The Auk 109(2):268-276, 1992

WATER AND ENERGY LIMITATIONS ON FLIGHT DURATION IN SMALL MIGRATING BIRDS

NURIT CARMI,[1] BERRY PINSHOW,[1] WARREN P. PORTER,[2]
AND JIM JAEGER[2]
[1]*Mitrani Center for Desert Ecology, Jacob Blaustein Institute for Desert Research,*
and Biology Department, Ben-Gurion University of the Negev,
Sede Boqer Campus, 84993 Israel; and
[2]*Department of Zoology, University of Wisconsin, Madison, Wisconsin 53706, USA*

ABSTRACT.—We examined the physiological limitations to flight duration in small migrating birds with a computer-simulation model. Given preflight body mass, fat and water contents, and flight-path meteorological data, we calculated water and energy budgets and possible flight time. The model can be applied to birds of any size that migrate by flapping flight. As an example, we simulated the flight of small Palearctic passerines (body mass = 10 g) during their annual migration over the Sahara desert. Sensitivity analysis of model input variables indicated that oxygen extraction and expired air temperature are the most important physiological variables in a bird's water budget and can profoundly influence flight duration. This manifests the importance of: (1) efficient cooling in the nasal passages of flying birds; and (2) the choice of flight altitude (which affects both ambient air temperature and expired air temperature). The model predicted that: (1) Prior to migration, these birds must have stored fat comprising at least 22% of their initial body mass; otherwise, they cannot complete their journey. (2) In relatively fat birds (stored fat >0.22 body mass), dehydration rather than energy will limit flight duration. (3) Birds should fly at an altitude not exceeding 1,000 m to cross the Sahara successfully. (4) Even in low-flying fat birds, flight duration will be limited by their stringent water budget. The model further predicted that small passerines cannot cross the Sahara in a 30- to 40-h nonstop flight, as commonly accepted, but should confine flying to the cooler hours (i.e. nights) and rest during the day in order to avoid elevated rates of water loss due to higher ambient air temperatures. Available data and observations of birds trapped at stopover sites in the Sahara support these predictions. *Received 26 February 1991, accepted 13 January 1992.*

LONG-DISTANCE flight over seas or deserts is perhaps the most risky and physiologically challenging event in the life cycle of migratory birds (Moreau 1961, Wilson 1981). Reports of high attrition among migrants and of exhausted birds found severely dehydrated and/or fat depleted (Serle 1956, Odum et al. 1964, Rogers and Odum 1964, Johnston 1968, Wilson 1981) raised the question: Is water or energy the greater physiological limitation to bird flight duration?

Energy, rather than water, is currently considered the major factor limiting bird flight duration because dehydration can be avoided by flying at high altitudes where air temperatures are low (Blem 1976, Torre-Bueno 1978, Skadhauge 1981, Dawson 1982, Biesel and Nachtigall 1987, Biebach 1990). However, this paradigm has not been substatiated with empirical field data.

To fully answer the above question one must know the energy and water budgets of the bird during long migratory flight, as well as the prevalent meteorological conditions. These include air temperature, relative humidity, and air pressure, as well as wind direction and velocity. Although data have been obtained for free-flight energy costs in birds (e.g. LeFebvre 1964, Utter and LeFebvre 1970, Masman and Klaassen 1987, Gessaman and Nagy 1988), none of these authors reported simultaneous measurements of meteorological variables, and no one has published information pertaining to free-flight rates of water loss.

It is almost impossible to make physiological measurements on the same bird just before and immediately after long-distance migratory flight, let alone measure the meteorological conditions it encountered along the way. To take a fresh look at this problem we developed a computer model, based on first principles, to predict water and energy budgets in flying birds as functions of ambient meteorological conditions. We then used the model to address the following questions: (1) Under what circum-

