Biology of landbird migrants: a stopover perspective

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ABSTRACT—This perspective on the stopover biology of migratory landbirds is organized around the response of migrants to challenges that can arise during stopover and how events during stopover are interconnected with other phases of the annual cycle. Landbird migrants seldom move nonstop from origin to destination, rather they stopover periodically, sometimes for a few hours, sometimes days. How well migrants meet challenges that arise during passage in a timely manner influences the success of their migration; a successful migration is measured in terms of survival and reproductive performance over the annual cycle. What transpires during migration is not isolated from other phases of the migrant’s annual cycle. Events taking place in one phase carry over to affect an individual’s biology in other phases, including linkage between breeding and wintering phases and the intervening migratory phase. Received 28 November 2017. Accepted 4 December 2017.

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The benefits of intercontinental migration, regardless of whether they accrue through increased survivorship by overwintering in the tropics, increased productivity by breeding in seasonally rich temperate areas, or both, are balanced against the costs of migration. Traveling between temperate and tropical areas comes with risks, and the mortality associated with long-distance migration, although difficult to estimate, may be substantial (Sillett and Holmes 2002, Paxton et al. 2017, Rockwell et al. 2017), is likely age-dependent (Greenberg 1980), and may limit populations (Newton 2006). Although intercontinental migratory birds move great, often awe-inspiring distances, invariably over large inhospitable landscapes, they seldom migrate nonstop from origin to destination,
but rather stopover periodically, sometimes for a few hours, sometimes days. Indeed, it is thought that most of migration time is spent on stopover (Hedenström and Alerstam 1997) when energy expended is high relative to migratory flight (Wikelski et al. 2003; see also Nudds and Bryant 2000, Bowlin et al. 2005).

My research program has integrated field and laboratory approaches to study the ecology, behavior, and ecophysiology of intercontinental landbird (i.e., passerines and near passerines with a terrestrial life history) migrants when they stopover during passage. This perspective on the stopover biology of migratory landbirds is organized around their response to challenges that can arise during stopover and the interconnection between events during stopover and other phases of the annual cycle. Why migrating bird stopover determines in large measure what they do during stopover: a migrant may be low on fuel stores, off course and find it easier to correct and reorient while on the ground, fatigued, and in need of rest and sleep after flying long hours or against unfavorable winds; experiencing or anticipating inclement weather; out of nighttime as a nocturnal migrant; or maybe the endogenous time–direction program (Gwinner 1996) simply dictates a pause en route to destination.

Response to challenges

Visualize a Red-eyed Vireo (Vireo olivaceus) gleaning small geometrid larvae from the edge of hackberry leaves in the middle of a long, narrow cheniere near Johnson’s Bayou, Louisiana, following a mid-April flight across the Gulf of Mexico. She finds herself in unfamiliar surroundings at a time when energy demand may be high, and possibly faced with the need to acquire food in a short period of time while balancing conflicting demands between predator avoidance and food acquisition, competition with other migrants and resident birds if resources are limited, unfavorable weather, exposure to parasites and pathogens, and loss of sleep, not to mention the need to make accurate and judicious decisions upon departure. How well she meets challenges in a timely manner determines the success of her migration (Alerstam and Lindström 1990), measured as successful in terms of survival and reproductive performance (Alerstam et al. 2003).

Arrival and habitat use

A migrant’s relationship to habitat during passage is best understood as a scale-dependent, hierarchically ordered process (Hutto 1985, Moore et al. 1995, Simons et al. 2000, Buler et al. 2007). For example, while traveling northward across the Gulf of Mexico, prevailing wind patterns and not habitat quality per se explain why a migrating Red-eyed Vireo finds herself approaching the southwest coast of Louisiana rather than barrier islands off the coast of Mississippi, not likely aware that landing in one place and not the other may have consequences (Simons et al. 2000). Although an interplay of intrinsic (e.g., fuel load) and extrinsic (e.g., weather) factors influence where landfall is made (Buler and Moore 2011), hardwood forest cover is strongly linked to migrant density (e.g., Buler and Dawson 2014, Lafleur et al. 2016) and likely serves as an indicator of habitat quality (Cohen et al. 2014) and cue to select a landing site (Buler et al. 2007, Kititorov et al. 2008, McCabe and Olsen 2015). Nocturnally migrating songbirds generally end their flight before dawn (Kerlinger and Moore 1989) when visual sensitivity may constrain a detailed evaluation of habitat features, so acoustic information may be used to recognize habitats when making landfall, including places already occupied by conspecifics (Herremans 1990, Mukhin et al. 2008, Alessi et al. 2010).

