Table 1: Percentage of plant morphotypes displaying adaptations that may reduce evapotranspiration from leaf surfaces at a low exposure site at the Estación Biologica Cuericí (n=24) and a high exposure site at the Cerro de la Muerte parámo (n=12), Costa Rica. Some plant morphotypes displayed more than one adaptation.

Site	Pubescence	Waxiness	Reflective coloration
Low exposure	50	58	4
High exposure	50	33	83

Table 1: Comparison of leaf pubescence density and type between pubescent plant morphotypes collected at a low exposure site at the Estación Biologica Cuericí (n=12) and a high exposure site at the Cerro de la Muerte parámo (n=5), Costa Rica. Pubescence types and descriptions were adapted from Harrington and Durrell (1957).

Site	Mean density (# hairs per magnifying lens view) + 1 S.E.	Classification of pubescence	# of morphs	Description of pubsecence
Low exposure	111.2 + 22.0	pubescent-type	7*	short to medium length hairs
		strigose	2*	short and stiff hairs
		puberulent	4	very short hairs
High exposure	543.2 + 153.7	tomentose	3	short to medium length interwoven hairs concealing true leaf surface
		sericeous	1	long, straight, soft hairs covering leaf surface; silky
		ciliate	1	hairs along leaf margin only

DIEL VARIATION IN BEHAVIOR OF *SELASPHOROUS FLAMMULA* , THE VOLCANO HUMMINGBIRD

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Abstract. Selasphorous flammula, the Volcano Hummingbird inhabits high elevation, open areas in the mountains of Costa Rica. Nighttime temperatures often approach freezing at these locals. For small, homeothermic vertebrates, maintaining body temperature overnight is metabolically demanding, and crucial for survival. We expected that Volcano Hummingbird daily behavior patterns would reflect the metabolic constraints placed on them by maintaining body temperature over the course of near freezing nights in their high mountain environment. We found three basic phases in the daily routine of these hummingbirds: 1)early morning foraging and territory establishment; 2) mid-day territory defense; and 3) late afternoon foraging. These behaviors may help maximize nectar rewards for the individual hummingbirds and ensure an adequate nectar supply to satisfy the hummingbird's nightly metabolic requirements.

Key Words: hummingbird behavior

INTRODUCTION

The Volcano Hummingbird, *Selasphorous flammula*, is common in high elevations throughout Costa Rica, inhabiting relatively open, secondary-growth areas (Stiles and Skutch 1989). It is a seasonal resident in the Estación Biológica Cuericí in the Cerro de la Muerte region where it feeds on insect pollinated flowers such as, *Fuschia, Castilleja, Salvia, Vaccinium, Rubus, and Miconia* (Stiles and Skutch 1989). At these high elevations, nighttime temperatures in the dry season can approach freezing. Hummingbirds must maintain body temperatures over the course of a night, although they may decrease body temperature somewhat by entering torpor. Hummingbirds also do not feed at night, making the metabolic stress upon the birds each night even greater. Presumably, a single night with inadequate calories to expend in temperature maintenance could prove fatal for these small homeotherms. Obtaining sufficient energy during the day to survive the cold nights may be a very important factor influencing their daily behavior patterns. The questions driving our study were : How do Volcano Hummingbirds secure the food resources to survive at high altitude and over cold nights, and what are the costs of securing these resources? To address these questions we examined the time budget of this species in a montane environment.

As hummingbirds do not forage at night, energy reserves should be lowest in the early morning. We predicted that in order to restore the energy depleted by the previous nights temperature maintenance, *S. flammula* would allocate the largest percentage of its time at dawn to foraging. Furthermore, males are known to defend perches and open areas with flowers (Wolf 1976). Such behavior is metabolically demanding, and may require an energy level which the hummingbirds cannot maintain throughout the night. Once the energetic demands of territorial defense had been met by foraging in the morning, we then expected territorial displays and conspecific interactions to become more common in the mid day, as the males attempted to maintain their territories.

METHODS

On 27-28 January 1997 near Cuerici Biological Station, Costa Rica, we chose six observation sites, offering good views of hummingbird activity. We observed Volcano Hummingbird behavior for two, 0.5 hour periods at each of these sites four times of day: dawn (05:45-06:45), morning (08:30-09:30), afternoon(13:30-14:30), and evening (16:30-17:30). During each of these one hour long observation periods, three people collected data at two observation points. Most of the data recorded was for males since they were conspicuous in their daytime perches. Females are known to move throughout the territories of the males (Wolf, et.al., 1976), and were only observed by us while foraging. The number of birds observed ranged between one and four at each of the six sites, and we estimate that data were obtained from the behavior of approximately 18 males.

Hummingbird activity was categorized into five distinct behaviors: Feeding, perching, dive display, conspecific interactions, and moving. Data were only collected from a single bird at a time, even if more than one bird could be seen. Behavior was noted

every 10 s whenever a bird was in sight. The dominant behavior during each 10 s observation was categorized as one of the five behavior patterns listed above. Proportions of these 10 s intervals in each behavior category were then used to construct a daily time budget.

Each time interval had six replicates (3 observers x 2 sites each). Overall means of behavior frequencies were generated for each of the four time intervals, by averaging the frequencies of a given behavior from all the sites, weighted by the total observation time at each site. The weighted mean percent behaviors at different times were compared using a one-way ANOVA. Individual time periods were then compared using multiple comparisons (Tukey Kramer HSD).