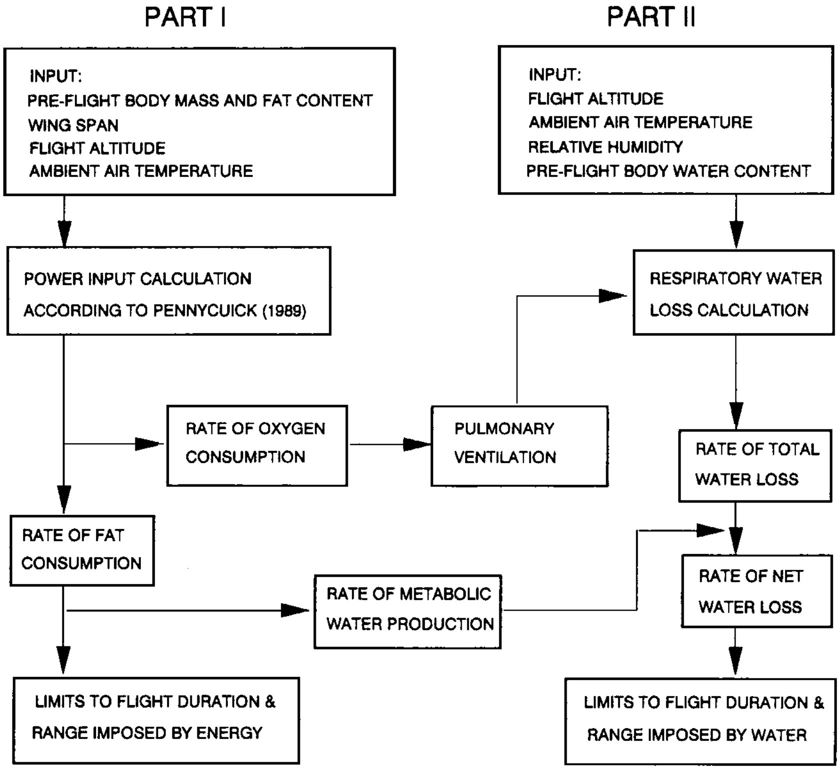

Fig. 1. Flow chart of model used to calculate possible flight duration and range in migrating birds. Energy-budget calculations (Part I) based on aerodynamic power inputs according to Pennycuick (1989). Water-budget calculations (Part II) outlined in Appendix.

stances would flight duration be limited by fat depletion and/or dehydration? (2) What are the meteorological conditions that a bird should choose in order to maximize flight duration and/or distance? (3) Is the predicted dependence of flight duration on meteorological conditions reflected in the migration strategies of avian species?

Model Methods

The model comprises two parts. Part I calculates flight power input, and part II calculates an in-flight water budget (Fig. 1). To take into account continuous changes during flight, we integrated over flight time using 1-min increments (see Appendix for details of model structure and assumptions).

Part I.—Power input was calculated using program 1 from Pennycuick (1989) after translation to FORTRAN and modification to run in batch mode. This program uses equations formulated by Pennycuick (1975), which are based on bird morphometry and aerodynamic first principles. The essence of Pennycuick's model is that for a bird of given dimensions, a curve relating mechanical power required for flapping flight to forward airspeed is computed. Total mechanical power output is the sum of parasite power (needed to propel the bird's body through the air), induced power (needed to support weight), and profile power (needed to sweep the wing through its arc). Metabolic power input is then computed by assuming a value for power conversion efficiency and adding the power requirements for circulation and respiration.

Recognizing the limitations of his model for the simulations presented, we used Pennycuick's default values for air density, fat energy density, induced power factor, circulation/respiration factor, and profile and metabolic power ratios. However, since power conversion efficiency has been the subject of recent debate (Rayner 1990, Walsberg 1990), we used a range of values this variable might assume. Input data for Pennycuick's model included the bird's lean body mass, fat content, and wingspan. Output data during level, steady-state flapping flight included aerobic power input, rates of fat consumption, minimum-power speed, maximum-range speed, and lift-to-drag ratio.

Part II.—We added a second section to the model,

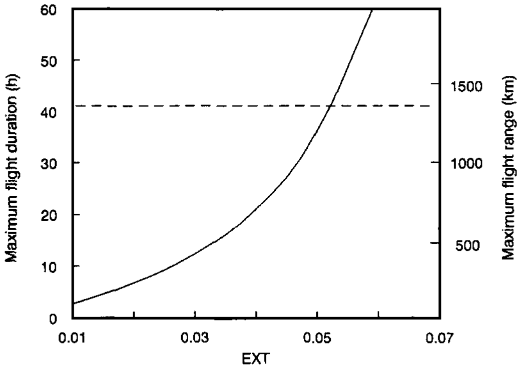

Fig. 2. Relations of maximum flight duration and range with the isolated effect of oxygen extraction (EXT, defined in Appendix) for a Willow Warbler traversing the Sahara desert in autumn. Assumed flight altitude 2,000 m, air temperature 14°C, and relative humidity 40%. Bird's initial body mass of 10 g included 2 g lean dry mass, 5 g water, and 3 g fat. Solid line designates limitation to flight duration imposed by a maximum-allowable water loss constituting 30% of initial body water. Dashed line designates energy limitiation imposed by use of all stored body fat.

which calculated rates of metabolic water production, respiratory evaporative water loss, total evaporative loss, and net water loss for birds flying at various altitudes under different ambient conditions of air temperature and relative humidity. Input data were air temperature, altitude, and the bird's preflight water content, in addition to aerobic power input and fat stored (as computed by Part I). We considered excretory water loss to be negligible, assuming that renal blood flow during flight is greatly reduced—as it is in exercizing mammals (e.g. Tanner 1975).

To estimate possible flight duration, one must relate the rate of net water loss to a level of permissible dehydration. Indices of hydration (or dehydration) state are usually expressed as fractions (i.e. water content divided by total, lean, or dry-lean body mass; Odum et al. 1964, Johnston 1968, Fogden 1972, Skadhauge 1981). Using any of these indices to deduce the effects of dehydration on migration, during which body mass, body composition, and body-water compartment volumes change, can lead to ambiguous conclusions. Therefore, we made an arbitrary, but conservative assumption that the maximum-allowable amount of water loss was 30% of the bird's preflight water content. This level of dehydration is a little beyond that considered debilitating in resting mammals (McNabb 1969, Horowitz et al. 1978, Arad et al. 1985). We then estimated maximum-possible flight duration for a given bird under given conditions, on the basis of this degree of dehydration.

