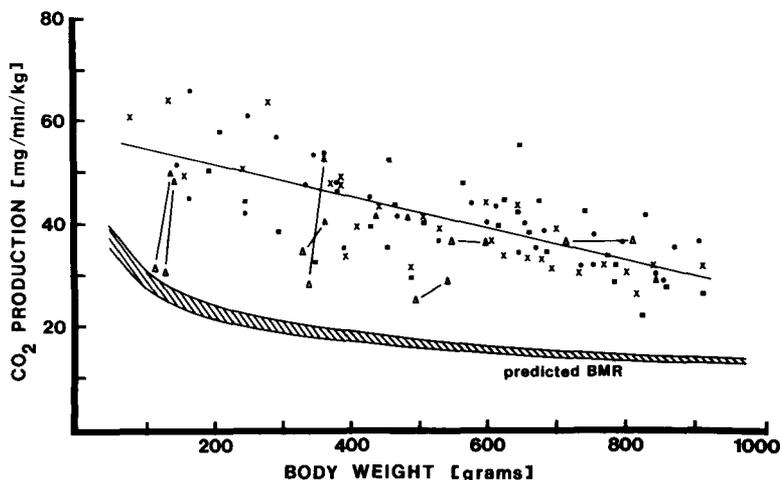


FIGURE 4. Rates of CO_2 production of nestling Swainson's Hawks during evaporative water loss tests compared to the predicted basal rates of CO_2 production for adult falconiform birds. Symbols are as follows: 25°C test (solid dots); 35°C test (X symbols); 42°C test (solid squares); well-fed nestlings in the sun at 30°C (solid triangles); fasted nestlings in the sun at 30°C (open triangles). Values obtained from the same nestling on two consecutive days are connected with a line. The regression line for Swainson's Hawk nestling CO_2 production rates was fitted by the least squares method after eliminating the low values of the five smallest, fasted nestlings, as follows:

$$\text{CO}_2 \text{ production} = -0.0309 W + 57.7 \quad r = 0.76.$$

Where

$$\begin{aligned} \text{CO}_2 \text{ production} &= \text{mg CO}_2/\text{min/kg} \\ &\quad \text{body weight} \\ W &= \text{body weight in g.} \end{aligned}$$

The region representing the predicted basal rate of CO_2 production at R.Q. values of 0.7–0.8 (diagonally patterned area) was determined from allometric equations modified from Wasser (1986) for the BMR of 11 species of falconiform birds.

Modified regressions:

$$\begin{aligned} \text{At R.Q.} = 0.7 &\quad \text{BMR} = 145.7 W^{-0.36} \\ \text{At R.Q.} = 0.8 &\quad \text{BMR} = 162.5 W^{-0.36}. \end{aligned}$$

Where

$$\begin{aligned} \text{BMR} &= \text{mg CO}_2/\text{min/kg body weight} \\ W &= \text{body weight in g.} \end{aligned}$$

5 g/day to about 20 g/day and was always substantially less than preformed water consumption (Fig. 3). Metabolic water production was 10–14% of the total water input to nestlings on the typical diet and 17–19% of the water input to nestlings on the high fat, low water diet in trials 3 and 4 of 1981.

The daily energetic requirements of these hawk nestlings (Fig. 2) were considerably higher than those expected for adult falconiforms (Wijnandts 1984). The energy cost of tissue deposition, an energetically inefficient process (75%, according to Ricklefs 1974), is probably the major cause of the elevated energy demands of Swainson's Hawk nestlings.

WATER STORAGE IN BODY TISSUES

The amount of water incorporated daily in new body tissue is estimated from the rate of increase in body mass and the proportion of water in new tissue. We assumed the percent water content of nestling carcasses (82.5%) and of new tissue to be the same. Tissue water content may change somewhat with nestling age, but we chose not to sacrifice nestlings merely to clarify this point.

The sigmoid pattern of body weight change in nestling Swainson's Hawks (Fig. 5) is characteristic of most growing birds (O'Connor 1984). Growth rates of nestlings reared in captivity were similar to those of nestlings reared in the wild.

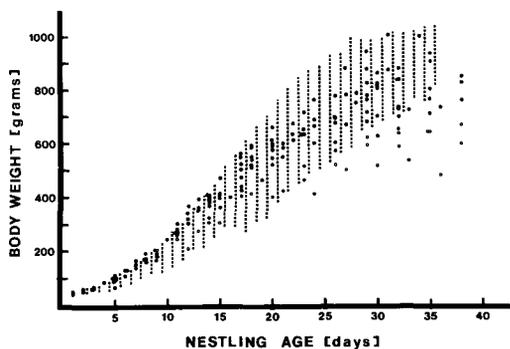


FIGURE 5. Body weight of nestling Swainson's Hawks. Vertical dotted lines designate the range of weights of 16 captive nestlings at each respective age. Solid dots indicate body weights of nestlings reared in the wild.

