Hummingbird Territoriality

There comes a terrible time in the lives of most graduate students when they know they will study something, but they haven't a clue in the world what it might be. It doesn't help to know that the work must make an original contribution to human understanding, that it must be good enough to survive peer review and be published, and that the quality of the work will make or break the student professionally. The task is to find what we call "the problem". What was my problem?

My case was really no different than many others. I spent months in the library, for example, hoping against hope that I would find my problem there but knowing on some level that it must be rooted not just in the literature but in my own personal ignorance. It is not an easy thing to discover issues about which we are so profoundly ignorant that to clarify them for ourselves will at the same time clarify them for everyone. World-class contributions require world-class ignorance, and it takes a lot of knowledge to identify gems of ignorance of such high quality.

Fortunately, graduate students do not just go to the library. They also attend seminar courses, where they discuss key papers in the technical literature and develop the habit of probing deeply enough into ideas to appreciate how they evolve. One week in ecology seminar, we were to discuss a paper by Martin Cody called, ominously, *A general theory of clutch size*, in which Cody wondered how different bird species come to lay different numbers of eggs. He described what he called the "principle of allocation", the idea that each individual animal in nature invests a certain amount of life force in various activities, such as feeding, avoiding predators, and reproducing, and that different species invest to varying degrees in these activities. Essentially, he argued that since all the activities take up all the time, doing more of one thing necessarily means doing less of something else, and that the best thing to do varies with the situation. The paper was about reproductive strategies, but the principle of allocation struck me as applying generally to nearly everything. I couldn't stop thinking about it.

Just before seminar, a group of us were in the elevator, descending toward the small room in the basement where we would meet. I stood with my back to the door, facing my peers, and we were jabbering about whatever. The elevator stopped, the door opened, and as I turned to step into the hall I suddenly "saw" what I would study.

In the summer before 7th grade, I visited Grizzly Lake for the first time. It was then and remains today one of the most beautiful places I have ever seen. The lake itself is a bright blue glacial tarn, resting at about 7000 feet altitude in a basin scooped by glacial ice out of white granite and literally perched on the edge of an overhanging cliff more than a hundred feet high in the overhanging part; the outlet stream from the lake flows only a few feet before plunging into space. Above the lake and below the jagged peaks all around, hummingbirds defend territories in rich meadows.

I had wondered for years what all that squabbling was all about. Suddenly, newly informed by Cody's theory, I saw hummingbird territoriality in a new light. They put enormous energy into territory defense, for example, so they must get a lot out of it too. But what determines the balance of costs and benefits that makes the difference to individuals as they make their way in the world? What informs their behaviour?

My PhD research in the Grizzly Lake meadows asked “how do territorial animals know how much space to defend?” Those meadows provided an ideal place to answer this question, and the late ‘60s and early ‘70s were the ideal time to answer it. These were not what most people would call “meadows”, but steep avalanche gullies clinging to the sides of mountains, where moist soil creeps slowly downward and columbine and Indian paintbrush grow wild. Southward-migrating hummingbirds go wild there, as do hummingbird biologists.

From measurements of territory size, flower density, and nectar production rates over several summers, I concluded that hummingbirds defend energy, not space directly. Over a wide range of conditions, the caloric value of the nectar territories produce remains remarkably constant, and individuals adjust their territory boundaries continuously to maintain that constancy in the face of changes in flower density and the number of competing hummingbirds in the meadows.

Better territories are more profitable to forage in because their flowers accumulate more nectar, and hummingbirds will defend all the flowers they can. But better territories are also more attractive to competitors, and it takes only a few stolen licks for an intruder to learn that a territory is too good to be economically defendable. Indeed, holders of especially good territories often had to fly nearly 100% of their time just to expel intruders, sometimes several of them at a time, and that is definitely an unprofitable response. They quickly gave up the fight, relaxed their defenses, and gave up part of the territory.

On average, territories produce enough energy to allow the birds to gain fat, but not enough for them to do that without working hard for it. I will develop this idea further in later essays.