SIMULATIONS

The model can be used to make calculations for a bird of any size. However, to demonstrate the utility of the models, we used the Willow Warbler (*Phylloscopus trochilus*) as an example. This species is a very common Eurasian passerine that makes an annual long-distance migratory flight across the Sahara desert, a 1,500- to 2,000-km-wide ecological barrier to Palearctic birds wintering south of the Sahel zone (Biebach 1988, Biebach et al. 1986). The Willow Warbler's mean premigration body mass is about 10 g, 30% of which we assumed to be fat and 50% water, fractions characteristic of small passerine migrants (Odum 1960, Caldwell et al. 1963, Ward 1964, Wood 1982a, b). The Willow Warbler has an average wingspan of 0.17 m.

For flight meteorological conditions, we chose those typically found over the Sahara desert at various altitudes in October (autumn; AMMO 1962). Except for one radar study in autumn by Schafer (cited in Moreau 1972), little is known about migration altitudes over the Sahara. Schafer reported a median migration altitude of 2,000 m, but did not document the species observed. We used this height for simulations at constant altitude. For further assumptions, see the Appendix.

Simulations to demonstrate the effects of energy and water budgets on flight duration were done as follows. First, the effects of individual physiological and meteorological variables were tested. In these simulations one variable (e.g. oxygen extraction, exhaled air temperature, power conversion efficiency, air temperature, altitude, etc.) was allowed to change over a range of values, while all others were held constant. Then physiological and meteorological variables were tested in combination to show overall effects.

MODEL RESULTS AND DISCUSSION

Dependence of flight duration on physiological characteristics.—Of the physiological variables examined, we found oxygen extraction and exhaled air temperature to have the most profound effects on flight duration. The higher the oxygen extraction coefficient (EXT), the longer a bird will be able to fly (Fig. 2). A lower EXT brings about increased pulmonary ventilation volume (i.e. more air must pass through the lungs to supply a given amount of oxygen). This results in higher respiratory water loss and shorter flight duration. Even a slight increase in EXT could lower respiratory water loss and prolong flight duration, which may explain why some birds have evolved higher EXT than found

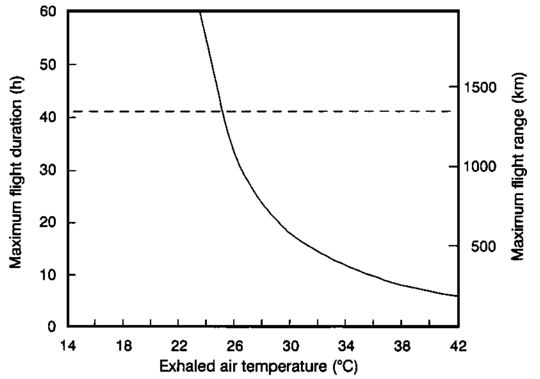

Fig. 3. Relations of maximum flight duration and range with the isolated effect of exhaled air temperature for a Willow Warbler traversing the Sahara desert in autumn. Assumed flight altitude 2,000 m, air temperature 14°C, and relative humidity 40%. Bird's initial body mass of 10 g included 2 g lean dry mass, 5 g water, and 3 g fat. Solid line designates limitation to flight duration imposed by a maximum-allowable water loss constituting 30% of initial body water. Dashed line designates energy limitation imposed by use of all stored body fat.

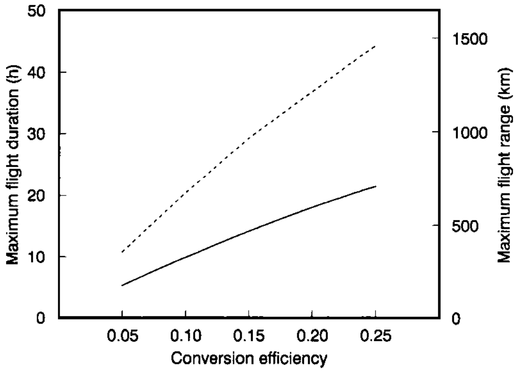

Fig. 4. Relations of maximum flight duration and range with the isolated effect of power conversion efficiency (mechanical power output/metabolic power input) for a Willow Warbler traversing the Sahara desert in autumn. Assumed flight altitude 2,000 m, air temperature 14°C, and relative humidity 40%. Bird's initial body mass of 10 g included 2 g lean dry mass, 5 g water, and 3 g fat. Solid line designates limitation to flight duration imposed by a maximum-allowable water loss constituting 30% of initial body water. Dashed line designates energy limitation imposed by use of all stored body fat.

in mammals of comparable size (e.g. Bernstein and Schmidt-Nielsen 1974). For further simulations, we assumed EXT to be constant, since it is not known whether EXT in flying birds varies in the face of changing oxygen partial pressure.