Once on the ground, migrants often display a preference for certain habitats and select among alternatives (Moore et al. 1990, Aborn and Moore 1997, Chemetsov 2006, Slager et al. 2015), which is not surprising if selection of a habitat has consequences for time and condition (Cohen et al. 2012). The process of seeking preferred habitat involves exploration (Aborn and Moore 1997; Paxton et al. 2008; Cohen et al. 2012, 2014), which may explain some landscape-scale movements observed at night (Mills et al. 2011) as well as ‘morning flights’ of migratory songbirds shortly after sunrise. Although some morning movements may be ongoing migration (Bingman 1980, Moore 1986, Sandberg et al. 2002), and morning hours do provide favorable atmospheric flight conditions (Kerlinger and Moore 1989), it is also likely that
migrants engage in morning flight to seek suitable stopover habitat (Alerstam 1978, Lindström and Alerstam 1986, Chernetsov 2011, Van Doren et al. 2015) or compensate for drift experienced during nocturnal migration (Moore 1990, Van Doren et al. 2015). Efforts notwithstanding, favorable stopover habitat, where a fat-depleted migrant, for example, can rapidly meet nutritional needs, is probably limited in an absolute sense (Simons et al. 2000), or effectively so because migrants are probably constrained to minimize exploration time during stopover (Paxton et al. 2008, Cohen et al. 2014; sensu Hedenström and Alerstam 1997).

Acquiring information in an unfamiliar place

After a migratory flight, a songbird almost invariably finds herself in a place different from the one occupied the previous day, much less the previous year (Stanley et al. 2012), which begs the question: Why not stopover in a familiar place where resources and sources of stress are better known? Certainly experienced adult songbird migrants have the navigational ability to return to previously experienced places (Åkesson et al. 2014), but the benefit of doing so for a small songbird en route is probably offset by 2 factors (Catry et al. 2004): (1) lost time to destination correcting for wind drift and/or waiting for favorable wind conditions at departure, and (2) the general availability of terrestrial habitats where a positive energy balance can at least be maintained during passage (Wang and Moore 1997). Moreover, changes in the abundance or suitability of stopover sites (e.g., deforestation, fragmentation, urbanization) along the migratory route would likely select for increased departure fuel load (greater margin of safety) and/or longer flights rather than en route philopatry.

Although the cues migratory birds use to make decisions about resources and sources of stress during stopover warrants more attention (Moore and Aborn 2000, McGrath et al. 2009, Wolfe et al. 2014), migrants that gather reliable information about unfamiliar places in a timely fashion (Cohen et al. 2014) increase the likelihood of a successful migration (Németh and Moore 2014). Individuals can estimate food availability or predator pressure using personal information gathered while sampling habitat or with social information obtained while observing the behavior of other migrants, or a combination of the 2 sources of information. For example, focal sampling of free-ranging songbird migrants following flight across the Gulf of Mexico suggests that birds respond to a lack of information by initially foraging in temporary feeding assemblages and are more likely to do so if fat-depleted (Németh and Moore 2007). Lean birds are probably more willing to trade off the reliability of information gained on their own for quicker and safer access to albeit less reliable information gained by foraging in a flock (Németh and Moore 2014).

Acquisition of nutrients

Arguably the most important constraint during migration is to acquire enough food to meet nutritional needs in a timely fashion. Birds in migratory disposition are especially efficient foragers (Moore and Simm 1985) and select a diet that achieves energy maximization relative to birds not in migratory condition (Bairlein 2003). Moreover, observation of free-ranging migrants during stopover reveals that energetic condition influences microhabitat selection (Tietz and Johnson 2007) and foraging behavior (Loria and Moore 1990, Wang and Moore 2005). Lean birds expand their foraging repertoire, broaden their use of substrate, and forage at a faster pace than do birds with residual fat stores (Loria and Moore 1990). Consequently, they achieve a favorable energy balance more quickly than they otherwise would (Wang and Moore 2005), thereby decreasing length of stopover and presumably time spent on migration. Younger migrants, however, are often less efficient foragers (Heise and Moore 2003), not to mention behaviorally subordinate to adults (Terrill 1987, Moore et al. 2003). Inefficiency and lack of experience would be especially consequential if food becomes scarce or when migrants experience heightened energy demand in anticipation of a possible energetic ‘short fall’ (Moore and Simm 1986, Woodrey and Moore 1997).

