value of fat reserves and the trade-off between starvation and predation. Acta Biotheoretica 38: 37–61.

METCALFE, N. B. 1984. The effect of mixed-species flocking on the vigilance of shorebirds: Who do they trust? Animal Behaviour 32:986–993.

PIERCE, V., AND T. C. GRUBB, JR. 1981. Laboratory studies of foraging in deciduous woodland birds. Auk 98:307–320.

POPP, J. W. 1988. Scanning behavior of finches in mixed-species groups. Condor 90:510–512.

PRAVOSUDOV, V. V. 1986. Individual differences in foraging and storing behavior in Siberian Tits *Parus cinctus* Bodd. and Willow Tits *Parus montanus* Bald. Soviet Journal of Ecology 4:60–64.

PRAVOSUDOV, V. V., AND T. C. GRUBB, JR. 1995. Vigilance in the Tufted Titmouse varies independently with air temperature and conspecific group size. Condor 97:1064–1067.

PRAVOSUDOV, V. V., AND T. C. GRUBB, JR. 1997. Energy management in passerine birds during the non-breeding season: A review. Current Ornithology 14:189–234.

PULLIAM, H. R., AND T. CARACO. 1984. Living in groups: Is there an optimal group size? Pages 122–147 *in* Behavioural ecology, an evolutionary approach (J. R. Krebs and N. B. Davies, Eds.). Blackwell Scientific Publications, London.

SASVARI, L. 1992. Great Tits benefit from feeding in mixed-species flocks: A field experiment. Animal Behaviour 43:289–296.

SMITH, S. M. 1991. The Black-capped Chickadee: Behavioral ecology and natural history. Cornell University Press, Ithaca, New York.

WAITE, T. A. 1987a. Vigilance in the White-breasted Nuthatch: Effects of dominance and sociality. Auk 104:429–434.

WAITE, T. A. 1987b. Dominance-specific vigilance in the Tufted Titmouse: Effect of social context. Condor 89:932–935.

Maintenance Energy Costs of Two Partially Folivorous Tropical Passerines

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In homeotherms, residual variation of maintenance-energy costs around allometric curves can be related to factors independent of body mass, such as food habits (McNab 1986), taxonomic affiliation (Bennett and Harvey 1987), season (Kendeigh et al. 1977), habitat type (Hulbert and Dawson 1974), climate (Weathers 1979), and body composition (Daan et al. 1990). Food habits are important because the rate of energy acquisition might limit the rate of energy expenditure (McNab 1986, Weiner 1992). For mammals, McNab (1978, 1986) hypothesized that the processing of food with low metabolizable energy content, including the leaves of woody plants, requires a low basal metabolic rate (BMR). Hence, arboreal mammals that meet large portions of their energy requirement from leaves have lower BMRs than predicted from allometric equations (McNab 1978, 1980a). Some of the reduction of BMR in folivorous mammals seems to be related to properties of leaves, such as their low metabolizable energy owing to the content of difficult-to-digest fiber and to the high content of secondary compounds (McNab 1978, 1986).

Food habits also influence rates of maintenance energy expenditure in birds (McNab 1988), but the relationship between folivory and avian BMR is not fully understood. To a large extent, this is because little is known about the energetics of folivorous species. Here, we report on the maintenance energy costs and thermal response to ambient temperature of two species of passerines that regularly include leaves and other plant tissues in their diets. Passerines are of interest because of their high mass-specific energy expenditure, because their small body size constrains the use of green tissues of plants, and because folivory is particularly scarce among them (Morton 1978, Parra 1978). Characteristics intrinsic to leaves should also affect avian consumers; therefore, it is of interest to determine if folivory is correlated with reduced BMR in birds, as it is in mammals.

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We studied two species of cardinalids, the Grayish Saltator (*Saltator coerulescens*; 47.0 ± SD of 2.6 g; n = 6) and the Orinocan Saltator (*S. orenocensis*; 32.7 ± 2.1 g; n = 4) from the central floodplains (llanos) of Venezuela. Both species are generalized arboreal herbivores at our study site, feeding mostly on fruits, leaves, and other plant tissues.

