SHORT COMMUNICATIONS

Flight Speeds and Energy Requirements for White Ibises on Foraging Flights

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In the spring and summer, up to 20,000 pairs of White Ibises (*Eudocimus albus*) congregate to breed on Pumpkinseed Island, Georgetown County, South Carolina (Christy et al. 1981, Bildstein 1987, Frederick 1987). Early in the breeding season, the adult White Ibises feed primarily on fiddler crabs (*Uca* spp.), which they obtain on salt marshes within 8 km of the colony. Later, when raising nestlings, they feed almost exclusively on crayfish (Cambarinae), which they catch in freshwater areas up to 50 km away from the breeding colony. As part of an ecological study of White Ibises, we required an estimate of the time and energy expended by adults that fly back and forth between the nesting island and the foraging areas. We observed flight speeds directly, and calculated the energy expended in short foraging flights. The methods can easily be adapted for use on other species.

Flight speeds were measured by ornithodolite, an optical device, whose construction was described by Pennycuick (1982a). An ornithodolite "run" consisted of two or more timed, three-dimensional determinations of the bird's position in space. Groundspeed "observations" were then obtained by measuring the distance and time between successive positions. To convert groundspeed into airspeed, we read wind speed and direction from an anemometer immediately after each run. All of these data were recorded in digital form for later analysis. The details of operation, and analysis of the data, were essentially as described by Pennycuick (1982b), with the variations described by Pennycuick (1987a). Observations were made from an 18.5-m-high steel tower located at the edge of the North Inlet Marsh, Hobcaw Barony, 5 km north of Pumpkinseed Island. For details of the area, see Christy et al. (1981). The top of the tower supported a platform with railings and a small hut. The ornithodolite was tripod-mounted on the platform, with its eye level 16.4 m above the level of the marsh, and about 10 m above the tops of a clump of trees that surround the tower. The anemometer mast was fixed to the railings on the windward side of the platform, with the sensor head clear of the top of the hut. The observation site was within the brackish water foraging area used by the White Ibises; and observations were made on birds flying past the tower to or from the nesting area. Observations were made on 20-22 April 1987, during the initial phase of the breeding season, which is a period of nest construction, egg laying, and early incubation.

Body measurements.—The measurements needed for flight calculations (mass, wing span, and body frontal area) were made on captive White Ibises taken as nestlings from Pumpkinseed Island, and maintained at the Savannah River Ecology Laboratory, Aiken, South Carolina. There was marked sexual dimorphism (Table 1; see also Kushlan 1977 and Bildstein 1987). The body frontal areas were only about 65% of the values predicted by a regression equation for hawks and ducks (Pennycuick et al. 1988). This difference is somewhat larger than in other species measured to date, and may reflect the more elongated and slimmer ibis body.

Observed and calculated flight speeds.—We made 82 observations of airspeeds in steady flight (Fig. 1). Observations in which the bird was about to land were excluded. The mean air speed was 13.1 $m \cdot s^{-1}$, with a standard deviation of 1.8 $m \cdot s^{-1}$. We were not able to discriminate between the sexes. We estimated the minimum power speed (V_{mp}) and maximum range speed (V_{mr}) (Fig. 1). The estimates were different for males and females because of the dimorphism (Table 1). Estimated values in Table 1 were from the method presented by Pennycuick (1975). Parasite power was calculated from measured body frontal areas (Table 1), combined with drag coefficients calculated by the method of Pennycuick et al. (1988). This makes only a small difference to the calculated speeds, in comparison to the simplified method for calculating equivalent flat-plate area (Pennycuick 1975).

The method for calculating bird performance given by Tucker (1973) is a revised version of an earlier theory by Pennycuick (1969) and introduced a number of modifications. The version of Pennycuick (1975) is a further revision of the same theory, which incorporated many of the modifications proposed by Tucker (1973). Some modifications were eliminated, notably Tucker's method of calculating profile power, which leads to erroneous results. These are not distinct theories, but successive revisions of the same theory, each superseding the previous version (Pennycuick 1989).

V_{mr} is the speed at which the bird must fly, it if is to maximize the air distance flown, when consuming a given amount of fuel. If the bird flies slightly slower, more energy is required to cover unit distance, but flight is less strenuous. There is no incentive, however, to cruise more slowly than V_{mp} because this is the speed at which muscular exertion and energy consumption are required at the lowest rate. The entire distribution of speeds for both sexes fell below

TABLE 1. Body measurements and performance estimates.

	Male		Female	
	$\bar{x}$	SD	$\bar{x}$	SD
Mass (kg)	0.977	0.056	0.767	0.084
Span (m)	0.982	0.025	0.920	0.029
Frontal area (m^2)	0.00519	0.00048	0.00431	0.00057
Body drag coefficient	0.304		0.317	
No. of specimens	5		4	
V_{mp} ($m \cdot s^{-1}$)	12.0		11.4	
V_{mr} ($m \cdot s^{-1}$)	19.8		18.8	
N_{max}	8.94		8.95	

the estimates for V_{mr} (Fig. 1). Twenty-one out of 82 observations (26%) also fell below the estimated V_{mp} for males, and 13 out of 82 (16%) fell below that for females. Possible reasons for these lower than expected speeds are errors in the speed measurements and variation of body measurements among individual birds. The speed estimates are based on the mean body measurements (Table 1), and V_{mp} for a light bird would be below the estimate. As the birds were flying over a feeding area, it is also possible that some of them flew slowly, to scout the marsh below for food.

