Condor 85:281–285

THE ROLE OF THE FEET IN BEHAVIORAL THERMOREGULATION OF HUMMINGBIRDS

MIKLOS D. F. UDVARDY

ABSTRACT.—Four species of hummingbirds (*Archilochus alexandri, Calypte anna, Selasphorus sasin,* and *S. rufus*) were observed to keep their feet and toes in a special patch of downy belly feathers at low ambient temperatures (T_a), gradually expose them as temperatures rise, and hold them fully exposed at high T_a when hovering and perching. Since the position of the feet depends upon T_a, it probably influences the birds' heat transfer coefficient.

In many species of hummingbirds, such as Allen's Hummingbird (*Selasphorus sasin*; Aldrich 1956), the posterior ends of the ventral pteryla bear plumulaceous feathers that cover the entire belly below the sternal margin, just anterior to the vent (Fig. 1). My scrutiny of fresh specimens of several species (e.g., Anna's Hummingbird, *Calypte anna*) revealed that these feathers are semiplumes that are dark basally, and white at the tip. They form a patch that is often white and conspicuous, especially in otherwise dark-plumaged species, such as the Fork-tailed Emerald (*Chlorostilbon canivetii*). It is clearly visible in many photographs of North American hummingbirds, e.g., those in Grant and Grant (1968) and Udvardy (1977). Drawings of hummingbirds show these patches in various positions (see, e.g., Peterson 1961, Robbins et al. 1966, Peterson and Chalif 1973) often creating the impression that there is a conspicuous, fluffy white ring of down on the distal end of the shank. Such "tibial tufts" or "puffs"—consisting of enlarged down or contour feathers—occur in certain neotropical hummingbirds (see, e.g., photographs of the Sapphire-vented Puffleg, *Eriocnemis luciani,* and Crimson Topaz, *Topaza pella,* in Greenewalt 1960; of *Boissonneaua* spp., *Eriocnemis* spp., and *Ocreatus* spp. in Schuchmann 1979a).

While in Honduras during 1971 and 1976, I noticed that in the foggy, cool, and often rainy climate of El Hatillo, a suburb of the capital city of Tegucigalpa (elevation 1,460 m; 14°04′N, 87°13′W), Green Violet-ear (*Colibri thalassinus*), White-eared Hummingbird (*Hylocharis leucotis*), Red-billed Azurecrown (*Amazilia cyanocephala*), and *C. canivetii* frequently hovered with their feet drawn into the belly as if into a "muff." In contrast, on the tropical seashore of the Caribbean (near Brus Laguna; 15°48′N, 84°30′W), the three most common species of hummingbirds (*C. canivetii*; Green-breasted Mango, *Anthracothorax prevostii,* and Cinnamon Hummingbird, *A. rutila*) often flew with their legs conspicuously extended.

I report here on follow-up observations, testing the hypothesis that the abdominal patch serves as a heat conserver for the feet and that the latter participate in thermoregulation (Udvardy 1977).

MATERIALS AND METHODS

Between 1975 and 1981, I observed hummingbirds at three sites in California: (1) near sea level in the Sacramento area (38°31′N, 121°30′W) throughout the year; (2) at 260 m elevation at Three Rivers (36°45′N, 118°55′W; July 1979); and (3) at 380 m elevation near Placerville (38°45′N, 120°56′W; summer only). Data were collected intermittently during all months of the year, but mostly during June-September and November-February, i.e., at the extremes of the hot, dry summer, and the rainy, cool winter, respectively. At all three sites, a clear glass feeder with red plastic flower-shaped bibs was hung outside a large window, behind which the observer sat in plain sight. Sugar/water solution (1:3, v/v) was fed to the birds. The feeder had no perch, and thus the birds fed while hovering, as they usually do when feeding from flowers. During each observation of a hummingbird, the time of the day, ambient temperature (T_a) in the shade at the feeder, and the species, sex, and, if possible, age of the feeding bird were noted, together with the position of its feet.

The feet of a hovering hummingbird were categorized according to their position (Fig. 2). Position 0—feet completely withdrawn into the muff on the belly; position 2—tibiae and tarsi extended and held at approximately right angles to the flanks, and the toes fully extended; position 1—intermediate situations, e.g., when the clenched "fist" was exposed and unfolded or when the toes were slightly straightened.

I report here on 459 observations of Anna's Hummingbird (136 males, 114 females, 113 juveniles, and 96 undetermined), 46 obser-

FIGURE 1. Ventral view of a frozen specimen of *Calypte anna* (juvenile male). The grey ventral contour feathers have been plucked away to expose the two patches of white abdominal semiplumes. The feet have been spread laterally to show that the feathered thighs do not have down or semiplumes.