Grayish Saltators feed almost exclusively on plant tissue throughout the year. Their diet is largely made up of fruit (35.6% of feeding observations), mature leaves of woody plants (27.7%), and flowers (16.6%). Most of the rest of the diet (20%) is made up of a variety of other plant tissues (leaf buds, flower buds, tendrils, and the skin of seed pods). Insects account for only 0.1% of feeding observations (Rodríguez 1994). Orinocan Saltators also consume mostly plant tissue throughout the year but are less folivorous than Grayish Saltators. Nevertheless, during the rainy season mature leaves account for 19.5% of feeding observations and leaf buds a further 2.3%. The rest of the diet is made up of flowers and flower buttons (34.5%), fruits (28.7%), and seeds (14.9%). Lichens and insects are consumed occasionally (García 1994). Both species have simple guts, and given their small body size and brief mean retention time of digesta (59 min for Grayish Saltator and 80 min for Orinocan Saltator), it is likely that the bulk of their energy requirements is extracted from cell solubles rather than from fiber fermentation (García 1994, Rodríguez 1994). Other species of saltators are also known to regularly include leaves, buds, and fruits in their diets (Jenkins 1969, Munson and Robinson 1992); however, none that has been studied in more detail is exclusively or obligatorily folivorous.

In this work, we compare maintenance energy costs of both species of saltator with those expected from allometric equations. We expected, by analogy with arboreal folivorous mammals, that BMRs would be lower than predicted for passerines of their size.

Methods.—We mist netted saltators at Fundo Pecuario Masaguaral (Guárico State, 8°34'N, 67°35'W), a cattle ranch in the seasonal savannahs of Venezuela, from June to August 1995. Vegetation is a mosaic of open savanna and gallery forest. Rainfall averages 1,400 to 1,500 mm annually and is largely concentrated in a single rainy season that lasts from May to November. Temperature varies only slightly during the year; average monthly minimum and maximum temperatures are 19.0 and 37.7°C, respectively (Troth 1979).

During the experimental period, birds were kept for one to four days in individual cages in a room exposed to natural photoperiod. During this period, birds were offered cultivated (papaya and guava) and wild fruits that are regularly included in their natural diet (i.e. *Annona jahni* and *Momordica charantia*). Saltators readily adapt to cages and maintain their body mass on a diet of fruit, which they prefer to leaves under caged conditions (García 1994, Rodríguez 1994). Birds were fasted for 4 to 6 h before the experiments. Because enough time elapsed between the last feeding and the experimental measurements for birds to have emptied their guts several times, we concluded that birds were under postabsorptive conditions. Sex of the birds was unknown, and no individual was molting during the experiments.

We measured oxygen consumption ($\dot{V}O_2$) of six Grayish Saltators and four Orinocan Saltators in relation to ambient temperature (T_a) during the nonactive phase with an open-flow Applied Electrochemistry model S-3A analyzer as described in Weathers et al. (1980). Birds were weighed to the nearest 0.01 g before being placed in a dark, 15.2-L metabolic chamber through which air was drawn with a flow rate of approximately 0.762 L · min^{-1} for Grayish Saltators and 0.658 L · min^{-1} for Orinocan Saltators. The chamber was placed in a thermostatically controlled temperature cabinet that allowed us to regulate ambient temperature. The system was allowed to equilibrate for at least 1 h before the beginning of measurements. Effluent air was run through tubes containing silica gel and soda lime granules to remove H_2O and CO_2 before measuring oxygen concentration. We recorded only the lowest stabilized readings of the presumably inactive individuals. At the end of each run, we opened the metabolic chamber and measured cloacal body temperature (T_b) with a thermocouple accurate to 0.1°C and reweighed the bird. We used the average of the initial and final body masses of each bird to calculate its specific metabolic rate. Ambient temperature in the chamber was continuously monitored with Cu-Cn thermocouples connected to a Campbell Scientific CR21 data logger. Not every bird was run over the whole ambient temperature range. Rates of oxygen consumption were calculated according to Hill (1972) and expressed under STP conditions.

For each species, the relationship between $\dot{V}O_2$ and T_a was examined by the method of Yaeger and Ultsch (1989). This method fits two straight segments to the data and determines the point where they intercept. This point can be considered the lower critical temperature where the shift from metabolic regulation of oxygen consumption to metabolic conformation occurs. We estimated "wet" thermal conductance by calculating a mean conductance from individual conductances obtained by applying $C = \dot{V}O_2 / (T_b - T_a)$ to each measurement of oxygen consumption and body temperature below thermoneutrality (McNab 1980b). We considered BMR as the average of $\dot{V}O_2$ values within the thermoneutral zone. To compare measured oxygen consumption rates with expectations from allometric equations, we used an energy equivalent of 1 watt (W) to 0.05 mL O_2 · s^{-1}. All birds were released unharmed at the end of the experiments.

