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REVIEW

How do en route events around the Gulf of Mexico influence migratory landbird populations?

Emily B. Cohen,[1]* Wylie C. Barrow, Jr.,[2] Jeffrey J. Buler,[3] Jill L. Deppe,[4] Andrew Farnsworth,[5] Peter P. Marra,[1] Scott R. McWilliams,[6] David W. Mehlman,[7] R. Randy Wilson,[8] Mark S. Woodrey,[9] and Frank R. Moore[10]

[1] Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, Washington, DC, USA
[2] U.S. Geological Survey, Wetland and Aquatic Research Center, Lafayette, Louisiana, USA
[3] Department of Entomology and Wildlife Ecology, University of Delaware, Newark, Delaware, USA
[4] Department of Biological Sciences, Eastern Illinois University, Charleston, Illinois, USA
[5] Information Science Program, Cornell Lab of Ornithology, Ithaca, New York, USA
[6] Department of Natural Resources Science, Coastal Institute in Kingston, University of Rhode Island, Kingston, Rhode Island, USA
[7] The Nature Conservancy, Albuquerque, New Mexico, USA
[8] Division of Migratory Birds, U.S. Fish and Wildlife Service, Jackson, Mississippi, USA
[9] Coastal Research and Extension Center, Mississippi State University, Biloxi, Mississippi, USA, and Grand Bay National Estuarine Research Reserve, Moss Point, Mississippi, USA
[10] Department of Biological Sciences, The University of Southern Mississippi, Hattiesburg, Mississippi, USA
* Corresponding author: cohene@si.edu

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ABSTRACT

Habitats around the Gulf of Mexico (GOM) provide critical resources for Nearctic–Neotropical migratory landbirds, the majority of which travel across or around the GOM every spring and fall as they migrate between temperate breeding grounds in North America and tropical wintering grounds in the Caribbean and Central and South America. At the same time, ecosystems in the GOM are changing rapidly, with unknown consequences for migratory landbird populations, many of which are experiencing population declines. In general, the extent to which events encountered en route limit migratory bird populations is not well understood. At the same time, information from weather surveillance radar, stable isotopes, tracking, eBird, and genetic datasets is increasingly available to address many of the unanswered questions about bird populations that migrate through stopover and airspace habitats in the GOM. We review the state of the science and identify key research needs to understand the impacts of en route events around the GOM region on populations of intercontinental landbird migrants that breed in North America, including: (1) distribution, timing, and habitat associations; (2) habitat characteristics and quality; (3) migratory connectivity; and (4) threats to and current conservation status of airspace and stopover habitats. Finally, we also call for the development of unified and comprehensive long-term monitoring guidelines and international partnerships to advance our understanding of the role of habitats around the GOM in supporting migratory landbird populations moving between temperate breeding grounds and wintering grounds in Mexico, Central and South America, and the Caribbean.

Keywords: Gulf of Mexico, landbird migration, Nearctic–Neotropical bird population, stopover habitat, airspace habitat, Gulf coast, migratory connectivity, avian monitoring

¿Cómo los eventos en ruta alrededor del Golfo de México influencian a las poblaciones de aves terrestres migratorias?

RESUMEN

Los hábitats alrededor del Golfo de México (GDM) proveen recursos críticos para las aves terrestres migratorias Neártico–Neotropicales, la mayoría de las cuales viaja a través o alrededor del GDM cada primavera y otoño cuando migran entre sus zonas de anidación templadas en Norte América y sus zonas de invernada tropicales en el Caribe y en Centro y Sud América. Al mismo tiempo, los ecosistemas del GDM están cambiando rápidamente, con consecuencias desconocidas para las poblaciones de aves terrestres migratorias, muchas de las cuales están experimentando declives poblacionales. En general, no se entiende bien la magnitud con que los eventos encontrados *en ruta* limitan a las poblaciones de aves migratorias. Al mismo tiempo, la información de radares meteorológicos, isótopos estables, rastreo, eBird y bases de datos genéticos es cada vez más accesible para atender muchas de las preguntas que quedan por responder acerca de las poblaciones de aves que migran a través del espacio aéreo y los hábitats costeros de descanso del GDM. Aquí hacemos una revisión del estado de la ciencia e identificamos necesidades de investigación clave para entender los impactos que los eventos *en ruta* alrededor del GDM tienen sobre las poblaciones de aves terrestres migratorias intercontinentales que anidan en Norte América, incluyendo (1) asociaciones de distribución, temporales y de hábitat; (2) características y calidad del hábitat; (3) conectividad migratoria; y (4) amenazas al espacio aéreo y a los hábitats de descanso, así como su estatus de conservación actual. Finalmente, también hacemos un llamado al desarrollo de lineamientos unificados y exhaustivos para el monitoreo de largo plazo, y a colaboraciones internacionales para mejorar nuestro entendimiento del papel que el hábitat del GDM juega para mantener poblaciones de aves terrestres migratorias que se mueven entre sus zonas de anidación templadas y sus zonas de invernada en México, Centro y Sud América, y el Caribe.

Palabras clave: Golfo de México, migración de aves terrestres, poblaciones de aves Neárticas–Neotropicales, hábitat de descanso, hábitat aéreo, costa del Golfo, conectividad migratoria, monitoreo de ave

Migratory birds can travel awe-inspiring distances, sometimes over sea and inhospitable landscapes, during many round-trip journeys over a lifetime. Although flight through airspace and foraging in stopover habitats that vary in suitability may come with considerable risks, the extent to which resources and threats encountered during migration limit populations remains unclear (Newton 2006). The mortality associated with migration may be substantial (Sillett and Holmes 2002, Newton 2006, Rockwell et al. 2017), but the reproductive benefits of exploiting seasonally abundant resources during the temperate summer and tropical winter presumably balance or outweigh the costs of migration. That said, unprecedented anthropogenic changes in atmospheric conditions aloft and availability of suitable stopover habitat on the ground may be increasing the threats and inflating the costs associated with migration (Wilcove and Wikelski 2008).