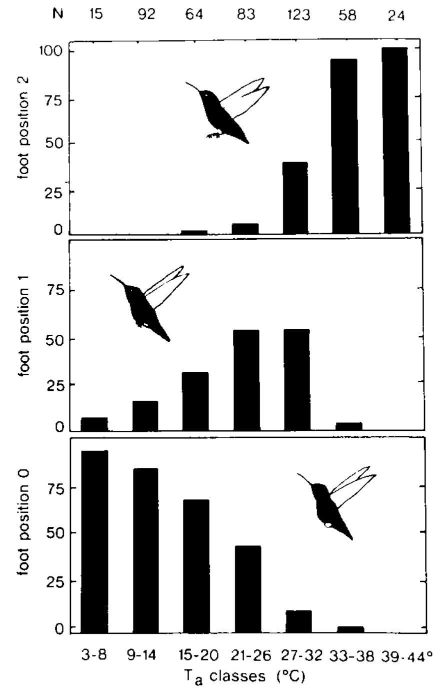

FIGURE 2. Percentages of observations of Anna's Hummingbirds in different foot positions at various ambient temperatures (T_a), pooled into 6°C classes.

vations of Black-chinned Hummingbird (*Archilochus alexandri*; 42 males and 4 females), and 102 observations of Rufous (*Selasphorus rufus*) and Allen's hummingbirds combined. The latter two species are transient in the Sacramento area between July and September. The adult males of these *Selasphorus* species are easy to distinguish, but females and juveniles are not. Consequently, I lumped my observations of these species into a single category, *Selasphorus* spp. The 102 observations comprise 16 of male *S. sasin,* 25 of male *S. rufus,* and 61 of unspecified females and juveniles.

RESULTS

Correlation of foot position with ambient temperature is best illustrated by my data for *C. anna* (Fig. 2; $r_s = 0.75–0.81$; $P < 0.001$, Spearman's Rank Correlation Test). Nevertheless, the correlation was highly significant in *all* species ($r_s = 0.75–0.86$; $P < 0.001$). Foot position 0 was the rule below 15°C, above which it graded into position 1, which predominated between about 26 and 30°C. Position 2 was typical at T_as above 30°C. The process of exposing the toes (i.e., the transition from position 0 to position 1) appeared to be more gradual than that from 1 to 2. Between 30 and 32°C, the toes opened and the tarsi were extended. Above 32°C, all hummingbirds (70+ observations covering all four species) held their feet in extreme position 2. Fewer observations were made of the Black-chinned Hummingbird and the *Selasphorus* species, but the pattern of exposing the extremities with rising temperature was the same (Fig. 3).

Male, female, and juvenile Anna's Hummingbirds did not differ with respect to the position of the feet as a function of T_a (the rank correlations were approximately the same for all sex and age classes). Several serial observations disclosed that position 2 was used exclusively during the afternoon and evening hours. However, whenever the temperature changed, the position of the feet varied accordingly.

During July and August 1981, I also observed non-feeding hummingbirds perched on telephone lines, watching them from a distance of 10–25 m with binoculars or a telescope. These observations, however, were not quantified. Birds perched in the sun during the cool morning hours, but moved into the shade when the T_a exceeded 25–30°C. During cool periods, they sat with their toes covered by the belly and flank feathers. Above 30–32°C, they stood on relatively outspread feet, the axis of the body approximately perpendicular to the feet. The wings drooped and the bend of the wing was held somewhat away from the body (Fig. 4).

DISCUSSION

While the position of the feet in my sample of hovering hummingbirds was artificially classified for the purpose of scientific notation, pooled data indicate a gradual shift in foot position in response to changes in ambient temperature. The feet of birds are well known to serve as a thermoregulatory device for either conserving or dissipating heat (summarized by Calder and King 1974). Similar changes in the position of the tarsus and toes as a function of T_a have been described in the Budgerigar

