Thoughts on the Air and the Birds That Make Their Living There

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Wilson's Storm-petrels feed on oceanic plankton.

The growing acknowledgment that populations of aerial insectivorous birds in the northeastern U.S. and southeastern Canada are declining has caused us to reflect on all aspects of the biology of this fascinating guild of birds. One of the aspects of their biology that has most fascinated many is the habitat they live in. Of course, all flying birds live in the air every time they take flight. But in this essay I will concentrate on the most aerial of birds, the aerial coursers.

These are the birds that make their living in the air almost full time, the birds that feed on the wing in long sustained flights that can last many hours or even days. Birds like flycatchers certainly foray into the air every time they fly after a passing insect, but they are very seldom more than a few meters above the Earth, as they always return to their perch between foraging attempts. In contrast, swifts and swallows (and less familiar birds like them elsewhere) spend most of their lives in the air, plying the waves of air above and around us just as storm-petrels make their way across the oceans of water. And storm-petrels resemble swallows more than in their graceful mode of traversing their realms: they are both planktivores of sorts. Swallows grasp small insects from the air and storm-petrels grasp small invertebrates from the water surface. The prey of both birds are plankton, meaning that the movements of the tiny prey are ruled more by the movements of the medium in which they live than by the results of their own exertions. Thus, to understand the distribution and variability of their food, we need to understand the movements of water versus air.

Water Versus Air

Water is perhaps the most quintessential substance of Earth. No single rock type distinguishes Earth as well as does the abundance of water in all three of its physical forms: vapor, liquid, and solid. Of these, liquid water is what makes ours the "blue planet," and its properties dominate the conditions for life on Earth. The cycling of its temperatures and densities

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Tree Swallows seine aerial plankton.

in a temperate lake is emblematic of its tremendous physical constancy and the relative predictability of its behavior: in summer a layer of warm, light water, often only a few meters deep, floats on top of a deeper, colder layer with a temperature of about four degrees Centigrade. The light, warm water on top is remarkably stable. Even with considerable wind, although the upper layer may slosh back and forth across the lake basin in slow, low waves, it still remains stratified atop the colder and heavier deep waters. This thermal stratification lasts all summer and eventually erodes into a fully mixing lake only after the bright sunshine and heat of summer are replaced by the dark, cold winds of fall and winter.

This unusual stability and predictability stand in stark contrast to the behavior of air. Air is almost outside our experience. We speak of things vanishing into thin air, and we spend much of each day forgetting that the air exists. But as soon as we open the window in a rushing car, or we cower in the house when a powerful thunderstorm with its strong local winds rolls past, we are reminded that air is viscous like water, just less so. One of the wonders of Earth is that air has sufficient viscosity that tremendous pressure differences can arise over very short distances—pressure differences that can produce tornadoes and hurricanes and typhoons. Anyone who has lived through one of these disastrous phenomena will never accept that the air is insubstantial!

Air follows all the same rules of fluid mechanics as does water, but everything about air is much more changeable. Even when it is not up to some of its more spectacular manifestations of viscosity, there are many signs of its ever-changing currents and gradients. In summer, a dandelion seed or scrap of cellophane can serve as a reliable indicator of the tortuous currents otherwise hidden in a bright summer's sky. And when air is moving at the surface, it is good to look farther skyward, as clouds often give us the best indicator of conditions aloft. On sunny days with puffy cumulus clouds popping up in the afternoon, one can be sure that there is a good deal of vertical movement of air, as it is vertical convective cells of air from lower levels that bring water vapor to the upper layers, where it condenses into water droplets and clouds. As vertical movement grows stronger, more vapor is taken farther faster; and when the solar energy being poured into the system is strong enough,

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Aerial insectivores are adept at catching flying insects.

water vapor can be carried many thousands of feet into the cumulonimbus clouds that are one mark of severe thunderstorms. In thunderstorms, the convective cells often engender strong lateral winds at the ground, feeding the rising air column, and large numbers of insects can be concentrated and carried far aloft, where swifts and swallows sometimes aggregate at altitudes, much higher than is their wont, to feed on concentrated and cold-stunned prey.