The Gulf of Mexico (GOM) is a conspicuous feature of the Neotropical–Nearctic migration system because the majority of landbird species (i.e. passerines and near-passerines with a terrestrial life history [doves, cuckoos, nightjars, hummingbirds, and woodpeckers]) that breed in temperate North America navigate it twice a year during migratory passage to and from wintering grounds in Mexico, Central and South America, and the Caribbean. West coast–breeding Neotropical–Nearctic landbird species rarely navigate the GOM, but eastern- and central-breeding species primarily navigate the GOM region during migration (Rappole 1995, Newton 2008, La Sorte et al. 2014). Additionally, many eastern species have breeding ranges that extend west across the boreal forest, and these western continental populations also move east to navigate the GOM region during migration (Ruegg and Smith 2002, Ruegg et al. 2006, Delmore et al. 2012). Before and after traveling across or around the GOM, billions of landbirds congregate on the barrier islands and in the marshes, scrub, coastal forests, and forested wetlands of the GOM coast from southern Texas to the Florida Keys in the United States, Tamaulipas to Quintana Roo in Mexico, and around western Cuba every spring and fall. These GOM coastal habitats provide critical resources before and after the nonstop flight across the GOM (Moore 1999).

Coastal ecosystems are among the world's most biodiverse, supporting an incredible and dynamic assembly of species. Yet, they are increasingly being altered by natural and anthropogenic stressors including climate change (e.g., increased frequency of severe weather events and sea level rise), pollution (e.g., oil spills, heavy metals, and pesticides), disrupted hydrology (e.g., dams, levees, and canals), and habitat destruction or degradation from human activities (e.g., urban development and commercial harvesting; Abdollahi et al. 2005, Stedman and Dahl 2008, Henkel et al. 2012, Carter et al. 2014). The human population along the GOM coast in the United States has increased at a rate more than double the national average, while wetland habitats are being lost faster here than anywhere else in the United States (Partnership for Gulf Coast Land Conservation 2014). In Mexico, the Yucatan Peninsula is among the world's most vulnerable regions to climate-induced changes, with the expectation that current drying trends will continue (Torrescano-Valle and Folan 2015). Although these changes have largely unknown consequences for the billions of birds that rely on habitats around the GOM coast during migration, it is possible that these changes are contributing to bird population declines.

Analyses of available long-term datasets have revealed population declines in many Nearctic–Neotropical migratory species over the last 40 yr (North American Bird and Conservation Initiative Canada 2012). Although the causes of declines are hard to identify (Wilcove and Wikelski 2008, Rappole 2013), research has predominantly focused on the breeding phase of the annual cycle, overlooking the importance of events during nonbreeding periods, and especially during migration (Marra et al. 2005). Yet, the habitat loss and degradation that affect Nearctic–Neotropical migratory landbirds during breeding and winter residency must also affect them during migration (Moore et al. 1995, 2005, Mehlman et al. 2005, Ewert et al. 2015). The rapid landscape and habitat changes occurring in coastal areas may disproportionately affect species that are dependent on coasts for emergencies or refueling before long sustained flights. That said, we know little, for example, about the distribution and spatial extent of human development in relation to the airspace corridors and stopover habitats used by migrating birds, nor do we understand when and where species or populations move

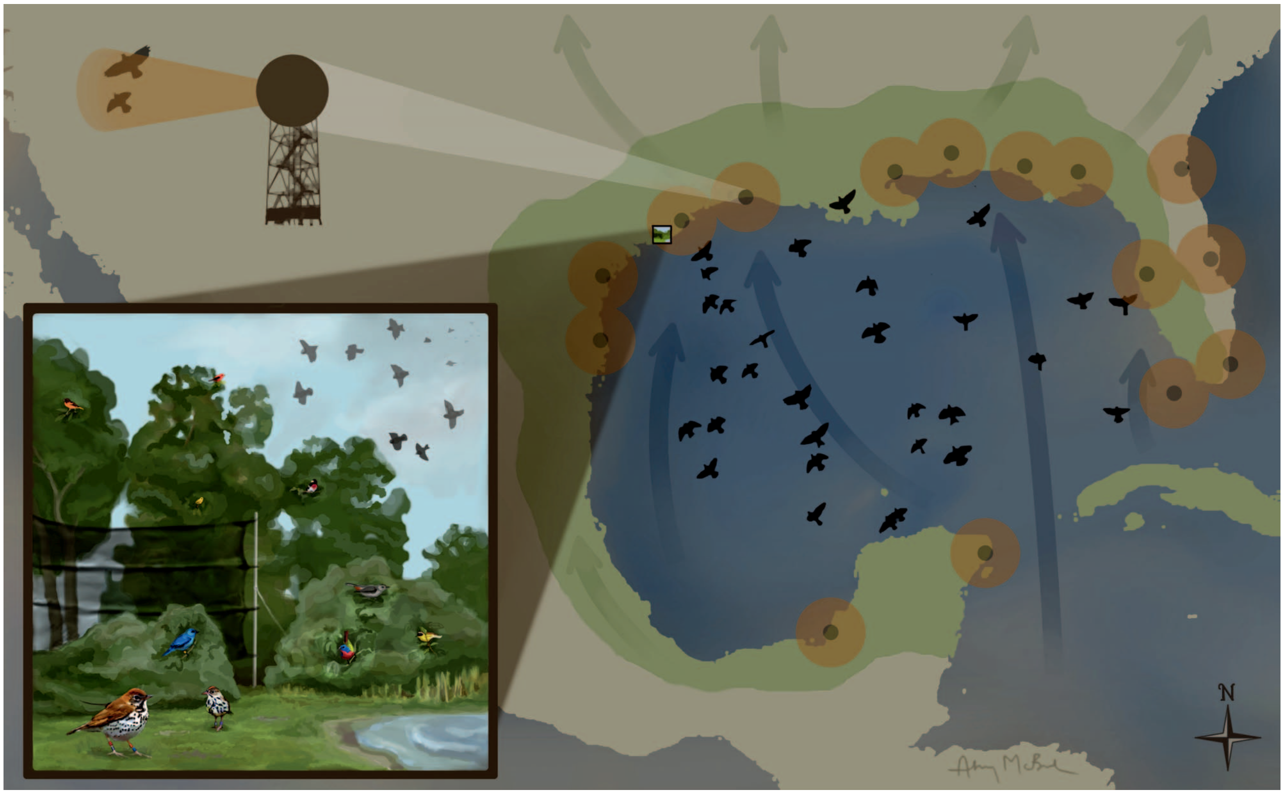

FIGURE 1. Billions of intercontinental migratory landbirds travel through the Gulf of Mexico region every spring (arrows) and fall (not shown), where their distribution in stopover and airspace habitat is detected remotely by weather surveillance radar (circles with inset symbol). In stopover habitat, their migratory behaviors are sampled by mist-netting and banding to measure physiological condition and stopover duration, and migratory connectivity is measured by collection of tissues and attachment of tracking devices (inset image). Artwork by Abby McBride

through the GOM coast region. It is now increasingly possible to fill these information gaps with gulf-wide analyses of citizen science (eBird; ebird.org), weather surveillance radar, tracking, stable isotope, and genetic data to understand the role of habitats along the GOM coast in migratory bird population trends across North America (Figure 1).

