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Size and Abundance: Breeding Population Density of the Calliope Hummingbird

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Population density is a basic component of life histories, competition, the structure and energy turnover of communities, and conservation. Hence, interspecific patterns in abundance or density are relevant to a wide range of ecological processes. The search for such patterns is fraught with variation due to heterogeneous resource distribution (Whittaker 1970), successional habitat changes (Johnston and Odum 1956), niche specialization (Perrins and Birkhead 1983), vulnerability to extirpation (Terborgh 1989), census methods (Dawson 1981, Calder 1990), biases towards study of abundant species (Brown and Maurer 1986), and consequences of body size (Juanes 1986). Relationships between density and size are attracting considerable attention (e.g. Damuth 1981, Brown and Maurer 1986, 1987, Juanes 1986, Lawton 1989, Cotgreave and Harvey 1992, Cotgreave 1993, Blackburn

et al. 1993a, b, Currie 1993). Two patterns of abundance have appeared: inverse log-linear regressions of population density on body size, and a triangular scatter plot when density/mass data sets include proportionately more rare species. Biological meanings are not yet clear.

Small mammals generally are more abundant than large mammals, and density/mass scaling correlations for common species are strong (e.g. $r^2 = 0.74$; Damuth 1981). Population density/size correlations are weaker for birds than for mammals. Juanes (1986) pooled densities of birds of all feeding types ($n = 564$) and found:

$$\log D = 1.96 - 0.49 \log M, \quad (1)$$

where D is density (birds/km²) and M is body mass (g). Although highly significant ($P = 0.0001$), the re-

gression r^2 was only 0.18. Other avian density regressions explain even less of the variation (lower r^2 values; cited in Juanes 1986 and Blackburn et al. 1993a). Indeed, without the points for nine raptors in Juanes' compilation, the scatter-plot of the data would suggest little, if any, size dependency. When Juanes treated data for herbivores and omnivores separately, r^2 s fell even lower. Only his carnivore and raptor correlations were stronger ($r^2 = 0.27$ and 0.58 , respectively).

The usefulness of regression equations for density has been questioned, with good reasons of both high interspecific variability in abundance of rare species and the fact that the data points become scattered into triangular versus linear plots as body size decreases; densities of common species increase towards a maximum as size passes below some threshold at which the trend reverses and densities decrease (Brown and Maurer 1987, Lawton 1989, Cotgreave and Harvey 1992, Cotgreave 1993, Blackburn et al. 1993a, b, Currie 1993). Brown and Maurer (1987) suggested that this reversal "implies some fundamental energetic constraints," such as a necessary shift to more concentrated foods to meet the higher energetic demands per gram mass of smaller birds and mammals. Cotgreave (1993) and Currie (1993), however, suggested ways in which triangular density/mass patterns could arise from sampling and (or) statistical methods. This may be not so much a matter of which pattern is correct, but of what heuristic function is to be served; linear regressions suggest design constraints (autecology) in the evolution of diversity, while triangular distributions reflect community processes (synecology).

Hummingbirds should be useful for exploring size-dependent, autecological constraints on abundance, body size range being a determinant of allometric precision (Calder 1987). Actual density data for hummingbirds have been lacking. Local abundance or scarcity of hummingbirds may not be represented accurately by numbers at feeders. Feeders attract fewer birds when natural resources are abundant (Inouye et al 1991). We studied the population density of the smallest bird in temperate North America, the Calliope Hummingbird (*Stellula calliope*) in an environment free of feeder artifacts.

Methods.—Our study site was at the base of the Mission Range (1,160 to 1,300 m elevation), Swan Valley, Montana, in regenerating clearcuts logged 5 to 13 years previously (C. Calloway pers. comm.). The vegetation consisted of young lodgepole pine (*Pinus contorta*), ponderosa pine (*P. ponderosa*), Douglasfir (*Pseudotsuga heterifolia*), alder (*Alnus tenuifolia*), snowberry (*Symphoricarpos*), beargrass (*Xerophyllum tenax*), and introduced weeds such as woolly mullein (*Verbascum thapsus*). The birds were feeding from Indian paintbrush (*Castilleja* spp.) and honeysuckle (*Lonicera ciliosa*) at the time.