Rate of nestling growth increases during the first 2 weeks, levels off during the 3rd week, and then rapidly declines (Fig. 6). Water storage in body tissue is greatest during the 2nd and 3rd weeks after hatching, and then rapidly declines as growth rate diminishes.

Weights of wild nestlings that we recorded are probably somewhat higher than their minimum morning weights, since nestlings could have eaten several meals prior to being weighed. One of the nests visited regularly in 1984 contained three nestlings which had abnormally slow rates of growth, presumably due to undernourishment (Fig. 5).

WATER OUTPUT IN EXCREMENT

We estimated rates of water output in excrement from the rate of production of excrement (DW) and the estimated fractional water content of fresh excrement. The water content of fresh excrement is highly variable, as this is the primary overflow route when water intake exceeds minimum needs. If water is in short supply, excrement can be considerably drier than normal (Skadhauge 1981). The variability in fractional water content of excrement coupled with the difficulty of obtaining large numbers of fresh excrement samples from all nestlings prevented us from accurately estimating the excretory water loss rates of each individual nestling during each trial.

The mean water content of 10 fresh excrement samples collected from captive nestlings in 1981 was 70.7% (range = 66.3–75.0%) (Fig. 7). In 1982 excrement from captive nestlings averaged 75.8% water (range = 63.4–91.8%; $n = 70$). The 89 samples collected in 1983 had a similarly broad range of water contents (62.9–94.3%), but when

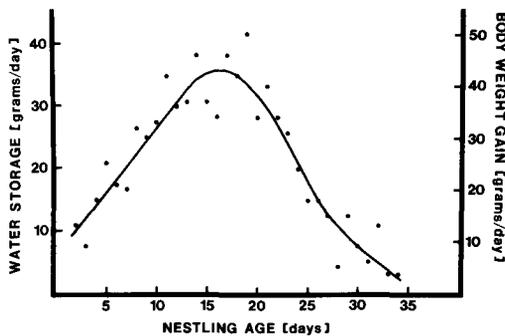


FIGURE 6. Average daily gain of body weight and body water storage of captive nestling Swainson's Hawks. Solid dots represent the average daily gain (right axis) or water storage (left axis, assuming 82.5% water in body tissue) of 16 captive nestlings at different ages. The regression line for nestling ages 3–20 days was fitted by the least squares method ($g \text{ body weight/day} = 2.19 [\text{age}] + 9.67; r = 0.90$). The remainder of the line was fitted by inspection.

partitioned into the three experimental groups, the averages within each treatment were significantly different (control—83.5%, 4 hr stress—78.8%; 8 hr stress—72.0%; $P < 0.025$). There was a trend toward drier excrement with increasing duration of heat stress, but individual variability within each group caused substantial overlaps in the excretory water content. The nestling which had the lowest average excretory water in each treatment group was also the youngest nestling of its group, though the data do not indicate that water content of excrement increases with nestling age.

Three of 169 excrement samples had the low-

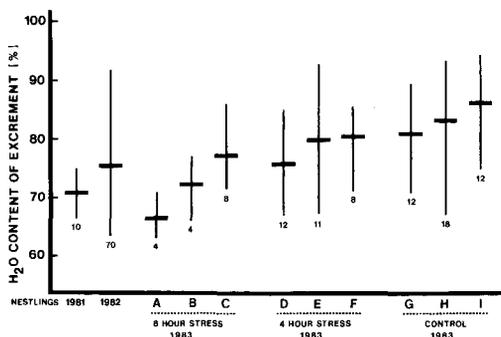


FIGURE 7. Water content of excrement samples from nestling Swainson's Hawks. Vertical lines represent the range; horizontal lines represent means; the number below each figure is the number of samples analyzed. The nine nestlings reared in captivity in 1983 are represented by letters A through I and are segregated into the three experimental groups denoting the daily duration of heat stress.

est percentage of water (i.e., 63%); 14 samples were in the 65–67% range. Since the lowest average water content of excrement from a heat stressed nestling was 66.5%, we assumed that 66% was the minimum average water content of excrement produced by nestlings that are conserving water maximally. This value is consistent with the percent water content of feces of dehydrated birds (Skadhauge 1981, p. 99). Figure 8 shows the measured rates of production of dry excrement of the captive nestlings and illustrates the potential variability in rates of excretory water loss associated with three different moisture levels in the fresh excrement (i.e., 66, 77, and 80% water).

Dry excrement production fluctuates with dry matter intake and digestive efficiency ($[ME/GEI] \times 100$), both of which depend upon food quality. In nestling feeding trials the digestive efficiency averaged 78% (range = 75–84%) and ratios of dry excrement to dry matter consumed ranged from 0.31–0.41. Lower rates of excrement production will result from diets higher in fat, because dry matter intake decreases with higher energy food, and digestive efficiency is enhanced by higher fat content (Collopy 1978), causing lower ratios of dry excrement to dry food.