If we are to understand how events encountered during migration through the GOM region are contributing to declines among Nearctic–Neotropical migrant species, we must identify the spatial and temporal distributions of species and populations, determine how migrants are affected by natural and anthropogenic events (e.g., hurricanes and oil spills) and habitats encountered during passage, and ultimately quantify the magnitude of those impacts on population trends. To that end, here we assess the state of the science for landbird migrants around the GOM region, including data needs that address: (1) the distribution, timing, and habitat associations of species; (2) habitat characteristics and quality; (3) migratory connectivity of populations; and (4) threats to and current conservation status of airspace corridors and stopover habitats. Further, Nearctic–Neotropical migratory birds are an internationally shared resource, the movements of which directly link habitats across the Northern and Southern hemispheres. Thus, we conclude with a call for the development of unified and comprehensive long-term monitoring guidelines and international partnerships to advance our understanding of the role of habitats around the GOM in population trends of migratory landbirds moving between North America and Central and South America and the Caribbean.

Distribution, Timing, and Habitat Associations

Perhaps the most fundamental information needed to advance our understanding of how events in the GOM region affect Nearctic–Neotropical migratory landbird populations is where and when species occur, on land and in the air, during spring and fall migration. There is a long history of seeking information about the routes taken by migrating landbirds in the GOM region. Beginning in the late 19th century, scientists in the ornithological community began a lengthy debate about whether migrating birds traveled over (e.g., Frazar 1881, Cooke 1904, 1915, Lowery 1946) or around (e.g., Williams 1945,

1950) the GOM. By the middle of the 20th century, the application of weather surveillance radar to the study of bird migration confirmed that large numbers of birds fly directly over the GOM (e.g., Hailman 1962, Gauthreaux 1970, 1971, Hebrard 1971). More recently, tracking of individual birds has confirmed that, although small landbirds have the capacity to fly directly between North and South America, GOM airspace figures prominently in their routes during both spring and fall migration (e.g., Bayly et al. 2013, DeLuca et al. 2015, Deppe et al. 2015, Stanley et al. 2015, Kramer et al. 2017).

Airspace is habitat that spans the interface between terrestrial and aerial domains and, although frequently overlooked, provides critical resources for migrating birds (Kunz et al. 2008, Diehl 2013). In fact, the atmosphere through which migrants fly is a structured and predictable medium that has surely been a selective force on individual success and survival. For example, migratory landbirds most often fly at times of day and at heights where travel is least costly, most rapid, and safest (Kerlinger and Moore 1989, Gauthreaux 1991). Defining airspace habitat for landbird species in the GOM requires information about their temporal and spatial bounds of movement in relation to meteorological, climatological, and geographical features. As such, it is not surprising that the study of airspace habitat has advanced with technologies for remote sensing of meteorological conditions and animal migration using weather surveillance radar (Shamoun-Baranes et al. 2010, Westbrook et al. 2014, Farnsworth et al. 2016, Kelly and Horton 2016). Nor is it surprising that airspace habitat has changed, and likely will continue to change, with the construction of communication cell towers, wind turbines, and buildings, as well as with shifting global climate patterns.

Although migratory birds ought to select altitudes that have the most supportive winds to reduce energetic costs and minimize flight time (Bruderer et al. 1995, Alerstam 2011), little is actually known about flight altitudes over the GOM. Generally, most migrants are found in the first 2,000 m above sea level (Kerlinger and Moore 1989, La Sorte et al. 2014), but it is not unusual to observe migrants flying as high as 5,000 m asl in response to atmospheric conditions (Gauthreaux 1971, Gauthreaux and Belser 1999). Gauthreaux (1991) recorded considerable day-to-day variation in altitude as migrants arrived along the GOM coast of the U.S. in spring, and migrants may increase altitude during the transition from nighttime to daytime flight as they approach the GOM coast (see Myres 1964, Larkin et al. 1979).

Regardless of actual flight altitude, prevailing atmospheric conditions at these altitudes have likely shaped when and where migrants navigate GOM airspace (e.g., Buskirk 1980, Gauthreaux 1991, La Sorte et al. 2014). Fall migration through the region often occurs when synoptic-scale weather systems (e.g., high pressure systems followed by strong cold fronts moving into the GOM) favor transgulf flights during mid-September to mid-October (Gauthreaux et al. 2005, Deppe and Rotenberry 2008, Martinez Leyva et al. 2009, La Sorte et al. 2014). The greatest densities of spring migrants consistently arrive during mid-April to early May along the western GOM coast, in Texas and Louisiana, USA (e.g., Gauthreaux and Belser 1998, 1999, Gauthreaux et al. 2006, Lafleur et al. 2016). Longitudinal passage patterns during spring vary annually and with atmospheric conditions (e.g., Gauthreaux et al. 2006, Lafleur et al. 2016). However, to date, no studies have comprehensively (1) compared airspace habitats in terms of bird density and species composition; (2) compiled migration traffic rates across the decades of available radar data; or (3) addressed intra- and inter-annual variation in airspace use during spring or fall migration. Moreover, how migrants use airspace over the GOM or along the Mexican and Cuban coasts of the GOM remains a significant research challenge given the sparsity of radar coverage. Where there are radars in Mexico and Cuba, data may not be archived or readily available for analysis.

Landbirds rarely migrate nonstop from origin to destination; rather, they stop over periodically for a few hours to a few days between flights (Newton 2007). In fact, the majority of the migration period is spent at stopover sites between flights (Hedenström and Alerstam 1997, Alerstam 2003), and where a migrant stops to rest and replenish fuel stores along the GOM coast is a hierarchical process influenced by endogenous and exogenous conditions (Buler et al. 2007). As migrants approach the U.S. coast at the end of a flight across the GOM, physiological stress (Moore et al. 1990, Kuenzi et al. 1991, Spengler et al. 1995) or severe weather (Lowery 1946, Gauthreaux 1971) may constrain their choice of where to land. These intrinsic and extrinsic constraints may influence how far inland birds travel before making landfall and can produce strong coastal concentrations of migrants. For example, adverse weather (e.g., widespread heavy rain and strong opposing winds) causes migrants to “fall out” in substantial numbers on barrier islands (Moore et al. 1990, Kuenzi et al. 1991) and in inland habitats (Gauthreaux 1971). These mass coastal fallouts of migrants typically occur with movements of air masses across the GOM, particularly frontal boundaries between air masses (e.g., Rappole and Ramos 1994, Russell 2005). Transgulf migrants facing adverse weather conditions often land on the first dry ground that they encounter, resulting in coastal concentrations that have been best documented in Mississippi, Alabama, and the panhandle of Florida, USA (Buler and Moore 2011, Lafleur et al. 2016), and on the northern Yucatan Peninsula, Mexico (Solomon 2016). In eastern Texas and southwestern Louisiana, migrants may also often pass over the inhospitable coastal marshes to land in forested landscapes farther inland (Gauthreaux 1971, Gauthreaux and Belser 1998).