We counted territorial males five times between 25 May and 5 June along 2.96 km of forest access road

(FS9550), which had minimal traffic (maximum of two vehicles per census period). In effect, we learned territorial locations in the first four counts, then used the final and highest count to calculate density. We travelled this route stepwise in about 2 h at near minimum speed of mountain bikes. One of us stopped to maintain surveillance on bird number n , while the other pedalled until male $n + 1$ was sighted and confirmed (by shouting back and forth) to be a different bird, bird n still being on his territory.

By itself, this would have been only a linear transect, missing a dimension (needed to express birds per unit area) and one-half or more of the population (the female adults and "floating" males not advertising claims). These problems of dimensionality and inconspicuity were addressed by addition of an intersecting mist-net/observation line. Former logging side roads were vegetated similar to the main FS9550 roadside, and had been administratively blocked to exclude vehicles, as part of the recovery plan for the Northern Rocky Mountain grizzly bear (*Ursus arctos*) population. We used one such side road as a secure mist-netting site, which we operated four mornings (0430-1030 MST, 28 May-6 June) to determine ratios of females and nonterritorial males (color-marked upon capture) to territorial males. Twelve 12-m nets were positioned to take advantage of vegetation and road banks that would shade the nets as late in the morning as possible, along a length of road bed estimated to be about three times the sum of the net lengths, or 432 m in all (road closure precluded an odometer measurement). Fortunately, this configuration spanned three territories, resulting in an average territory width indistinguishable from the mean spacing along the main road. We then assumed that the ratio of observed territorial males (M_t) to marked nonterritorial males (M_{nt}) to females (F) along the side road was representative of the local population, and estimated the total adult population density (D_p) using the following calculations. First, from data gathered on the side road, we estimated B , the number of birds per territory, as

$$B = (M_t + M_{nt} + F)/M_t. \quad (2)$$

The density of territorial males (D_t ; males/ha) along the main road was estimated as

$$D_t = M_{mt}/(X_{Mt}/100)^2, \quad (3)$$

where M_{mt} is the number of territorial males along the main road and X_{Mt} is the mean distance (in meters) between territorial males along the main road (divided by 100 and then squared to obtain the mean area in hectares for converting linear counts to density). The population density (D_p ; birds/ha) was then estimated as

$$D_p = BD_t. \quad (4)$$

Note that, using X_{Mt} as the side of a square, territories include all of the area (cf. X_{Mt} as diameter of a circular territory or using mapped territories that ex-

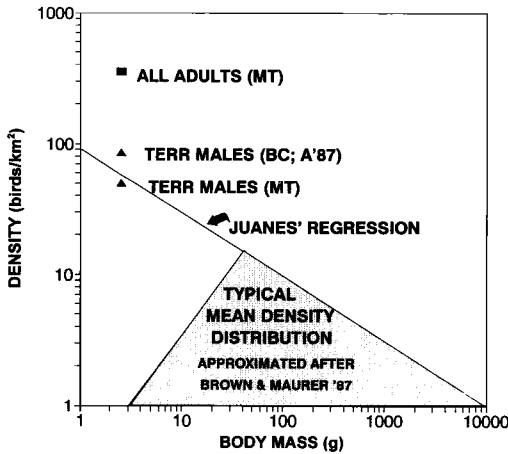


Fig. 1. Estimates of population density of territorial male Calliope Hummingbirds fall near an extrapolation from Juanes' (1986) general avian regression for density as function of body size (inverse line). Midvalue for territorial males calculated from Armstrong (1987); bottom estimate for territorial males from present study. A conservative estimate for all adults (including females and "floater males") is even farther from conformity to energetic constraint implied by triangular distribution of bird abundances, here represented by stippled triangle at bottom. This triangle was approximated for purpose of visualization by (1) eye-fitting slopes to upper bounds of data points in figure 2 in Brown and Maurer (1987), (2) taking one-half of each slope value to adjust their linear (birds/route) expression of abundance to dimensional equivalent of Juanes' (1986) plot (birds/km²), and then (3) extending adjusted "absolute constraint" slope from a point on regression corresponding to "threshold" size for peak density from Brown and Maurer plot. The inverse slope above the "size threshold" was almost the same as Juanes' (-0.46 vs. -0.49), so we assumed that the two were the same, using Juanes' slope for Brown and Maurer's "energetic trade-off" upper bound.

clude unused patches). If energy-concentrated food sources are distributed in patches, each bird in effect occupies only the useful fraction, for which the calculated ecological density (Lawton 1989) is high. However, crude population density, calculated from the total area of square territories, which enclosed both patches and local marginal habitat, would give the most conservative estimate of density, which is important for arguments that will follow.

