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Correlates and Consequences of Body Size in Nectar-Feeding Birds

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SYNOPSIS. Nectar-feeding birds are among the smallest birds and the largest pollinators. Energetic costs of maintenance, temperature regulation, foraging and reproduction increase in direct proportion to body mass raised to fractional exponents, which may vary from 0.5 to 1.0; overall costs probably vary with an exponent of 0.75. Avian nectarivores acquire most of their energy from flower nectar; in so doing they compete with other nectar feeders and pollinate plants. Larger pollinators are more reliable and move pollen greater distances, but to attract them plants must secrete more nectar and protect it from utilization by smaller animals. Minimum body size of avian nectarivores (2g) appears to reflect both competition with insects and the limited capacity of the smallest birds to acquire and store energy relative to the demands of fasting, temperature regulation, and reproduction. Hummingbirds have attained significantly smaller size than other nectar feeding birds because lower metabolic rates and use of hypothermic torpor reduce their energy expenditure relative to income. Maximum body size of avian nectarivores (approximately 80g) apparently reflects the upper limit of plant energy expenditure for reliable, long distance pollination. Between these limits, size variation reflects divergence to reduce interspecific competition and coevolution with plants to promote specificity.

INTRODUCTION

It is appropriate that this symposium begins with a discussion of body size, for no other characteristic of an organism influences more aspects of its biology. To appreciate the diverse and pervasive effects of body size, consider the energetics of a nectar-feeding bird. In order to survive and reproduce, the bird requires energy which it obtains primarily by feeding on sugar solutions secreted by flowers. The bird must ingest sufficient energy to sustain its tissues, to regulate its body temperature and to perform other vital functions such as reproduction. The

amount of tissue being supported varies with body mass, heat exchange varies with body surface area, and capacity to obtain food depends largely on linear dimensions of locomotor and feeding appendages. Since the bird's mass varies as the cube and its surface area as the square of its linear dimensions, birds of different body size can exist only if all energetic functions are adjusted for these relationships. Allometric scaling in relation to variation in body size is required for all biological functions and can be described quantitatively by means of simple exponential equations. In birds, for example, empirically determined allometric equations describe relationships between body size and such quantitative traits as metabolic rate (Aschoff and Pohl, 1970), length of appendages (Greenewalt, 1975), egg size (Rahn *et al.*, 1975), incubation time (Rahn and Ar, 1974), longevity (Lindstedt and Calder, 1976), and size of territory (Schoener, 1968).

Although correlates of body size variation are numerous and well documented, their biological causes and consequences often are complex and poorly understood. Because virtually all structures and func-

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tions of an organism interact with each other and are influenced by body size, it is difficult to isolate cause and effect. A profitable way to investigate the effects of body size is to study intensively organisms which lie at the extremes of established allometric relationships. Comparative studies which include organisms of extreme size not only reveal mechanisms which enable them to achieve physiological integration and ecological function, but also indicate compromises and constraints which prevent the evolution of larger or smaller forms.

Nectar-feeding birds provide an exceptional opportunity for a comparative analysis because they lie at the narrow intersection of two largely nonoverlapping spectra of body sizes. Hummingbirds, sunbirds, honeycreepers, and the other birds which feed extensively on nectar are among the smallest birds and the largest pollinators (Fig. 1). Birds vary in size from the 2g bee hummingbird to the 100kg ostrich. Animals that provide pollination services for plants while foraging for nectar or pollen vary in size from fig wasps, some of which weigh less than 1 mg, to some birds and bats, which rarely weigh more than 80g. Although the 40 fold variation in size of nectarivorous birds is minute compared to the more than 50,000 fold variation in both birds and pollinators, it is accompanied by significant differences in the extent to which the birds are specialized for foraging from flowers and dependent on floral nectar as a food re-

source. Body size also influences relationships between birds and plants. Relative to insect pollinators, birds require large quantities of energy, so we should look for special benefits of avian pollinators which make it advantageous for flowers to secrete sufficient nectar to attract birds.

In the present paper we examine the influence of body size on the biology of these birds. First, we discuss physiological effects of body size on avian energetics, and then we consider their consequences for ecological roles (nectar consumers and pollinators). We also investigate the significance of variation in body size among avian nectarivores and discuss the compromises and constraints which determine minimum size of birds and maximum size of pollinators.

PHYSIOLOGICAL CORRELATES

Nectar-feeding birds obtain most of their energy by feeding on floral nectar, a plant secretion rich in sugars (Ford and Patton, 1976). Birds metabolize these sugars and use the resulting energy for their own maintenance, temperature regulation, foraging, and reproduction. The rate at which birds expend energy and the way they allocate it to different functions varies with body size.

Nectar is eaten by many birds. Fisk and Stein (1976) list 20 species of North American birds in 7 families exclusive of hummingbirds, which have been observed feeding on floral nectar. However, the majority of nectar feeders and the most specialized ones are concentrated in four families (Table 1). Note that hummingbirds are unique in not belonging to the order of perching birds (Passeriformes), in being the only group inhabiting the New World, and in attaining a minimum body weight one-third that of other avian nectarivores. The majority of temperate North American hummingbirds weigh approximately 3.5g which is only half the size of the smallest sunbird. Hummingbirds also differ from other nectar feeders in their capacity for sustained hovering flight and for entering hypothermic torpor as a means of emergency energy conservation (Fig. 2).