Because passerine birds are, in general, less efficient flyers than other bird taxa (Hedenström and Alerstam 1992, Ward et al. 2001, Rayner and Maybury 2003), they may be under greater pressure to minimize the distance traveled when crossing the GOM by departing from and arriving on the immediate coast. Among landbirds, smaller-bodied species appear more constrained to landing closer to the coast than larger species during both spring and fall migration (Buler et al. 2007). During fall migration, the same coastal effect is true for young birds, which are disproportionately abundant in coastal areas, while adult birds are more abundant in inland areas (Woodrey and Moore 1997).

Although wind patterns and proximity to the coast influence the distribution of migrants among landscapes of the GOM coast, bird densities in the United States during spring migration are also positively correlated with the amount of hardwood forest cover (Buler and Moore 2011, Lafleur et al. 2016). The composition of the landscape may serve as a cue that allows migrants to assess landscape quality prior to landing (Chernetsov 2006, Buler et al. 2007). For example, landscapes with a greater amount of forest cover are associated with greater food availability (Buler et al. 2007) and faster refueling rates of migrants (Ktitorov et al. 2008, Cohen et al. 2014). Tall and structurally diverse forested landscapes may support greater numbers of migratory landbirds than unforested landscapes (Petit 2000, Rodewald and Matthews 2005). After landfall, habitat selection within a landscape is influenced by intrinsic habitat factors (Aborn and Moore 1997, Chernetsov 2005, Seewagen et al. 2010, Cohen et al. 2012), including food abundance, physiognomy, and floristics, which become important for determining habitat use patterns of migrants (Hutto 1985, Petit 2000, Chernetsov 2006, Buler et al. 2007, Cohen et al. 2014). For example, migrants arriving at the Yucatan Peninsula concentrate in mangroves, scrub forests, and coastal dunes, and refine habitat use within these vegetation types based on structural and floristic attributes (Deppe and Rotenberry 2008). That said, migratory birds are capable of using a variety of environments throughout their annual cycles, and habitat use during migration is highly variable both within and among species (e.g., Bairlein 1983, Petit 2000). Migrants occur in more diverse landscapes during migration than during stationary phases of the annual cycle, which not is surprising given the greater diversity of environments encountered en route (Zuckerberg et al. 2016). This observed variability may represent adaptive behavioral and physiological plasticity that permits migrants to successfully occupy a diverse array of habitat types as well as respond to novel circumstances during migration (Martin and Karr 1990).

Radar mapping studies have also revealed high-density use of forests in human-dominated landscapes, particularly urban parks within large cities in areas outside the GOM coast region (Bonter et al. 2009, Buler and Dawson 2014), and citizen science data corroborate this affinity of migrants with human-dominated landscapes across the United States (La Sorte et al. 2014, Zuckerberg et al. 2016), which may be influenced by attraction to anthropogenic light (Watson et al. 2016). Similarly, field surveys in Veracruz, Mexico, have documented high use of forest patches in highly fragmented, agriculturally dominated landscapes (Ruelas Inzunza et al. 2000) and in urban parks (González-García et al. 2014). Therefore, although migrating birds often congregate during stopover in hardwood forest, habitat patches embedded in urban or agricultural landscapes may also be important stopover sites (e.g., Seewagen and Slayton 2008, Seewagen et al. 2010).

In general, knowledge about the distribution and habitat requirements of migrants along the Mexican and Caribbean coasts of the GOM lags behind that of our knowledge for the United States Gulf Coast, and is based primarily on brief inventories (e.g., MacKinnon and Aburto 2003, Estrada and Coates-Estrada 2005) and observational records (i.e. eBird). However, a handful of studies in Mexico (González-García et al. 2014) and Cuba (González-Alonso et al. 2006) have identified regionally important stopover sites and documented the importance of successional vegetation (Winker 1995a), forest patches in agricultural landscapes (Ruelas Inzunza et al. 2005, Deppe and Rotenberry 2008), and small natural areas embedded in coastal urban centers (Raymundo Sanchez 2010). Whereas sparse spatiotemporal sampling has left significant gaps in our understanding of migrant distributions and habitat affiliations, analyses of gulf-wide radar and eBird data have the potential to provide much of this missing information.

Habitat Characteristics and Quality

Assessments of how and when events in the GOM region affect population dynamics require an additional understanding of the survival and condition of migrants within stopover sites. Whether a given stopover site meets the needs of Nearctic–Neotropical migrant landbirds depends on their nutritional requirements and the distribution, quality, and quantity of resources at the stopover site. Here we consider the individual migrant's ability to successfully refuel at a stopover site in relation to the availability of resources, and describe how energy-based models could be used to quantify the habitat quality of landscapes around the GOM coast.

Important biotic variables that determine the suitability of stopover habitats include (1) the intensity of competition for food resources, (2) shelter provided from predators, and (3) the type, abundance, and spatial distribution of food resources (Cohen et al. 2012). Landbird densities at stopover sites often far exceed the highest densities reached during the breeding or wintering periods of the annual cycle (Moore et al. 1993). Therefore, although rarely studied, food-based competition is expected at stopover sites when high densities of migrants are refueling during migration. For example, Moore and Yong (1991) found that the density of potential competitors negatively affected fuel deposition rates during stopover on the GOM coast. Further, the selection of habitat at inland stopover sites has been positively related to the abundance of arthropods (Graber and Graber 1983, Hutto 1985, Cohen et al. 2012), thereby potentially increasing competition for food resources.