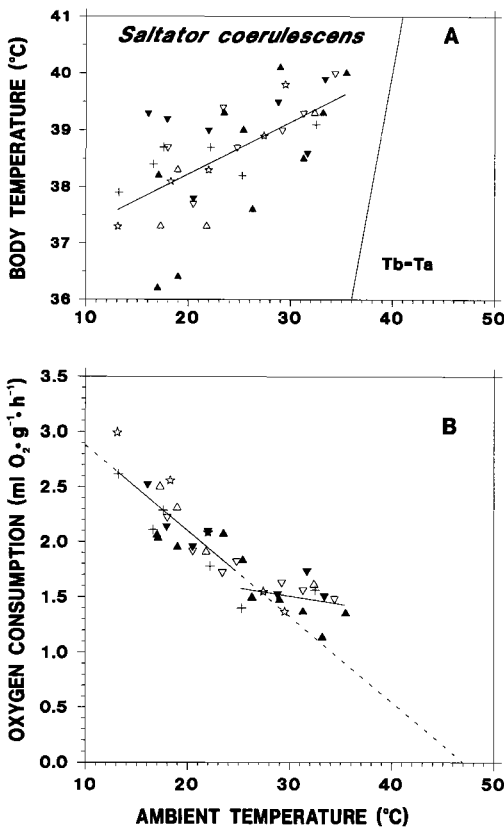*Results for Grayish Saltators.*—Based on the method

FIG. 1. Body temperature (A) and oxygen consumption (B) in relation to ambient temperature of six postabsorptive Grayish Saltators during their nonactive phase. The two lines in the lower figure were fitted by the method of Yeager and Ultsch (1989; see text for equations). Each symbol represents one individual bird.

of Yeager and Ultsch (1989), we fitted two lines to the data set (Fig. 1B). The line to the left ($\dot{V}O_2 = 3.657 - 0.078T_a$; $n = 22$, $r = 0.790$, $P < 0.001$) and the line to the right ($\dot{V}O_2 = 1.941 - 0.015T_a$; $n = 18$, $r = 0.296$, $P = 0.233$) intersected at 27.1°C. This point marks the shift from metabolic conformation to metabolic regulation and can be considered to be the lower limit of thermoneutrality. Average nightly body temperature of individuals within the thermoneutral zone was 39.4 ± SE of 0.141°C ($n = 14$). Grayish Saltators maintained a high but variable body temperature (Fig. 1A). Although birds clearly could thermoregulate, their body temperature was not controlled precisely, and it varied significantly with ambient temperature ($T_b = 36.4 + 0.091T_a$; $n = 40$, $r = 0.617$, $P < 0.001$). Not even within the thermoneutral zone was there a clear indication that birds maintained a constant body temperature. Average body tempera-

ture at night fell within the range recorded for other passerines (see Prinzinger et al. 1991).

Basal metabolic rate was 1.489 ± 0.04 mL $O_2 \cdot g^{-1} \cdot h^{-1}$ ($n = 14$), or 0.3887 W · ind^{-1} for a 47.0-g bird. This value is 64.4% of that expected from body mass for passerines during the night period as predicted by Aschoff and Pohl (1970) and 63.6% of that expected for passerines during summer nights (calculated from Kendeigh et al. 1977). BMR measured for the Grayish Saltator fell below the 95% confidence interval of the standard regression of BMR and body mass for birds (Reynolds and Lee 1996).

Thermal conductance was 0.116 ± 0.002 mL $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$, which is 18.9% higher than expected from body mass for passerines during the rest phase (i.e. 0.098 mL $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$; Aschoff 1981). Extrapolated body (=ambient) temperature at a rate of metabolism equal to zero (i.e. 46.9°C; Fig. 1B) was considerably higher than recorded body temperatures.