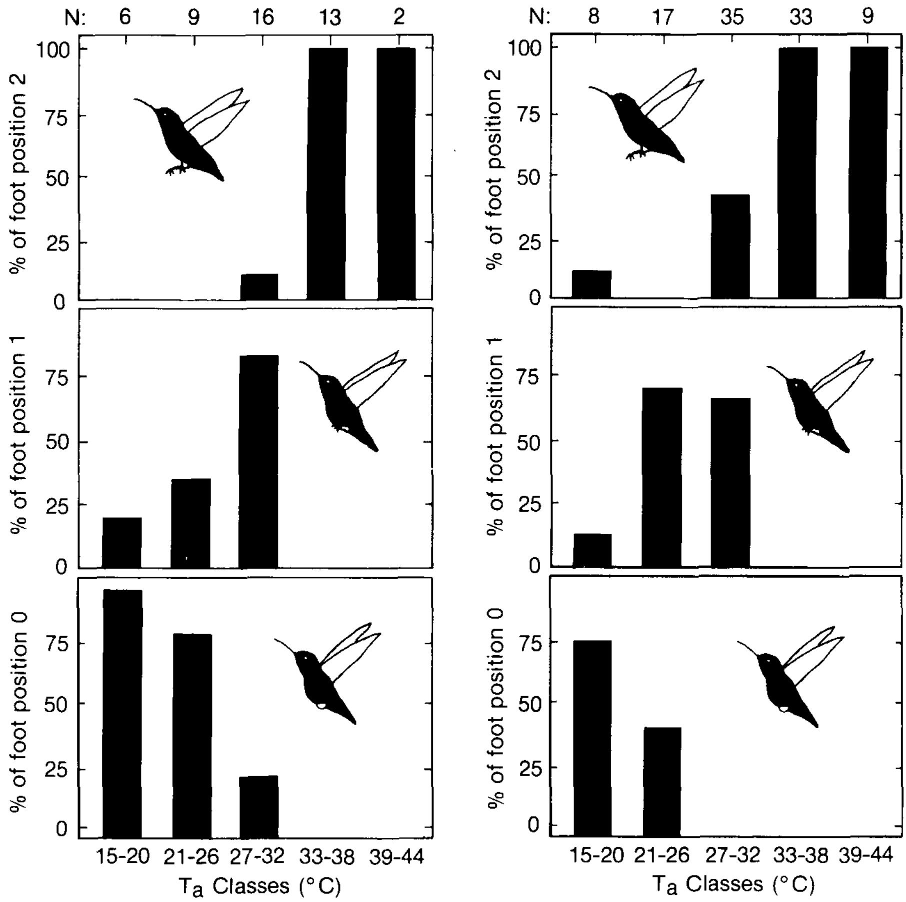

FIGURE 3. Percentages of observations of Black-chinned Hummingbirds (left) and *Selasphorus* hummingbirds (right) in different foot positions at various ambient temperatures.

(*Melopsittacus undulatus*; Tucker 1968) and in eight species of African birds (Frost and Siegfried 1975). We can now extend these observations to hummingbirds: when faced with heat losses, they withdraw their feet into the downy feathers on the belly.

Lasiewski (1964) demonstrated that resting hummingbirds have a lower critical temperature of about 27–30°C. Flight, however, increases the heat production of birds (e.g., Baudinette et al. 1976) in general, and hummingbirds (cf. Morrison 1962, Schuchmann 1979b) in particular. This may explain why foot position 1 was most common at T_as between 26 and 30°C. Below this range of T_as, the feet were increasingly withdrawn, and protected. The exceptions (toes showing or tarsi extended by some Anna's and Rufous hummingbirds at T_as between 16 and 24°C) may have been caused by exertion before birds visited the feeder, i.e., the birds may have developed a heat load that had to be dissipated while they fed.

My observations suggest that the extension of feet at high T_as is a form of behavioral thermoregulation. Hovering birds of all four California species, in addition to those observed in tropical Honduras, exposed their tarsi and feet on hot days (56 of 57 Anna's Hummingbirds, and all Black-chinned Hummingbirds and *Selasphorus*; Table 1). The few exceptions at high T_as (e.g., one Anna's Hummingbird had clenched feet at 35°C) may have been due to sudden changes in temperature immediately around the birds, as, for example, caused by gusts of wind.

Lasiewski (1964) found resting body temperatures (T_b) in the species studied here to be between 34.4 and 41.2°C. Those of nine species of Brazilian hummingbirds are between 39.5 and 44.6°C (Ruschi 1949). Even the lower extremes of these values are higher than the T_a at which feet and toes are completely extended. Hummingbirds may regulate the temperature of the blood, and hence body temperature with countercurrent exchangers and arteriovenous shunts in their hind limbs as do other birds (Steen and Steen 1965). When the T_a is below the T_b, the extended legs, when allowed full circulation, may increase heat loss from the

TABLE 1. Observations of hummingbird foot positions at various ambient temperatures (T_a). Total number of observations = 607. Position 0—feet hidden in downy abdominal feathers, position 1—toes visible, position 2—feet and toes exposed.