Predation risk also alters habitat quality during stopover. Coastlines often concentrate raptors during their migrations (Kerlinger and Moore 1989), and several species of raptor that migrate around the GOM occur frequently in coastal habitats (e.g., Aborn 1994, Woltmann 2001). This may increase the conflict between meeting energetic demands and predator avoidance. For example, Blue-gray Gnatcatchers (*Polioptila caerulea*) have been found to move deeper into cover and away from food resources as the risk of hawk predation increases (Cimprich et al. 2005). Lean birds also take greater risks of exposure to predators to satisfy energetic demands than birds with fuel reserves (Cimprich and Moore 2006). In many situations, the energetic cost of avoiding predation may outweigh the energetic benefit of foraging in a habitat possessing high-quality food, such as a coastal thicket with fruiting shrubs (Mudrzynski and Norment 2013, Smith and McWilliams 2015), so that habitats with lower-quality food but little or no predation may be preferred.

Arguably the most important constraint during migration is finding sufficient resources to meet energetic demands (McWilliams et al. 2004, McGrath et al. 2009, Cohen et al. 2014). Many landbirds are known to change their diets to high-energy foods during migration, including fruits and nectar, which may also satisfy their protein requirements during migration even though the protein content of these foods is relatively low (Langlois and McWilliams 2010). In northern latitudes, birds that are predominantly insectivorous during the breeding season change their diets to eat more fruit during fall migration (Parrish 1997). Along the Gulf Coast of Louisiana and Texas, Barrow et al. (2000) found that 44% of migrant species consumed fruit during spring and only 24% of species consumed fruit during fall, although more recent studies suggest that frugivory of landbirds during fall migration along the GOM coast may be more common (F. Moore personal observation). For example, some fall migrants that stop on small islands off the northern coast of the Yucatan Peninsula gain mass by foraging on fruit that is abundant in coastal scrub (Solomon 2016). An improved understanding of the plant species that migrants forage on and their role in satisfying the energetic requirements of migration is needed for creating guidelines for the management and restoration of habitats in the GOM coast region (Martinez Leyva et al. 2009, Wood et al. 2012).

Habitat quality in the form of food resources is difficult to quantify when it is measured at a landscape scale. In the vicinity of the GOM, the density of migrants within hardwood forest patches is positively associated with arthropod and fruit abundance (Buler et al. 2007), and migrants have higher fuel deposition rates in landscapes with more hardwood forest cover (Cohen et al. 2014). In habitat containing sparse and spatially restricted food resources, migrants forage locally where food is abundant, whereas in habitat with more broadly abundant food resources, migrants are less restricted in their foraging movements (Cohen et al. 2012). Sites may also vary in function and quality between spring and fall migration (Winker 1995b, Shaw and Winker 2011). Bioenergetic models are a tool for measuring the relationship between food resources and bird fitness to quantify the quality of stopover habitat and its carrying capacity for migratory birds (e.g., Williams et al. 2014).

Bioenergetic models integrate information about the basic energetic requirements of birds with estimates of the energy available on the landscape. Although they have not yet been applied to landbird migrant habitat around the GOM coast, we outline the potential of these models for integrating available information about the energetic condition of migrants with habitat characteristics to quantify habitat quality. Energy-based habitat models require information about the daily energetic requirements of birds (e.g., the sum of energy required for maintenance and activity; King 1973, McKinney and McWilliams 2005, Servello et al. 2005, Williams et al. 2014). Wikelski et al. (2003) provide one of the few direct estimates of daily energetic requirements of actively migrating landbirds, for *Catharus* species migrating north through the Great Lakes region. They estimated that 30-g thrushes expended 133 kJ per day on days that included a migratory flight (an average of 4.6 hr of flying on a given night) and ~88 kJ per day on stopover days without a migratory flight. These direct estimates of daily energetic requirements for freely migrating thrushes confirm that information about daily fat accumulation can be used to quantify the energetic value of a habitat for migrating landbirds. Further, estimates of daily energetic requirements for one individual can be extrapolated to reflect the numbers of individuals using a habitat, thereby estimating the amount of that habitat needed to support a target number of individuals within a landscape. Such models have been used widely and successfully for migratory waterbirds

(Williams et al. 2014) and should be useful for population-based habitat assessments along the GOM coast. We recommend that managers use local sampling to measure the condition of birds and the availability of resources in habitats to build and assess landscape-scale models. These models can be used with an adaptive management approach to ensure adequate resources for migrating landbirds.

Migratory Connectivity

Understanding how events during migration affect population dynamics requires information not only about where species occur, but also when and where populations occur and how they are connected to other phases of the annual cycle, i.e. en route migratory connectivity (Webster et al. 2002). Events that migrating birds encounter along the GOM coast may either affect populations during migration or carryover to affect them during subsequent phases of the annual cycle (e.g., Paxton and Moore 2015, Hewson et al. 2016, Sorensen et al. 2016). Furthermore, events along the GOM coast are unlikely to have an equal influence on all populations of Nearctic–Neotropical migratory species that move through the region (Henkel et al. 2012). For these reasons, measuring the impacts of events encountered during migration requires information that links stopover and airspace habitats with specific breeding and wintering populations (Runge et al. 2014).

En route migratory connectivity to breeding and wintering areas has both a spatial and a temporal component, and an understanding of both is needed to appreciate the potential impacts and carryover effects of stopover and airspace habitats on the survival, timing, and condition of migrating populations. With the exception of a few sites and species, the spatial and temporal patterns of migratory connectivity through the GOM coast region are poorly understood. However, tracking between breeding and wintering areas has revealed that, during spring migration, Ovenbirds (*Seiurus aurocapilla*) that winter in Mexico and Central America and breed in western North America move across, or sometimes around, the GOM, while those that winter in the Caribbean and breed in northeastern North America migrate along the Atlantic coast of Florida (Hallworth et al. 2015). It is not clear whether western-breeding populations of Ovenbirds differentiate where they cross the GOM (Hallworth et al. 2015). Wood Thrushes (*Hylocichla mustelina*) that winter in Mexico and Central America migrate across, and sometimes around, the GOM in spring, primarily taking a route into the Mississippi River delta of Louisiana and into eastern Texas (Stanley et al. 2015). During fall migration, Wood Thrushes cross the GOM and pass farther east, from Florida to Louisiana (Stanley et al. 2015). In both spring and fall, Wood Thrush passage longitudes through the GOM coast region are positively correlated with breeding longitudes (Stanley et al. 2015). During spring migration, Eastern Kingbirds (*Tyrannus tyrannus*) tracked from Oklahoma and Nebraska, USA, crossed the GOM through the mid-Texas coast, with one bird migrating through the Florida and Alabama border (Jahn et al. 2013). Eastern-, central-, and western-breeding populations of Golden-winged Warbler (*Vermivora chrysoptera*) all navigate the GOM region, with spatial differentiation among populations during fall but not spring migration (Kramer et al. 2017). Inland and coastal subspecies of Swainson's Thrush (*Catharus ustulatus*) use divergent migration routes, with only the inland subspecies crossing (during fall) or circumventing (during spring) the GOM (Delmore et al. 2012). Little information is available about the consistency of passage routes or timing, other than for 10 Wood Thrushes tracked for 2 yr, which showed substantial annual variability in migration routes across the GOM (Stanley et al. 2012). Information about en route migratory connectivity patterns through the GOM coast region derived from tracking data has been limited by small sample sizes of few species and incomplete sampling across the range. Therefore, multisite and multiyear studies are necessary to understand population-specific airspace and stopover habitat use throughout the GOM region.