En route competition

If migrants with similar nutritional requirements and heightened energy find themselves locally concentrated during stopover, competition could depress food resources and reduce the rate at which migrants restore essential fuel loads (Hans-
son and Petersson 1989, Moore and Wang 1991, Kelly et al. 2002). Further, social asymmetries often mediate competitive interactions, and subordinate status is known to affect priority access to food during passage and handicap fuel deposition rates in landbird migrants (Lindström et al. 1990, Carpenter et al. 1993, Wang et al. 1998, Moore et al. 2003). Male Pied Flycatchers (Ficedula hypoleuca), for example, have advantages over females competing for food resources, and females are more likely to challenge dominants and successfully access resources in a same-sex environment than in an opposite-sex environment (Moore et al. 2003). Given the energetic demands of migration, social asymmetries would be expected to be condition dependent; lean migrants value food more than fat individuals and gain priority access to food despite pre-existing status (Moore et al. 2003).

During passage, migrants encounter resident birds during stopover, including conspecifics that settled at a breeding destination earlier in spring. The influx of migrants may adversely affect the behavior and habitat use of residents (Bensusan et al. 2011), whereas residents defending territorial space may constrain use of preferred stopover habitat (E. Cohen, Smithsonian Conservation Biology Institute, 2007–2008, pers. obs.).

How often migrants actually compete for resources during stopover depends in part on how often they are locally concentrated during passage, which is tied to the number of birds aloft and the availability and configuration of stopover habitat. The volume of birds aloft depends on the occurrence of favorable synoptic weather events (e.g., Richardson 1978, 1990; Gauthreaux 1991), which creates ‘waves’ of migrants over a landscape that may consist of attractive habitat fragments embedded within a less hospitable matrix (e.g., Tankersley and Orvis 2003).

**Predation pressure**

Predation is a hazard during migration (Lindström 1989, Aborn 1994), and migrants assess risk of predation during stopover (Cimprich et al. 2005). Moreover, a combination of factors during stopover creates a complex, dynamic environment within which migrants trade-off safety and foraging, which may be especially problematic for less experienced, young birds; (1) predation risk is variable and unpredictable during migration; (2) migrants carry relatively large fuel loads, which is known to affect escape performance (Kullberg et al. 1996, Lind et al. 1999); (3) migrants often experience elevated foraging demands; (4) there is pressure to travel quickly; and (5) information about predation risks and foraging opportunities is lacking. Changes in risk of predation during stopover alter both foraging location and intensity (Cimprich and Moore 2006), which could affect fuel deposition rates and stopover length. Fatter birds should be more cautious because they are more vulnerable, or lean birds may simply be more risk prone because of increased energetic demand (Moore 1994, Dierschke 2003, Cimprich and Moore 2006). While predation risk clearly affects the behavior of migrants during stopover, the proximate cues used to assess risk and how accurately they accomplish this task are poorly known.

**Microbes, pathogens, and parasites**

Migration is no time to be fighting an infection given time and energetic constraints, especially if birds in migratory disposition suppress immune responsiveness (Owen and Moore 2006; Owen and Moore 2008a, 2008b). Although migrating birds may be expected to invest in immune function given exposure to parasites and pathogens during their travels, immune function may be suppressed in response to anticipated energetic demands or downregulated to avoid immunopathology during periods of stress. Whereas flight performance per se may not be particularly stressful or immunosuppressive (Hasselquist et al. 2007), birds that arrive at a stopover site in poor condition display reduced immune responsiveness, although it rebounds with improving condition during stopover (Owen and Moore 2008a).

