Table 1. Regression coefficients (r) associated with environmental variables that best predict fish distribution in tide pools at Corcovado National Park, Costa Rica.

	Individual Fish Species								
Variable	1	2	3	4	5	6	7	Shannon Diversity Index	Species Richness
Depth	0.34**	- 0.08	0.18	0.46**	0.14	- 0.18	- 0.15	0.14	- 0.23
Area	0.25*	0.50**	0.28	0.36**	0.30*	0.31*	0.44**	0.27*	0.35**
Zone	0.00	- 0.25*	0.24*	- 0.17	- 0.23	- 0.23	- 0.23	0.00	- 0.21

* $p < 0.05$; ** $p < 0.01$

Table 2. Day-to-day variation in fish compostition in tide pools at Corcovado National Park, Costa Rica.

Pool Number	Area (m^2)	# of Days	# of Spp.	# of Individuals (range)	G	df	P
5	7.5	4	2 - 3	31 - 109	63.73	6	< 0.05
6	4.5	4	1 - 2	8 - 71	19.07	3	< 0.05
7	3.0	4	3	28 - 54	54.27	6	< 0.05
8	2.0	4	1	4 - 35	15.91	3	< 0.05
9	9.5	3	1 - 2	17 - 34	12.09	2	< 0.05
10	19.5	4	1 - 2	7 - 114	66.35	3	< 0.05

Table 3. Temperature and salinity variation at low tide in tide pools at Corcovado National Park, Costa Rica.

	Temperature (°C)				Saliniry (bricks)	
Time	Smal Pool [a]	Medium Pool[b]	Large Pool[c]	Ocean	Small Pool[a]	Medium Pool[b]
0730	27.6	27.0	--	27.4	2.75	3.50
0830	30.3	28.3	--	27.4	2.50	3.50
0930	32.9	30.8	27.8	27.4	--	--
1030	35.6	32.3	--	27.4	2.00	3.50
1100	37.3	34.0	--	27.4	--	--

[a]High Zone; [b] Mid Zone; [c] Low Zone

Day-to-day variation in fish communities primarily reflects changes in the number of individuals of each species present, not which species are present. This variation in abundance indicates that individual fish may not choose or defend specific territories in the intertidal zone. However, different species and sizes of fish select tide pool environments that provide a suitable balance between tolerable physical conditions, favorable foraging opportunities, and acceptable predation risks.

RAINSTORM EFFECTS ON THE BEHAVIOR OF *AMAZALIA TZACATL*

JON S. BEADELL, SARAH E. KOPPLIN AND MATTHEW K. LITTLE

Abstract. Rufous-tailed hummingbirds are often exposed to daily extremes in rain conditions which may alter their behavior. Rufous-tails spent more time foraging and defending their territories on dry days than on rainy days. During rainstorms, flying may become more costly or forage may become less energy-rich, thereby decreasing the benefit of either defending or foraging within a territory. In addition, more species of hummingbirds visited rufous-tail territories more frequently on rainy days than on dry days. This suggests that competitors take advantage of the relaxed territorial behavior of rufous-tail hummingbirds during rainy conditions.

Key words: Amazalia tzacatl, *rainstorm, foraging, territoriality*

INTRODUCTION

La Selva's historic rainstorm of 11-14 February 1996 provided a unique opportunity to study the effects of rain on the foraging and defense behavior of hummingbirds. Rufous-tailed hummingbirds, common members of La Selva's avifauna, defend feeding and mating territories in the branches of *Haemelia* trees. We hypothesized that during rainy days, rufous-tailed hummingbirds should spend less time exposed to the heat-draining rain and, consequently, less time foraging and defending its territory. We also hypothesized that on rainy days, those hummingbirds that are typically excluded from rufous-tail territories may take advantage of the relaxed defense in order to feed on the *Haemelia* flowers.