Exhaled air temperature (T_{ex}) may range between air temperature and body temperature; the lower T_{ex} is, the less water is lost in expired air and the longer the bird can fly (Fig. 3). The extent to which expired air is cooled depends on vasocontrol in the walls of the anterior respiratory tract, and the structure of the narial air passages (e.g. Schmidt-Nielsen et al. 1970, Murrish 1973). The effectiveness of cooling in the anterior respiratory pasages, which will function to condense respiratory water vapor which is recovered, may be very important in long-distance migrants. Its efficacy might even constitute the limiting physiological factor on bird flight duration. Unfortunately, except for the study of Berger et al. (1971), data are not available on the relation between inhaled and exhaled air temperatures in flying birds.

Conversion efficiency.—The default value of power conversion coefficient (PCC) in Pennycuick's program is 0.23. PCC values reported for flying birds vary a great deal, probably because muscle efficiency, determined by muscle contraction strain and stress, varies with flight speed (Rayner 1986, 1988). Rayner (1990) suggested that conversion efficiencies range from 7% to 15% for small passerines. Walsberg (1990:table 1) gives higher PCC values, from 17% to 59%; however, 30% seems to be a reasonable upper limit to muscle efficiency (Stainsby et al. 1980). Figure 4 illustrates the theoretical dependence of flight duration on PCC. Clearly, PCC will strongly affect flight duration, and empirical data are needed to complete the picture. Also, no matter what PCC value is used, water rather than energy is the limiting variable.

Dependence of flight duration on meteorological conditions.—The independent effects of altitude and air temperature on flight duration are shown in Figures 5 and 6, respectively. As a bird flies higher, air density (which was calculated taking both altitude and air temperature into account) decreases, the lift-to-drag ratio increases, and aerobic power input increases. The increase in oxygen demands combined with the decrease in oxygen partial pressure with increasing altitude lead to increased pulmonary ventilation volume and increased respiratory water loss, resulting in shorter flight duration. To sum-

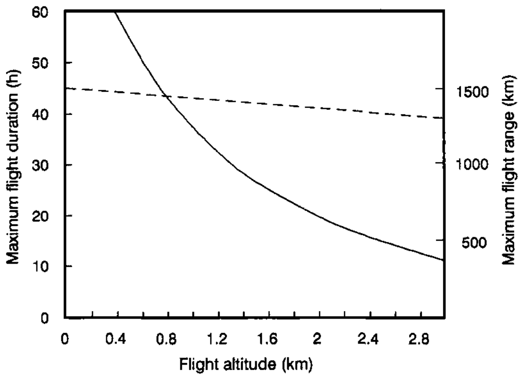

Fig. 5. Relations of maximum flight duration and range with the isolated effect of air temperature for a Willow Warbler traversing the Sahara desert in autumn. Assumed flight altitude 2,000 m and relative humidity 40%. Bird's initial body mass of 10 g included 2 g lean dry mass, 5 g water, and 3 g fat. Solid line designates limitation to flight duration imposed by a maximum-allowable water loss constituting 30% of initial body water. Dashed line designates energy limitation imposed by use of all stored body fat.

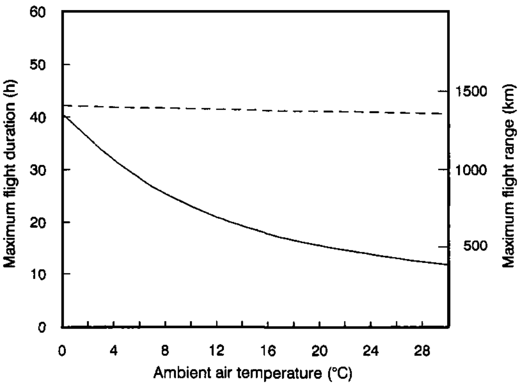

Fig. 6. Relations of maximum flight duration and range with the isolated effect of flight altitude for a Willow Warbler traversing the Sahara desert in autumn. Air density at flight altitude calculated taking both altitude and ambient temperature into account. Assumed air temperature 14°C and relative humidity 40%. Bird's initial body mass of 10 g included 2 g lean dry mass, 5 g water, and 3 g fat. Solid line designates limitation to flight duration imposed by a maximum-allowable water loss constituting 30% of initial body water. Dashed line designates energy limitation imposed by use of all stored body fat.

marize, if only altitude effects on flight duration are taken into account, from both energy and water considerations, a bird should fly as low as possible.

The effect of air temperature (T_a) on flight duration is insignificant from an energetic standpoint. However, for the bird's water budget, the impact of T_a on flight duration is significant through its effect on expired air temperature. If one considers only the effects of T_a, our model suggests that the lower T_a, the longer the possible flight duration and, because T_a decreases with increasing altitude, birds should choose to fly as high as possible. Thus, a combination of opposing factors apparently affects a bird's choice of flight conditions. The compounded effects of T_a and altitude on flight duration for a 10-g bird flying at various combinations of altitude and T_a are illustrated in Figure 7, where the contours show the limitation to flight duration, in hours, imposed by a maximum-allowable water loss constituting 30% of the bird's initial body water.

