

SHORT COMMUNICATIONS

Is Long-distance Migration Possible for Soaring Hawks Using Only Stored Fat?

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Fat is the fuel for avian migration (Weis-Fogh 1952, Blem 1980), but little quantitative information is available concerning the energy expenditure involved in these flights. Most studies of the energetics of avian migration have dealt with birds that use powered (flapping) flight (Berger and Hart 1974). These investigations have been based on laboratory analyses of flight metabolism (e.g. Tucker 1971), field studies of changes in body mass (Nisbet 1963, Rogers and Odum 1966), or inquiries into the quantities of fat necessary to fuel long-distance migratory flights that are less than a week or so in duration (Berthold 1975). In the present study we combine these approaches to analyze the energetics of a different type of migration, the long-distance, long-term soaring flight of Swainson's Hawk (*Buteo swainsoni*) and the Broad-winged Hawk (*B. platypterus*). Such a flight ought to involve large expenditures of metabolic energy (Pennycuik 1969, 1975; Newton 1979; Smith 1985c). The migration, however, may be accomplished largely without feeding (Smith 1980, 1985c). We are particularly interested in assessing this possibility.

Patterns of migration.—Although some *B. swainsoni* migrate to the southeastern United States to spend the nonbreeding season (Browning 1974), most are long-distance migrants that travel back and forth between the plains, shrublands, and pampas of North and South America. Some of these long-distance migrants remain in suitable habitats in Central America during the boreal winter (Bent 1937, Smith pers. obs.), but hundreds of thousands continue on through the Isthmus of Panama to their migratory terminus in Argentina. This transequatorial migration lasts 30–65 days. The hawks pass over Las Cruces, New Mexico in early October, reach Panama approximately 18 days later, and arrive in Argentina during the last week of November (Smith 1980, 1985b).

Although some *B. platypterus* remain in North America during the nonbreeding season, most migrate to northern South America from their breeding areas in southern Canada, and central and eastern U.S. Migrating birds pass through Texas in late September and 12–14 days later arrive in Panama. Substantial numbers of Broad-winged Hawks spend the nonbreeding season in Panama.

Evidence for fasting.—Hundreds of thousands of hawks of both species migrate together through Mexico and Central America (Smith 1985a; Fig. 1).

During southward migration, the rivulets of migrating birds coalesce into large migratory flocks at approximately 30°N (Lasley and Sexton 1985). During northward migration, similar large flocks form by the time the migrants reach the slopes of the Andes, approximately 3–5° north of the equator. The migrating hawks are funneled into extremely dense concentrations by the shape of the land mass and by meteorological features. Except for the possibility of occasional outbreaks of insects (Smith 1980, 1985b; Lasley and Sexton 1985), it is unlikely that an individual bird would be able to procure a significant amount of food while foraging among such a dense concentration of conspecifics. Furthermore, the main period of passage of these flocks through the Isthmus of Panama is well defined and relatively short (approximately 16 days; Smith 1985a), with peak movement occurring during 9 days. Thus, it is unlikely that significant numbers of birds leave the migrating flocks for several days to feed, accumulate fat, and renew their flight.

Further evidence for fasting comes from examination of migratory hawks collected at their roosts in Panama in early October, before the nonbreeding seasonal residents had commenced feeding or started to establish territories. On the day after the collection the roost was empty, further confirming that these birds were migrants. None of the birds in this sample had food in their guts, and neither feces nor pellets were found where hundreds of hawks had spent the night.

Evidence for fat deposition.—For Swainson's Hawk our data are limited to birds in the middle of their migration. Southward migrating *B. swainsoni* were captured in Panama in October. Most of the birds had some subcutaneous fat (Table 1). However, 51% of adults and 41% of juveniles were scored as having little or no fat (fat index = 0 or 1). No Swainson's Hawks were found dead or dying in Panama. However, at least some of them arrive in Argentina in such a weak condition that they can be picked off their perches (Olrog in Smith 1980).

Premigratory Broad-winged Hawks that had been in Panama for 5 or 6 months were captured on their foraging territories in March and early April, just before their normal departure time for northward migration. None of these birds was laparotomized, but all individuals with a mass greater than 450 g were assumed to be females (Table 2). Of the birds



Fig. 1. A typical concentration of migrating Broad-winged Hawks in a thermal bubble. Panama City, Panama, 14 October 1984.

captured, 62% (6 of 11 adult females, 9 of 14 adult males, and 8 of 12 juveniles) were moderately to very fat (fat index = 2 or 3).

