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COMMENTARY

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ABSTRACT
The occurrence of molt during migration, known as "molt-migration," has increasingly received attention across many avian taxa since first being described in waterfowl in the 1960s. However, despite the many different types of molt stages and strategies, most, if not all, uses of the term "molt-migration" apply to the definitive prebasic molt of flight feathers in post-breeding adults, whereas fewer studies address migration for body-feather molts. Here, we argue that the current definition of molt-migration, as applied, is limited in focus relative to the diverse ways in which it can manifest in avian populations. We suggest a new, broader definition of molt-migration and highlight examples of molt-migration as traditionally defined, and the many examples that have not been defined as such. We propose a new, 2-tiered typology for defining different forms of molt-migration, based on (1) its progression relative to stationary portions of the annual cycle, and (2) the stage of molt involved. In order to advance our understanding of the ecology and evolution of this increasingly documented phenomenon and apply this knowledge to conservation and management, avian researchers must begin to utilize a common framework for describing molt-migration in its various forms.

Keywords: migration, molt, molt-migration, seasonal interactions, stopover

Expandiendo la definición tradicional de muda migratoria

RESUMEN
La existencia de la muda durante la migración, conocida como "muda-migratoria," ha recibido una atención creciente a través de muchos taxa de aves, desde que se describió por primera vez en aves acuáticas en la década de 1960. Sin embargo, a pesar de los muchos tipos diferentes de etapas y estrategias de muda, la mayoría, sino todos, de los usos del término "muda-migratoria" se refiere a la muda prebásica definitiva de las plumas del vuelo en adultos post-reproductivos, mientras que pocos estudios apuntan a la muda de las plumas del cuerpo durante la migración. Aquí, argumentamos que la definición actual de muda-migratoria, cómo se aplica, tiene un enfoque limitado en relación con la diversidad de maneras en la cual puede manifestarse en las poblaciones de aves. Sugerimos una nueva definición más amplia de muda-migratoria y destacamos ejemplos de muda-migratoria como se define tradicionalmente, y los muchos ejemplos que no han sido definidos como tales. Proponemos una nueva tipología de dos niveles para definir diferentes formas de muda-migratoria, basados en (1) su progresión en relación con porciones estacionarias del ciclo anual y (2) la etapa de muda involucrada. Para mejorar nuestro entendimiento de la ecología y la evolución de este fenómeno cada vez más documentado y para aplicar este conocimiento a la conservación y el manejo, los investigadores de aves deben comenzar a utilizar un marco común para describir la muda-migratoria en sus varias formas.

Palabras clave: interacciones estacionales, parada, migración, muda, muda-migratoria

Overview

Migratory birds must balance 3 energetically expensive events during the annual cycle: breeding, migration, and molt. Although breeding and migration have received an enormous amount of attention, relatively little work has been dedicated to understanding the evolution of molt strategies (Leu and Thompson 2002). This is an important knowledge gap, given the energetic costs associated with molt (Dietz et al. 1992, Vézina et al. 2009) and the vast variation in when, where, and which feathers birds molt

(e.g., Howell et al. 2003, Pyle et al. 2009, Lourenço and Piersma 2015, Wiegardt et al. 2017b). Indeed, molt appears to be highly labile, with different molt strategies arising within and among species independently over relatively short evolutionary time (Pyle et al. 2009, Pyle 2013a).

Many birds balance energetically expensive events through temporal separation, for example by performing the definitive prebasic molt prior to fall migration (Pyle 1997, Leu and Thompson 2002, Froehlich et al. 2005). However, this strategy does not hold for all species, with

some species actively molting feathers while migrating and others interrupting migration to molt at stopover locations. The nature of this type of molt strategy can take many forms, even within a single family (e.g., Leu and Thompson 2002). Further complicating matters, there is substantial variation in which feathers are molted (e.g., complete or partial molt; contour feathers or flight feathers), as well as intraspecific variation among (Nordell et al. 2016), and even within (Tonra et al. 2015), individuals. This variation is often captured by the single term "molt-migration" (for flight-feather molts), or lacks any classification at all (e.g., for partial molts). As a result, the term "molt-migration" is lacking in specificity and is in need of an updated definition that better captures its various forms. The impetus behind this commentary was to shed light on the numerous molt strategies used by migratory birds and to disentangle and simplify the language used to describe these strategies. We also hope to draw more attention to the complexity of molt—a chronically understudied but critical aspect of avian life history.