Results for Orinocan Saltators.—The two lines fitted by Yaeger and Ultsch's (1989) method, $\dot{V}O_2 = 1.83 + 0.06T_a$ and $\dot{V}O_2 = 2.91 - 0.04T_a$, intercepted at $T_a = 10.9°C$, which is not biologically meaningful. Therefore, on the basis of visual inspection we divided the data set in points above and below 25°C and fitted by least squares a line to each subset (Fig. 2B). The line to the left ($\dot{V}O_2 = 3.925 - 0.080T_a$; $n = 11$, $r = 0.74$, $P = 0.009$) and the line to the right ($\dot{V}O_2 = 1.540 + 0.006T_a$; $n = 9$, $r = 0.102$, $P = 0.794$) intersected at 27.7°C, which we considered to be the lower limit of thermoneutrality. Average nightly body temperature of individuals within the thermoneutral zone was 38.8°C ± 0.269 ($n = 6$). As in the former species, body temperature of Orinocan Saltators varied significantly with ambient temperature, even within the thermoneutral zone ($T_b = 32.4 + 0.198T_a$; $n = 20$, $r = 0.774$, $P < 0.001$; Fig. 2A). Average body temperature at night also fell within the range recorded for other passerines (see Prinzinger et al. 1991).

Basal metabolic rate was 1.715 ± 0.064 mL $O_2 \cdot g^{-1} \cdot h^{-1}$ ($n = 6$), or 0.3136 W · ind^{-1} for a 32.7-g bird. This value is 67.9% of that expected from body mass for passerines during the night period as predicted by Aschoff and Pohl (1970) and 65.4% of that expected for passerines during summer nights as calculated from Kendeigh et al. (1977). BMR of the Orinocan Saltator also fell below the 95% confidence interval of the standard regression of BMR and body mass for birds (Reynolds and Lee 1996).

Thermal conductance of Orinocan Saltators was 0.143 ± 0.004 mL $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$, which is 23.9% higher than expected from body mass for passerines during the rest phase (i.e. 0.115 mL $O_2 \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$; Aschoff 1981). As for Grayish Saltators, extrapolated body (=ambient) temperature at a rate of metabolism equal to zero (i.e. 49.1°C; Fig. 2B) was considerably higher than recorded body temperatures.
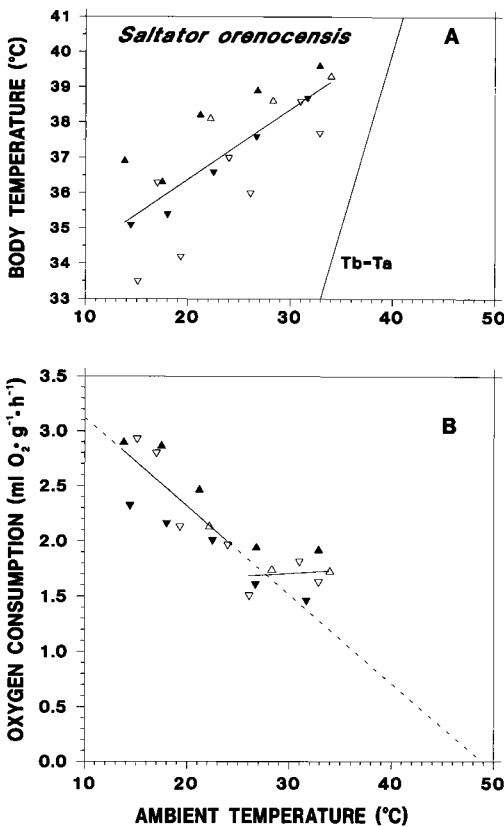
FIG. 2.   Body temperature (A) and oxygen consumption (B) in relation to ambient temperature of four postabsorptive Orinocan Saltators during their nonactive phase. The two lines of the lower figure were fitted by dividing the data set into points below and above 25°C (see text for equations). Each symbol represents one individual bird.