WATER OUTPUT IN PELLETS

Pellets were first egested at 5–7 days after hatching for seven of the captive nestlings and at 8–12 days after hatching in the other nine captive nestlings. Most nestlings less than 2 weeks of age produced pellets infrequently. Sometimes the interval between pellets was 4–5 days. Older nestlings produced pellets daily or on alternate days with few exceptions. The total dry weight of pellets produced during a 7-day feeding trial ranged from about 6 g/week for 1-week-old nestlings to 14 g/week for 3-week-old nestlings.

The average water content of 222 pellets classified as fresh or semifresh was 65%. The lowest water content of a fresh pellet was 56% and the highest content was 81%. Because we did not find all pellets in fresh condition, we determined pellet water loss of each nestling by multiplying the dry weight of pellets produced by the average ratio of water to dry matter in the fresh pellets of that nestling. Average daily water loss from pellet egestion ranged from 0.6 g/day in 1-week-old nestlings to 3.8 g/day in 3-week-old nestlings. Pellet water losses are a minute fraction of the total water budget.

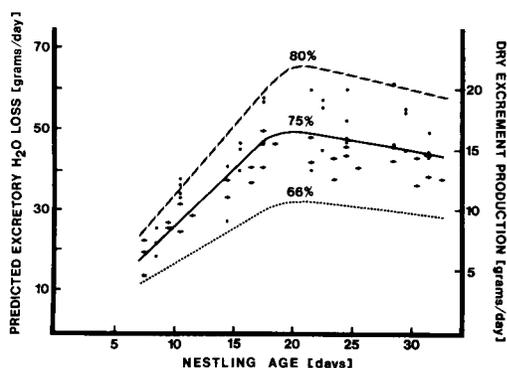


FIGURE 8. Rates of dry excrement production and predicted rates of excretory water loss for captive nestling Swainson's Hawks. Solid dots represent the average rate of dry excrement production (right axis) for each nestling in each trial. Dots with a horizontal line through them designate the nestlings reared in 1981. Least squares regressions were determined for values in the first two trials ($g \text{ dry excrement/day} = 0.91 [\text{age}] - 0.08$; $r = 0.89$) and the last two trials ($g \text{ dry excrement/day} = -0.61 [\text{age}] + 19.8$; $r = 0.26$), and the regression lines were joined by inspection (solid line). The left axis for excretory water loss is scaled such that the dots and solid line are directly convertible to daily water loss assuming 75% water content in the excrement. Plots for water loss assuming 66 and 80% water content in the excrement are also shown (dotted and dashed lines, respectively) and apply only to the left axis.

EVAPORATIVE WATER LOSS

Rates of evaporative water loss (EWL) at air temperatures of 35°C and 42°C are positively correlated with nestling body mass (Fig. 9) as described by the formulae which follow:

At 35°C

$$EWL = 0.155 W - 1.56 \quad r = 0.985$$

$$n = 24 \quad (1)$$

At 42°C

$$EWL = 0.173 W + 31.49 \quad r = 0.936$$

$$n = 22 \quad (2)$$

where

$$EWL = \text{rate of evaporative water loss in mg/min}$$

$$W = \text{body weight in g.}$$

EWL of Swainson's Hawk nestlings at 42°C should approximate the maximal rates for these birds. Swainson's Hawk nestlings weighing less than 200 g had evaporation rates similar to those predicted from an allometric equation of maximal evaporation rates for other avian species

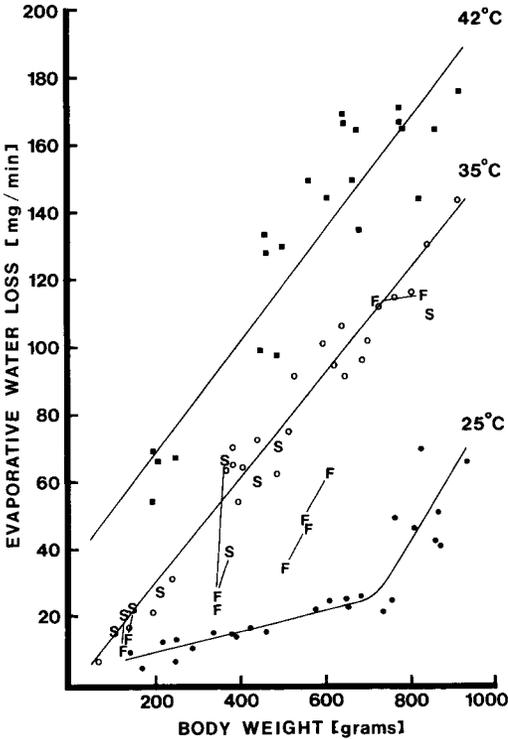


FIGURE 9. Rates of evaporative water loss (EWL in mg/min) for nestling Swainson's Hawks in relation to body weight (W in g) and ambient temperature. Evaporation rates at 42°C (squares), 35°C (open circles), and 25°C (solid dots) are plotted with respect to the lowest body weight of the nestling on the day it was tested. Regression lines were determined by the least squares method. At 42°C, $EWL = 0.155 W - 1.56$; $r = 0.985$, $n = 24$. At 35°C, $EWL = 0.173 W + 31.49$; $r = 0.936$, $n = 22$. At 25°C, $EWL = 0.0308 W + 2.84$; $r = 0.937$, $n = 18$. Additionally the graph shows the rates of evaporative water loss for well-fed (S) and fasted (F) nestlings exposed to direct midday sunlight and an air temperature of 30°C. Values obtained from the same nestling on two consecutive days are connected with a line.