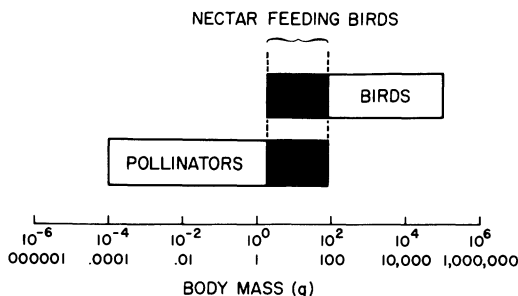


FIG. 1. Range of body size in nectar-feeding birds (shaded portion) relative to other birds and other pollinators. Note that nectar feeding birds vary about 40 times in body mass and include both the smallest birds and some of the largest pollinators.

TABLE 1. *Sizes and other characteristics of the four primary families of nectar-feeding birds.*

Family	Order	Number of species	Distribution	Range of body length (mm)	Minimum body mass (g)
Trochilidae	Apodiformes	319	North and South America	63-216	2.0
Nectarinidae	Passeriformes	104	Africa, southern Asia, Malaysia	95-254	6.9
Meliphagidae	Passeriformes	167	Australia and Oceania	102-432	8.5
Drepanididae	Passeriformes	22	Hawaiian Archipelago	102-203	8.5

Minimum body mass (m_b) was estimated from length (l) using the equation $m_b = 8 \times 10^{-6} l^3$. Data are from Van Tyne and Berger (1976).

Since all nectar-feeding birds are relatively small and hummingbirds are the smallest birds of all, it is of interest to consider the physiological correlates of small size and to ask what special characteristics of hummingbirds have permitted the evolution of uniquely small size. Such an analysis should suggest functional processes important in determining the size of birds.

Metabolism, temperature regulation, and torpor

Except when stressed by energy shortages resulting from scarce food and/or

low temperatures, all birds maintain relatively constant body temperatures of approximately 40°C (Calder and King, 1974). Temperatures well in excess of average environmental temperatures are maintained by a balance between heat production and heat loss from the body surface. Metabolic rate (H_m) of resting birds increases with body mass (m_b) according to a fractional exponent ($H_m = km_b^{0.75}$; see Calder, 1974, for a review). The value of k differs between passerine and nonpasserine birds (Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970) so standard (resting) metabolic rates (SMR) of passerine nectar feeders should be 55 to 65% greater than those of hummingbirds of the same size (Fig. 3).

Metabolic rate is elevated above resting levels during activity and for temperature regulation when environmental temperature is below the thermoneutral range (Fig. 3). Since passerines and other birds do not differ significantly in body temperature and insulation (Calder, 1974), differences in metabolic rate are large only in the relatively narrow thermoneutral range (Lasiewski, 1963, 1965; Wolf and Hainsworth, 1972; see Fig. 3). Because insulation increases and relative body surface decreases with increasing body size, rates of heat loss below the thermoneutral range scale to body mass with smaller fractional exponents ($m^{0.42}$ to $m^{0.53}$; Kendeigh, 1969) than SMR.

The energetic consequences of these metabolic and thermoregulatory patterns for birds of varying body size are summarized in Table 2, which presents calcu-

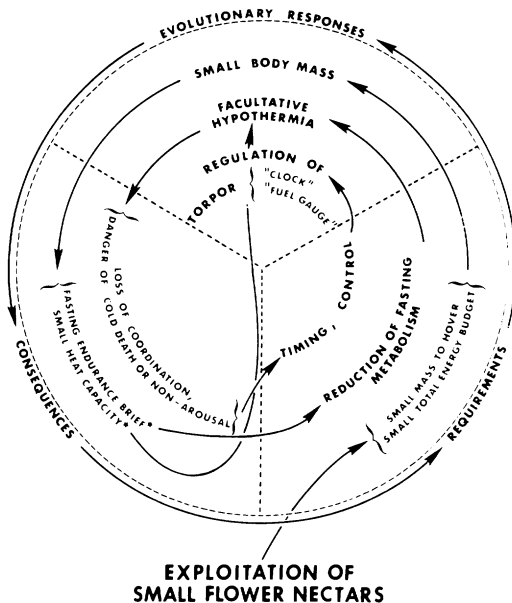


FIG. 2. A hypothetical scheme of some energetic aspects of hummingbird evolution which indicates consequences of small body size (from Calder, 1974).