The mean speed for both sexes (13.1 $m \cdot s^{-1}$) is 9% faster than the V_{mp} estimate for males, and 15% faster than that for females (Fig. 1). This is similar to the results on 11 species of North Atlantic seabirds (Pennycuick 1987a), where in all cases the mean airspeed was well above the estimate for V_{mp}, but few or no observations exceeded or even approached V_{mr}. The seabirds were engaged in short foraging flights of a few minutes' duration. Probably fuel economy is not of critical importance on such short flights, and the birds elected to fly at a less strenuous speed, below the optimum for economical cruising. If this interpretation is correct, we expect that birds engaged in longer flights (hours) would cruise at speeds closer to their estimated V_{mr}. This was reported (Alerstam 1981) from radar observations of long-distance migrants, ranging from passerines to swans. We would expect the White Ibises to fly somewhat faster later in the season, when they forage at a greater distance from their nests.

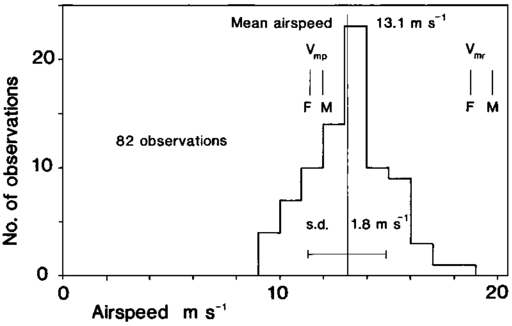

Fig. 1. Observed airspeed, compared with calculated minimum power speed (V_{mp}) and maximum range speed (V_{mr}).

Energy consumption on short flights.—To estimate the energy consumed on a short foraging flight, it is not necessary to consider explicitly the actual rate at which energy is consumed. In particular, we do not estimate "flight metabolism" by multiplying an estimate of the basal metabolic rate by some factor. This procedure has no experimental or theoretical basis and can lead to errors exceeding a factor of 10 (Pennycuick 1978, 1989). The most direct method to estimate the energy consumed on short flights is to obtain first a maximum estimate for the effective lift : drag ratio (N), defined as:

$$N = MgV/P, \qquad (1)$$

where M is the body mass, g is the acceleration due to gravity (taken to be 9.81 $m \cdot s^{-2}$), V is the flight speed, and P is the total power, i.e. the rate at which energy is expended for all purposes. N is a dimensionless ratio, closely related to the "cost of transport" function (Schmidt-Nielsen 1972). This is a heterogeneous ratio that compares a chemical to a mechanical power, whereas N is the ratio of the weight to the average horizontal force needed to propel the bird along. This "effective lift : drag ratio" is an older concept than "cost of transport" and dates from the early days of aeronautics. The name "performance number" has been proposed (Pennycuick 1987b) as more appropriate when applying the original concept to forms of locomotion other than flight.

N cannot be estimated from "flight metabolism" at an undefined speed because its value is different at different speeds. It reaches its maximum value (N_{max}) at V_{mr}, which is how V_{mr} is defined. We estimated N_{max} by computing N for speeds from V_{mp} to V_{mr} (program 1 *in* Pennycuick 1989). It can also be found directly from formulae and charts (Pennycuick 1975) without working out any speeds or powers. The calculation requires values for the mass, wing span, and frontal area of the body (Table 1). The body drag coefficient (Table 1) was estimated by the method of Pennycuick et al. (1988). From body measurements (Table 1) we estimated N_{max} of 8.94 for males and 8.95 for females. These values (or any value of N) can be used to estimate the energy expended in short flights, by inverting Equation 1:

$$P/V = Mg/N. \qquad (2)$$

Thus, for males, where $M = 0.977$ kg and $N = 8.94$, $P/V = (0.977 \times 9.81)/8.94 = 1.07$ J/m. This is the work done per meter flown, since the ratio of power to speed (P/V) is the same as that of work done to distance traveled. The extreme simplicity of this calculation depends on the use of units that all belong to the same system.