T_a	*Calypte anna*			*Archilochus alexandri*			*Selasphorus* spp.		
°C	0	1	2	0	1	2	0	1	2
44			3						
			1						
42			2						1
									1
40			7			1			2
			11			1			5
38			6						4
			6			2			8
36			11			3			6
		1	4			3			1
34			5			3			7
	2	1	22			2			7
32		4	14		1				4
	1	4	8		1			2	
30	1	8	5		1			2	2
	1	17	3		5	1		2	2
28	5	19	10	2	4			6	4
	5	14	4	1				10	1
26	3	15	3	1			1	7	
	10	9			1		2	1	
24	7	7	1	1			1	1	
	6	6		1			2	1	
22	8	4		3	2				
	1	3						1	
20	8	2		1			1		
	5	1		2					
18	11	3					1		
	4	5		2	1		1	1	
16	8	4	1				2		1
	8	4					1		
14	4								
	7	4							
12	16	4							
	17	4							
10	24	2							
	10								
8	5								
	1								
6	1								
	4	1							
4									
	3								
2									
n	186	146	127	14	16	16	12	34	56

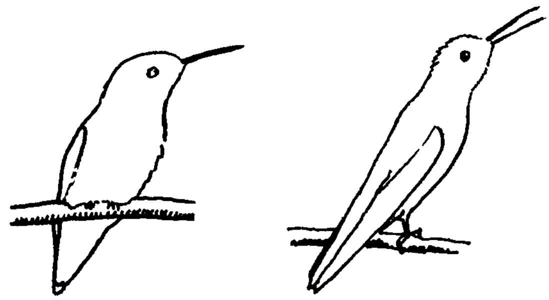

FIGURE 4. Postures of resting Anna's Hummingbird in response to ambient temperature. Left: in the cold; feet protected by abdominal feathers, plumage fluffed. Right: hot and panting; feet fully exposed and spread apart, plumage sleek, wings drooped and slightly away from the body.

blood by conduction and convection. This mechanism may be used by both hovering and perching birds, since the latter also expose their feet and toes in hot weather. While hovering, such postulated heat loss may be augmented by convection currents generated by the wings.

Recent experimental work on several species of tropical hummingbirds (Schuchmann 1979b, c, Schuchmann and Schmidt-Marloh 1979a, b, Schuchmann et al. 1979, Schmidt-Marloh and Schuchmann 1980) casts doubt on the general validity of the classical concept of thermal neutrality and associated metabolic responses in Trochilidae. Individuals of seven species responded to rising T_as by elevating their T_b. Maximum T_b ranged from 39.9° to 43.3°C at T_as between 34 and 41°C, respectively. These birds, then, became *hyperthermic* at high T_a. Since this stored heat increases the difference between their T_b and the prevailing T_a, it enables them to dissipate additional, excess heat by exposing their tarsi and feet. In the light of these findings, it would be desirable to repeat Lasiewski's experiments on North American hummingbirds, exposing them to high T_as and watching for a thermoregulatory role of their feet.

SUMMARY

The hummingbirds that I observed hid their feet in the downy plumage on the lower abdomen at T_as below about 24°C. As the temperature rose, the birds gradually exposed their feet and toes, presumably to facilitate heat loss. Above 32°C, the feet and toes were exposed as fully as possible. The two extremes and the intermediate postures of the feet are closely correlated with ambient temperature.

The T_a values at which these behavioral changes occur in the Anna's Hummingbird are independent of sex, age, season, or the time of the day. In the three other species, the trend is the same, yet owing to their much smaller size future detailed studies may reveal differences. A lower and narrower range of T_as for the intermediate foot position would reflect a greater need for behavioral thermoregulation at low as well as high ambient temperatures in these species.

ACKNOWLEDGMENTS

I am grateful to Mary Bacon and Maud E. Udvardy for their original observations, which are reported here with mine. Mrs. Udvardy also typed the manuscript and helped in many other ways. I also thank Harold W. Kerster for doing the statistical analysis, Charles S. Papp for the illustrations, Monica L. Udvardy for editorial and grammatical comments, and Peter Stettenheim for suggestions concerning the feathers. Elmer C. Aldrich, George A. Bartholomew, Robert D. Montgomerie, Oliver P. Pearson, and an anonymous reviewer gave thorough critiques of the manuscript that helped to clarify my discussion and conclusions. My 1971/1972 fieldwork in Honduras was during a Fulbright lectureship, and in 1976, it was supported by a grant from the Frank M. Chapman Memorial Fund of the American Museum of Natural History. Mrs. C. S. de Beausset, Mrs. G. Eoff, and J. Eoff generously provided the logistical base during my stays in Honduras.

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Department of Biological Sciences, California State University, Sacramento, California 95819. Received 29 October 1981. Final acceptance 24 November 1982.