When do fat depletion or dehydration limit flight duration?—Because physiological variables respond to environmental conditions, the answers to the first two questions we initially posed are inseparable. Figure 8 illustrates the energy and water limitations to flight duration of a Willow Warbler in terms of the initial quantity of fat the bird carries. According to the model, maximum-range speed of a 10-g passerine is about 10 m/s, requiring at least 40 h to cross the Sahara in still air. Warblers whose preflight fat content is less than 22% of their initial body mass could not complete the flight. Such lean birds are limited by energy if they fly at low altitude, and by water if they fly high. Flight duration of birds with a fat content exceeding 27% of their body mass is limited by dehydration and can be prolonged by flying as low as possible. Regardless of flight altitude, even if fat reserves can supply energy for a much longer time, after about 40 h birds should stop flying because of dehydration. In other words, at combinations of air temperature and relative humidity typical over the Sahara desert in autumn, the model predicted that even the fattest birds have only a small safety margin in terms of water.

Migration strategies.—Moreau (1961, 1972) hypothesized that the predominant physiological limitation to flight duration is energy, and that small migrant birds traverse the Sahara in a single nonstop flight. Moreau's hypotheses bore an additional concept, also expresseed by Curry-Lindahl (1981), which is that small birds found on the ground during trans-Saharan migration represent a less capable group, termed

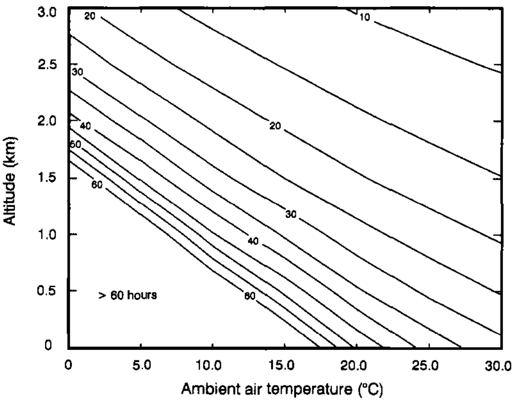

Fig. 7. Contour plot of dependence of maximum flight duration on flight altitude and air temperature for a Willow Warbler traversing the Sahara desert in autumn. Air density at flight altitude calculated taking both altitude and ambient temperature into account. Initial body mass of 10 g included 2 g lean dry mass, 5 g water, and 3 g fat. Contours show limitation to flight duration, in hours, imposed by a maximum-allowable water loss constituting 30% of initial body water.

"fallouts," rather than representing migrants in general.

Recently, Moreau's views have been reconsidered (Haas and Beck 1979, Biebach et al. 1986, Biebach 1988, 1990, Bairlain 1988). Biebach (1990) evaluated the physiological limitations on flight duration of small passerines crossing the Sahara in autumn, and reached the same conclusion as did other researchers (Blem 1976, Torre-Bueno 1978, Skadhauge 1981, Dawson 1982, Biesel and Nachtigall 1987), namely that energy, rather than water, is the major factor limiting bird flight duration, since dehydration can be avoided by flying at high altitudes where air temperatures are low. This argument, however, is based on the premise that the higher the bird flies the lower the air temperature and, thus, the lower its evaporative water loss. It does not take into account the decrease in oxygen partial pressure that occurs with increasing elevation and its consequent effects on evaporative water loss. We suggest that flying high, specifically at air temperature less than 10°C, would not necessarily eliminate dehydration risk; decreasing oxygen partial pressure with increasing altitude and consequent increased pulmonary ventilation volume must be considered as well.

Predictions of our model implied that the threat of dehydration places the greatest physiological constraints on trans-Saharan flight by small birds. The water budget for such flights leaves only a narrow margin of safety in terms of a small bird's ability to cross the Sahara successfully. These predictions further suggest that: (1) Small birds would do better flying at night and resting by day. At night, low air temperatures occur at lower altitudes than during the day. Thus, the energy advantage of low-altitude flight plus the reduced pulmonary ventilation volume at low altitude might both function as selective forces favoring night time flights by Saharan migrants. (2) Birds found on the ground will not necessarily be fat depleted and/or dehydrated. (3) Sites at which small birds land do not have to provide food and/or water.

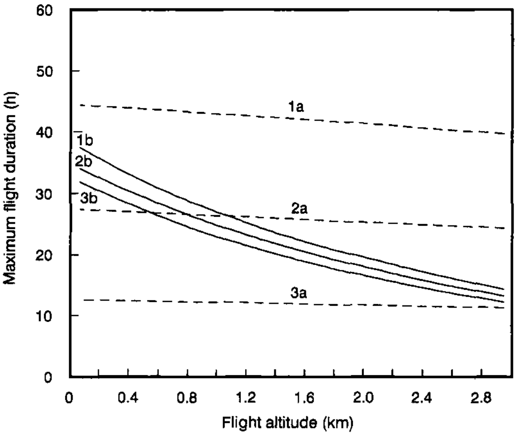

Fig. 8. Plot of dependence of maximum flight duration on flight altitude in terms of initial quantity of fat carried by a Willow Warbler traversing the Sahara desert in autumn. Air density at flight altitude calculated taking both altitude and ambient temperature into account. Assumed air temperature 14°C and relative humidity 40%. Bird's initial body mass in all three cases included 2 g lean dry body mass and 5 g water. However, fat content and, therefore, total body mass varied. Solid lines designate limitation to flight duration imposed by a maximum-allowable water loss constituting 30% of initial body water. Dashed lines designate energy limitation imposed by use of all stored body fat. Lines for birds with total initial body mass of: (1a and 1b) 10 g with 3 g fat; (2a and 2b) 9 g with 2 g fat; (3a and 3b) 8 g with 1 g fat.