(Calder and King 1974, equation 66). Larger nestlings had rates that were only 79–84% of the predicted maximal rates.

At 25° EWL increases linearly with nestling body weight up to 750 g; the relationship is described by equation (3).

$$EWL = 0.0308 W + 2.84 \quad r = 0.937 \quad (3)$$

$n = 18$

EWL at 25°C should approximate the minimum, or basal rates for these nestlings, yet they are considerably higher than the evaporation rates predicted from an allometric equation for other species of adult birds at 25°C (Crawford and Lasiewski 1968, equation 6). For example, at 25°C

the EWL of Swainson's Hawk nestlings weighing 100–200 g was 34% higher than predicted, and 700-g nestlings have rates approximately 75% higher than predicted.

At 25°C the EWL of seven larger nestlings weighing between 780 and 935 g averaged about 50% higher than predicted from equation 3 that we derived for smaller (younger) Swainson's Hawk nestlings, and about three times the allometric prediction for adult birds. The reason for the sudden upswing in EWL for larger nestlings is unclear. One possibility is that elevated evaporation rates may be the result of increases in the effective surface area for evaporation due to rapid feather growth which may expose blood-filled portions of the feather quills. This type of surface area phenomenon affects the dynamics of heat transfer in nestling Mourning Doves, *Zenaidura macroura* (Breitenbach and Baskett 1967).

Evaporation rates of the 12 nestlings heat stressed by a combination of direct sunlight and 30°C are also shown in Figure 9. The EWL of well-fed nestlings was similar to nestlings at 35°C without sunlight. Evaporation rates of seven nestlings which had fasted for at least 24 hr were always less than their rates prior to fasting, except in one nestling (the largest) which was not measurably affected.

It is difficult to assess how closely the thermal conditions present during the tests in direct sunlight simulated those at natural nests fully exposed to the midday sun. Because chamber walls were kept cool (18–22°C) to prevent overheating the chamber, the radiative environment in the chamber may have differed from that at an actual nest. Differences between the rates of nestling heat loss by forced convection (i.e., wind) in the laboratory and field could be expected to cause differences in panting rates.

Qualitatively, the behavior of nestlings in the four experimental conditions used to examine evaporative water loss differed considerably. At 25°C most nestlings sat quietly, sometimes appearing to sleep. Very small nestlings sometimes visibly shivered. At 35°C the same young nestlings appeared to be more comfortable and panted infrequently; older nestlings panted intermittently, but not at maximum rates. At 42°C nestlings panted rapidly, strongly, and continuously; with few exceptions, they moved nervously about the chamber, struggling against the walls as if trying to escape. Nestlings subjected to sunlight and 30°C also moved about the chamber as though seeking shade, but panted only at

TABLE 3. Parameters used in the water budget scenarios.

Figure	Water budget scenario	% water in excrement	% water in nestling tissue	% water in diet	% fat ¹ in diet	Wet energy ² of diet (kJ/g)	% energy ³ digestive efficiency	Excrement ⁴ food ratio
10	Water utilization	66	82.5	73	13	5.86	78	0.38
11	Moderate fat diet	66	82.5	73	13	5.86	78	0.38
11	Low fat diet	66	82.5	78	10	4.18	74	0.40
11	High fat diet	66	82.5	58	40	10.88	86	0.29

¹ Percent fat expressed on a dry weight basis.
² Wet energy is food energy expressed on a wet weight basis.
³ Digestive efficiencies of low and high fat diets reported for eagles by Collopy (1978).
⁴ Ratio = dry excrement produced/dry food consumed.

intermediate rates and did not appear to be as heat stressed as the nestlings at 42°C.

NESTLING BODY TEMPERATURES (T_b)

The average pretest T_b (± SD) for nestlings in all three indoor test conditions was 40.0 ± 0.57°C. Pretest T_b's of 19 nestlings tested in the sun averaged somewhat lower (39.3 ± 0.99°C). The pretest temperatures of seven fasted nestlings averaged 0.7°C lower than their T_b's on the previous day (a decline of marginal statistical significance, P < 0.1).