There is evidence for temporal patterns of migratory connectivity from stable isotopes in the tissues of birds captured on the GOM coast: Analysis of stable isotopes in tissues of migrating birds captured at stopover sites on the GOM coast has revealed spatial patterns of migratory connectivity and carryover effects of winter habitat quality. Populations of 5 forest-breeding migrants, the Acadian Flycatcher (*Empidonax virescens*), Ovenbird, Black-and-white Warbler (*Mniotilta varia*), Hooded Warbler (*Setophaga citrina*), and American Redstart (*Setophaga ruticilla*), from the southeastern United States to the Canadian boreal forests moved through a single spring stopover site in eastern Louisiana, with southern-breeding populations passing through the site earlier than northern-breeding populations for all species except the Acadian Flycatcher (Langin et al. 2009). Additionally, passage timing to spring stopover on the northern coast of the GOM was later for Black-and-white Warblers from poorer quality winter habitat (Paxton and Moore 2015). In contrast, Wood Thrush energetic condition during winter did not influence spring passage timing across the GOM, suggesting that this species compensates for the effects of winter habitat quality during spring migration (McKinnon et al. 2015). Two long-term analyses of spring passage phenology suggest that migrant timing and condition may be influenced by both long-term climate change and extreme global weather events. Species that winter in Central America, but not South America, have delayed the timing of their spring migration across the GOM over the past 20 yr (Cohen et al. 2015), while species that winter in South America, but not Central America, arrive in poorer condition during El Niño years (Paxton et al. 2014). These studies were not population-specific, but suggest that carryover effects from winter into spring migration may be common. Analyses of stable isotopes in tissues of migrating birds captured at stopover sites on the GOM coast have the potential to provide considerable information about spatial and temporal patterns of en route migratory connectivity with breeding latitudes. Toward this end, we recommend that migration banding stations on the GOM coast use common protocols, including tissue collection from as many species as possible, for future analyses of migratory connectivity.

Knowledge of migratory connectivity is essential to understand the role of the GOM coast on the population dynamics of Nearctic–Neotropical migratory species, as well as to assess the potential impacts of future conservation investments (Sheehy et al. 2011, Henkel et al. 2012). Advancing tracking technologies and stable isotope and genomics analyses (Rushing et al. 2014, Hallworth and Marra 2015, Ruegg et al. 2016) are making it increasingly possible to understand full life cycle migratory connectivity, and measures of population-specific distributions around the GOM can be paired with information about the distribution of threats and habitats to assess the impacts on specific populations.

Current Conservation Status and Threats Faced by GOM Habitats

In addition to knowledge of where migratory species occur, their survival and condition in those areas, and how populations are linked to other phases of the annual cycle, a thorough understanding of the influence of events around the GOM region on migrant populations requires information about current and future threats to habitats. Coastal ecosystems are changing dramatically, and factors associated with the impacts of coastal development threaten migratory landbird habitats. The most obvious of these factors is direct habitat loss from clearing of forest and scrubland, filling of wetlands, dredging, and hardening of shorelines. In particular, urban development along coastlines can be greater than in inland areas (Buler and Moore 2011) and may lead to increased exposure of migrants to anthropogenic sources of mortality, including collisions with human-made structures and vehicles, pesticides, and cat predation (Loss et al. 2015). Habitat degradation may occur with forest cutting and fragmentation, increases in predators or competitors attracted to human communities, and introduction of invasive species (Buler and Moore 2011). Global climate change will also alter the character of coastal ecosystems and affect habitat availability and quality for migratory landbirds. For example, protected areas on the northern coast of the Yucatan Peninsula are predicted to switch from subtropical dry forest to subtropical thorn woodland or tropical dry forest if CO_2 concentrations double in the atmosphere (Villers-Rúz and Trejo-Vázquez 1998). Finally, tall structures such as communication cell towers and wind turbines effectively decrease the permeability of the lower altitudes of airspace that migratory birds move through, leading to increased mortality (Loss et al. 2013, 2014a, 2014b). These changes can have either direct or indirect effects on the demography of migratory landbirds. The direct consequence is increased mortality, while indirect consequences are more subtle and influence demographic parameters in the future by reducing the probability of survival or reproduction (e.g., Marra et al. 1998, Smith and Moore 2003, 2005). Land managers and conservation planners need to know whether these factors are changing or have changed in ways that shift population limits.

The only region-wide synthesis of the conservation status of stopover sites thought to be important for Nearctic–Neotropical migratory birds in the United States and Mexico is based on expert opinion (Duncan et al. 2002). This analysis found that only 23% of identified stopover sites in the United States and 19% in Mexico had some level of protection (Duncan et al. 2002). Therefore, >75% of the stopover sites hypothesized to be important remain unprotected in the United States and Mexico, indicating that more conservation effort needs to be dedicated to this region. For example, only 3% of the estimated 2,107 ha of forested chenier habitat (coastal hardwoods on relict beach ridges in southwestern Lousiana), known to be an important spring stopover area for migrant birds in Louisiana (Moore 1999, Barrow et al. 2005), is protected by a conservation entity (M. Parr personal communication). Although Cuba was not analyzed in this synthesis, some stopover sites known to have a high abundance and richness of migratory birds (e.g., Península de Guanahacabibes, Cayo Santa María, Cayo Coco; González-Alonso et al. 2006) are located in protected areas (Sykes et al. 2007). In addition to protected conservation status, management of stopover sites is needed to maintain long-term value, though this topic has seldom been directly addressed (Moore et al. 1993, Barrow et al. 2005). Of the 2.3 million ha of identified stopover sites in the United States that are under some level of protection, only 33% is managed for biodiversity, suggesting that more work will be needed to maintain even protected sites as suitable habitat (Duncan et al. 2002). The need for management is especially essential given the current and potential threats to these sites from invasive species and increased storm frequency (e.g., Barrow et al. 2007). An analysis of the conservation status of stopover sites identified to be important through gulf-wide synthesis