Our third main question involved the degree of concurrance of predictions from our model with documented migration strategies. Observations of small passerines during their trans-Saharan crossing are few and far between. However, those available seem to support our predictions. Biebach (1988) studied small passerines at stopover sites during trans-Sahara migration. He reported finding many birds on the ground, resting during the day. Typically, they were perching on bushes or large stones above the surface boundary layer where they apparently benefited from convective cooling. These birds resumed flight after dark. He also noted that trapped birds were in good body condition (i.e. neither dehydrated nor fat depleted) and that, often, sites where birds were observed did not provide food. Further, according to observations by Safriel and Lavee (1988), autumn migrants in good body condition that landed at an oasis left the same day. However, "fallouts," in relatively poor body condition, usually remained for more than a day, while they replenished fuel supplies and were conspicuous in their food-gathering activity.

Other considerations.—According to our model, flight duration will increase with decreasing flight altitude, and birds will do best if they fly lower than 1,000 m. Unfortunately, few data exist on flight altitudes of migrating birds in general and none on transdesert migrants. Thus, data are not available to test our altitude prediction.

Another factor favoring low-altitude north-to-south flight over the Sahara in autumn is the wind regime. In autumn, northerlies prevail at below 1,000 m, whereas, at about 3,000 m winds become westerly (AMMO 1962). Low-flying autumn migrants will not only reduce dehydration risk, but also can exploit tailwinds to increase flight range.

Vernal migration strategy is more difficult to understand, and no data relevant to this analysis are available. On the one hand, air temperatures are lower than in autumn and, due to predominantly winter rainfall in Mediterranean North Africa, that region is probably much more hospitable to migrants in spring than in autumn (Moreau 1966:271). However, the wind regime is less favorable, since the same low-altitude northerlies that assist autumn migrants prevail in the spring as well. Thus, we can only guess that, unlike autumn migration in which the Sahara is traversed on a wide front, in spring, birds avoid flying directly north across the Sahara by flying west and north, or east and north. This idea is supported by the fact that far more migrants are seen flying north through the Arava (rift valley) in Israel in spring than south in autumn (Shirihai and Gellert 1987).

Observations of flight altitude, migration patterns, behavior, and body condition of birds caught at stopover sites along desert migration routes are rare. More field studies no doubt will clarify the picture of trans-Saharan migration strategies in particular, and of long-distance flights over seas or deserts in general.

ACKNOWLEDGMENTS

This work was supported by a United States-Israel Binational Science Foundation (BSF) grant (No. 89-00350), by the J.N.F. Ecology Fund, and by OHER of the U.S. Department of Energy (grant No. DE-FGO2-88ER60633) to W.P.P. This is contribution No. 128 of the Mitrani Center for Desert Ecology.

LITERATURE CITED

AMMO (Air Ministry, Meteorological Office). 1962. Pages 78-166 *in* Weather in the Mediterranean, vol. 1, 2nd ed. Air Ministry, Meteorological Office, London.

ARAD, Z., S. S. ARNASON, A. CHADWICK, AND E. SKADHAUGE. 1985. Osmotic and hormonal responses to heat and dehydration in the fowl. J. Comp. Physiol. 155:227-234.

BAIRLAIN, F. 1988. How do migratory songbirds cross the Sahara? Trends Ecol. & Evol. 3(8):191-194.

BERGER, M., J. S. HART, AND O. Z. ROY. 1971. Respiratory water and heat loss of the Black Duck during flight at different ambient temperatures. Can. J. Zool. 49:767-774.

BERNSTEIN, M. H. 1987. Respiration in flying birds. Pages 43-73 *in* Bird respiration, vol. 2 (T. J. Seller, Ed.) C.R.C. Press, Boca Raton, Florida.

BERNSTEIN, M. H., AND K. SCHMIDT-NIELSEN. 1974. Ventilation and oxygen extraction in the Crow. Respir. Physiol. 21:393-401.

BIEBACH, H. 1988. Ecophysiology of resting Willow Warblers (*Phylloscopus trochilus*) crossing the Sahara. Proc. 19th Int. Ornithol. Congr. 2162-2168.

BIEBACH, H. 1990. Strategies of trans Sahara migrants. Pages 352-367 *in* Bird migration (E. Gwinner, Ed.). Springer-Verlag, Berlin.

BIEBACH, H., W. FRIEDRICH, AND G. HEINE. 1986. Interactions of body mass, foraging and stopover period in trans-Sahara migrating passerine birds. Oecologia (Berl.) 69:370-379.

BIESEL, W., AND W. NACHTIGALL. 1987. Pigeon flight in a wind tunnel. 4. Thermoregulation and homeostasis. J. Comp. Physiol. B 157:117-128.

BLEM, C. R. 1976. Patterns of lipid storage and utilization in birds. Am. Zool. 16:671-684.