We repeated this procedure from 27 May to 2 June 1994, adding the measurement of perpendicular distances from the road to male territorial perches, using an optical tape measure (split-image rangefinder; Edmond Scientific) to each male's territorial perch from the road to determine our mean and maximum de-

tection distance. Readings subsequently were corrected from calibration of the meter against a metric tape.

Rufous hummingbirds (*Selasphorus rufus*) also were territorial in the vicinity. The two species appeared to be spatially segregated, with the Rufous Hummingbird territories replacing or adjoining Calliope Hummingbird territories at the high end of our transect route and down a south-facing slope towards Cooney Creek.

Results and Discussion.—In five successive main-road transects in 1993, we located and counted 14, 14, 18, 20, and 21 male Calliope Hummingbirds posted on their territories (all present and accounted for on the fifth transect). We assume that the progressive increase represented our learning the territory locations, but it could be due to a continuing influx of new territory-holders, again making our counts conservative. Dividing the 2,960-m distance by these 21 territorial males yields an average distance of 141 m between males (for use as X_{mt} in equation 3). If the local area had been packed evenly with territorial males, each would have had 141 m × 141 m or a 19,881 m² square (1.988 ha) as a territory, 27% larger than if calculated as circular. Using equation 3, the density of territorial males alone was 0.503 birds per hectare (1,986 ha/male).

Along the logging side road, our nets captured 16 females and 9 males. We color marked the males with colored paint-pens when banded. However, the three territorial males that perched with high visibility along the mist-net series remained unmarked, having been able to avoid the nets, which they must have seen from their look-outs. We divided the total of nine nonterritorial males by the number of netting days (four) to get an average figure of 2.25 per three territorial males. If in fact these nine nonterritorial birds had all remained as "floaters," the total population would have been 32% greater, so again, we have leaned towards a conservation estimate.

The total of 3 territorial males, 2.25 floater males, and 16 females was 21.25 birds in three territories, or 7.08 per territory (equation 2). Assuming that these proportions were representative, a territory of 1.988 ha along the main road would have been populated by 7.08 birds on average, for a density estimate of 3.56 Calliope Hummingbirds per hectare (equation 4).

In two mornings of netting in 1994 on the side road, we netted too few females to determine a proper multiplier for estimating total population from territorial male counts. Females tend to arrive later than males, and our general impression (as well as that of local birders and another bander) was that hummingbirds and songbirds were few or late in recolonizing the Swan Valley vicinity. We did count 19 males (compared to 21 in 1993). They were spaced an average distance of 109 m between posts (range 64–176 m). Mean distances between adjacent pairs of three males along the netting side road and four males on

a side road on the opposite side of the main road were 89 and 90 m, respectively. This was well within the range and similar to the average for spacing along the main road, confirming the legitimacy of squaring the distance between males along the main road to estimate density from linear spacing.

The mean distance to territorial posts, perpendicular to the main road as determined with the range-finder, was 14.1 m (range 2.6–33.5 m). The maximum was less than one-half the 89- to 90-m distance between males along the perpendicular logging roads; so if transects err, it certainly is on the low side.

Thus, for this species, a linear transect would tend to give a conservative estimate of hummingbird density. We also calculated a crude density of 0.86 territorial males/ha in British Columbia, from data and a map given by Armstrong (1987:fig. 1), which exceeded territorial male density in this study by 71%. These two values straddle Juanes' (1986) regression, which, extrapolated only slightly from his smallest bird (3 g), predicts a density of 0.55 birds/ha for the 2.78-g mean body mass of the birds we captured. Cotgreave and Harvey (1992) reported a steeper mass slope of -0.6 , without reporting the intercept (or plotting the regression line), which is needed in order to calculate predictions. However, our points for territorial males alone, or for all adults, appear to fall appropriately on their figure 1.