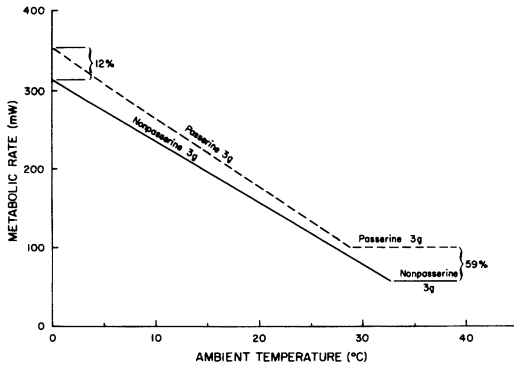


FIG. 3. Relationship between metabolic rate and ambient temperature predicted for hypothetical 3g passerine and nonpasserine birds from allometric equations relating standard metabolic rate and heat loss to body mass (from Calder, 1974). Nonpasserines have significantly lower metabolic rates than passerines at warm temperatures within the zone of thermoneutrality (level portion at lower right), but when these birds must expend energy for temperature regulation in cold environments their metabolic rates are very similar.

lated values derived from allometric relationships for hummingbirds. Note that standard metabolic rate, rate of heat loss, and daily energy cost decrease with decreasing body size. This would appear to favor birds of small body size because they could subsist on small quantities of nectar inadequate to support large birds. However, because standard metabolic rate and heat loss rate scale with fractional exponents, whereas energy reserves (fat and crop contents) should scale linearly with respect to body size, small birds must feed more frequently and have less ability to endure periods of food scarcity than large birds. This disparity increases as environmental temperature decreases.

Note that we discuss energetics in terms of metabolic costs to individual birds. Physiologists often try to make size-independent comparisons by dividing these rates by body mass and purport to show an inherent disadvantage of small body size because it is cheaper to fuel a gram of a large rather than a small bird. However, the unit of ecological function is the individual, not the gram (McNab, 1971). A large bird always requires more food energy, has a higher total rate of heat loss, and expends more total energy for

foraging and reproduction than a small bird whatever the cost per gram (Table 2). However, it is also true that, in comparison to a larger relative, a small bird: 1) ingests a greater proportion of its body weight per day in food; 2) increases its metabolic rate by a relatively greater factor to thermoregulate at a given environmental temperature below the thermoneutral range; and 3) uses up its fat reserves at a relatively greater rate while fasting. Since food energy and time available to forage are limited, allometric scaling of these energetic costs could present severe problems for very small birds.

Most hummingbirds which have been studied have the capacity to enter into and arouse spontaneously from torpor. Originally torpor was regarded by physiologists as the failure of temperature regulation. However, demonstrations that hummingbirds regularly enter and recover from torpor both in the laboratory (Lasiewski, 1963; Hainsworth and Wolf, 1970) and field (Calder and Booser, 1973; Carpenter, 1974, 1976a), and that they regulate body temperature at hypothermic levels (Wolf and Hainsworth, 1972; Carpenter, 1976a) suggest torpor is a normal metabolic response. Indeed, it is clear that torpor is an adaptive mechanism which permits energy conservation, but it appears to be used only when food is scarce and birds have difficulty remaining in positive energy balance (Fig. 3; Calder, 1974; Calder and Booser, 1973; Carpenter, 1976a; Hainsworth *et al.*, 1977). In such circumstances hummingbirds can enter torpor at night when they are unable to forage, temperatures are lowest, and risk of predation is least (Fig. 2).

Nocturnal torpor has been reported only in relatively small birds which have limited capacity for energy storage but the ability to reduce energy expenditure by entering hypothermia. High rates of heat loss enable small birds to cool rapidly to low body temperatures with consequent low metabolic rate (Lasiewski and Lasiewski, 1967). Energy conservation associated with torpor is substantial. For example, metabolic rate of a 5g hummingbird (*Pantherpe insignis*) torpid at 6° C is only 20% that

TABLE 2. Energy and reproductive estimates for hypothetical small hummingbirds.*

Body Mass	SMR Kj/day ^a	Flight (5 × SMR) ^b	Heat loss rate (mW ^c C ⁻¹) ^e	Daily energy cost (Kj) ^d	Crop energy reserves (Kj) ^e	Fat energy reserves (Kj) ^f	e + f (days) ^g	endur- ance at 5°C (days) ^h	life- span (yr) ⁱ	Pre- dicted egg mass(g) ^k	(% ad ♀)	Egg surface (cm ²) ^m	Adult surface (cm ²) ⁿ	Egg/Ad contact ratio ^o	Egg energy cooling (%SMRP °C/°C ^q)	
1g (0.50)	2.48 (0.60)	12.39 (0.60)	4.72 (0.73)	19.08 (0.75)	1.361 (0.64)	17.39 (0.50)	7.6 (0.84)	1.31 (0.70)	4.4-4.8 (0.88)	.175 (0.59)	17.5 (1.17)	1.47 (0.70)	10 (0.63)	0.29 (1.12)	31.04 (0.97)	13.81 (1.24)
2g (0.67)	4.11 (0.74)	20.54 (0.74)	6.49 (0.83)	25.54 (0.84)	2.137 (0.77)	34.78 (0.67)	9.0 (0.93)	1.88 (0.81)	5.1-5.4 (0.93)	.298 (0.73)	14.9 (1.10)	2.10 (0.81)	15.87 (0.76)	0.26 (1.04)	31.87 (0.98)	11.12 (1.14)
3g (0.75)	5.52 (0.81)	27.32 (0.81)	7.82 (0.88)	30.30 (0.89)	2.77 (0.83)	52.17 (0.75)	10.0 (0.93)	2.32 (0.86)	5.5-5.8 (0.95)	.408 (0.60)	13.6 (1.07)	2.59 (0.86)	20.80 (0.83)	0.25 (1.04)	32.45 (0.99)	9.79 (1.09)
4g (0.80)	6.82 (0.85)	27.32 (0.85)	8.93 (0.90)	34.20 (0.91)	3.347 (0.86)	69.55 (0.80)	10.7 (0.95)	2.70 (0.89)	5.8-6.1 (0.95)	.509 (0.84)	12.7 (1.05)	3.00 (0.89)	25.20 (0.86)	0.24 (1.04)	32.82 (0.99)	8.95 (1.07)
5g	8.02	33.60	9.90	37.57	3.871	86.94	11.3	3.03	6.1-6.4	.604	12.1	3.37	29.26	0.23	33.09	8.35

* Figures in (parens) signify percentage change going from larger to smaller bird.