Discussion.—In accordance with expectations, both species of saltator had substantially lower BMRs than predicted from their body size. This reduction of resting metabolism should contribute to an economy of daily energy expenditure. Other arboreal folivores also have low BMRs. Speckled Mousebirds (*Colius striatus*; 50 to 55 g) and Blue-naped Mousebirds (*Urocolius macrourus*; 51.3 g), two partially folivorous species of tropical and temperate Africa, feed on leaves, buds, and fruit and have BMRs that are 75 and 63%, respectively, of expected (Bartholomew and Trost 1970, Prinzinger 1988). Furthermore, mousebirds are able to enter torpor, an important energy-saving mechanism (Bartholomew and Trost 1970, Prinzinger et al. 1981). Likewise, the obligate folivorous, fiber-fermenting Hoatzin (*Opisthocomus hoazin*; 598 g) of the Neotropics has a BMR that is 69.8% of expected (Grajal 1991). In mammals, reduction of BMR is highest in medium-sized arbo-

real species, particularly those that rely extensively on fiber fermentation (McNab 1978). Microtine rodents of small body mass that feed heavily on leaves of woody plants, and that probably digest cell solubles only, have high basal rates (McNab 1986). Furthermore, in mammals it appears that BMR is reduced only in species whose diets consist of at least 20 to 30% leaves (McNab 1978: figure 6). In contrast, BMRs are considerably reduced in small birds (e.g. saltators and mousebirds) that are incapable of fiber fermentation and that incorporate leaves in their diet to a moderate extent only.

The interaction between food quality and digestive physiology might influence metabolic rates of homeotherms because digestive and absorptive processes might limit rates of energy acquisition, thus setting an upper ceiling to the energy budget of organisms (e.g. Weiner 1992, Veloso and Bozinovic 1993). In particular, McNab (1978, 1986) proposed that the use of a poor food source by mammalian arboreal folivores might require them to have a low basal rate of metabolism. He posed three nonexclusive explanations to interpret the correlation between folivory and reduced BMR in mammals. First, leaves might have a low metabolizable energy content because they are rich in fiber, which is difficult to digest. Limitations on the maximum bulk of energy-dilute food that can be processed daily by the digestive tract might limit energy intake in folivores. Second, the low basal rates of folivorous mammals may be an adaptation to reduce the intake of toxic secondary compounds present in the green tissues of plants. Reduced intake of secondary compounds may reduce dose-related negative effects and the costs of detoxification. Third, arboreal mammalian folivores, particularly larger species, are rather sedentary and have a low proportion of muscle mass relative to body mass. In mammals, low basal rates of metabolism are correlated with reduced muscle mass.

Explanations proposed by McNab in relation to mammals might also apply to folivorous birds. First, difficulties associated with the digestion of fiber (and of soluble cell contents contained within fibrous cell walls) determine that metabolizable energy of foliage ranks lowest among bird foods (Karasov 1990). Likewise, limitations of tract volume and processing rate of energy-dilute foliage are known to limit intake rates in folivorous birds (Kenward and Sibly 1977). Second, folivorous birds are known to limit intake in order to reduce ingestion of toxic plant secondary metabolites (Jakubas et al. 1993), and detoxification costs might be a substantial portion of their energy and nutrient budget (Guglielmo et al. 1996). Third, in birds small muscle mass in association with sedentary habits might also be correlated with a low basal rate of metabolism (McNab 1988, 1994). Few data exist on time budgets of arboreal folivorous birds, but it is of interest that the obligatorily foli-

vorous Hoatzin has a thickened callus of skin on the tip of the sternum that helps it to maintain a sitting posture for 70 to 80% of the day (Strahl 1988). In our study site, nonbreeding individuals of both species of saltator remain motionless for major portions of their time budget. Grayish Saltators and Orinocan Saltator spend about 50 and 42% of daylight hours, respectively, sitting and a further 30 and 35% engaged in low-cost static activities such as preening and singing (García 1994, Rodríguez 1994).

A considerable portion of the diet of saltators is made up of fruits and other plant tissues. Data on the energetics of frugivores is scant, but it appears that frugivory in birds is also associated with low BMR (McNab 1988). However, this is not well established because three species of highly frugivorous Neotropical manakins (Pipridae) have BMRs that correspond to their body size (Vleck and Vleck 1979). Nevertheless, several of the conditions that apply to folivory might also apply to frugivory. Fruit has a high water content and a considerable portion of indigestible seeds; hence, metabolizable energy of whole fruits per unit of fresh mass is quite low (Karasov 1990), and processing by the digestive tract might limit intake in highly frugivorous species (Levey and Grajal 1991). Similarly, secondary metabolites of fruit pulp can limit intake in frugivores (Izhaki and Safriel 1989, Cipollini and Stiles 1993). Perhaps the low basal rates in saltators are associated with folivory in combination with frugivory.