Posttest T_b's in the 25, 35, and 42°C tests averaged 39.3 ± 0.88, 40.4 ± 0.43, and 41.8 ± 0.70°C, respectively. Posttest T_b's of all birds tested in the sun averaged 40.2 ± 0.7°C. The posttest T_b's of the seven nestlings tested in the sun on two consecutive days (i.e., separated by 24 hr of fasting) were similar on both days, averaged 40.6 and 40.3°C, respectively. Average body temperature elevation during the sunlight test periods (i.e., the differences between pretest and posttest T_b's) was not significantly greater after 24 hr of fasting (1.5°C vs. 1.0°C). We believe the lower mean pretest T_b's of the seven fasted nestlings accounts for their slightly greater T_b rise during the second trial period.

The lowest T_b (34.1°C) was recorded on an 8-day-old nestling after more than 100 min at 24°C. The highest T_b (43.7°C) was measured on a 23-day-old nestling after at least 45 min at 42.8°C.

DIETARY EFFECTS ON WATER BALANCE

Water utilization. We estimated the minimum water requirements of a nestling hawk by summing the four components of water utilization (i.e., water storage in new biomass, water output in pellets, excrement, and evaporation) of nestlings at different ages. We assumed that: (1) nestling body tissue averages 82.5% water; (2) excrement averages 66% water; (3) the ratio of dry excrement production to dry food intake is 0.38;

and (4) digestive efficiency is 78% (Table 3). The level of water utilization shown by the upper boundary of the area labeled EWL: 25°C in Figure 10 is a conservative estimate of nestling water needs under nonstressful thermal conditions, since we assumed a low water content of excrement and basal rates of EWL. The predicted rates of water utilization of a nestling heat stressed for 8 hr at 35°C and at 42°C are greater than at 25°C,

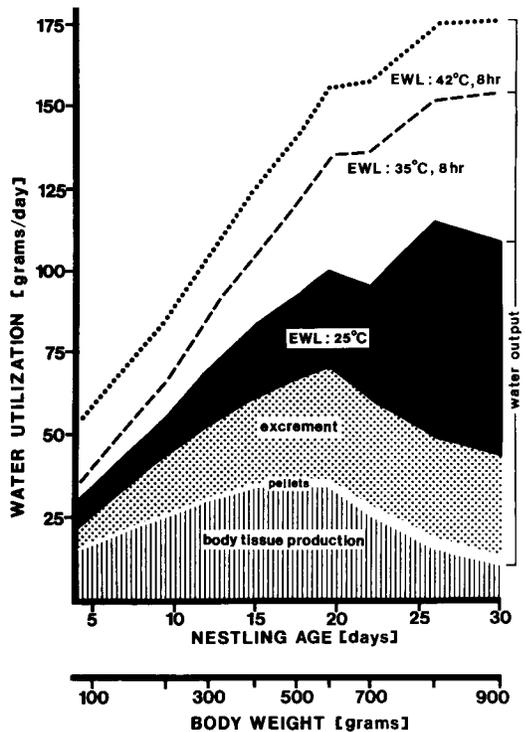


FIGURE 10. The minimum water utilization of a nestling Swainson's Hawk. See text for assumptions made in computing the four components of minimum water utilization. Water use components are additively stacked. The effects of prolonged daily periods of heat stress are simulated by the two upper plots, derived by replacing 8 hr of basal evaporative water loss with 8 hr of elevated evaporative water loss at either 35°C (dashed line) or 42°C (dotted line).

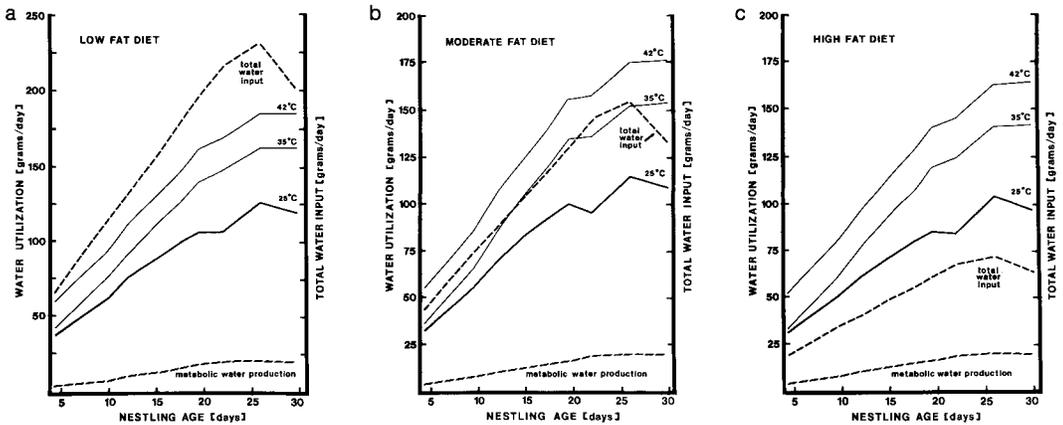


FIGURE 11. Water budget scenarios of a nestling Swainson's Hawk fed a low fat diet, a moderate fat diet, and a high fat diet. The sum of metabolic water production (lower dashed line) and preformed water consumption equals total water input (upper dashed line). Rates of minimum water utilization (solid lines) are redrawn from Figure 10 for the moderate fat diet and were recalculated for the low fat diet and the high fat diet. See Table 3 for assumptions made in computing total water input and water utilization.

because EWL is greater (the other three components of water utilization remain the same).