Post- or midmigratory Broad-winged Hawks were captured at roosting areas in Panama during the first three weeks of October in 1972–1983. Seventy-six of these birds were dead or sick individuals, and an additional 46 healthy birds were captured and released. Of the dead and apparently sick birds, we examined fat deposits on 25 adults (11 females, 7 males, and 7 birds that could not be sexed satisfactorily). Two of the females (mass 377 and 349 g) were moderately fat. The other 23 adults had no visible fat, and their pectoral muscles were wasted and concave. Of the 46 healthy birds, only 35% were classified as having moderate or heavy fat deposits (Table 3).

Model of the energetics of hawk migration.—While our data are less than compelling, they are consistent with the hypothesis that Swainson's and Broad-winged hawks store fat before migration and fast while migrating. Swainson's and Broad-winged hawks fly for about 9,000 and 5,000 km, respectively. To estimate the physiological possibility that these birds deposit sufficient fat to fuel these entire flights, we construct-

ed for each species a simple, generalizable model in which the magnitude of the critical parameters can be selected by the user and the amount of fat required for a given migratory distance can be estimated. Our models, each of which consists of two families of nomograms, are based on body mass, fat stores, flight speed, basal metabolic rate (BMR), and the energy cost of soaring flight.

We assume that migrating hawks engage in only two activities: soaring flight during the day and roosting at night. The number of hours per day during which soaring hawks are airborne depends on local meteorological conditions. In our experience Swainson's and Broad-winged hawks seldom fly before 0745 and never fly after 1800. We therefore assume that during migration they fly 10 h/day and roost 14 h/day.

The energy cost of soaring is calculated as $BMR \times cff$, where BMR is the daytime basal metabolic rate (calculated from Lasiewski and Dawson 1967) and cff (cost of flight factor) is the metabolic cost of soaring expressed as a multiple of daytime BMR. Direct measurements of the metabolic cost of gliding have been reported for only one species, the Herring Gull (*Larus argentatus*; Baudinette and Schmidt-Nielsen 1974). The oxygen consumption of two Herring Gulls (masses 965 g and 859 g) gliding in a wind tunnel at 10.8 m/s averaged 13.95 W, which is 2.17 times BMR calculated from the Lasiewski-Dawson equation. We use the value 2.0 as cff and assume that $2.0 \times BMR$ is the metabolic cost of soaring. However, the model is designed so that the user can select any cff value between 1 and 3.

The energy cost of nighttime roosting is assumed to equal the allometrically calculated nocturnal BMR (Aschoff and Pohl 1970), which is approximately $0.8 \times$ daytime BMR.

There is no entirely satisfactory way to deal with the metabolic costs associated with stored fat. Although stored fat is relatively inert metabolically, little is known about the effect of increased body fat on BMR. Fat also increases total body mass, which increases wing loading. This in turn increases the amount of work that must be done by the tonic wing muscles during soaring. The magnitude of the effect

TABLE 1. Total body mass and fat index of southward migrating Swainson's Hawks captured at roosts in Panama 20 and 25 October in 1972–1983. Index for visible fat: 0 = none, 3 = very fat.

Plumage	Sex	n	Body mass (g)			Visible fat index			
			Range	Mean	SD	0	1	2	3
Adult	F	12	801–1,240	979	134.0	2	3	6	1
Adult	M	9	672–793	727	41.5	1	4	4	0
Adult	?	14	730–999	850	78.6	3	5	4	2
Juvenile	F	6	816–998	941	51.4	2	0	4	0
Juvenile	M	14	675–780	721	37.6	3	4	7	0
Juvenile	?	9	755–1,001	838	77.1	1	2	4	2

TABLE 2. Total body mass and fat index of premigratory Broad-winged Hawks captured in Panama between 17 March and 1 April in 1980-1984. Adults with mass >450 g were assumed to be female. Index for visible fat: 0 = none, 3 = very fat.