Neither species of saltator fully balanced heat losses through an increase in metabolism as ambient temperature decreased (their body temperatures dropped in a seemingly controlled manner). The decrease in T_b between 34 and 13°C T_a that we estimated from the regression equations was 1.9°C in the Grayish Saltator (from 39.5 to 37.6°C) and 4.1°C in the Orinocan Saltator (from 39.1 to 35.0°C). This controlled decrease in T_b, although moderate, should contribute to an economy of energy expenditure and also could be considered an adaptation to save energy. A moderate decrease in T_b with falling T_a, controlled hypothermia, is known for approximately 40 other species of birds, including mousebirds (Prinzinger et al. 1991). Failure to increase heat production enough to balance heat loss also has the effect of lowering the slope of the line to the left of the lower critical temperature (Figs. 1B and 2B), which coupled with a combination of physical and chemical thermoregulation (McNab 1980b), should account for the high extrapolated body temperatures at an estimated rate of metabolism equal to zero for both species.

Tropical birds seem to have reduced BMRs for their body size, particularly species that regularly forage in the sun (Weathers 1979, 1997). Latitude, or factors associated with it (e.g. lower mass of metabolically active tissue; Rensch and Rensch 1956 *in* Daan et al. 1990), might be a confounding factor in the interpretation of our finding that saltators have reduced metabolic rates. At this point, we cannot discern the effects of diet and latitude on our results. However, the fact that saltators spend 77 to 80% of their time sitting, singing, and preening suggests that, under such a relaxed time budget, it is unlikely that they would be forced to forage or to spend considerable portions of time exposed to unfavorable radiative environments. The fact that BMR is reduced in other arboreal folivores, including temperate species, suggests that diet is important.

Among folivorous birds, it appears that only the more arboreal species have reduced metabolic rates. The ground-dwelling folivorous grouse and ptarmigan (Tetraoninae) of temperate latitudes have metabolic rates that are similar to or higher than those expected from considerations of body mass alone (see Weathers 1979, McNab 1988). Likewise, flightless, forb-eating ratites and largely terrestrial, grass-feeding anseriforms do not have reduced BMRs (see McNab 1988). To some extent, this pattern is similar to that found in mammals in which only the more sedentary arboreal species have low basal rates. In contrast, the consumption of grass and forbs by terrestrial herbivorous mammals is associated with high basal rates (McNab 1978, 1986). Further research is needed to unravel the effects of latitude, folivory, and arboreal habits on the metabolic rates of birds.

LITERATURE CITED

ASCHOFF, J. 1981. Thermal conductance in mammals and birds: Its dependence on body size and circadian phase. Comparative Biochemistry and Physiology 69A:611–619.

ASCHOFF, J., AND H. POHL. 1970. Der Ruheumsatz von Vögelen als Funktion der Tageszeit und der Köpergrösse. Journal für Ornithologie 111:38–47.

BARTHOLOMEW, G. A., AND C. H. TROST. 1970. Temperature regulation in the Speckled Mousebird, *Colius striatus*. Condor 72:141–146.

BENNETT, P. M., AND P. H. HARVEY. 1987. Active and

resting metabolism in birds: Allometry, phylogeny and ecology. Journal of Zoology (London) 213:327–363.

CIPOLLINI, M. L., AND E. W. STILES. 1993. Fruit rot, antifungal defense, and palatability of fleshy fruits for frugivorous birds. Ecology 74:751–762.

DAAN, S., D. MASMAN, AND A. GROENEWOLD. 1990. Avian basal metabolic rates: Their association with body composition and energy expenditure in nature. American Journal of Physiology 259: R333–R340.

GARCÍA, M. A. 1994. La dieta y la eficiencia digestiva del Lechosero Pechiblanco (Saltator orenocensis). Thesis, Universidad Simón Bolívar, Caracas, Venezuela.

GRAJAL, A. 1991. The nutritional ecology and digestive physiology of the Hoatzin (Opisthocomus hoazin), a folivorous bird with foregut fermentation. Ph.D. dissertation, University of Florida, Gainesville.

GUGLIELMO, C. G., W. H. KARASOV, AND W. J. JAKUBAS. 1996. Nutritional costs of a plant secondary metabolite explain selective foraging by Ruffed Grouse. Ecology 77:1103–1115.