Water input. We estimated the rate of total water input to captive nestlings for three different diets (i.e., moderate fat, low fat, and high fat) by computing the rates of metabolic water production and preformed water consumption for each diet (see Table 3 for assumptions). Figure 11b shows the rate of water input for a moderate fat diet (i.e., 73% water; 13% fat in DW, 5.9 kJ/g fresh weight) as compared to the rates of water utilization at 25, 35, and 42°C (from Fig. 10) and illustrates the following water balance relationships: (1) a thermally nonstressed nestling at 25°C requires less water than the total water input, and must eliminate excess water by producing excrement with a water content greater than 66%. This excess water provides a margin of safety, reducing the risk of dehydration; (2) a nestling which pants at intermediate rates for 8 hr/day at 35°C would have barely enough water to meet its minimum needs, and must maintain a low excretory water content to avoid dehydration; (3) a nestling that is forced to pant at maximal rates for 8 hr/day at 42°C would require more water than is available from its diet. It would become dehydrated and likely die, unless it was able to conserve water in other ways (e.g., producing excrement considerably lower in water than 66%, tolerating a substantial reduction in the water content of body tissues, decreasing the rate of evaporation, etc.).

Total water input to a nestling consuming a diet low in fat and high in water content (i.e.,

78% water, 10% fat in DW, 4.2 kJ/g fresh weight), such as the juvenile ground squirrels we analyzed (Table 2), is shown in Figure 11a. Total water input exceeds water utilization at 25, 35, and 42°C. Food intake must increase to compensate for the lower energy content of the less fatty food and the slightly lower digestive efficiency (74%). The latter causes a higher ratio of dry excrement output to dry food intake (0.40). Increased excrement production causes higher rates of excretory loss and, therefore, slightly higher rates of water utilization (Fig. 11a). But these higher rates of water utilization for the low fat diet are more than compensated by the significant increase in total water input. Although metabolic water production is virtually unaffected by differences in dietary composition (assuming that only fat and protein are variable and that carbohydrate is a constant low value), preformed water consumption rises significantly with the increase in food consumption and the higher proportion of water in the low fat food. The main conclusion from the analysis of this scenario (Fig. 11a) is that a nestling on a low fat diet would probably never be stressed by water shortages, even if rates of evaporative water loss were maximal (e.g., if severely heat stressed 8 hr/day).

When a nestling consumes a diet high in fat and low in water content (i.e., 58% water, 40% fat in DW, 10.9 kJ/g fresh weight) the rates of total water input decrease significantly (Fig. 11c). This diet matches the body composition of adult Townsend ground squirrels (*Spermophilus townsendi*) collected in late May by Collopy (1978),

but it does not represent the most extreme case, because adult Uinta ground squirrels can attain fat levels of at least 50% dry weight during the months of June and July when Swainson's Hawks are rearing their young (Gessaman 1984).

Food consumption diminishes as the fat content of the food increases, as was demonstrated by the nestlings we reared on the higher fat diet in 1981 (Fig. 1). The high fat and low water content which characterizes this high energy diet rapidly satisfies nestling energy requirements, but yields very little preformed water. The rate of excrement production decreases, since less food is consumed, and because the fatty food is digested more efficiently (86%). The water savings which result from diminished rates of excretory water loss, however, are minor in comparison to the major reduction in total water input.

The conclusion from this scenario is that a nestling Swainson's Hawk cannot subsist on a high fat diet, such as the one proposed in this example, since the total water input would fail to meet the minimum water requirements of the nestling. The most important conclusions from these three scenarios are that: (1) the composition of the food, especially the water, fat, and energy content, has a major effect on water intake rates, and (2) this effect far surpasses the small changes in the rates of excretory water loss from different diets, or the variable rates of EWL under different thermal conditions.

Natural diet. Swainson's Hawks tend to be opportunistic generalists in their dietary habits. The broad diversity in Swainson's Hawk diets and the tendency for individuals to specialize on a locally abundant prey species (Fitzner 1978) make it difficult to select any one of the previous three scenarios as most representative of Swainson's Hawks. The body composition of the major prey items (i.e., voles and pocket gophers) of Swainson's Hawks nesting in Cache Valley, Utah, was most similar to the moderate fat diet (Fig. 11b), much like the food we fed to captive nestlings.