Results

Within a given one hour observation period, the percentage of time that a humming bird was actually observed varied during the day: dawn=20%, morning=43%, afternoon=60%, and evening=12%.

The proportion of time observed feeding at various times of day varied significantly with time of day (F=4.06, df=20, P=0.021). The Tukey-Kramer test showed that hummingbirds fed in the evening more than the morning or the afternoon (Fig. 1). The proportions of time spent feeding did not differ between other pairs of time intervals, although there was a strong trend for lower proportion of time spent feeding in the late morning and afternoon compared to dawn. Conspecific interactions decreased throughout the course of the day, although the pattern was not significant (Fig. 1, ANOVA F=2.15, df=20, P=0.12).

Discussion

The hypothesis that there will be a decrease in feeding behavior and an increase in territorial defense and display over the course of a day was generally supported by our data. Although not predicted, time spent feeding in the evening was significantly greater than time spent feeding in the morning or afternoon. Presumably the birds are accruing vital energy before the cold night, when they will remain inactive and will not forage until the next morning. By vigorously defending patches of food during the day, the birds may be insuring access to these food resources during the evening foraging period. The relatively high percentage of foraging behavior at dawn compared with the morning is probably due to the birds having depleted their energy reserves during the night, and thus there may be a caloric prerequisite to be met before the birds can engage in territorial establishment and defense.

Although three person hours of total observation occurred at each of the four time intervals, the duration of actual time that hummingbirds were under observation was substantially lower, as frequently there were no birds in sight. We observed the lowest amount of total activity during the dawn and evening intervals, when we recorded the highest percent of feeding. Feeding behavior is much more difficult to observe than territorial behavior, so it is logical that during times of increased feeding, our total time of hummingbird observation would less than at times of increased perching. Therefore, our estimates for feeding are most likely conservative estimates, and it is likely that larger differences exist between foraging times for highly visible times (late morning, afternoon) and low visibility times (dawn, evening).

Relatively high conspecific interaction at dawn is possibly a result of competition for territories. A subsequent decrease in conspecific interaction may be a function of better established territorial boundaries. Territorial defense included perching by males in high, conspicuous branches, conspecific interaction, and dive displays. Territorial behavior including conspicuous perching and dive display may arise from a need to defend food resources which may otherwise be depleted over the day by conspecifics or other nectar feeders. Defense of food resources within an individual hummingbird's territory may be essential for optimizing foraging immediately before sunset. The hummingbird's behavior on conspicuous perches was characterized by constant head rotation, alertness and scanning. Dive displays, in which males spiral 10-20 m up into the air and then dive vertically downwards to the vegetation also appears to be a territorial display. Such activity was sometimes met by chases from other males. The dive display may be involved in courtship and reproduction as well, possibly serving as a mechanism for mate selection. It is interesting to note that as proportion of perching behavior increased and decreased, so did frequency of dive displays, suggesting that while the birds are displaying they are also watching the displays of neighbors.

Proportion of perching time observed remained relatively constant throughout the day. Although only one form of perching was recorded, there were qualitative differences in the location of the perches and their context. Perching during time intervals of high feeding (dawn and evening) was lower in the brush, and seemed associated with foraging behavior. Perching during the morning and afternoon intervals was conspicuous atop bushes and small trees, and seemed

to be associated with conspecific interaction and what appeared to be territorial reconnaissance.

In conclusion, we believe that there exist three important daily stages, marked by varying behavior patterns of *S. flammula*, in the high altitude disturbed forests of Cerro de la Muerte. We believe these behavior patterns arise as a response to satisfy the metabolic demand of the near freezing nights in the hummingbird's high elevation environment. These three daily stages include: early morning foraging and territory establishment, midday territory maintenance (including diving display), and evening foraging.

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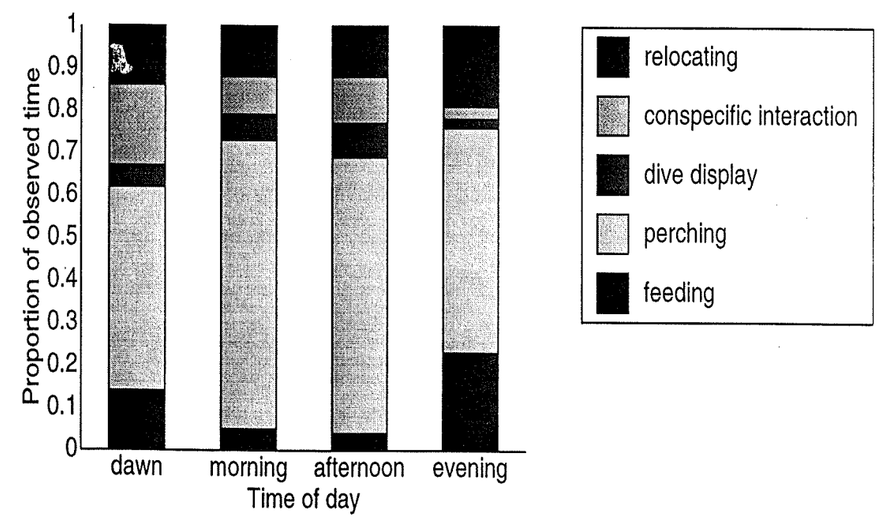

FIG. 1. Proportion of *S. flammula* time spent in five behaviros at four times of day at Cuerici Biological Research Station, Costa Rica. Each proportion represents the weighted mean of siz observations of approximately 18 individual birds.

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