BLEM, C. R. 1980. The energetics of migration. Pages 175-224 *in* Animal migration, orientation and navigation (S. A. Gauthreaux, Ed.). Academic Press, New York.

CALDWELL, L. D., E. P. ODUM, AND S. G. MARSHALL. 1963. Comparison of fat levels in migrating birds killed at a central Michigan and a Florida Gulf Coast television tower. Wilson Bull. 75:428-434.

CURRY-LINDAHL, K. 1981. Bird migration in Africa. Academic Press, London.

DAWSON, W. R. 1982. Evaporative water losses of water by birds. Comp. Biochem. Physiol. 71A: 495-509.

DAWSON, W. R. 1984. Physiological studies of desert birds: Present and future considerations. J. Arid Environs. 7:133-155.

DOLNIK, V. R., AND V. M. GAVRILOV. 1971a. Caloric equivalent of body weight variation in Chaffinches (*Fringilla coelebs*). Pages 273-287 *in* Bird migration, ecological and physiological factors (B. E. Bykhovskii, Ed.). Halsted Press, New York.

DOLNIK, V. R., AND V. M. GAVRILOV. 1971b. Energy metabolism during flight of some passerines. Pages 288-296 *in* Bird migration, ecological and physiological factors (B. E. Bykhovskii, Ed.). Halsted Press, New York.

FOGDEN, M. P. 1972. Premigratory dehydration in the Reed Warbler (*Acrocephalus scirapaceus*) and water as a factor limiting migratory range. Ibis 114:548-552.

GESSAMAN, J. A., AND K. A. NAGY. 1988. Transmitter loads affect the flight speed and metabolism of homing pigeons. Condor 90:662-668.

HAAS, W., AND P. BECK. 1979. Zum frühjahrszug paläarktischer vögel über die westliche Sahara. J. Ornithol. 120:237-246.

HOROWITZ, M., S. SAMUELLOFF, AND J. H. ADLER. 1978. Acute dehydration: Body water distribution in acclimated and non-acclimated *Psammomys obesus*. J. Appl. Physiol. Respir. Environ. Exercise Physiol. 47:738-744.

JOHNSTON, D. W. 1968. Body characteristics of Palm Warblers following an overwater flight. Auk 85: 13-18.

LEFEBVRE, E. A. 1964. The use of D_2O^{18} for measuring energy metabolism in *Columbia livia* at rest and in flight. Auk 81:403-416.

LIST, R. J. 1966. Smithsonian meteorological tables, 6th ed. Smithsonian Institution, Washington, D.C.

MASMAN, D., AND M. KLAASSEN. 1987. Energy expenditure during free flight in trained and free living Eurasian Kestrels (*Falco tinnunculus*). Auk 104:603-616.

MCNABB, F. M. A. 1969. A comparative study of water balance in three species of quail. II. Utilization of saline drinking solutions. Comp. Biochem. Physiol. 28:1059-1074.

MOREAU, R. E. 1961. Problems of Mediterranean-Saharan migration. Ibis 103a:373-427.

MOREAU, R. E. 1966. The bird faunas of Africa and its islands. Academic Press, London.

MOREAU, R. E. 1972. The Palearctic African bird migration systems. Academic Press, London.

MURRISH, D. E. 1973. Respiratory heat and water exchange in penguins. Respir. Physiol. 19:262-270.

ODUM, E. P. 1960. Lipid deposition in nocturnal migrant birds. Proc. 12th Int. Ornithol. Congr. 563-576.

ODUM, E. P., D. T. ROGERS, AND D. L. HICKS. 1964. Homeostasis of the nonfat components of migrating birds. Science 143:1037-1039.

PENNYCUICK, C. J. 1975. Mechanics of flight. Pages 1-75 *in* Avian biology, vol. 5 (D. S. Farner and J. R. King, Eds.). Academic Press, New York.

PENNYCUICK, C. J. 1989. Bird flight performance. Oxford Univ. Press, Oxford.

RAYNER, J. M. V. 1986. Vertebrate flapping flight mechanics and aerodynamics, and the evolution of flight in bats. Pages 27-74 *in* Bat flight—Fledermausflug (W. Nachtigall, Ed.). Fischer, Stuttgart.

RAYNER, J. M. V. 1988. Form and function in avian flight. Curr. Ornithol. 5:1-77.

RAYNER, J. M. V. 1990. The mechanism of flight and bird migration. Pages 283-299 *in* Bird migration physiology and ecophysiology (E. Gwinner, Ed.). Springer-Verlag, Berlin.

ROGERS, D. T., AND E. P. ODUM. 1964. Effect of age, sex and level of fat deposition on major body components in some wood warblers. Auk 81:505-513.

SAFRIEL, U., AND D. LAVEE. 1988. Weight changes of cross-desert migrants at an oasis—Do energetic considerations alone determine the length of a stopover? Oecologia (Berl.) 76:611-619.

SCHMIDT-NIELSEN, K. 1990. Animal physiology, adaptation and environment, 4th ed. Cambridge Univ. Press, Cambridge.