Plumage	Sex	n	Body mass (g)			Visible fat index			
			Range	Mean	SD	0	1	2	3
Adult	F	11	459-560	504	26.6	4	1	1	5
Adult	M	14	313-447	378	37.3	3	2	5	4
Juvenile	F	6	471-516	488	17.2	2	0	1	3
Juvenile	M	6	319-409	375	30.1	1	1	4	0

of the increased wing loading associated with body fat on the energy cost of flight, and the metabolic costs associated with stored fat, have not yet been determined. Therefore, we incorporated these two inadequately quantified incremental energy costs associated with stored body fat into our model by calculating BMR from total body mass, including fat. This procedure allowed us to combine the energy costs associated with fat deposits during rest and during flight by treating the cost of flight as a multiple of BMR. In the present context this procedure is conservative in that it probably overestimates the energy costs associated with body fat and hence underestimates the migratory distance attainable on a given fat reserve. In our model both BMR and the cost of flight diminish continuously as body mass, in the form of fat, is lost during migration. Because the migration route is through low latitudes and is accomplished at relatively low (warm) altitudes, we included no thermoregulatory costs in our model.

We based our calculations on fat-free body masses of 600 g for Swainson's Hawks and 300 g for Broad-winged Hawks, probably representative of male birds of each species. Our model assumes that fat is the sole source of energy for migration, and that complete oxidation of fat yields 39.7 kJ/g.

During the southward migration under rainy-season conditions, soaring hawks obtain lift from air movements associated with slopes, thermal bubbles, and cloud streets. These soaring patterns require that a substantial amount of time be devoted to gaining

altitude (Pennycuik 1972). Smith's observations suggest that 8.33 m/s (30 km/h or 300 km/day) is a generous estimate of the average horizontal speed for the hawks on their way south. During the northward migration, the strong tradewinds in Central America allow these hawks to engage in dynamic-soaring, or even wave-soaring, on the lee sides of the mountains. These could produce speeds of as much as 70 km/h during some parts of the northward journey. In our model the user can select any of eight flight speeds.

To use the nomograms, first determine the time required to fly a given distance at a particular speed (Figs. 2A and 3A). Then, for this duration of flight and using an estimated cost of flight factor (cff), determine the mass of fat required by the bird (Figs. 2B and 3B). For example, for a Swainson's Hawk to fly at 240 km/day from Las Cruces, New Mexico to Ancon, Panama (4,310 km), 18 days are required (dotted lines, Fig. 2A). At a cff of 2.0, this flight requires the oxidation of 145 g of fat (dotted lines, Fig. 2B). Similarly, for *B. swainsoni* to fly from Las Cruces to a point midway between Cordoba and Tucuman, Argentina (9,010 km) at 240 km/day and a cff of 2.0, 37.5 days and 330 g of fat are required.

For *B. platypterus*, migration from New Brunswick, Canada to Ancon, Panama (6,700 km) at 240 km/day and a cff of 2.0 requires 29 days and 155 g of fat (line X, Fig. 3). The flight from Brownsville, Texas to Venezuela (4,300 km) requires 16 days and 80 g of fat (line Y, Fig. 3). To fly from Brownsville to Panama

TABLE 3. Total body mass and subcutaneous fat index of southward migrating Broad-winged Hawks captured at roosts in Panama during the first two weeks of October in 1972-1983. Index for visible fat: 0 = none, 3 = very fat.

Plumage	Sex	n	Body mass (g)			Visible fat index			
			Range	Mean	SD	0	1	2	3
Adult	F	9	430-455	447	21.8	2	4	3	0
Adult	M	13	319-373	357	26.0	3	3	5	2
Adult	?	5	387-407	394	8.7	0	3	2	0
Juvenile	F	5	323-476	431	6.8	2	3	0	0
Juvenile	M	5	311-371	332	23.0	0	1	3	1
Juvenile	?	9	321-391	353	30.8	3	6	0	0

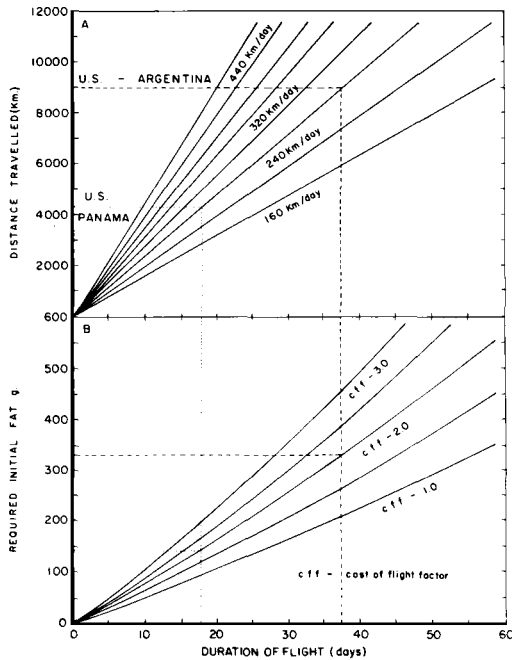


Fig. 2. Nomograms for the migration of a Swainson's Hawk with a lean mass of 600 g. The dotted and dashed lines are to guide the eye in working out examples; see text for details and operation.