Clearly, our data for the Calliope Hummingbird fall far outside of a "triangular distribution" of density versus mass (Fig. 1). Instead, this hummingbird seems to extend an "upper bound . . . set by limits to per capita use of resources" (Lawton 1989). Alternatively, this could be described as a continuation of the "energetic trade-off" along the inverse slope of the right side of the triangular distribution of Brown and Maurer (1987).

At least for this hummingbird species, there does not seem to be a "fundamental energetic constraint" on population density at the small extreme in body sizes. One could argue that hummingbirds are quite specialized in their nectar feeding, polygynous breeding, and habit preference for early stages in plant succession. Naturally, with canopy closure later in succession, flower abundance would be expected to decline, causing hummingbird density to thin locally as many emigrate to sites with greater floral abundance. The possibility remains that some fundamental energetic constraint may interrupt the allometric extrapolation from a regression for larger birds, but more data and a diversity of analytical approaches are needed for firm conclusions about proportionate energy turnover by species of different sizes within the same avian community. For the time being, our hummingbird data tend to confirm or even elevate the inverse slope of Juanes (1986).

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Definitions for Migrant Birds: What is a Neotropical Migrant?

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As a North American who has spent three years living in the Temperate Zone of the Neotropics (Paraguay), I often have wondered what the term "Neotropical migrant" refers to. Although some authors define a Neotropical migrant as any species of bird that migrates within the Neotropical biogeographical realm (Stangel 1992, Koford et al. 1994), the prevailing view of a Neotropical migrant is a species that breeds in North America and spends the nonbreeding season south of the Tropic of Cancer (e.g. Hagan and Johnston 1992a, b, Finch and Stangel 1993), a view which excludes austral (southern) and intratropical migrants (Levey 1994). Levey (1994) adopted a broader view of the term "Neotropical migrants" by including the latter two groups of migrants in the definition. I agree with Levey's arguments that austral and intratropical migrants need to be studied for both scientific and conservation reasons. However, by lumping all of these birds into the same category, we blur the already obscure definition of what a Neotropical migrant is and is not, which leaves us begging for a more precise set of terms and definitions for the various groups of migrants.

In the New World, there are two fundamentally distinct systems of long-distance latitudinal migration: (1) breeding birds in temperate North America that migrate southward to spend the winter in warmer climates, often in Central and South America; and (2) breeding birds in temperate South America that migrate northward to spend the winter in warmer climates, but only rarely in North America. The distinctiveness of these two groups of migrants is accentuated by the timing of their seasonal cycles, which are essentially half a year apart. Biogeographers have

long agreed that most of North America (north of central Mexico) belongs to the Nearctic realm, whereas Central America, the Caribbean and all of South America (south to Tierra del Fuego) belong to the Neotropical realm (e.g. Brown and Gibson 1983; see Fig. 1). In my mind, the two groups of migrants could logically be referred to as: (1) "Nearctic migrants," which breed in temperate North America and migrate southward; and (2) "Neotropical migrants," which breed in temperate South America and migrate northward. But instead, North Americans have persisted in selectively applying the term "Neotropical migrants" to the species breeding on the North American continent and wintering to the south of the Tropic of Cancer, which all but precludes the use of the term for migrant species breeding in temperate South America. The use of this term in this context is so pervasive that it frequently graces the titles of articles in the major North American ornithological journals, as well as the titles of two recently published symposium volumes (Hagan and Johnston 1992b, Finch and Stangel 1993). The term has been echoed repeatedly by conservation organizations and alliances, such as Partners in Flight. As a consequence, workers such as myself have been forced to use the term "austral migrants" in reference to migrant species breeding in South America (e.g. Chesser 1994, Hayes et al. 1994, Hayes 1995).

As Levey (1994) and others have proposed, we could simply refer to all of these migrants as "Neotropical migrants," which is certainly logical because these species all winter in the Neotropics and their ancestors probably evolved in the New World tropics (e.g. Brown and Gibson 1983). But then what definitions