Dietary water supply could be highly variable for nesting hawks which feed almost exclusively on ground squirrels. Like other small mammals, ground squirrels tend to have lower body water content as fat levels increase (Flehart et al. 1973), and during June and July juvenile ground squirrels are significantly less fatty than adults (Gessaman 1984). It is possible that hawks could preferentially select either juvenile or adult ground squirrels as the bulk of their diets, thus providing nestlings a low fat diet or high fat diet, respec-

tively. In the former case, nestlings would have a surplus of water, whereas in the latter case nestlings may die from insufficient water. Prey selection which results in a mixed diet (composed of different ages and species of prey) would help to offset the dehydrating effects of occasionally consuming a fatty prey item.

CONSEQUENCES OF FOOD DEPRIVATION

Undernourished nestlings have an acute water balance problem in addition to the obvious disadvantages resulting from nutrient shortages. Excrement production and tissue production will decline with decreased food intake, and the reduction of both help to reduce the nestling's water needs.

Evaporation rates. Evaporation would continue to be a significant water loss factor in undernourished nestlings, though evaporative water loss rates of undernourished birds may be substantially reduced in certain circumstances, as was illustrated in Figure 9. The explanation for these lower rates of evaporation in fasted nestlings is unclear. The slightly lower average body temperatures of fasted nestlings during the trial periods would favor reduced rates of evaporation if the fasting nestling's evaporative surfaces were cooler than before the fast. Lower rates of endogenous heat production in fasted nestlings (Fig. 4) should also help diminish the respiratory ventilation rate as well as the amount of evaporative water required to dissipate body heat and control temperature. Despite the lower rates of evaporation in fasted nestlings, their increases of T_b during the direct sunlight tests were small (less than 3°C) and not significantly different from those of well-fed nestlings.

Body temperatures and heat stress. Tomback and Murphy (1981) measured crop temperatures of three nestling Ferruginous Hawks (5–6 weeks old) tethered in the sun on three consecutive days. They withheld food from the nestlings on the morning of the 3rd day to food-stress the birds. They conclude that these crop temperatures and cloacal temperatures (recorded for 3 hr on two other nestlings) "suggest that food deprived nestling Ferruginous Hawks cannot cope with heat stress" (Tomback and Murphy 1981, p. 96). Their conclusion was primarily based on the occurrence of slightly higher than average crop temperatures (0.6–0.7°C higher) in two of the three fasted nestlings (the third nestling had a decrease of 0.5°C) and larger variations in the crop tem-

peratures of two of the fasted nestlings (a different pairing than before).

The small sample size, the lack of controlled thermal conditions, the small and conflicting temperature differences, and the relatively short period of food deprivation, preclude firm conclusions from their data. The much longer periods of food deprivation (24–40 hr) in our study had minimal effects on the posttest body temperatures of the seven Swainson's Hawk nestlings that we heat stressed under controlled conditions. Thus, we predict that short-term food deprivation should not radically affect the ability of hawk nestlings to control their body temperatures during short periods of heat stress. However, we believe that chronic food shortages which substantially dehydrate the nestlings might impair their thermoregulation and increase the risk of extreme hyperthermia and ultimately death. The degree of food limitation or thermal stress that would lead to death has not been clearly established.

Shapiro and Weathers (1981) reported gradual declines (0.2–0.3°C/day) of the cloacal temperature of American Kestrels deprived of food. These declines averaged only 1.0°C after 3 days of food deprivation, about the same reduction we observed in fasted Swainson's Hawk nestlings (i.e., about a 0.7°C decrease after 24 hr of fasting). Chaplin et al. (1984) reported that the mean 24-hr T_b of Red-tailed Hawks decreased 0.2°C in summer and 0.7°C in winter during a fasting period. These decreases in T_b may represent adaptive responses to starvation. In conclusion, while short-term food deprivation does reduce heat production, excrement production, evaporative water loss, and growth of nestling hawks, the effects on body temperature regulation should only become life threatening if prolonged starvation inhibits the nestling's abilities to shiver or to pant effectively.

Dehydration. As it is true for other homeotherms, hawk nestlings can undoubtedly tolerate some degree of dehydration of their body tissues below the 82.5% level which we have used in the three water budget scenarios described above. Two Swainson's Hawk nestlings which had apparently suffered extended periods of sibling aggression and starvation, judging from their severe head injuries and weakened, emaciated condition, had body water contents of 70 and 76% at the time of their deaths shortly after being brought to the laboratory. Similarly, three cap-

tive Swainson's Hawk nestlings, which died suddenly of unknown causes during an earlier study, had body water contents of 68, 72, and 74% at the time of their deaths. It is likely that all these nestlings had survived at least several days of decline in their body water reservoirs well below the level of 82.5%. Emaciated, and presumably dehydrated, raptors can recover weight losses if given foods with sufficient moisture content before they become too weak to eat (Shapiro and Weathers 1981). Although it is possible that acute dehydration could impair the nestling's evaporative cooling mechanisms, we did not extend fasting to the point at which failure might occur, nor do we think that impaired thermoregulation can account for the reductions in the evaporative water loss rates of the fasted nestlings in this study.