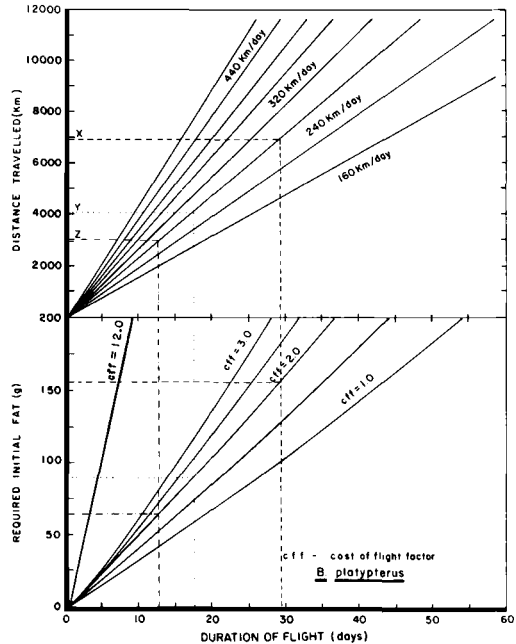


Fig. 3. Nomograms for the migration of a Broad-winged Hawk with a lean mass of 300 g. See text for operation and details.

(3,900 km) requires 14 days and 65 g of fat (line Z, Fig. 3).

Alternatively, from an estimate of the mass of fat accumulated by the two species, we can estimate the maximum range attainable by anorexic soaring. We speculate that if a 600-g *B. swainsoni* could deposit 200 g of fat, at a flight speed of 240 km/day and a cff of 2.0 the bird would have a maximum range of ~5,800 km. If a 300-g *B. platypterus* could accumulate 125 g of fat, it would have a soaring flight range of ~5,300 km (flight speed = 240 km/day, cff = 2.0).

Our model indicates that a migration by the hawks without feeding from the southern U.S. to northern South America would require deposition of fat amounting to 20-25% of lean body mass. Although such fat deposition has not been recorded for raptors, this is within the range commonly measured in migratory birds of other taxa (Nisbet 1963). Thus, our calculations suggest that a long-distance fasting migration is physiologically reasonable in Swainson's and Broad-winged hawks. The capability for this migration derives largely from the hawks' use of energetically inexpensive soaring, rather than powered, flight. For example, although 100 g of fat would sustain a soaring Broad-winged Hawk (cff = 2) for more than 20 days, powered flight (cff = 12; King 1974) would exhaust this fuel reserve in less than 5 days (Fig. 3). Thus, a hawk using powered flight

would need to forage extensively during its migration. The difficulty of procuring adequate prey among so many conspecifics suggests that it is energetically preferable to soar and forgo feeding rather than to attempt feeding to maintain powered flight. Indeed, during either northward or southward migration on days when no lift is available, the hawks simply sit. We did not observe flapping flight in migration.

Our model indicates that, in theory, both hawk species can accomplish all or much of their migrations without feeding. To confirm that they routinely have the energy resources to do so, however, further information, particularly on fat-free masses, actual (rather than predicted) measurements of rates of energy expenditure, rates and levels of fat accumulation, and flight speeds, is needed. Our model provides a framework for integrating this information as it accumulates.

P. Bloom and W. Clarke supplied information about Swainson's Hawks in North America. C. Sexton provided the dates for the movements of both species at the Texas-Mexico border. D. Brinker and T. Erdman kindly let us see their data gathered over many years for Broad-winged Hawks. R. Ridgely and W. Belton supplied information about both species in South America. H. Hill, N. Gale, and J. Steffen advised and helped catch Broad-winged Hawks. J. Fryxell, N. Towe, R. Foster, N. Currie, and F. Delgado were helpful hawk watchers at various times in Panama.

D. Bradford contributed to development of the computer model. C. Pennycuick, A. S. Rand, D. Brinker, and T. Erdman provided useful criticisms of the manuscript.

