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Migratory hummingbirds make their own rules: the decision to resume migration along a barrier

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Knowing how naïve migrants respond to intrinsic and extrinsic factors experienced en route will allow a more thorough understanding of the endogenous migratory programme. To understand how inexperienced individuals respond to ecological features, we tracked the migratory departures of juvenile ruby-throated hummingbirds, *Archilochus colubris*, one of the smallest (~ 3 g) and least-studied migrants, along the Gulf of Mexico during southbound migration using an international automated radiotelemetry system. The recent miniaturization of radiotags provides a novel method to track one of the smallest migratory birds, rendering the first information on departure decisions of known hummingbirds in relation to an ecological barrier. Using weather conditions and individual attributes, we also determined which factors influenced the time and direction of departure from a coastal stopover site. Most migrants (83%) departed in the morning, and daily departure time was only influenced by stopover duration, the amount of time spent at a stopover site. The majority (77%) of departure orientations paralleled the coastline, and we found little influence of any factor on departure direction. Our results reveal that (1) juvenile hummingbirds departing coastal Alabama move in a direction indicative of a circum-Gulf path during southbound migration and (2) departure decisions support a fly-and-forage strategy in which hummingbirds likely take advantage of resources along the coast while moving towards their destination.

Many migratory animals face at least one barrier during migration (e.g. Deppe et al., 2015; Marschall, Mather, Parrish, Allison, & McMenemy, 2011; Rittenhouse & Semlitsch, 2006), with migratory birds negotiating large inhospitable ecological features, such as oceans and deserts, to reach breeding or wintering locations (e.g. Biebach et al., 2000; Deppe et al., 2015; Gill, Piersma, Hufford, Servranckx, & Riegen, 2005). In eastern North America, the majority of breeding birds that winter in the tropics must make a critically important decision when arriving at the Gulf of Mexico: fly across or around this feature. Birds that fly across the Gulf of Mexico require stores of fat sufficient to meet the energetic demands of a trans-Gulf flight (Deppe et al., 2015; Sandberg & Moore, 1996; Smolinsky, Diehl, Radzio, Delaney, & Moore, 2013) and those reserves are largely obtained during stopovers (e.g. Woodrey & Moore, 1997; Zenzal & Moore, 2016). Habitats along the northern coast of the Gulf of Mexico provide the last possible stopover before migrants engage in a nonstop flight of ~900 km, and evidence suggests that landbird migrants may not begin to build large fuel loads until they encounter barriers (Caldwell, Odum, & Marshall, 1963; Odum, Connell, & Stoddard, 1961; but see Hou & Welch, 2016). Alternatively, individuals may move along the coastline in a circum-Gulf flight (Alerstam, 2001; Sandberg & Moore, 1996). Whether migrants fly around or over the Gulf, they face important decisions (Deppe et al., 2015): when to depart and in what direction to travel, and each will have repercussions for a successful migration. Both intrinsic and extrinsic factors, which can influence the endogenous programme that governs migratory behaviour, have been found to impact these decisions (e.g. Deppe et al., 2015; Müller et al., 2016; Sandberg & Moore, 1996; Smolinsky et al., 2013).

Intrinsic factors (age, sex and fuel load) influence the decision to depart as well as departure direction (e.g. Deppe et al., 2015;

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Dossman et al., 2016; McKinnon, Fraser, Stanley, & Stutchbury, 2014; Müller et al., 2016; Smolinsky et al., 2013; Thorup, Alerstam, Hake, & Kjellén, 2003). Less experienced juvenile (hatching-year) birds on their first migration may be inadequately prepared to negotiate the Gulf of Mexico (Woodrey, 2000) and/or more prone to orientation errors (Able & Bingman, 1987; Moore, 1984; Ralph, 1978). The role of sex on departure decisions has received less attention. Although Helbig (1991) found no differences in migratory directions between male and female blackcaps, *Sylvia atricapilla*, sex can influence access to resources (Moore, Mabey, & Woodrey, 2003) and wing morphology (Stiles, Altshuler, & Dudley, 2005), both of which may influence an individual's departure decisions (e.g. Bowlin, 2007; Sandberg & Moore, 1996). Fuel stores have the strongest influence on the departure decisions of migrants since it determines the distance a bird can travel (Pennycuick, 2008), which in turn influences how an individual negotiates ecological features (Deppe et al., 2015; Dossman et al., 2016; Sandberg & Moore, 1996; Sjöberg et al., 2015; Smolinsky et al., 2013). Individuals with sufficient fuel stores are able to traverse inhospitable ecological features, while individuals with insufficient fuel stores may choose to spend time fuelling on stopover, reorient in search of better habitat, or if possible, circumnavigate the feature (Deppe et al., 2015; Nilsson & Sjöberg, 2015). Rarely do intrinsic factors act alone; young migrants, for example, are often in leaner condition compared to adult birds (Woodrey & Moore, 1997; Zenzal & Moore, 2016).