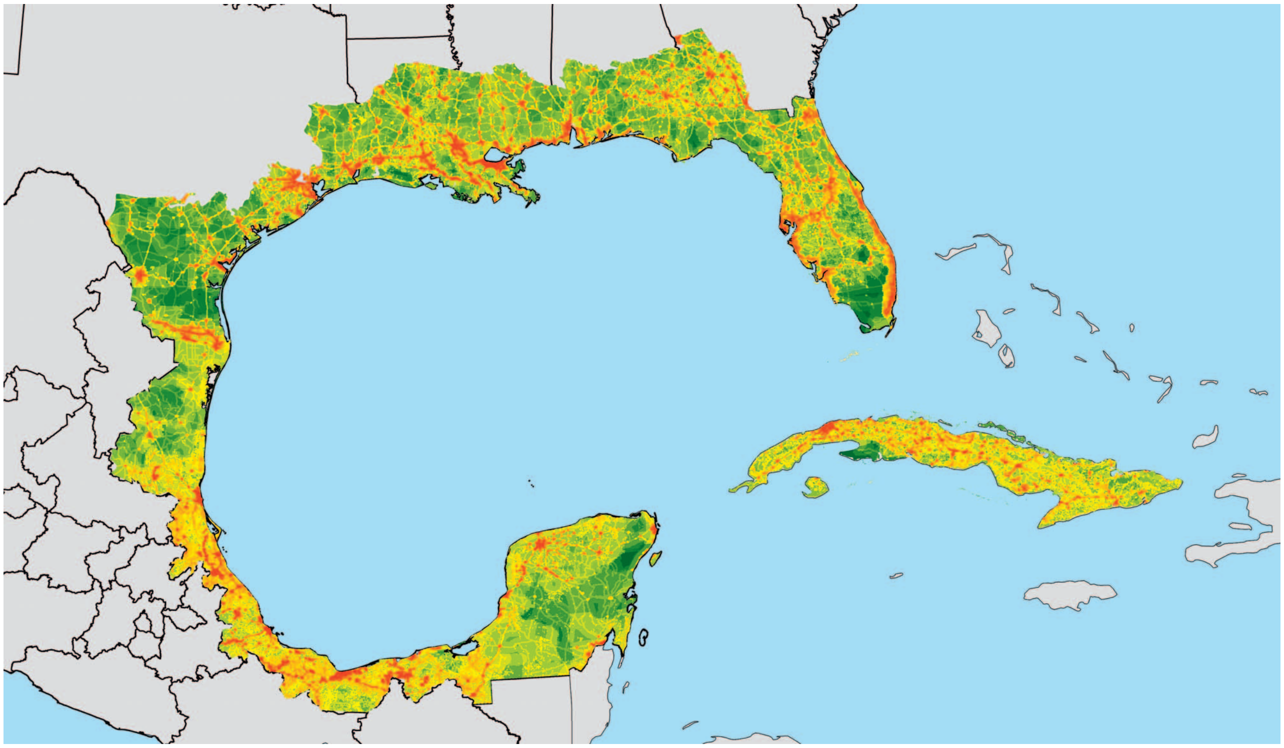

FIGURE 2. Human footprint analysis of population density, urbanization, roads, railroads, navigable rivers, coastlines, land use, and nighttime light to quantify the level of threat to migrating birds from human population growth and development (http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic) around the coast of the Gulf of Mexico shows that the threat level ranges from green (low to no threat) through yellow and orange to red (high threat). The Columbia Bottomlands in Texas, USA, and the Central Veracruz region in Mexico, in particular, are relatively highly developed with few protected areas.

of migrant distributions and habitat quality is necessary, as is increased information about the conservation and management status of sites in Cuba.

Brenner et al. (2016) conducted a threats analysis that incorporated the loss of wetlands, forests, and mangroves, and the distribution of urban and suburban areas, roads, tall structures, wind turbines, and electrical lines, and found that these threats were broadly distributed across the GOM region but were particularly concentrated on the Florida peninsula. We mapped the GOM region using an available human footprint dataset that combines population density, urbanization, roads, railroads, navigable rivers, coastlines, land use, and nighttime light to quantify the level of threat to migrating birds from human population growth and development (http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic). The footprint map suggested that the stopover sites hypothesized to be important in the United States had only a slightly higher human footprint than the rest of the U.S. GOM coast, while in Mexico, stopover sites considered to be important had a lower human footprint than the rest of the Mexican GOM coast (Figure 2). The Columbia Bottomlands in Texas and the central Veracruz region in Mexico, in particular, are relatively highly developed with few protected areas (Figure 2). Moreover, threats to birds, including the illegal capture and trade of some migratory species in Mexico and Cuba, can be a significant source of mortality and must also be considered (Sykes et al. 2007, Garrido and Kirkconnell 2011). We urgently need a comprehensive, high-resolution, gulf-wide analysis of the distribution of threats and mortality rates specific to migratory landbirds.

A Call for Coordinated Monitoring

A comprehensive, standardized, and collaborative gulf-wide monitoring program for migratory birds is needed to provide baseline information about landbird populations in the GOM region to inform long-term conservation planning. Region-wide monitoring is the best means to measure the impacts on migrating landbird populations of ecosystem stressors such as urban development, oil spills, hurricanes, and sea level rise, as well as the intended and unintended effects of the many current and planned conservation and restoration investments around the coast of the GOM. At best, the current approach of localized and uncoordinated efforts for monitoring provides an incomplete picture of bird abundance and response to management; at worst, these data misrepresent or overestimate the value of specific management and restoration practices (Braun et al. 1978, Strassmann 1987, Meretsky et al. 2006).

Monitoring is often the most discussed but least implemented element of a conservation project or management plan (Arnett and Sallabanks 1998). Consequently, the ability of natural resource management agencies and the bird conservation community to manage resources is severely compromised (Lindenmayer and Likens 2009, McDonald-Madden et al. 2010, Williams 2011). To address this issue, the Gulf of Mexico Avian Monitoring Network (GoMAMN) has utilized a structured decision-making process (Keeney 2009) to identify and agree upon fundamental objectives that maximize the relevance, scientific rigor, and integration of monitoring efforts across agencies and organizations. Specifically, GoMAMN has suggested that relevant monitoring efforts should focus on (1) establishing reliable estimates of population size and trends; (2) evaluating the effectiveness of habitat restoration and management efforts for restoring avian populations and their habitats; and (3) understanding how ecological processes affect birds and their habitats (Wilson 2015; www.gomamn.org/). GoMAMN provides a forum within which conservation partners can collaborate and implement a coordinated monitoring framework that recognizes and builds on established monitoring programs. This monitoring framework will connect, leverage, and integrate existing efforts into a comprehensive avian monitoring program to address contemporary and long-term conservation needs of avian populations and their habitats within the GOM region.