^a @ 28.67m^{0.73} in mW from Calder, 1974.^b Assuming metabolic expansibility for thermoregulation similar to finches (Dawson and Carey, 1977).^c From non-passerine heat-transfer coefficient (Calder, 1974).^d From MacMillen and Carpenter (1977).^e Highest value for each of n=27 birds from Hainsworth and Wolf (1972b), least squares log regression, vol. = 0.270m^{0.9}. r = 0.789, at 5.04 Kj/ml, obtained from weighted average sucrose-equivalent concentration 0.893 molar from 9 flower spp. in Ecuador, 19 in southwestern U.S. (Hainsworth and Wolf, 1972c), and 5 spp. in Colorado Rocky Mts. (Waser, personal communication).^f @ 43.8% of body mass (Odum *et al.*, 1961) × 39.7 Kj/g.^g Endurance on reserves at SMR. Note that even at summit metabolism, reserves last > 1 day.^h Endurance on reserves at 5°C, (e+f) ÷ C(40° - 5°).ⁱ @ 17.6m^{0.20} for all wild birds and 16.6m^{0.18} for wild nonpasserines (Lindstedt and Calder, 1976).^k Rahn *et al.* (1975) general equation m_e = 0.277m_b^{0.77} predicts a value 58% high for a hummingbird (*Calypte anna*) as estimated, assuming a density of 1.88g/ml (Romanoff and Romanoff, 1949) from measurements of egg given by Hoyt (1977), and ♀ body mass of 3.82 from Pearson (1950). Hence above values are scaled as 0.175m_b^{0.77}.^m As 4.72 m_e^{0.667} derived from Hoyt's (1977) egg dimensions and scaled parallel to Meeh equations for surface area (Kleiber, 1961).ⁿ Assumed surface area = 10m_b^{0.67}.^o Contact ratio = (¼ egg surface × 2 eggs) ÷ ¼ adult surface.^p Egg energy estimated from 1.05 Kcal/g in altricial eggs (King, 1973, p. 88).^q Extrapolated from Fig. 38 of Drent (1975).

of a nontorpid bird resting at the same environmental temperature (Wolf and Hainsworth, 1972). Small body mass also permits rapid heating and arousal at the completion of a bout of torpor (Heinrich and Bartholomew, 1971). The capacity of small birds for heat production is amazing. Maximum metabolic rates (H_{\max}) of 14 species of small birds vary with respect to size according to the relationship $H_{\max} = km_b^{0.65}$ (from Calder, 1974).

Even the largest hummingbirds can utilize the energy saving advantages of torpor, as can their even larger relatives, the swifts and goatsuckers. Passerine nectar feeders, and passerine birds in general, appear to utilize torpor less frequently and effectively (Fig. 4). One small sunbird, *Nectarinia mediocris* (weight approximately 7.5g), studied in the laboratory by Cheke (1971) entered hypothermia and reached a body temperature 17.5°C below active body temperature, but we are not aware of evidence that any other nectar feeding birds regularly use torpor under natural conditions.

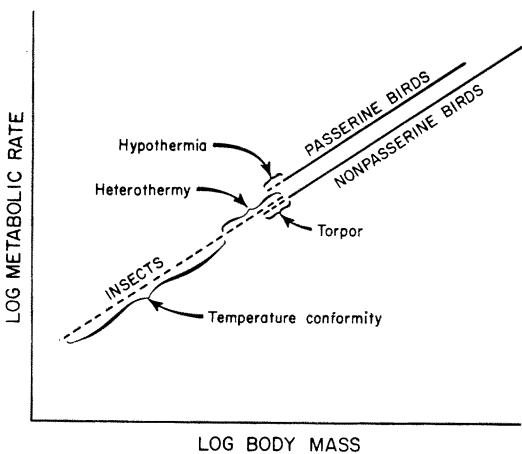


FIG. 4. Relationship between metabolic rate for passerine and nonpasserine birds (SMR; from Aschoff and Pohl, 1970) and for flying insects. Note that with decreasing body size flying nectarivores appear to rely increasingly on energy conservation resulting from reduced body temperature (dashed lines). The exact relationship for insects is uncertain because body temperature and metabolic rate of most insects vary with ambient temperature. The line plotted here was obtained using Heinrich's (1975a) value for incubating bumblebees and assuming that metabolic rates of other insects vary as $m_b^{0.75}$.