OTHER FACTORS AFFECTING WATER BUDGET

Nest microclimate and heat stress. Nestling heat stress should be more prevalent in raptor species that typically nest in hot environments and exposed locations, e.g., Ferruginous Hawks, Swainson's Hawks, Golden Eagles (*Aquila chrysaetos*), Prairie Falcons (*Falco mexicanus*), and Osprey (*Pandion haliaetus*) (Fyfe and Olendorff 1976). Throughout the breeding range of Swainson's Hawks, which extends from northern Mexico to Alaska, nestlings are exposed to a broad range of thermal regimes in habitats ranging from deserts and grasslands to high montane parklands (Fitzner 1978). Even in shaded conditions high ambient temperatures can cause nestlings to increase respiratory rates and breathe with their mouths open. In 1981, nestlings, within their shaded cubicles, panted only on the hottest days when air temperatures were in the range of 29–35°C. Thus, panting solely due to high air temperatures should only be common in hot environments.

In contrast, panting in response to direct sunlight can occur even at cool temperatures. For instance, a pair of 17-day-old Red-tailed Hawk nestlings, that we were observing from a blind in early June 1980, began to pant in the early morning sunlight (08:30) when nest air temperatures were only 13°C. Our estimates of protective foliage cover at 77 Swainson's Hawk nest sites showed that the majority (69%) would expose nestlings to direct sunlight for major portions of the day if adults did not shade the young

(Kirkley 1985). Nestlings avoid exposure to direct sunlight by moving to shaded portions of the nest, but when the nest is fully exposed to direct sunlight, attending adults frequently shade their young (Fitzner 1978, Kirkley 1982). Heat-stressed nestlings tend to position themselves on the elevated outer margin of the nest, presumably enhancing the effectiveness of convective cooling from wind.

OTHER ROUTES OF WATER LOSS

We observed that nestling Swainson's Hawks have functional salt-secreting glands which expelled small amounts of salty fluids from the nostrils, as reported in other raptors (Cade and Greenwald 1966). The net effect of salt gland function is to promote water conservation by removing excess salts from the body in a more concentrated state than by the urinary system.

During bouts of maximal panting, some nestlings salivated profusely, causing saliva to drip from the tips of their tongues and lower mandibles. By measuring drip rates and droplet size we estimate that the maximum rate of water loss from dripping saliva was approximately 160 mg/min, at least equaling the already elevated rates of EWL in those maximally heat-stressed nestlings (Fig. 9).

Blood-sucking insects remove water and nutrients from the nestling's body through their parasitic feeding. Practically all hawk nestlings that we examined in the field had some blood-sucking ectoparasites, mainly flies. We predict that only major parasitic infestations on small downy nestlings would have any significant effect on nestling water budget.

CONCLUSIONS

Water balance in nestling hawks is a dynamic process controlled by six major factors which vary in importance under different conditions and at different times during the nestling period. For instance, the incorporation of water in new body tissues is a significant water budget component during the first half of the nestling period when growth rates are maximal, but thereafter its importance rapidly diminishes as growth slows and the nestling approaches full size.

The magnitude of evaporative water loss significantly increases with nestling age as the evaporative surfaces of the body enlarge. The rate of evaporation at any particular time is highly dependent upon the thermal conditions affecting

the nestling, as evaporative cooling by panting is one of its major methods of heat dissipation. Parental and nestling behaviors, which protect nestlings from the heating effects of direct sunlight, diminish not only the immediate risk of heat prostration but also the long-term risk of nestling dehydration.

The most important, and highly variable, factor governing nestling water balance is the body composition of the prey consumed, especially its water and fat content. Because fat and water content tend to vary inversely, the water yielding potential of different prey items, even different individuals of the same species, can differ markedly. For instance, our hypothetical scenarios showed that a nestling raptor diet composed of lean, juvenile ground squirrels would provide more than three times as much water as that provided by a diet of fatty, adult ground squirrels. To fulfill nestling energy requirements adult hawks would need to capture more of these small, low energy juvenile squirrels, but that disadvantage of dietary selectivity may be offset by the added margin of protection from dehydration provided by the surplus water in this diet.

We predict that a diet composed exclusively of fatty, high energy, adult squirrels would result in nestling death from dehydration, because this diet would fail to provide enough water to meet the minimum requirements of the nestlings. Diets which include prey of various species and ages probably provide intermediate levels of water input, necessitating adult and nestling behaviors which help the nestling avoid heat stress and minimize evaporative water losses (e.g., adult shading, nestling shade seeking).

Although short-term food deprivation (24–40 hr) did not significantly impede the ability of nestlings to dissipate heat and control their body temperatures, we predict that excessive dehydration from prolonged starvation could hinder nestling thermoregulation and increase the risk of heat prostration.

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