Nearctic–Neotropical migratory birds are an internationally shared resource. Even if it were possible to conserve and manage all stopover habitats on the GOM coast of the United States, migratory birds would be unlikely to benefit without comparable efforts in Mexico and Cuba (e.g., Ruelas Inzunza et al. 2005, González-Alonso et al. 2006, Deppe and Rotenberry 2008). Therefore, understanding the population dynamics of migratory birds requires the adoption of a truly collaborative, multinational approach (Boom 2012). Traditionally, the amicable relationship between Mexico and the United States has facilitated the development of collaborations and opportunities for applying many U.S.-based research funds to projects based in Mexico. For example, the U.S. Fish and Wildlife Service Neotropical Migratory Bird Conservation Act and North American Wetlands Conservation Act grants allow funds to be directed toward (1) research and monitoring, (2) capacity building, (3) land protection, restoration, and management, and (4) infrastructure development in Mexico. There are many experts studying migratory birds in Cuba (González-Alonso et al. 1992), and Mexican resource management agencies such as the Secretary of the Environment and Natural Resources (Secretaría de Medio Ambiente y Recursos Naturales) and National Council of Science and Technology (Consejo Nacional de Ciencia y Tecnología) provide funding opportunities to coordinate with Cuban researchers. With recent political changes, the potential for United States–Cuba collaboration is poised to expand (Boom 2012). Workshops jointly led by Cuban, Mexican, and U.S. researchers have not only proven to be a successful way to standardize methods and share expertise, but have also served as a way to motivate participants to pursue research on migratory birds (González-Alonso et al. 1992). Future GoMAMN workshops focused on international scientific exchange would help to advance international gulf-wide monitoring and collaboration.

Future Research and Monitoring Needs

Comprehensive information about the distributions of migratory species and their populations, habitat quality, and threats will not be trivial to collect or synthesize given the seasonal and annual variability of landbird migration through the GOM region. Yet this information is essential to understand the role of GOM coast habitats in declining migratory landbird population trends and to predict the impacts of future changes. Fortunately, many of the logistical, technological, and analytical constraints on the collection and utilization of these data no longer exist. Until recently, detection of migrants was limited to scattered field studies that primarily characterized local distribution patterns and to a handful of tracking studies that characterized the migratory behaviors of species large enough to carry devices. Today, advances in technology permit a number of new and innovative means to advance our understanding of how landbirds utilize the GOM: (1) weather surveillance radar is a tool for region-wide mapping of the distribution of landbird species in stopover and airspace habitat (e.g., Buler and Dawson 2014, Farnsworth et al. 2016, Horton et al. 2016, Lafleur et al. 2016); (2) archival tracking devices are light enough to follow the migratory behaviors of small birds (Hallworth and Marra 2015); (3) automated radio-telemetry arrays are a tool for detecting the passage locations of migrants tagged on breeding or wintering ranges (e.g., Taylor et al. 2011, Deppe et al. 2015); (4) stable isotopes in tissues and genetics are a means of assigning migrating individuals to destination populations (e.g., Langin et al. 2009, Rushing et al. 2014, Ruegg et al. 2016); and (5) citizen science data (e.g., eBird) are increasingly available for mapping regional distributions, timing, and habitat affiliations of many species (La Sorte et al. 2014, Zuckerberg et al. 2016). Concurrent with the emergence of these new technologies to study and understand migratory birds around the GOM region, a new integrated and coordinated network of scientists and land managers is providing a forum within which to collaborate and communicate information for the implementation of unified, increasingly multinational bird monitoring efforts. We now have the opportunity not only to understand the role of the GOM region in the demography of migratory birds, but also to provide this essential science to inform conservation strategies and educate decision-makers, managers, landowners, and the public sector about the billions of migratory birds that move through and across the barrier islands, beaches, marshes, open water, and airspace habitats of the GOM region and are one of the Western Hemisphere's greatest living resources.

We emphasize these key research and monitoring needs for intercontinental landbird migrants in the GOM region during spring and fall:

(1) Comprehensive analysis of weather surveillance radar data to identify and characterize stopover habitat hotspots, including their consistency of use over time and in relation to anthropogenic and natural changes;
(2) Comprehensive analysis of weather surveillance radar data to identify airspace corridors, their characteristics in relation to meteorology and climatology, and their consistency of use over time and in relation to anthropogenicand natural changes;
(3) Analysis of eBird data to map species-specific distributions, timing, and landscape associations;
(4) Comprehensive monitoring (e.g., visual, banding, acoustic) on oil platforms to measure distribution, abundance, and mortality during passage over the GOM;
(5) Comprehensive monitoring at a network of long-term, coordinated coastal banding sites to collect tissues and measure species-specific passage phenology over time and the condition of migrants in relation to competition, predation pressure, and food resources;
(6) Analysis of stable isotopes in tissues collected from migrating birds captured at stopover sites to measure species-specific patterns of spatial and temporal en route migratory connectivity with breeding latitudes;
(7) Comprehensive installation of tracking towers and tagging of many species to measure migratory connectivity across and around the GOM and movements of populations relative to habitat quality and conservation and restoration investments;
(8) Field studies of plant and insect food for migrants, energetic value of these foods for migrants, and how restoration can enhance these resources;
(9) Development of energy-based models to measure landscape-scale stopover habitat quality for use in adaptive management;
(10) Field and radar studies to measure attraction and understand the potentially detrimental role of artificial light at night in urban landscapes and on oil platforms;
(11) Comprehensive, high-resolution analysis of the spatial distribution of risk and mortality attributed to buildings, vehicles, pesticides, feral and domestic cats, illegal capture and trade, communication cell towers, and wind turbines; and
(12) Increased collaboration through GoMAMN around the GOM region, including between the United States, Mexico, and Cuba, as well as the establishment of similar forums in countries where Nearctic–Neotropical migratory landbirds breed and winter (e.g., Canada, Central and South America, and the Caribbean), to identify core values and needs to enhance integrated, coordinated monitoring efforts.

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