Foraging

Nectar feeding birds must expend energy on foraging to obtain energy. Foraging takes two forms: perching movements and flight. Metabolic costs of hopping about in vegetation and probing flowers while perched seldom are measured, but they are generally assumed to be in the range of 1.5 to 2 times resting metabolic rate and to scale with respect to body size with the same exponent as SMR (Gill and Wolf, 1975; Carpenter and MacMillen, 1976). Flight costs are greater, and empirical measurements suggest metabolic rate during flight may be as much as 5 to 7 times SMR for both hovering in hummingbirds and linear flight in other birds (Lasiewski, 1963; Tucker, 1970; Bernstein *et al.*, 1973; Greenewalt, 1975). Because they usually fly continuously while foraging, hummingbirds in particular may expend much energy on flight. Recently several authors have attempted to estimate the energy required (power output) for hovering in hummingbirds (*e.g.*, Weis-Fogh, 1972; Hainsworth and Wolf, 1972a, 1975; Epting and Casey, 1973; Greenewalt, 1975; Feinsinger *et al.*, 1978). Most of these estimates are based on aerodynamic theory, and use measurements of wing length and body weight rather than direct measurements of metabolism of hovering birds. There is some question and disagreement about exactly how energy expenditure for hovering scales with respect to body size; it appears likely that power output varies as at least the three-fourths power, and perhaps as the first power, of body mass. Field estimates of energy budgets for territorial, nectar feeding birds suggest that flight may account for 50% or more of daily energy expenditure (Wolf and Hainsworth, 1971; Carpenter and MacMillen, 1976).

Reproduction

Nectar feeding birds expend energy also for the production of offspring. Energetic costs of reproduction in birds include energy invested in eggs and metabolic ex-

penditures for courtship, mating, nest building, incubation, brooding and foraging for dependent young. Many of these costs are difficult to measure or estimate, but in general they probably scale with a fractional exponent in relation to body mass. Egg mass (m_e) varies with body size according to the relationship $m_e \propto m_b^{0.77}$ (Rahn *et al.*, 1975; see Table 2). Small females invest less total energy, but a larger proportion of their reserves, in eggs than larger birds (Skutch, 1962). Small females must also expend relatively more energy to carry their eggs until they are laid. Small females have relatively less body surface area in relation to relatively higher cooling rates of their eggs during incubation. Once the eggs hatch, it should cost proportionately more to care for the relatively larger young. We expect metabolic rates, and hence food requirements, of dependent young to scale similarly to adult SMR, approximately as $m_b^{0.75}$ (where m_b is adult body mass).

Not all costs can be measured in energetic terms. It is reproductive success or fitness which is the ultimate currency of evolution that determines whether a species persists and how it evolves. Survivorship and fecundity, the components of fitness, are strongly affected by body size. Longevity in birds scales as $m_b^{0.20}$ (Lindstedt and Calder, 1976), and small birds have a shorter life in which to reproduce. Since clutch size tends to decrease with body size and is typically two in hummingbirds (Bent, 1940), nesting success and survival, especially of juveniles, should increase as body size decreases. The consequences of these relationships for small birds are illustrated by data for Broad-tailed Hummingbirds (*Selasphorus platycercus*, body weight 3.5g) at Gothic, Colorado, elevation 2,910 - 3,000m (Waser and Inouye, 1977; Inouye, pers. comm.). Females successfully fledge an average of 1.15 young per nest, and the season is too short to rear more than one brood per year. Maximum recorded longevity of six years compares well with allometrically predicted lifespan of 5.8 - 6.1 years (Lindstedt and Calder, 1976), but average lifespan appears to be less than three years. As

might be expected, these birds are just about replacing themselves. Consequences of allometric scaling on survivorship and reproduction are extremely important in the evolution of body size.

ECOLOGICAL AND EVOLUTIONARY CONSEQUENCES

The previous section discussed effects of body size on the energetic processes essential for maintenance and reproduction. The present section is concerned with ecological consequences of nectarivorous birds foraging to obtain energy. By their feeding activities birds have important effects on both the plants which produce nectar and the other animals which feed on it. These ecological interactions provide the selective basis for the coevolution of communities of plants and pollinators. Because body size influences energy requirements and foraging behavior, it has important consequences for ecological and evolutionary relationships among nectarivores and plants.

Coevolution of pollinator energetics and plant nectar secretion

The basis of relationships between nectar feeding birds and plants is coevolved mutualism. Floral nectar has evolved specifically to attract animals which move pollen between plants and promote outbreeding. While pollinating, animals obtain energy from the sugars in nectar. While each partner in such a mutualistic relationship benefits from the activities of the other, natural selection acts on each partner to obtain the maximum benefit for the minimum cost. Most, but unfortunately not all, of the costs and benefits potentially can be measured in energetic terms. Rates of energy intake and expenditure have been estimated and net rates of energy gain have been calculated for free living, foraging nectarivores (*e.g.*, Gill and Wolf, 1975; Carpenter and MacMillen, 1976; Gill, 1978). Allocation of energy by plants to nectar and other floral attractants presumably could also be measured, but the

benefits of pollen transport and resulting outbreeding can be evaluated only in terms of reproductive success. Lack of a common, easily measured, currency to quantify costs and benefits to each partner complicates the study of plant-pollinator coevolution, and raises interesting challenges for future investigators.