A variety of parasites and pathogenic microorganisms are associated with intercontinental songbird migrants (Hubalek 2004). For example, it is not uncommon to detect several blood parasites (Haemoproteus, Plasmodium, Leucocytozoon, and Trypanosoma) in migratory birds in spring, and fuel load is negatively associated with density of Haemoproteus spp. infection in several species (Garvin et al. 2006). When reduced energetic condition caused by blood parasites results in delayed arrival on the breeding grounds (DeGroote
and Rodewald 2010, Hatch et al. 2010), infections may have important consequences for host fitness. Migratory songbirds also serve as transport carriers for immature ticks, including exotic ticks carrying tick-borne pathogens from tropical wintering areas to temperate breeding areas (e.g., Mukherjee et al. 2014, Cohen et al. 2015), although it remains uncertain if migratory birds are negatively affected by ticks during stopover (Morris et al. 2007) or whether they serve as competent reservoir hosts for tick-borne pathogens (Budachetri et al. 2017). Migratory birds are competent reservoir hosts and potential dispersal vehicles for West Nile Virus (Owen et al. 2006).

Of course, not all microbes are harmful. Migrating birds are characterized by a diverse gut microbiota (Lewis et al. 2016), the composition of which rapidly converges across individuals that stopover in the same place (Lewis et al. 2017). The rapid change in composition is probably a response to local conditions, including available food resources, and similar reconstitution of gut function after food withdrawal and prolonged flight. It remains to be seen if the composition of this microbiota has functional consequences for migratory birds.

**Sleepy migrants**

Most bird species are active during the day and much less so at night, except during migration when the migratory flights of most songbirds take place. Generally, a migratory bird begins a night’s flight after sunset before astronomical twilight and flies for half or more of the night. By migrating at night, a migrant experiences decreased predatory pressure, improved atmospheric conditions for flight, and more time to feed during the day (Kerlinger and Moore 1989). Nevertheless, a night migrant necessarily experiences loss of sleep, yet surprisingly may not experience negative consequences (e.g., Rattenborg et al. 2004). If loss of sleep has negative consequences, a migrating bird should show compensatory adjustments (Fuchs et al. 2006), including the possibility of semi-hemispheric sleep while aloft (Fuchs et al. 2009). Compensatory sleep during the day, however, is not without costs; less time is available for foraging, which could have consequences in units of time and condition, and may explain why observations of sleep during stopover are uncommon. When observed, sleep events are short (e.g., Schwilch et al. 2002, Németh 2009, Covino and Cooney 2015), not unlike the daytime micro-naps recorded in captive Swainson’s Thrushes (Catharus ustulatus) when in migratory disposition (Fuchs et al. 2006, 2009).

**Weather**

Atmospheric conditions acting across widely different scales have a profound influence on the biology of migratory birds (Richardson 1978, 1990; Gauthreaux et al. 2005; Shamoun-Baranes et al. 2017; LaSorte et al. 2014), including when and where a migrant stops over (e.g., Gauthreaux 1971, 1972), the abundance and availability of resources (Dobbs et al. 2009, Lain et al. 2017), likelihood of departure (e.g., Matthews and Rodewald 2010), and when during the day and in what direction to depart a stopover site (Danhardt and Lindström 2001, Smolinsky et al. 2013, Sjöberg et al. 2015, Deppe et al. 2015). Yet, surprisingly little is known about the effect of precipitation (Smith and McWilliams 2014), temperature, and wind condition on, for example, activity budgets during stopover, much less fuel deposition rates and departure fuel loads. For example, migrants might change their activity pattern during the day in anticipation of departure when experiencing atmospheric conditions consistent with favorable conditions for migratory flight; that is, they increase foraging activity to reach appropriate departure fuel load or decrease activity to reduce energy expenditure if carrying an adequate fuel load for departure.

**Departure decisions**

Migration is about reaching destinations in a timely fashion and in good nutritional condition, so stopover must come to an end. Some individuals stay but a few hours and depart as soon as possible, usually the night following arrival (‘transients/flyers’), while ‘non-transients/feeders’ stay for a few to several days (Rappole and Warner 1976). This dichotomy hints at the striking variation in stopover duration within individuals from site-to-site over a migration season, among individuals within species, age and sex cohorts as well as among species—variation that reflects the complexity inherent in the stopover biology of migratory birds and the capacity for individual
strategic variation in decision making (sensu Winkler et al. 2014).