METHODS

On 13-14 February 1996, we monitored the behavior of one rufous-tailed hummingbird within a territory including 4 *Haemelia* trees immediately behind the laboratory at La Selva Biological Preserve, Costa Rica. We recorded the time spent flying and resting during rainy and dry periods on both days. In general, the weather on 13 February consisted of intense showers with infrequent periods of no rain. The weather on 14 February was mostly dry with an occasional misting rain. In addition, we noted the frequency of visits to the territory defended by this rufous-tailed hummingbird by non-territorial hummingbirds: Blue-chested (*Panterpe insignis*), Little Hermit (*Phaethronis longuemareus*), and the Red-footed Plumeleteer (*Chalybura urochrysia*). We observed bird behavior for approximately 8 hours in the late morning and early afternoon of both days. Because we did not observe all species in both rain and dry conditions on both days, we were unable to perform rigorous statistical analyses.

RESULTS

On average, the focal rufous-tailed hummingbird spent 11% of its time in flight (foraging or territorial defense) on the rainy day and 25% of its time in flight on the dry day. On the generally rainy day, the percentage of time spent flying was the same during periods of rain and during perdiods between rain. On the generally dry day, however, the same hummingbird spent 31% of its time flying during periods of rain and 18% of its time flying during periods between rain. We noted 13 visits to the territory by 3 species of hummingbird on the rainy day and only 2 visits by 2 species of hummingbird on the dry day.

DISCUSSION

Rufous-tailed hummingbirds appeared to alter their behavior to maintain their precarious energy balance during rainy conditions. Rufous-tails fly to defend their territory and to forage (collecting and consuming nectar). Only the latter provides an immediate return in energy. Presumably foraging provides a net energy gain and this gain must be larger than the energy lost to defending a territory. Therefore, if the energy of the forage is fixed, should flying become more of an energy drain, foraging may no longer provide a net energy gain. As a result, both territorial defense and foraging behavior should decline. Rain may increase the energy cost of flying. Moving the high surface area of a damp wing at the high velocities required to sustain hovering must increase heat loss and could increase the energetic demands of thermoregulation.

Similarly, if the cost of flying remains fixed, yet the

energy return from forage falls, activity should decline. *Haemelia* flowers may not provide nectar of the same quality or quantity during excessively wet periods. On average, a hummingbird like the rufous-tail expends 18 calories per minute while hovering (Baker 1983). Nectar production may be so low during extended rainy periods that the energy required to fly is not returned by the energy gained from consuming the nectar.

While rufous-tailed hummingbird activity was reduced during the overall rainy day, visits to Haemelia trees by smaller non-territorial hummingbirds increased. Perhaps these opportunistic birds rely on rainy conditions to increase their nectar uptake when the chances of being chased off are reduced. Given the relatively high surface to volume ratio of these smaller birds, it is likely that these birds are less well insulated than larger birds. Therefore, while the rufous-tailed hummingbird can afford to remain inactive when flying is not energetically favorable, smaller birds may be forced to fly in order to maintain a stable body temperature during extended rainy periods. Also, if the wing area of smaller birds is proportionately smaller, the cooling effects of flying may be outweighed by the warming of metabolizing. And it is more likely that the small birds will have energy to metabolize because they are less likely to be driven off during the rain. Thus, small non-territorial birds counteract the energy demands of flying with energy from a more accessible source.

Interestingly, rufous-tails spent more time flying during the infrequent periods of rain on the overall dry day than during the dry periods of the same day. This seems to be consistent with the above analysis. Perhaps the smaller birds, being more susceptible to cooling during rainy periods, must be active even during these short periods of rain. If they remain active by foraging in rufous-tail territories, then it is likely that the rufous-tail must increase its activity to defend against these intrusions. Perhaps the brief mists do not pose such a cooling threat to the larger bird when flying. Quantification of rain intensity, duration, and temperature would improve this analysis. Future studies should focus more closely on the consequences of rain on the relative success of territorial and non-territorial birds. To do this accurately, the effects of bird size on metabolic requirements must be separated from the effects of territoriality on defense and foraging behavior.

LITERATURE CITED

Baker, H.G., K.S. Bawa, G.W. Frankie and P.A. Opler. 1983. Reproductive biology of plants in tropical forests. Pages 183-201 *in* F.B. Golley, editor. Ecosystems of the world. Vol. 14A, Tropical rain forest ecosystems. Elsevier Scientific Press, Amsterdam.