HILL, R. W. 1972. Determination of oxygen consumption by use of paramagnetic oxygen analyzer. Journal of Applied Physiology 33:261–263.

HULBERT, A. J., AND T. J. DAWSON. 1974. Standard metabolism and body temperature of perameloid marsupials from different environments. Comparative Biochemistry and Physiology 47A: 583–590.

IZHAKI, I., AND U. N. SAFRIEL. 1989. Why are there so few exclusively frugivorous birds? Experiments of fruit digestibility. Oikos 54:23–32.

JAKUBAS, W. J., W. H. KARASOV, AND C. G. GUGLIELMO. 1993. Ruffed Grouse tolerance and biotransformation of the plant secondary metabolite coniferyl benzoate. Condor 95:625–640.

JENKINS, R. 1969. Ecology of three species of saltators in Costa Rica with special reference to their frugivorous diet. Ph.D. dissertation, Harvard University, Cambridge, Massachusetts.

KARASOV, W. H. 1990. Digestion in birds: Chemical and physiological determinants and ecological implications. Studies in Avian Biology 13:391–458.

KENDEIGH, S. C., V. R. DOL'NIK, AND V. M. GAVRILOV. 1977. Avian energetics. Pages 127–204 in Granivorous birds in ecosystems (J. Pinowsky and S. C. Kendeigh, Eds.). Cambridge University Press, Cambridge, United Kingdom.

KENWARD, R. E., AND R. M. SIBLY. 1977. A Wood Pigeon (Columba palumbus) feeding preference explained by a digestive bottle-neck. Journal of Applied Ecology 14:815–826.

LEVEY, D. J., AND A. GRAJAL. 1991. Evolutionary implications of fruit-processing limitations in Ce-

dar Waxwings. American Naturalist 138:171–189.

MCNAB, B. K. 1978. Energetics of arboreal folivores: Physiological problems and ecological consequences of feeding on an ubiquitous food supply. Pages 153–162 in The ecology of arboreal folivores (G. G. Montgomery, Ed.). Smithsonian Institution Press, Washington, D.C.

MCNAB, B K. 1980a. Food habits, energetics and the population biology of mammals. American Naturalist 116:106–124.

MCNAB, B. K. 1980b. On estimating thermal conductance in endotherms. Physiological Zoology 53: 144–156.

MCNAB, B. K. 1986. The influence of food habits on the energetics of eutherian mammals. Ecological Monographs 56:1–19.

MCNAB, B. K. 1988. Food habits and basal rate of metabolism in birds. Oecologia 77:343–349.

MCNAB, B. K. 1994. Energy conservation and the evolution of flightlessness in birds. American Naturalist 144:628–642.

MORTON, E. S. 1978. Avian arboreal folivores: Why not? Pages 123–130 in The ecology of arboreal folivores (G. G. Montgomery, Ed.). Smithsonian Institution Press, Washington, D.C.

MUNSON, E. S., AND W. D. ROBINSON. 1992. Extensive folivory by Thick-billed Saltators (Saltator maxillosus) in southern Brazil. Auk 109:917–919.

PARRA, R. 1978. Comparison of foregut and hindgut fermentation in herbivores. Pages 153–162 in The ecology of arboreal folivores (G. G. Montgomery, Ed.). Smithsonian Institution Press, Washington, D.C.

PRINZINGER, R. 1988. Energy metabolism, body-temperature and breathing parameters in nontorpid Blue-naped Mousebirds Urocolius macrourus. Journal of Comparative Physiology 157B:801–806.

PRINZINGER, R., R. GÖPPEL, A. LORENZ, AND E. KULZER. 1981. Body temperature and metabolism in the Red-backed Mousebird (Colius castanotus) during fasting and torpor. Comparative Biochemistry and Physiology 69A:689–692.

PRINZINGER, R., A. PREßMAR, AND E. SCHLEUCHER. 1991. Body temperature in birds. Comparative Biochemistry and Physiology 99A:499–506.

RENSCH, I., AND B. RENSCH. 1956. Relative organmasse beitropischen warmbluetern. Zoologischer Anzeiger 156:106–124.