Nectar-feeding birds share with bats and a few other mammals the distinction of being the largest pollinators. They have much higher energy requirements than the much smaller insects which pollinate most plant species. Plants specialized to be pollinated by birds and mammals must produce sufficient rewards to pay the high energetic costs of their pollinators. Thus, there is a significant positive correlation between body size of pollinator and caloric

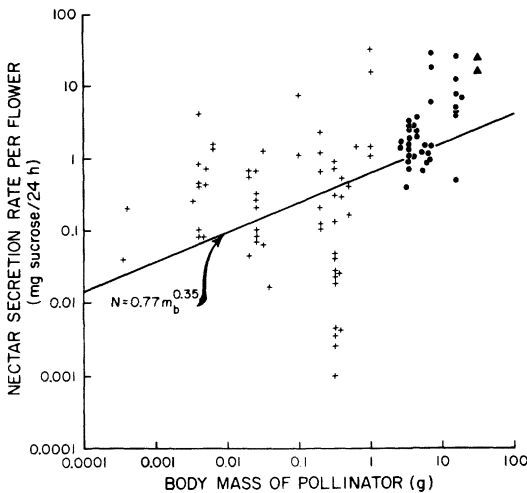


FIG. 5. Relationship between nectar secretion rate (N) of flowers and body mass (m_b) of pollinators for a large number of flower species pollinated by birds (circles), mammals (triangles), and insects (crosses). The fitted regression equation, $N = 0.77m_b^{0.35}$, probably is biased by the difficulties of measuring small nectar secretion rates of flowers pollinated by small insects. We would expect more points in the lower left hand corner of the graph and a regression equation with a higher exponent. Data compiled from Carpenter (1976*b*), Feinsinger (1976), Gill and Wolf (1975), Hainsworth and Wolf (1972*b*), Heinrich (1975*b*), Hocking (1968), Kodric-Brown and Brown (1978), Percival (1965), Stiles (1975), and the authors' unpublished data; when necessary body weights were estimated from body length using empirically determined allometric equations.

value of nectar secreted per flower per day (Fig. 5). The great variability around this relationship can be explained in large part by variation in the spatial distribution of flowers or other factors which influence foraging costs (see Heinrich, 1975; Heinrich and Raven, 1972, for excellent discussions). In addition, this pattern is biased by the difficulty of measuring accurately nectar secretion rates for those flowers which produce minute amounts and are pollinated by small insects. Except for this bias, the relationship should have a steeper slope and nectar secretion might scale with an exponent of 0.5 to 0.75 of pollinator body mass as we would predict from metabolic requirements (Fig. 4).

There appear to be two primary consequences of large body size which make it advantageous for some plants to pay the expense of avian pollinators. First, large size confers high mobility which is important on two scales. In their daily foraging activity large animals are able to move greater distances to satisfy their higher energy demands, and consequently they have larger home ranges and territories. In birds, territory area (A_t) scales to body mass (m_b) according to the allometric equation $A_t \propto m_b^{1.09}$ (Schoener, 1968). It is potentially beneficial for plants to use large pollinators because they increase the proportion and distance of outcrossing. This should be particularly advantageous to plants which are sparsely distributed or those in which seed dispersal is inadequate to achieve outbreeding. As might be expected, bird pollinated species tend to be medium- to large-sized, long-lived perennials which often are sparsely or patchily distributed. For example, Grant and Grant (1968) list 127 species of plants from western North America thought to be primarily hummingbird pollinated. Of these, only five are annuals, perhaps an equal number are biennials, and the remainder are perennials; a large proportion of the perennials are woody shrubs.

High mobility conferred by large size also enables avian nectarivores to migrate long distances to exploit erratically or seasonally available nectar sources. Thus many nectarivorous birds, including both

temperate and tropical hummingbirds (Grant and Grant, 1969; Gass *et al.*, 1976; Kodric-Brown and Brown, 1978; Carpenter, 1976a; Feinsinger, 1976; Feinsinger and Colwell, 1978), honeyeaters (Keast, 1968), and sunbirds (Skead, 1967), migrate in response to local and geographic patterns of flower availability. This ability to migrate makes nectarivorous birds reliable pollinators where conditions suitable for plant reproduction occur only seasonally or unpredictably.

A second consequence of large body size which makes birds particularly effective and reliable pollinators in certain habitats is thermoregulatory capacity. The ability of birds to maintain a constant body temperature makes their activity much more independent of environmental temperature and insolation than smaller heterothermic pollinators (Cruden, 1975; Brown *et al.*, 1978). This appears to account in large part for the relatively high abundance and diversity of nectar feeding birds and bird-pollinated plants at intermediate to high elevations on several continents (North and South America, Africa, and southern Asia).

Competition among nectar feeders and evolution of plant-pollinator specificity

Nectar is an energetically rich, easily utilized food that is potentially attractive to many animals. Competition for nectar among animals which both do and do not provide effective pollination is severe and of great importance in the coevolution of plants and nectarivores. If floral nectar is equally available to animals of large and small body size, then small nectar feeders often keep the standing crop of available nectar so low that large nectarivores cannot forage profitably and are competitively excluded (Brown *et al.*, 1978). Plants are strongly affected by such competition, and those which utilize large pollinators often have evolved mechanisms to prevent consumption of their nectar by small nectarivores. As a result, communities of plants and nectar feeders are organized in part on the basis of specificity relative to pollinator body size.