A migrant’s decision to depart or remain at a stopover site is governed by the bird’s behavioral and physiological states as well as its temporal and spatial position within a programmed migration schedule (Jenni and Schaub 2003). This program provides a framework within which other factors influence stopover decisions (Deppe et al. 2015), including species-, age-, and sex-specific use of habitat and day-to-day variation in the threat of predation, competitor density, and weather. Migrating birds gather information, integrate environmental and internal state data, and make departure decisions presumably in relation to current and anticipated conditions (Moore et al. 2017). How migrant’s gauge current, much less future, conditions is poorly known, but they do so with success (Ward et al. forthcoming).

Just prior to the departure of free-ranging birds (e.g., Cochran et al. 2004) and onset of migratory activity (zugunruhe) in captive birds (e.g., Ramenofsky et al. 2008), a period of inactivity, sometimes termed quiescence, is observed. This poorly understood quiescent period may reflect a cessation of movement as light levels decline, but it also is probably the time when migrants gather flight information and prepare for departure; that is, they calibrate compasses, assess internal energetic state and meteorological conditions, switch metabolically from fuel deposition to a mobilization phase, and maybe take a nap (Schofield et al. forthcoming 2018).

When during the day and in what direction to depart are important decisions also influenced by the interplay of intrinsic and extrinsic factors (Sandberg and Moore 1996a). Nocturnally migrating landbirds generally depart on a migratory flight shortly after sunset and before astronomical twilight, a window of time linked to the onset of favorable atmospheric conditions (Kerlinger and Moore 1989) and the opportunity to integrate directional information known to be important in migratory orientation (Moore 1987, Pakhomov and Chernetsov 2014). Not all nocturnal migrants depart during this window of time, and that variation informs on the interplay of factors influencing this decision (Bolshakov et al. 2007, Müller et al. 2016).

For example, Swainson’s Thrushes carrying sufficient fuel loads to cross the Gulf of Mexico depart within the window of time between sunset and astronomical twilight regardless of age and move in a southerly direction out over the Gulf of Mexico (Smolinsky et al. 2013). Doing so takes advantage of the entire night in relation to a long-distance, trans-Gulf flight, recognizing that trans-Gulf migrants almost invariably arrive on the opposite coast the next day and often continue flight well beyond the coast (Gauthreaux 1971, 1972; Lafleur et al. 2016). Birds departing later in the night invariably carried fuel loads insufficient for an entire night’s flight, much less a trans-Gulf flight, and moved in northerly directions away from the coast (Smolinsky et al. 2013), presumably in search of more extensive forested habitat (Buler and Moore 2011). In an ambitious follow up study, Swainson’s Thrushes as well as Red-eyed Vireos and Wood Thrushes (Hylocichla mustelina) were radio-tracked before and after crossing the Gulf of Mexico in fall to assess departure decisions in relation to trans-Gulf movement (Deppe et al. 2015, Bolus et al. 2017; Ward et al. forthcoming 2018). These studies found that adequate fuel load is essential, seasonal timing and synoptic weather matter, wind profit affects crossing time, species differ in their willingness to cross the Gulf of Mexico, and age does not affect success. Migratory songbirds are not intimidated by large stretches of inhospitable terrain (e.g., Bulte et al. 2014, Gómez et al. 2017); the key is risk management and a margin of safety (see Moore and Kerlinger 1992).

**Carryover effects and seasonal transitions**

The development and application of new tracking technology is moving us closer to the reconstruction of migratory routes and spatial connectivity across the annual cycle while reinforcing the notion that what transpires during migration is not isolated from other phases of the annual cycle (Marra et al. 2015). Events in one phase carry over to affect an individual’s biology in other phases (e.g., Sandberg and Moore 1996b), including linkage between breeding and wintering phases and the intervening migratory phase. For example, climatic variation in passage areas has important carryover effects on breeding phenology and performance of intercontinental songbird migrants, presumably driven by en route effects
on time and condition (Finch et al. 2014). More to the point, climatic variability across tropical wintering areas affects the energetic condition of Nearctic-Neotropical migratory songbirds during spring migration (Paxton et al. 2014). Species that over-wintered in South America experienced significantly drier environments during El Niño years than birds over-wintering in the Caribbean and Central America. During El Niño years, birds from South America arrive in poorer condition and are more likely to stopover immediately along the northern coast of the Gulf of Mexico, whereas Caribbean–Central American wintering birds showed no such differences between El Niño and La Niña years (Paxton et al. 2014). If lean migrants stay longer than usual to refuel and do not make up for lost time, arrival at the destination is delayed. Migrants that arrive late on the breeding grounds may jeopardize opportunities to secure a territory or a mate (Smith and Moore 2005a). If migrants depart a stopover site with low departure fuel loads, they have a smaller ‘margin of safety’ to buffer the effect of adverse conditions on the availability of food at the next stopover or the destination (Smith and Moore 2003, 2005b; Holzschuh and Deutschlander 2016). If a migrant expects to ‘catch-up’ with the overall time schedule of migration and maintain a margin of safety vis-a-vis anticipated energetic demands, she must refuel faster than average during the next stopover, and a domino effect may ensue.