REYNOLDS, P. S., AND R. M. LEE III. 1996. Phylogenetic analysis of avian energetics: Passerines and nonpasserines do not differ. American Naturalist 147:735–759.

RODRÍGUEZ, A. 1994. Dieta y comportamiento alimentario del Lechosero Ajicero (Saltator coerulescens). Thesis, Universidad Simón Bolívar. Caracas, Venezuela.

STRAHL, S, D. 1988. The social organization and be-

haviour of the Hoatzin (*Opisthocomus hoazin*) in central Venezuela. Ibis 130:483–502.

TROTH, R. G. 1979. Vegetational types on a ranch in the central llanos of Venezuela. Pages 17–30 *in* Vertebrate ecology in the northern Neotropicis (J. F. Eisenberg, Ed.). Smithsonian Institution Press, Washington, D.C.

VELOSO, C., AND F. BOZINOVIC. 1993. Dietary and digestive constraints on basal energy metabolism in a small herbivorous rodent. Ecology 74:2003–2010.

VLECK, C. E. M., AND D. VLECK. 1979. Metabolic rate in five tropical bird species. Condor 81:89–91.

WEATHERS, W. W. 1979. Climatic adaptation in avian standard metabolic rate. Oecologia 42:81–89.

WEATHERS, W. W. 1997. Energetics and thermoregulation by small passerines of the humid, lowland tropics. Auk 114:341–353.

WEATHERS, W. W., C. J. SHAPIRO, AND L. B. ASTHEIMER. 1980. Metabolic responses of Cassin's Finches (*Carpodacus cassini*) to temperature. Comparative Biochemistry and Physiology 65A: 235–238.

WEINER, J. 1992. Physiological limits to sustainable energy budgets in birds and mammals: Ecological implications. Trends in Ecology and Evolution 7:384–388.

YEAGER, D., AND G. R. ULTSCH. 1989. Physiological regulation and conformation: A BASIC program for the determination of critical points. Physiological Zoology 62:888–907.

Low Extrapair Paternity in the Cactus Finch (*Geospiza scandens*)

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Several investigations of Darwin's finches have relied upon observations of adults at the nest for identifying parents. These include estimations of heritable variation and covariation (Grant and Grant 1989, 1994), lifetime reproductive success and genetically effective population sizes (Grant and Grant 1992), and the evolutionary response to selection (Grant and Grant 1995). Studies of other emberizids and cardinalids (related sparrows, finches, and buntings) in the temperate zone have shown that simply observing adults at the nest is not sufficient to be sure of correctly identifying biological parents (Westneat and Webster 1994). Extrapair copulations sometimes result in fertilizations and the rearing of nonpaternal offspring. To determine whether this occurs in Darwin's finches, we undertook a study of microsatellite DNA variation in a socially monogamous, multibrooded species, the Cactus Finch (*Geospiza scandens*), on the Galapagos island of Daphne Major (0°15'S, 90°13'W). The frequency of polygyny has never exceeded 5% in this population (see Boag and Grant 1984, Gibbs and Grant 1987, Grant and Grant 1996 for breeding characteristics and population data).

Methods.—Blood samples were taken from 248 birds in 1988 to 1996. A single drop of blood was tak-

en by brachial vein puncture from nestlings at day 8 and from adults captured in mist nets. Nearly all males on the island throughout the study period were sampled. The largest number of potential breeders was present in 1993 (68 males and 27 females), when 90% of the males and 93% of the females were sampled.

Prior to puncture with a 30.5-gauge hypodermic needle, the area was cleaned with alcohol, and a drop of 0.5M EDTA was placed over the vein. Blood was transferred to EDTA-soaked filter paper, air dried, and stored in drierite at ambient (field) temperatures before being transferred to the laboratory and stored at −80°C.

Eight microsatellite loci developed in the Medium Ground-Finch (*Geospiza fortis*) were used to test parentage in *G. scandens*. Laboratory techniques used for genomic library screening and genetic screening of individual birds generally followed those of Primmer et al. (1995). Detailed methods and primer sequences are available elsewhere (Petren 1998). Measures of variation at these eight loci and exclusion probabilities are given in Table 1. We found no evidence of "null" alleles (Callen et al. 1993) in the pedigree.

Results and discussion.—All 159 offspring had one allele in common with the maternal parent (with the exception of the Z-linked locus). Therefore, mater-

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