LITERATURE CITED

- ASCHOFF, J., & H. POHL. 1970. Der Ruheumsatz von Vögeln als Funktion der Tageszeit und der Körpergröße. *J. Ornithol.* 3: 38-47.
- BAUDINETTE, R. V., & K. SCHMIDT-NIELSEN. 1974. Energy cost of gliding flight in Herring Gulls. *Nature* 248: 83-84.
- BENT, A. C. 1937. Life histories of North American birds of prey. *Bull. U.S. Natl. Mus.* 167: 69.
- BERGER, M., & J. S. HART. 1974. Physiology and energetics of flight. Pp. 416-477 in *Avian biology*, vol. 4 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- BERTHOLD, P. 1975. Migration: control and metabolic physiology. Pp. 77-128 in *Avian biology*, vol. 5 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- BLEM, C. R. 1980. The energetics of migration. Pp. 175-224 in *Animal migration, orientation and navigation* (S. A. Gauthreaux, Jr., Ed.). New York, Academic Press.
- BROWNING, M. R. 1974. Comments on the winter distribution of the Swainson's Hawk (*Buteo swainsoni*) in North America. *Amer. Birds* 28: 865-867.
- KING, J. R. 1974. Seasonal allocation of time and energy resources in birds. Pp. 4-70 in *Avian energetics* (R. A. Paynter, Jr., Ed.). Cambridge, Massachusetts, Nuttall Ornithol. Club.
- LASIEWSKI, R. C., & W. R. DAWSON. 1967. A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor* 69: 13-23.
- LASLEY, G. W., & C. SEXTON. 1985. South Texas region. *Amer. Birds* 39: 75-77.
- NEWTON, I. 1979. Population ecology of raptors. Berkhamsted, England, T. & A.D. Poyser.
- NISBET, I. C. T. 1963. Weight loss during migration. Part II: Review of other estimates. *Bird-Banding* 34: 139-159.
- PENNYCUICK, C. J. 1969. The mechanics of bird migration. *Ibis* 111: 525-556.
- . 1972. Animal flight. *Inst. Biol. Studies in Biol.*, No. 33. London, Edward Arnold.
- . 1975. Mechanics of flight. Pp. 1-75 in *Avian biology* (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). New York, Academic Press.
- ROGERS, D. T., & E. P. ODUM. 1966. A study of autumnal postmigrant weights and vernal fattening of North American migrants in the tropics. *Wilson Bull.* 78: 415-433.
- SMITH, N. G. 1980. Hawk and vulture migrations in the Neotropics. Pp. 51-65 in *Migrant birds in the Neotropics: ecology, behavior, distribution and conservation* (A. Keast and E. S. Morton, Eds.). Washington, D.C., Smithsonian Inst. Press.
- . 1985a. Dynamics of the transisthmian migration of raptors between Central and South America. Pp. 271-290 in *Conservation studies on raptors*, ICBP Tech. Publ. No. 5 (I. Newton and R. D. Chancellor, Eds.). London, Intern. Council for Bird Protection.
- . 1985b. Some uncertain aspects of migration by Swainson's Hawks (*Buteo swainsoni*) and Turkey Vultures (*Cathartes aura*). Rochester, New York, Proc. North American Hawk Migration Conf. No. 4.
- . 1985c. Thermals, cloud streets, trade winds, and tropical storms: how migrating raptors make the most of atmospheric energy in Central America. Rochester, New York, Proc. North American Hawk Migration Conf. No. 4.
- TUCKER, V. A. 1971. Flight energetics in birds. *Amer. Zool.* 11: 115-124.
- WEIS-FOGH, T. 1952. Fat combustion and metabolic rate of flying locusts (*Schistocerca gregaria* Forsal). *Phil. Trans. Royal Soc. London, Ser. B* 237: 1-36.

Received 15 August 1985, accepted 11 December 1985.

The First Documented Case of Polyandry for Wilson's Phalarope (*Phalaropus tricolor*)

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Phalaropes are noted for their unusual mating system in which males provide all parental care and females compete for mates (Oring 1982). This reversal of the sex roles is characteristic of classical polyandry, a rare mating system among birds (Oring 1985). Despite evidence that phalaropes exhibit sex-role reversal and polyandry (Oring 1982), sequential poly-

andry was proven only recently for Red-necked (*Phalaropus lobatus*; Hildén and Vuolanto 1972, Reynolds et al. 1985) and Red phalaropes (*P. fulicaria*; Schamel and Tracy 1977). I present here the first documented case of polyandry for Wilson's Phalarope (*P. tricolor*).

I studied Wilson's Phalaropes from 1982 to 1985