Defining Molt Migration

Since the term "molt-migration" was first introduced, the definition of this phenomenon has evolved in ways that slightly alter what types of movements are included. Salomonsen (1968; summarized by Jehl 1990) defined molt-migration as "birds moving from the breeding grounds to a special moulting area where they can rapidly replace their flight feathers at a low predation risk before resuming their migration to the winter quarters." This definition confines molt-migration to post-breeding flight-feather molts, and to the use of "special moulting areas." Thus, instances where molting sites also serve as refueling locations, or molt occurs during active migration, are seemingly excluded. Per Salomonsen's definition, molt-migration is distinct from migration to overwintering sites, as opposed to occurring during/overlapping with migration. Leu and Thompson (2002) updated the definition to describe when "bird species interrupt the annual fall migration at specific locations to molt their flight feathers." Unlike the previous definition, Leu and Thompson more explicitly imply molt-migration occurs within the larger migration life history stage and they included both elevational and latitudinal movements in their review of molt-migration. However, not captured in this definition are birds that molt continuously during active migration (though they include such examples in their literature review). Further, it excludes spring migration and continues to refer to molt as the primary function of the area utilized, excluding birds that molt at staging/stopover sites also utilized for refueling. Pyle et al. (2009) largely used the same definition as Leu and Thompson (2002) in describing the "monsoon migrant" systems of western North America,

but are more general in saying birds "stop and molt," broadening the definition beyond flight-feather molt, as in the 2 previous definitions.

In previous definitions (e.g., Salomonsen 1968), molt-migration is treated primarily as a form of movement relative to molt, and separate from migration. However, there are many examples of instances where migratory movement and molt of feathers overlap, such that the destinations are not solely visited for molting, and serve as refueling sites as well (e.g., Lourenço and Piersma 2015; see below for more examples). Thus, we feel that a more comprehensive definition is required to capture the full breadth of strategies whereby these 2 life history stages overlap and interact. Ramenofsky and Wingfield (2006) reviewed and conceptualized such overlap in life history stages, in the context of the transition leading into breeding for migratory birds. Later, Wingfield (2008) described the organization of annual cycles in terms of a "finite state machine," where annual cycles have a finite number of distinct stages that exist on a continuum, with the development of one stage often overlapping completion of another. We feel such an annual cycle approach is germane to the instances of transitioning between molt and migration. Therefore, we define molt-migration as "temporal overlap in the molt and migration life history stages." This definition includes all instances where scheduled feather replacement occurs at "special molting areas" (sensu Salomonsen 1968), refueling sites, or during active migration. Further, it can be applied where molts that do not include flight feathers occur during migration. With this broader definition that better represents the way in which molt-migration is referred to in the literature, we capture a wide variety of systems, thus requiring a typology to more specifically classify each one. In order to develop such a system, we first review some examples of how molt-migration is manifest in birds.

Examples of Molt-Migration Strategies as Traditionally Defined

Flight-feather Molt Occurring Entirely on Migratory Stopover. Perhaps the first use of the term "molt-migration" was by Salomonsen (1968) in describing waterfowl post-breeding movements. Specifically, the term was applied to the movements of many ducks, and later other Anseriformes (e.g., geese; Ogilve 1978), to secluded marshes in order to complete flight-feather replacement during their definitive prebasic molt, including a period of flightlessness. This phenomenon, which has been detailed in many species of waterfowl since Salomonsen (e.g., Hohman et al. 1992, Robert et al. 2002, Dickson et al. 2012), revealed a critical component of the habitat needs specific to molt in waterfowl, separate from wintering and breeding. In addition, several species of grebe (Family Podicipedidae) have a similar molt-migration as waterfowl

(e.g., Storer and Jehl 1985, Piersma 1988). For example, Eared Grebes (*Podiceps nigricollis*) halt migration at hypersaline lakes in the western U.S. to complete flight-feather molt (e.g., Mono Lake, Great Salt Lake; Storer and Jehl 1985). These grebes also endure a flightless period during this stopover as they molt all of their flight feathers. Some shorebirds migrate to staging areas during fall migration and replace flight feathers, such as Wilson's Phalaropes (*Phalaropus tricolor*), which partially replace their primaries while stopping over at many of the same lakes utilized by Eared Grebes (Jehl 1987).