Poorly known is how events during other phases of the annual cycle affect migration strategy during stopover and vice versa (Moore et al. 2005). The challenge is not simply to track the movement of a migrant through the annual cycle (difficult enough), but rather to understand a migrant’s strategy (fuel deposition rate, departure fuel load, stopover duration) based on conditions experienced prior to stopover and the migrant’s destination. Intrinsic markers (e.g., carbon and hydrogen isotopic signatures) can be used to link stopover biology to winter habitat quality and breeding destination (Paxton and Moore 2015, 2017). Among Black-and-White Warblers (Mniotilta varia) migrating to the same breeding region, males and females arriving early on stopover come from higher quality wintering habitat; the benefits of occupying high-quality habitat during the winter positively influence the timing of migration. Male warblers arriving early to the stopover site, however, do not carry larger fuel loads than later arriving birds that originate from poor-quality habitat, regardless of breeding destination, a pattern consistent with males minimizing time at the expense of energy. By contrast, female arrival condition on stopover does not vary with timing of migration or breeding destination, consistent with a strategy that minimizes energy expenditure during migration. Moreover, refueling rate and duration of stopover is influenced by breeding destination and timing of arrival at stopover site, although the relationships are subtle and sex-dependent (Paxton and Moore 2017).

Imagine watching a Wilson’s Warbler (Cardellina pusilla) forage in a cottonwood at a stopover site in southern California along the Colorado River on her way to a distant breeding location. Knowing whether the bird is early or late in relation to its programmed migration schedule, how far she must travel to reach her breeding destination, and where she has been are essential pieces of information when trying to draw inferences about the individual’s stopover biology and migration strategy (Paxton and Moore 2017). Tracking the origin of a migratory songbird using noninvasive, intrinsic marking techniques is a challenging endeavor, but methods are now available that combine information from high resolution genetic markers with stable isotopes and habitat suitability models to spatially infer the breeding origin of migrants captured anywhere along their migratory pathways (Ruegg et al. 2014, 2017). Identifying migratory connections across the annual cycle is vitally important for studies of migrant ecology and conservation (Bayly et al. 2017, Cohen et al. 2017).

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productive and memorable. Our first long term study site was established in the mid-1980s at Peveto Woods, part of a cheniere (coastal forest) in Cameron Parish, Louisiana, with the help of my doctoral mentor, Sidney Gauthreaux, Jr, and the Baton Rouge Audubon Society. Radar ornithology later confirmed what birders suspected for years, namely that southwest Louisiana consistently experiences some of the highest density of spring migration along the northern coast of the Gulf of Mexico. It was in Peveto Woods that I experienced my first “fallout” of trans-Gulf migrants. The chenieres of coastal Louisiana provide a truly remarkable setting to appreciate bird migration, not to mention to fall in love with crawfish, blue crab, boudin, and Cajun music. We established other study sites along the northern coast of the Gulf of Mexico, notably on Ft. Morgan Peninsula, Alabama, and on the barrier islands off the coast of Mississippi, and over time studied stopover biology elsewhere in North America as well as in Europe. Our research over the years gained support from the National Geographic Society, US National Park Service, National Science Foundation, US Fish & Wildlife Service, USDA Forest Service, National Fish and Wildlife Foundation, US Department of the Navy, NOAA/Sea Grant, US Department of Defense, Center for Disease Control/Mississippi Department of Health, Birmingham Audubon Society, and the Louisiana Ornithological Society.

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