SCHMIDT-NIELSEN, K., F. R. HAINSWORTH, AND D. E. MURRISH. 1970. Counter-current heat exchange in the respiratory passages: Effect on water and heat balance. Respir. Physiol. 9:263-276.

SERLE, W. 1956. Migrant land-birds at sea off west Africa. Ibis 98:307-311.

SHIRIHAI, H., AND M. GELLERT. 1987. Ringing of passerines in Eilat. *In* Eilat, an intercontinental highway for migrating birds. International Birdwatching Center, Eilat, Israel.

SKADHAUGE, E. 1981. Osmoregulation in birds. Springer-Verlag, Berlin.

STAINSBY, W. N., L. B. GLADDEN, J. K. BARCLAY, AND B. A. WILSON. 1980. Exercise efficiency: Validity of base-line substractions. J. Appl. Physiol. 48: 518-522.

TANNER, G. A. 1975. Kidney function. Pages 455-487 *in* Basic physiology for the health sciences (E. E. Selkurt, Ed.). Little, Brown and Company, Boston.

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

UTTER, J. M., AND E. A. LEFEBVRE. 1970. Energy expenditure for free flight by the Purple Martin (*Progne subis*). Comp. Biochem. Physiol. 35:713–719.

WALSBERG, G. E. 1990. Problems inhibiting energetic analyses of migration. Pages 413–421 *in* Bird migration physiology and ecophysiology (E. Gwinner, Ed.). Springer-Verlag, Berlin.

WARD, P. 1964. Lipid levels in birds preparing to cross the Sahara. Ibis 105:109–111.

WILSON, B. W. 1981. Migration and navigation. Pages 56–59 *in* Birds (B. W. Wilson, Ed.). W. H. Freeman, San Francisco.

WOOD, B. 1982a. Weights and migration strategy of Blackcaps *Sylvia atricapilla* wintering in Tunisia. Ibis 124:66–71.

WOOD, B. 1982b. The trans-Saharan spring migration of Yellow Wagtails (*Motacilla flava*). J. Zool. (Lond.) 197:267–283.

APPENDIX. Model calculations and assumptions.

Net water loss was calculated as the difference between metabolic water production and net evaporative water loss. Metabolic water production was calculated from the rate of fat use, an output of program 1 of Pennycuick (1989). We assumed each gram of fat oxidized released 1.07 g of metabolic water (Schmidt-Nielsen 1990) and that metabolic water production is the bird's only source of water input during flight.

Total water loss was considered the sum of respiratory and cutaneous evaporative water loss. Cutaneous evaporation was assumed to be 10% of the total evaporative water loss; this is a conservative estimate (Dawson 1984:table 1). Respiratory water loss was calculated as the difference between the quantities of water in the inspired and expired air.

Vapor density of inspired air was calculated using the following equation from List (1966:381, eq. 2) relating e_ω to T_a:

$$\rho_\omega = 216.68 e_\omega / (C_v T_a) \qquad (1)$$

where C_v is the compressibility factor for water vapor (dimensionless), e_ω is the saturation water vapor pressure (P), T_a is the air temperature (°C), and ρ_ω is the saturation water vapor density (g/m^3).

Expired air was assumed to be saturated with water vapor at the expired-air temperature (T_{ex}; Schmidt-Nielsen et al. 1970), which was calculated as

$$T_{ex} = 23.0 + 0.43 T_a \qquad (2)$$

(Berger et al. 1971). This regression equation is the only one available in the literature for flying birds.

Pulmonary ventilation volume ($\dot{V}_I$) was calculated from the oxygen-consumption rate ($\dot{V}O_2$), taking into account the partial pressure of oxygen at the given altitude. To calculate rates of oxygen consumption we assumed that, for each 20.08 kJ of heat produced, 1 L of oxygen was consumed (Schmidt-Nielsen 1990). The main energy source during long-distance migratory flight is fat (Blem 1976, 1980, Dolnik and Gavrilov 1971a, b). Thus,

$$\dot{V}CO_2 / \dot{V}O_2 = R = 0.71. \qquad (3)$$

Unless used as a continuous variable (as in Fig. 2), oxygen extraction, calculated as

$$\mathrm{EXT} = \dot{V}O_2(0.2095R + 0.7905)/\dot{V}_I), \qquad (4)$$

was assumed a constant 0.039, the average EXT of flying birds (Bernstein 1987:table 2).

Other assumptions embodied in the calculations are: (1) Birds fly at maximum-range velocity (Pennycuick 1989). (2) Birds are in heat balance, and convection accounts for most heat loss. (3) The maximum-allowable amount of fat used was assumed to be 100% of the bird's preflight fat reserves since, except for a negligible amount (structural lipids), nearly all body fat is metabolized before protein starts to be consumed (Odum et al. 1964, Rogers and Odum 1964, Blem 1980). Although a small amount of protein is probably catabolized during flight, we assumed it negligible because, if a significant amount of protein was catabolized, flight would be impaired. (4) To compute the flight duration (h) allowed by a bird's water budget, we divided the maximum-allowable amount of water loss (g) by the rate of net water loss (g/h).

Owners of Pennycuick's (1989) book and programs are welcome to contact us to obtain the additional program used for our simulations.