In the arid regions of western North America, temperatures soar and resources become increasingly limited by late summer, at which time birds are faced with the prospect of completing their definitive prebasic molt with limited food resources in a harsh, demanding environment. Several western migrants have developed an effective strategy for dealing with limited resources for molt during the post-breeding period (summarized in Rohwer et al. 2005, Pyle et al. 2009). By flying south post-breeding and stopping en route (to wintering grounds) to molt, these species are able to temporally separate energetically demanding events. As an example, at the end of the breeding season, Bullock's Orioles (*Icterus bullockii*) migrate to northwest Mexico/southwest United States (Pillar et al. 2016), where they take advantage of the high insect and fruit abundance that coincides with late-summer rainstorms in this region (Rohwer and Manning 1990). As the current increase in tracking studies using geolocators and miniaturized GPS devices continues (e.g., Black-headed Grosbeak [*Pheucticus melanocephalus*]; Siegel et al. 2016), it is quite likely we will discover additional species using this strategy. Though molt in the Mexican monsoon region is strongly biased toward western migratory birds, geolocators revealed that Painted Buntings (*Passerina ciris*) breeding in Oklahoma, USA, travel westward several hundred kilometers to the Mexican monsoon region to molt prior to traveling southeast to overwinter in southern Mexico (Contina et al. 2013). A similar system appears to occur in Trans-Saharan migrants, whereby flight-feather molt is delayed until arrival at stopover sites south of the Sahara, and birds arrive in freshly molted plumage at overwintering sites (e.g., Eurasian Reed-Warbler [*Acrocephalus scirpaceus*], Dowsett-Lemaire and Dowsett 1987; Great Reed-Warbler [*Acrocephalus arundinaceus*], Hedenström et al. 1993).

As noted above, food limitation likely plays a critical role in determining when and where molt occurs (Jenni and Winkler 1994). Thus, in addition to moving latitudinally to a stopover site to molt, movement may also involve changing elevations post-breeding, most commonly in the form of upslope movements, to cooler, moister habitat to complete molt. This appears to be the case for migrants in western North America, including Orange-crowned War-bler (*Oreothlypis celata*; Steele and McCormick 1995), Townsend's Warbler (*Setophaga townsendi*; Leu and Thompson 2002), Hermit Warbler (*S. occidentalis*; Pearson 2013), Cassin's Vireo (*Vireo cassinii*; Rohwer et al. 2008), and Wilson's Warbler (*Cardellina pusilla*; Wiegardt et al. 2017a). Recent work suggests that this strategy may be much more common and complex than previously appreciated (Wiegardt et al. 2017b). Consistent with Leu and Thompson (2002), we consider these movements to be migratory, and thus the time spent at the molting location a "stopover" or "staging" event, given that birds are moving to meet an energetic challenge prior to further movement (Warnock 2010).

Flight-feather Molt Bridging Post-Breeding and Migration. Many waterfowl are rendered flightless during molt and must rely on stopover/staging areas, bearing the risks associated with flightlessness. By contrast, in other taxa (e.g., passerines), there is no flightless period, but the molt period is generally associated with secretive behavior and reduced activity to minimize energy expenditure and predation risk (Newton 1966). Yet, perhaps due to energetic costs of molt, some species appear to avoid overlap of active migratory movement with molt by suspending molt begun near the breeding grounds until arrival at stopover sites or the wintering grounds (e.g., Loggerhead Shrike [*Lanius ludovicianus*]; Pérez and Hobson 2006). In addition, migration with gaps in the wing due to remex molt may have negative impacts on flight performance (e.g., Hedenström and Sunada 1999). Yet, despite the apparent risks and energetic costs of continuing to molt while actively migrating, some species of Neotropic–Nearctic passerines (Northern Rough-winged Swallow [*Stelgidopteryx serripennis*], Purple Martin [*Progne subis*], Tree Swallow [*Tachycineta bicolor*], Swain-son's Thrush [*Catharus ustulatus*], Red-eyed Vireo [*Vireo olivaceus*], Yellow Warbler [*Setophaga petechia*], Rose-breasted Grosbeak [*Pheucticus ludovicianus*], American Redstart [*S. ruticilla*; but see Reudink et al. 2008]; table 2 in Leu and Thompson 2002) may molt flight feathers during active migration, combining 2 highly energy-intensive events. If food resources are limited post-breeding, but flight feather replacement is critical for flight performance during migration (e.g., crossing the Gulf of Mexico or long-distance flights over the Atlantic Ocean), selection may favor a strategy whereby individuals molt throughout migration. Furthermore, extremely protracted molts may necessitate/facilitate molting during active migration. Such appears to be the case in Families Accipitridae and Falconidae, where flight-feather molt can take as long as 4–8 mo (e.g., Peregrine Falcon [*Falco peregrinus*], White et al 2002; Sharp-shinned Hawk [*Accipiter striatus*], Bildstein and Meyer 2000).

