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The airspace is habitat

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Revising our notions of habitat

A preconception concerning habitat persists and has gone unrecognized since use of the term first entered the lexicon of ecological and evolutionary biology many decades ago. Specifically, land and water are considered habitats, while the airspace is not. This might at first seem a reasonable, if unintended, demarcation, since years of education and personal experience as well as limits to perception predispose a traditional view of habitat. Nevertheless, the airspace satisfies the definition and functional role of a habitat, and its recognition as habitat may have implications for policy where expanding anthropogenic development of airspace could impact the conservation of species and subject parts of the airspace to formalized legal protection.

The core concept of habitat has remained remarkably unchanged for decades. Early formal definitions focused on occupancy. Odum [1] offered what remains perhaps the most recognizable, simple, and frequently implied definition, '...the place where an organism lives, or the place where one would go to find it.' Whittaker *et al.* [2] described habitat similarly as 'the range of environments or communities over which a species occurs'. More recent definitions are consistent with Odum and Whittaker *et al.* but elaborate by identifying proximate causes for occupancy usually associated with resource use. Morrison *et al.* [3] defines habitat as an 'area with a combination of resources and environmental conditions that promotes occupancy by individuals of a given species and allows those individuals to survive and reproduce.' Beyer's *et al.* [4] definition is more subtle regarding resources, 'regions in environmental space that are composed of multiple dimensions, each representing a biotic or abiotic environmental variable; that is, any component or characteristic of the environment related directly or indirectly to the use of a location by the animal.' These and other widely cited definitions [5] specify that occupancy, and perhaps resource use, are essential attributes of habitat. The airspace satisfies these criteria, and accepted definitions of habitat contain no language that precludes airspaces from being considered habitat.

The airspace in question here primarily concerns the lower parts of the troposphere where an organism's presence in a specific part of the airspace (i) indicates use of some airborne resource, (ii) indicates use as a movement corridor, and/or (iii) is fortuitous (e.g., aerial plankton). Organisms capable of powered flight and occupying aerial habitats may be largely behaviorally decoupled from the earth's surface and responding primarily to the availability of resources aloft (e.g., favorable winds, food). Aerial habitats also represent expedient, and perhaps traditional and frequently used, corridors or routes linking two or more resources that may be airborne, terrestrial, or aquatic (e.g., migratory stopover sites, bats moving between roosts and foraging areas). Microscopic organisms such as bacteria, fungi, spores, and pollen as well as small invertebrates comprise much of the aerial plankton carried aloft by winds or convection. Some suspended microbes are metabolically active, for example drawing resources from a habitat of cloud droplets, and can remain in the airspace for days or weeks, long enough to complete reproductive cycles [6].

Recognizing the airspace as habitat offers a fresh context for evaluating the generality of ecological concepts typically applied to terrestrial and aquatic habitats. Habitats vary in quality in ways that influence survival and reproductive success, so natural selection strongly favors behaviors leading animals to occupy high quality habitat. Like most any habitat the airspace is heterogeneous, so flying organisms exhibit strong preference and selection for certain parts of the airspace over others (e.g., [7,8]). Migrating songbirds and insects often concentrate in altitudinal layers within the air column that favor rapid movement in specific directions [7]. Soaring birds seek out convective thermals and other uplifting air masses (e.g., thermal updrafts, see Figure 1) during foraging and migration [8]. Some insect species find favorable lekking habitat in the airspaces over specific terrestrial features where the resource these airspaces provide is mates. Localized temporary trophic interactions also occur. Invertebrates and some forms of aerial plankton, which may be concentrated by atmospheric motion (e.g., gust fronts), become food for a wide range of insectivorous bats, swifts, swallows, nightjars, dragonflies, robberflies, and other taxa. In effect, these and other attributes of the airspace constitute highly ephemeral habitat patches within the atmospheric equivalent of a landscape, an airscape. As with terrestrial landscapes, aerial habitats within these airscapes can be impacted by anthropogenic disturbance. In large wind facilities, the turbines themselves as well as the downwind influence of their rotation on the local wind field can lead to disruption of the airspace. Such impacts are analogous to the onset of terrestrial habitat fragmentation, and while some birds have been shown to avoid these hazardous aerial habitats [9], some bats may be attracted to such areas which in turn become ecological traps. Unlike habitat selection, territoriality as it relates to defense of resources in the airspace appears non-existent or at best extremely uncommon for reasons consistent with ecological theory; namely, that there are few benefits for animals defending highly unpredictable and transient resources that are locally abundant in space and time. Even so, it should be possible to predict territoriality or other habitat-related ecological and behavioral processes