> ***The fundamental mismatch in the ways that insects and birds adjust their life histories to their environments has led some to fear that another sort of mismatch maybe affecting aerial insectivorous birds in the Northeast.***

Thus, currents in the air can be just as strong as any currents in water, and we have a great deal to learn about how currents in less extreme conditions than thunderstorms may affect the foraging behavior and ecology of aerial insectivorous birds.

We do know a couple of interesting things, though. First, those big concentrations of insects in the air associated with high altitudes in thunderstorms are major exceptions to one of the known properties of air as a habitat for coursing insectivores: that available insect densities drop off steeply with altitude. Thus it is not too surprising that most aerial insectivores spend most of their time foraging in the first tens of meters above the Earth. And within that band, there appears to be a loose apportionment of foraging space, at least among North American swallows: Barn Swallows most often near the ground, Tree and Rough-winged at mid-level, then Bank generally higher, and Purple Martins up at the highest levels, often with swifts and nighthawks. This stratification raises the question of what may be taking such high-foraging birds so high. If food densities are generally much lower at higher altitudes, are these birds taking larger prey to compensate for the lower prey densities where they forage? Do the high fliers have any special sensory or cognitive skills that allow them to find and capture larger prey more efficiently?

Air Temperatures Change Rapidly

The other interesting thing about air versus water is the relative rapidity with which air temperatures can change, and many of the most rapid changes come about through the displacement of large masses of air. Temperatures can drop dramatically overnight with the arrival of a cold front from the north, and these changes in air temperature contrast with those in water, the high thermal inertia of which helps buffer lakes and rivers from large daily swings (and of course water has a hard time moving out of lake basins the way air can shift over the Earth's surface!). Many aerial insects hatch out from aquatic habitats, and they may thus emerge from water warm enough to support their eclosion into air that is too cold to allow them to fly. Different insects have very different thermal optima for flight, and aerial insectivores are subject to dramatic changes in available food from one day to the next, depending on what groups of adult insects are present and on the air temperatures on any given day. Thus it is not uncommon in a northern spring for aerial insectivores to go overnight, with the simple arrival of a cold front, from a feast of available insects to a famine. This rapid alternation in available prey can have large effects on breeding productivity if a cold snap lasts a couple of days or more, and the generally high breeding productivity of swallows can be slashed to large-scale failure if such conditions arise during the time of chick development when their feeding requirements are highest.

Many insect species have an aquatic lifestage.

The Price Of Being Warm-Blooded

It is a price of being a warm-blooded animal that one's metabolic requirements remain high no matter what the weather. Insects can "go on ice" when it is too cold to fly, but birds must continue to feed their metabolic fires to keep their temperatures high. This difference between homoeothermic and ectothermic animals helps explain an interesting difference in the timing of annual cycles of abundance and activity in insects and birds around the northern hemisphere: insects respond flexibly to changes in weather and climate, whereas vertebrates take longer to adjust the settings on their programs of self-regulation. These slower adjustments can lead to mismatches in breeding schedules and food availability, causing birds to attempt to breed in spring after peaks in food abundance have already passed.

This fundamental mismatch in the environmental adjustments of insects and birds has led some to fear that another sort of mismatch may be affecting aerial insectivorous birds in the Northeast. It may be that insects across the board are responding to warmer springs and summers in the North by shifting their emergence earlier in the year, thus reducing the availability of aerial insects in late summer and early fall, just when aerial insectivores need high quantities of food to fuel molt and migration. This mismatch could explain declines in aerial insectivores of diverse migratory schedules and destinations across the Northeast, but it would not answer why aerial insects might be affected differently than the foliage-bound insects on which the bulk of other migrant birds rely.

> ***Insects respond more flexibly to changes in weather and climate. Vertebrates take longer to adjust.***

If aerial and foliage-associated insects respond differently to climate change, one of the first places to look for an explanation would be in their environments. Both insects and birds living in these habitats must cope with different gradients with different dynamics, and we are only beginning to understand what some of the key differences might be. We know that air, like land and water, is rich in heterogeneity, and the rates at which air's heterogeneity changes are much faster than in the other two environs. We are just beginning to sift through the implications of these differences, and, as we begin to do so, we will no doubt gain a much more synthetic understanding of the most continuous and pervasive habitat on Earth.

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