We wish to highlight here that the distinction between suspended and continuous molt bridging migration is a
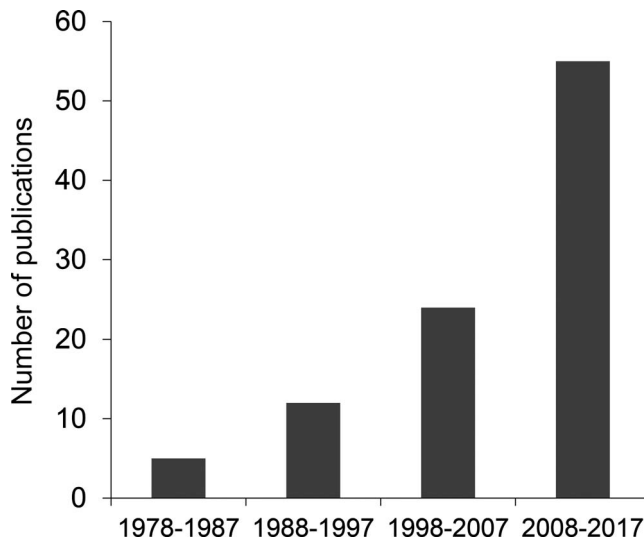
FIGURE 1. Total number of publications since 1978, by 10-year intervals, using the terms "molt-migration" or "moult-migration", and "bird". Numbers based on keyword search for terms in Web of Science, March 2018.

difficult one to document in many cases. For instance, Swainson's Hawk (*Buteo swainsoni*) had been assumed to molt flight feathers continuously during migration (e.g., Palmer 1988). However, surveys of large-capacity roost sites on the migration route failed to find evidence of this in the form of dropped feathers (Smith 1980, Bechard and Weidensaul 2005), and thus there appears to be support for a suspended molt (Bechard et al. 2010). Tree Swallows appear to begin molt following departure from breeding areas and complete molt late in migration, but are assumed to molt continuously, as opposed to suspending molt until arrival at stopover sites, without direct evidence (Stutchbury and Rowher 1990). Further, although stable isotopes present a valuable technique to examine the distinction between continuous and stopover molt, the coarse nature of isoscapes is problematic. For instance, in Loggerhead Shrikes intermediate stable-hydrogen isotope ratios provided evidence that some individuals continued to molt on migration. Yet, for those shrikes that suspended molt, the isotope values for feathers molted south of breeding areas overlapped both possible stopover sites and wintering areas (Perez and Hobson 2006).

Examples of Molt-Migration Not Previously Defined as Such

Although focus on molt-migration as a process has increased over the last decades (Figure 1), research utilizing the term has generally only dealt with one portion of the molt cycle: post-breeding flight-feather (remex) molt (prebasic molt; Howell et al. 2003, Pyle 2005). The reason for this is likely that flight-feather molt is easier to document than body-feather molt and is of great

importance, as it directly impacts flight performance (e.g., Tucker 1991, Swaddle et al. 1996). However, molt of body feathers is also critical to avian life history, as body feathers play important roles in communication (e.g., Hill 2006, Senar 2006) and thermoregulation (e.g., Vézina et al. 2009). Although the term molt-migration is not applied, there are several examples of body-feather molts (Humphrey and Parks 1959, Howell et al. 2003) occurring during the migration stage. In this section we review several types of molt that can overlap with migration that have not traditionally been considered in previous definitions of molt-migration, but would fit our revised definition.