Community patterns which reflect the effects of body size on competition among nectarivores and on plant-pollinator specificity are particularly evident in nectar-feeding birds. Many characteristics of bird-pollinated flowers are adaptations either to avoid attracting insect competitors (red color, lack of odor) or to prevent their taking nectar (long constricted floral tubes with tough, thickened walls (see Faegri and van der Pijl, 1971; Proctor and Yeo, 1972; Heinrich and Raven, 1972; Heinrich, 1975a).

Where several species of nectar feeding birds coexist in the same habitat, they often differ in body size. These species tend to subdivide the bird-pollinated plants on the basis of size, thereby minimizing interspecific competition for nectar and achieving a degree of plant-pollinator specificity. Perhaps the clearest patterns are those shown by hummingbirds in the West Indies. Lack (1973) noted that although a few small, low elevation islands have but one hummingbird species, most islands have at least two (Fig. 6). When only two species are present they usually differ in wing length by a factor of at least 1.25 (which corresponds to 2-fold difference in weight). Large, mountainous islands often have more than two species, but those of similar size almost invariably occur at different elevations or occupy different habitats. In western Puerto Rico two large hummingbirds (*Anthracothorax dominicus* and *A. viridis*) replace each other altitudinally, and one small species (*Chlorostilbon maugaeus*) occurs at all elevations (Fig. 6). Hummingbird-pollinated flowers likewise fall into two size categories. One set of flower species has corolla tubes 17-20mm long, produces 1-2mg of sucrose per flower per day, and is visited almost exclusively by the small *Chlorostilbon*. Another group of flower species has corollas 30-38mm long, secretes 4-27mg of sucrose per flower per day, and is pollinated almost exclusively by one of the two large *Anthracothorax* species. This specificity appears to be maintained because the small flowers produce just enough nectar to support small, but not large, hummingbirds; the large flowers,

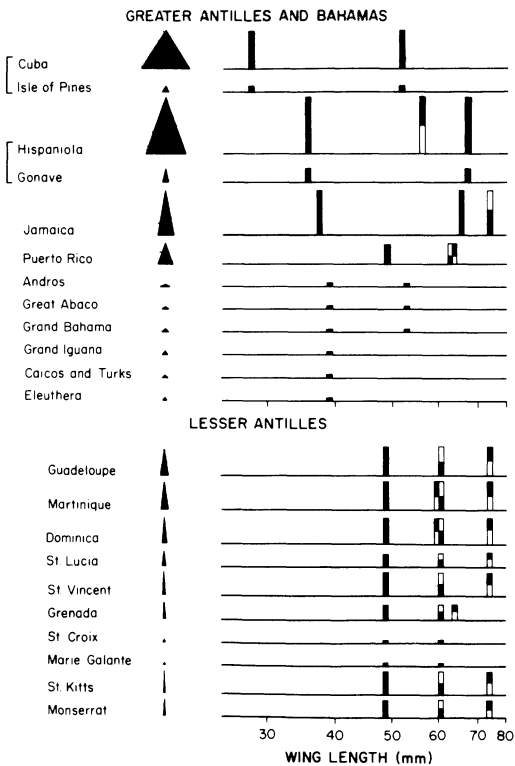


FIG. 6. Pattern of body sizes in the hummingbird faunas of representative West Indian islands. Hummingbird species are indicated by rectangles (shaded to indicate altitudinal distribution) on a logarithmic scale of wing length. Triangles indicate the elevation (overemphasized) and diameter of each island respectively. Note that most islands have at least two species of hummingbirds, and that those species which coexist at the same elevation usually have wing lengths which differ by a factor of at least 1.25. Drawn from data in Lack (1973).

which produce more nectar, have long corollas which prevent small birds from harvesting nectar. In more diverse tropical communities where several species of hummingbirds coexist, they often differ not only in body size and bill length, but also in bill shape, foraging behavior, and aggressiveness (*e.g.*, Snow and Snow, 1972; Feinsinger and Colwell, 1978).

LIMITS OF SIZE

The smallest nectar feeding bird weighs 2g, the largest may weigh as much as 80g, and the vast majority of species weigh from 3 to 30g. Since most appear to be surviving and reproducing successfully, we assume

their body sizes are adaptive. The body size of each species should be very close to the optimum for its particular ecology; this optimum should reflect the diverse effects of size which combine to maximize reproductive success. On the other hand, the narrow range of body sizes suggests that constraints of being both a bird and a nectar feeder place limits on the range of sizes which is adaptive. Reexamination of the patterns discussed in the previous sections should provide insights into those processes which determine the upper and lower limits of body size.

Minimum size

"Since smaller birds lose more heat relative to their body size than do larger birds, there is a minimum size below which birds are incapable of ingesting and metabolizing sufficient amounts of food to offset this heat loss." (Lanyon, 1963, p. 41) Such reasoning is common (*e.g.*, D'Arcy Thompson, 1961; Pearson, 1948, 1953; Greenewald, 1975), but usually it is based on qualitative arguments or untested and tenuous assumptions. It is almost impossible to prove that any one factor prevents evolution of smaller size. In fact we suspect that minimum size of nectar feeding birds reflects joint effects of several processes. If smaller size were advantageous except for the influence of one factor, then natural selection should act strongly to reduce the deleterious effect of that factor and thereby promote evolution of still smaller size. This indicates a potential hazard in extrapolating from allometric equations based on a wide range of sizes to make inferences about organisms of extreme sizes. With this warning to accept our results with care, we shall proceed to make such extrapolations.