The result is expressed in terms of mechanical power and work, even though P in Equations 1 and 2 is the total power expended for all purposes. Most of this power represents the rate at which the flight muscles do mechanical work, with contributions for work done by the respiratory muscles and the heart. There is also a contribution for basal metabolism which has to be converted into its mechanical equivalent in order to make it compatible with the other components of power expenditure. If the goal of the calculation is to estimate fat consumption over a given distance, then the energy content of the fat has to be reckoned on the basis of the amount of mechanical work done by the muscles when consuming a given amount of fat and not by the heat measured in a bomb calorimeter. When fuel is consumed by muscles, some fraction of the chemical energy liberated (commonly assumed to be 20–25%) is converted into mechanical work; the rest is converted into heat. The ratio of mechanical work produced to chemical energy consumed is the "conversion efficiency" (η) of the muscular system. Pennycuick (1975) suggested a value of $\eta = 0.23$, based on physiological evidence available at that time. The energy density of fat (denoted by e) is assumed to be 3.9×10^7 J kg^{-1} (Schmidt-Nielsen 1983). Then, 23% of this amount, or 9.0×10^6 J kg^{-1}, may be expected to appear in the form of mechanical work if fat is consumed by locomotor muscles. If F is the mass of fat consumed/meter flown, then

$$F = P/Ve\eta.$$

P/V for the male White Ibis above is 1.07 J/m. Substituting this value in Equation 3, along with the above values for e and η, indicates that the bird consumes 1.19×10^{-7} kg of fat for each meter flown. Once again the calculation is simplest if carried out in the basic SI units, although the final result may be more intelligible if expressed as $F = 0.12$ g/km. The corresponding figure for females is 0.094 g/km.

In a long migratory flight, the bird's mass will decline appreciably owing to the consumption of fuel. P/V will decrease progressively (Eq. 2) and N may also increase as the body slims down. Methods that compensate for these changes, so that a long-distance migrant's range can be estimated are available (Pennycuick 1975, program 1 *in* Pennycuick 1989). For the purpose of estimating the energy consumed on short foraging flights, however, the only change of mass to consider is that of the food carried back to the nest. P/V will be higher inbound than outbound, but can be considered constant for the duration of each short flight. The theory (Pennycuick 1975) can also be used to calculate power consumption in flight, for comparison with physiological experiments that indirectly estimate power by measuring the rate of oxygen consumption. It is difficult to design experiments of this kind that are free from errors caused by transient effects or disturbances caused by the apparatus. The recent results of Rothe et al. (1987), who measured the oxygen consumption of pigeons (*Columba livia*) that were trained to fly steadily for prolonged periods in a wind tunnel, agree well with the predictions of the theory (Pennycuick 1989).

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The Taxonomic Status of the Small Ground-Finch, *Geospiza* (Aves: Emberizidae) of Genovesa Island, Galápagos, and Its Relevance to Interspecific Competition

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From their study of the feeding habits of *Geospiza difficilis* and *G. fuliginosa* on Genovesa, Pinta, and Marchena islands, Galápagos Archipelago, Schluter and Grant (1982, 1984) concluded that these species probably competed in the past. Crucial to this conclusion is the taxonomic identification of the Genovesa population, classified as *G. acutirostris*, *G. fuliginosa*, or *G. difficilis* by various authors (see below). We present morphological evidence to indicate that, contrary to its current classification as *G. difficilis*, the Genovesa population may more justifiedly be placed in *G. fuliginosa*, as done by Snodgrass and Heller (1904). We also discuss the evolutionary and ecological consequences of this suggested taxonomic rearrangement.

The small ground-finch of the genus *Geospiza* living on Genovesa Island was first described by Ridgway (1894: 363; see also Ridgway 1897) as *Geospiza acutirostris*, a form "Similar to *G. parvula* (Gould) [synonymized since with *G. fuliginosa*], but bill longer, with straighter outlines, and extremely acute at tip." Rothschild and Hartert (1899) concurred with Ridgway's view. Snodgrass and Heller (1904: 316) characterized the taxon *acutirostris* as "Very similar to *G. f. fuliginosa*, but bill more acute, with straighter outlines" and ranked it as a subspecies of *G. fuliginosa* Gould, 1837. Swarth (1931: 178) felt that "The Tower [Genovesa] Island *acutirostris* is, to my notion, of the *Geospiza debilirostris* [currently considered a subspecies of *G. difficilis*] aggregation, but the differentiating characters are such as to make it seem desirable to treat the form as specifically distinct." Lack (1945, 1947, 1969) recognized the transfer of *G. acutirostris* to the *G. difficilis* group, but argued that its measurements overlapped widely those of *G. d. difficilis* of Pinta Island (Sharpe 1888), and combined *G. acutirostris* with the latter. Paynter and Storer (1970) followed Lack's arrangement. Harris (1973: 265) made "... no attempt ... to discuss the taxonomic status of species." Schluter (1984), Grant et al. (1985) and Grant (1987) studied the classification of Darwin's finches, found it solid, and suggested no modifications. Neither of these authors examined specifically the status of the Genovesa population. Bowman (1961, 1983) adopted Lack's classification, but noted (pers. comm.) that the "Genovesa *Geospiza* song is quite different from other *difficilis* songs as well as *fuliginosa* songs. Like *fuliginosa* it lacks the 'special basic' song of other *difficilis* populations, and this I think is very significant, indicating allegiance to *fuliginosa*. (See Bowman 1983, p. 437, fig. 62 and p. 423, fig. 48.)" It thus appears that the early authors assigned the Genovesa form to the *G. fuliginosa* group, on the basis of overall similarities, primarily in beak morphology. Swarth and Lack broke with these views when they assigned the Genovesa form to the *G. difficilis* group. We believe that they focused on a single feature, bill length, giving little