Extrinsic factors, specifically atmospheric conditions, can influence the endogenous programme governing the departure decisions of migrants along the northern Gulf of Mexico coast (Able, 1972; Deppe et al., 2015; Müller et al., 2016), especially for individuals preparing for overwater flights (Deppe et al., 2015; Kranstauber, Weinzierl, Wikelski, & Safi, 2015; Richardson, 1978, 1990). Supportive winds decrease the energetic cost of transport and allow a higher migration speed (Kranstauber et al., 2015; Liechti & Bruderer, 1998), while opposing winds, turbulence and/or low visibility from cloud cover or precipitation increase transport costs and may cause orientation problems (e.g. Able, 1982; Ravi et al., 2015; Richardson, 1978; Åkesson, Walinder, Karlsson, & Ehnbom, 2001; Liechti & Bruderer, 1998). Migrants experiencing unfavourable weather conditions may delay their departure until conditions are favourable, depart in a nonpreferred direction, or attempt to compensate for unfavourable wind conditions by altering flight direction to maintain progress towards the destination (Mueller & Berger, 1967; Schaub, Liechti, & Jenni, 2004; Schmaljohann & Naef-Daenzer, 2011; Åkesson & Hedenström, 2000), all of which can have negative carryover effects (e.g. Drake, Rock, Quinlan, Martin, & Green, 2014; Norris & Marra, 2007; Smith & Moore, 2003).

The ruby-throated hummingbird, *Archilochus colubris* (hereafter 'hummingbird'), is the smallest (~3 g) migratory bird in eastern North America, travelling between temperate breeding grounds in the United States and Canada and wintering grounds in Mexico and Central America (Weidensaul, Robinson, Sargent, & Sargent, 2013). While thought to be the only hummingbird that crosses the Gulf of Mexico (e.g. Osborne, 1998; Sargent, 1999), there is no evidence supporting this hypothesis. We suspect that the Gulf of Mexico presents a barrier to hummingbirds because their small size increases susceptibility to unfavourable weather aloft (Ravi et al., 2015). Flight range estimates based on oxygen consumption of hovering flight suggest that a hummingbird with 2 g of fat could fly 1050 km (Lasiewski, 1962), and hummingbirds carry enough fuel, primarily derived from nectar, to cross the Gulf of Mexico under calm wind conditions (Zenzal & Moore, 2016). However, unfavourable atmospheric conditions, particularly headwinds or crosswinds and turbulence, would necessarily decrease the probability of a successful crossing. Given that hummingbirds increase wing beat frequency in turbulent conditions (Ravi et al., 2015), encountering unfavourable winds over the Gulf of Mexico would dangerously increase the energetic cost of flight. The departure decisions of hummingbirds at a coastal stopover site may depend on precisely estimating internal energetic state and prevailing weather conditions. Moreover, our understanding of hummingbird migration, especially in relation to departure decisions from a stopover site, pales in comparison to what is known about other landbird migrants.

In this study, we are the first to examine how intrinsic and extrinsic factors impact the departure decisions, and hence the endogenous programme, of hummingbirds on their first migration. The miniaturization of radiotags and an international automated radiotracking network provide a novel way to understand the movements of known individuals during stopover as they negotiate crossing the Gulf of Mexico. We focus on juvenile birds for three main reasons: (1) the U.S. Bird Banding Laboratory only approved tagging of juveniles; (2) large numbers of juvenile birds were captured at our study site compared to adult birds (see Zenzal & Moore, 2016), ensuring adequate sample sizes; (3) studying departure decisions made by young migrants should improve our understanding of migratory strategies based on endogenous programming or factors experienced en route, especially considering no prior experience with negotiating ecological features. We hypothesized that hummingbirds would behave similarly to songbirds moving along the Gulf coast (Deppe et al., 2015; Sandberg & Moore, 1996; Smolinsky et al., 2013), that is (1) departure direction – trans-Gulf (south), circum-Gulf (east or west) or reverse movement (north) – depends on energetic condition as well as weather variables, and (2) the time of departure depends on weather conditions, specifically individuals should depart during days and times when weather is most favourable for migration. A secondary objective of this study was to determine the extent to which we can generalize what we know about songbird migration to hummingbirds.

METHODS

Study Site and Capture Methods

Ruby-throated hummingbirds were captured at a long-term migration station (30°10′N, 88°00′W; Fig. 1) on the Bon Secour National Wildlife Refuge (NWR) in Fort Morgan, Alabama, U.S.A. The site was composed of scrub-shrub habitat and pine forest with *Pinus elliottii*, *Quercus* spp., *Ilex* spp., *Smilax* spp. and *Serenoa repens* as the dominant species (for a complete description see Zenzal, Fish, Jones, Ospina, & Moore, 2013). Autumn migrants that stopover at this site are immediately confronted with a departure decision in relation to the Gulf of Mexico.

We captured hummingbirds using nylon mist nets ($N = 29$–32; 12 m or 6 m × 2.6 m with 30 mm mesh) from approximately 25 August to 1 November 2011–2014 (see Zenzal & Moore, 2016). We typically operated mist nets from sunrise until noon (Central Daylight Time, CDT), depending on weather conditions and capture rates. We supplemented resources in the study site with 14 artificial feeders. Ten of the feeders were part of a separate study and not associated with netting locations, the remaining four were used to increase hummingbird capture probability; the majority of the netting effort was passive. We banded hummingbirds with U.S. Geological Survey aluminium leg bands, aged (juvenile/hatch year or adult/after hatch year) and sexed them according to Pyle (1997), estimated visible subcutaneous fat (Helms & Drury, 1960), and measured natural wing chord (0.01 mm) and mass (nearest 0.01 g using an electronic balance). Given the high turnover rate of