Allometric scaling of metabolic and other processes creates a number of potential problems for very small birds. We have illustrated some of these in Table 2 by using available allometric equations to calculate predicted values of some physiological parameters for hummingbirds of various size, including the smallest existing species (2g) and a hypothetical bird weigh-

ing 1g. These extrapolations suggest that a 2g hummingbird evolving to half its size would have to contend with: 1) reduced endurance to fasting (by 16 and 30% at thermoneutrality and at 5°C respectively); 2) a shorter lifespan (by 12%) in which to reproduce; 3) egg mass contributing a relatively larger (by 17%) burden for female to produce and lift; 4) a relative decrease in surface of adult which can be applied to heat the egg (37% *vs.* 30% decrease); and 5) a more rapid cooling rate (by 24%) of its eggs.

Small avian nectarivores not only must solve these physiological problems, they also must be able to obtain sufficient energy to meet their metabolic requirements. They must evolve mutually advantageous relationships with plants which produce nectar, and they must compete successfully with other nectar feeders, particularly insects which have smaller body sizes and are subject to different physiological constraints. We should expect particularly intense competition between the smallest nectar-feeding birds, hummingbirds, and the largest insect pollinators, which include bumblebees (genus *Bombus*) and hawkmoths (family Sphingidae). These animals are similar in size: many hummingbirds weigh 2-4g (Greenewalt, 1962, cited in Carpenter, 1976a), bumblebee queens often weigh 0.5g or more (B. Heinrich, personal communication), and some hawkmoths weigh as much as 6g (Heinrich and Bartholomew, 1971). In addition, all have generally similar metabolic rates and hence similar nectar requirements. All are endothermic, so that they provide reliable pollination despite low or variable environmental temperatures (Fig. 4; see also Heinrich, 1975a). Finally, all have elongate proboscides which they use to extract nectar from tubular flowers specialized to exclude other nectarivores.

Recent studies indicate that competition between large nectar feeding insects and hummingbirds can be severe and may play a major role in plant-pollinator coevolution. Inouye (1976) notes that hummingbirds and bumblebees forage on many of the same flowers on his study area in Colorado. He calls attention to the

occurrence in northern Europe of bumblebee species with substantially longer proboscides than any North American species. The inference is that such long-tongued bees have been able to evolve in Europe because of the absence of competing hummingbirds. Brown, Kodric-Brown, Witham, and Bond (unpublished data) have documented competition between hummingbirds and insects (particularly bumblebees) and suggested that this interaction plays a major role in the evolution of plant-pollinator specificity. Brown and Kodric-Brown also have evidence for similarly important competition between hummingbirds and hawkmoths.

These studies suggest that under certain conditions either birds or large insects can competitively exclude the other from a flower species, and that the outcome ultimately is determined largely by the plant, which can evolve characteristics to favor the competitor which provides the most effective pollination. It is difficult to specify the extent to which such competition may act to prevent evolution of even smaller birds than presently exist. However, since the smallest birds and largest insects are similar in size, energy requirements and capacity for pollination, competition may be as important as physiological constraints in limiting minimum size in nectar feeding birds. This should be a profitable subject for future research.

Maximum size

We suggest that maximum body size in nectar feeding birds (about 80g) is a consequence of diminishing advantages to plants of producing sufficient nectar to attract large avian pollinators. The largest nectar feeding birds include orioles, drongos, babblers, and some honeyeaters. These are not only less specialized for foraging from flowers than hummingbirds and sunbirds, but they are also less dependent on a continuous supply of nectar and are likely to supplement their diet more with insects or fruit. These birds require large amounts of energy, and plants must secrete copious nectar to attract them. For only a few plants does the benefit of long

distance pollen movement appear to outweigh the costs of attracting birds of this size. These plants include some trees and large herbs, particularly species which occur at low density or reproduce only once at the end of a long life.

It is of interest that mammalian pollinators have approximately the same upper limit to body size as nectarivorous birds and show similar patterns of specificity. The largest mammalian pollinators, most of which are bats, are not highly specialized and feed on insects or fruit when nectar is not available (Heithaus *et al.*, 1975). The plants that they pollinate share many characteristics of those visited by the largest avian nectarivores, including large size, sparse distribution, and copious nectar secretion (Baker, 1961).

CONCLUDING REMARKS

The influence of body size on nectar-feeding birds is so pervasive and important that it affects virtually all aspects of their biology. We have presented a synthetic overview of the diverse correlates and consequences of body size from physiological and ecological perspectives which emphasize energetics. Body size influences basic processes of metabolism, temperature regulation, locomotion, and reproduction, which determine energy requirements of free living birds. In foraging to meet these requirements, birds play important roles in ecological communities as consumers of nectar and pollinators of plants. In the last decade, great progress has been made in analyzing these relationships, but there is much opportunity for further work. The correlates of body size at all levels of ecological organization suggest that it will be particularly fruitful to use these patterns and the extensive information on energetics of individual birds as a basis for investigating aspects of community ecology and plant-pollinator coevolution which remain poorly documented and understood.

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