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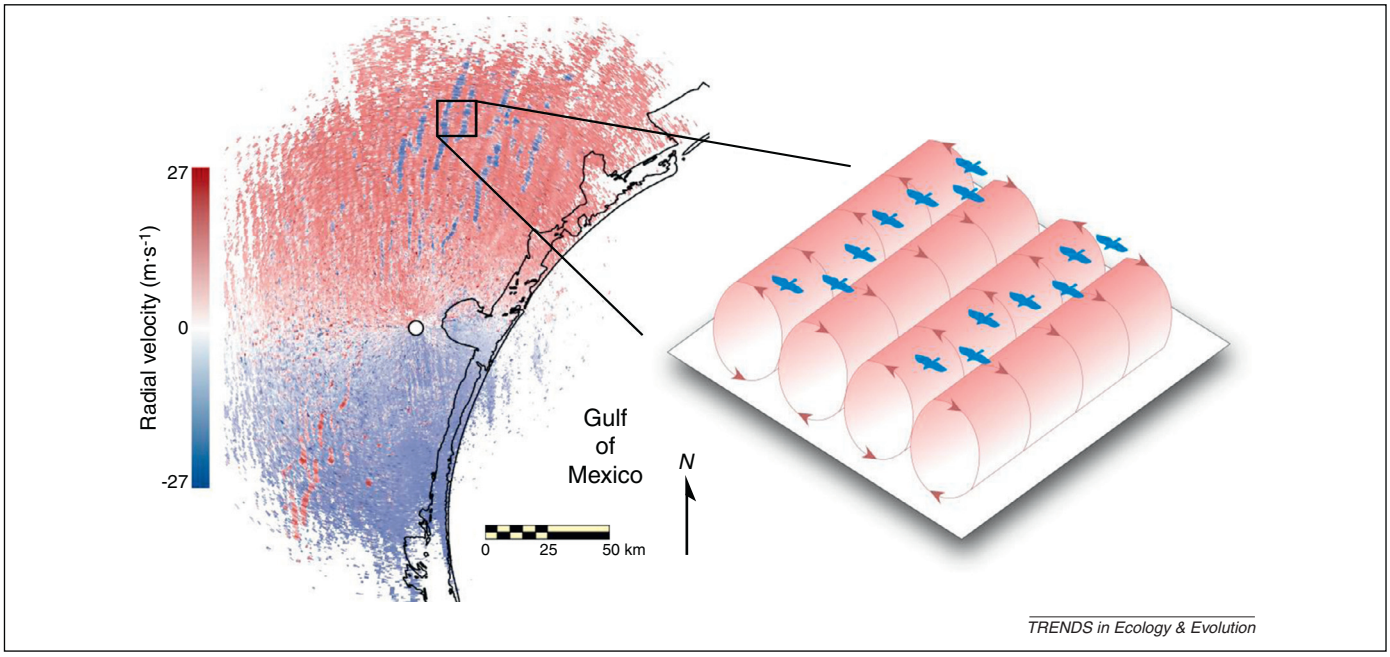

Figure 1. Updrafts in roll vortices constitute habitat patches of favorable for migration by soaring birds. Doppler weather radars routinely show migrating raptors exhibiting habitat preference within highly structured airspaces. On the day shown (28 September, 2009), counter-rotating convective air masses called horizontal roll vortices were present and appear as striations in the Doppler data, where blue indicates movement toward the radar (white dot) and red away. Raptors, appearing as streaks of blue against a red background and vice versa, followed thermal updrafts associated with roll vortices that enabled them to move south against 13 $m \cdot s^{-1}$ winds. Surveys conducted near Corpus Christi, Texas documented that nearly 100 000 raptors, mostly broad-winged hawks (*Buteo platypterus*), migrated through the area on this day (Corpus Christi Hawk Watch, see: http://www.ccbirding.com/thw/watches.html).

in the airspace provided the conditions for that process are met.

The everyday habitats familiar to most humans, such as forests, agricultural fields, and riparian areas, are both visible and relatively static (seasonal changes notwithstanding). The airspace is neither, but these are not disqualifying attributes. Formal definitions and ecological reasoning aside, bias and limits to human perception influence everyday conceptions of habitat. Decades of ecological literature, academic training, and personal experiences firmly link our notion of habitat to terrestrial and aquatic areas. Indeed, biologists often understand an animal's ecology well enough to recognize its habitat in the field. The airspace, however, leaves relatively few clues to its structure, and many features of the airspace that influence animal distributions aloft, such as winds, temperature, precipitation, light conditions, geomagnetism, the presence of prey or predators, are both highly dynamic and often not obvious to humans. Owing to such perceptions, consideration of the airspace as habitat might be questioned for this apparent lack of structure, the often relative paucity of biological diversity, the almost inevitable reliance by its users on terrestrial or aquatic habitats, or its unusually dynamic nature. Definitions of habitat are not constrained on these grounds. Moreover, some of these points describe places that are unquestionably considered habitat. In the open sea, for example, many pelagic fish behave like flying animals. They ride favorable currents and otherwise move through a dynamic yet seemingly featureless fluid environment where habitat structure may be difficult for humans to discern and biological diversity often quite low. Also, the life cycle of many pelagic species is tied to other habitats (e.g., reefs, upwellings) in much the way migratory birds, bats, and insects are temporary residents of the airspace between time spent on breeding and non-breeding areas. The habitat concept should apply to the airspace as readily as it does the open sea.

Anthropogenic impacts and airspace reserves

Recognition of airspace as habitat has implications for policy, regulation, and species conservation (e.g., [9]). Flying animals represent threats to commercial and military aviation, and these organisms are themselves threatened by stationary anthropogenic structures. Applications of species conservation laws explicitly hinge on biologists' notions of habitat. Therefore, codifying an understanding of habitat that includes the airspace equips governmental agencies with a scientific framework for identifying and regulating airspaces that may be important to flight safety, civil infrastructure, and species conservation. The effects on flying animals of developing the airspace mirror those on terrestrial wildlife of developing the landscape. Habitats deemed critical to flying animal populations, such as traditional feeding or migratory flight corridors or airspaces proximal to large bat or bird roosts, may require preservation or some other form of legal protection. In many cases, such 'airspace reserves' could reimagine reserve designs where natural and anthropogenic uses are scheduled according to the predictably cyclic habits of flying animals such as seasonal migration or daily foraging flights.

The emerging field of aeroecology [10] acknowledges growing conflicts between natural and anthropogenic use of airspace even as it proposes to advance our understanding of the ecology of flying animals from the perspective of the airspace. Recognizing airspace as habitat should clarify these efforts, but it requires that biologists expand

their conception of habitat. Either the airspace is habitat or flying animals are exceptional for their ability to be outside it.

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