Prealternate and Staged Prebasic Molts. There are extensive examples of shorebirds completing their prealternate molt during migratory stopover (Lourenço and Piersma 2015). For instance, after spending a relatively brief time in basic plumage, adults of the Rufa Red Knot (*Calidris canutus rufa*) begin prealternate molt in February, just prior to departing wintering sites in extreme southern South America (Buehler and Piersma 2008). They then complete this molt into their breeding plumage while staging on the mid-Atlantic coast of the United States, prior to migrating to breeding locations in the Canadian Arctic (Buehler and Piersma 2008). In reviewing this phenomenon across shorebird species, Lourenço and Piersma (2015) suggest that this may be a byproduct of migration distance and time, such that birds minimize feather age and wear during mate acquisition on arrival to the breeding grounds. Furthermore, in addition to the long recognized molt-migration during the prebasic remex molt in waterfowl (Salomonsen 1968), many species are known to molt contour feathers during migration in both spring and fall (Pyle 2005). This includes both the autumnal portion of the prebasic molt into colorful nuptial plumages, and the prealternate molt of some females into cryptic breeding season plumage (based on updated terminology; Pyle 2005). For instance, Northern Shoveler (*Anas clypeata*) males initiate the contour feather portion of their prebasic molt while at post-breeding molting grounds, but either continue this complete contour feather molt during fall migration or suspend it until after migration is completed, with some birds still molting as late as November (DuBowy 1980, 1996). Northern Pintail (*A. acuta*) follow a similar pattern, with most of the contour feather molt delayed until after flight-feather replacement peaking in October and continuing into the winter in some cases (Clark et al. 2014), and Long-tailed Ducks (*Clangula hyemalis*) also appear to continuously molt during migration (Payne et al. 2015).

Recently, there are indications that this phenomenon occurs in other families as well. Most studies of passerine prealternate molt have documented, or assume, that this molt occurs on the wintering grounds, prior to departure for spring migration (e.g., Mowbray 1997, Mazerolle et al.

2005, Boone et al. 2010, Bulluck et al. 2016). However, few studies have directly addressed questions about the spatial variation in prealternate songbird molt. At least one recent study documented an obligate partial prealternate molt, completed during spring stopover, in Rusty Blackbirds (*Euphagus carolinus*; Wright et al. 2018). In that case, much like many shorebirds, individuals begin prealternate molt prior to leaving wintering grounds (Mettke-Hoffman et al. 2015), but molt peaks in the middle of the stopover period. Molt was negatively associated with fat score in this study, potentially indicating it is antagonistic with migratory fattening and a limit on migration phenology (Wright et al. 2018). Furthermore, another recent study has found evidence of a definitive prealternate molt during migratory stopover in Rufous Hummingbird (*Selasphorus rufus*; Sieburth and Pyle 2018). At this time, it is unclear how many other taxa follow such a pattern, as there is scant treatment in the primary literature. For instance, in songbirds, Indigo Bunting (*Passerina cyanea*) first prealternate molt appears to begin on the wintering grounds, but often completes on breeding sites (Pyle 1997), but it is not clear that definitive prealternate molt follows the same pattern. There is a great need for further documentation and quantification of such examples to determine how widespread prealternate molt-migration is in most families.

Presupplemental Molts. Several shorebird species complete presupplemental molts during migratory stopover/staging. In these cases, feathers already replaced on wintering sites in a prealternate molt are replaced again (Humphrey and Parkes 1959, Howell et al. 2003) during migratory stopover. Such appears to be the case in shorebird species that stage in east Asia, such as the Great Knot (*C. tenuirostris*; Battley et al. 2006) and Ruff (*Calidris pugnax*; Jukema and Piersma 2000), and the Bar-tailed Godwit (*Limosa lapponica*), which stages in western Europe. In the case of the godwit, for example, birds in better condition re-molt contour feathers in the Netherlands, and appear to enhance the quality of their plumage prior to arrival at breeding sites (Piersma and Jukema 1993, Piersma et al. 2001). In addition, there are some indications that ducks in the genus *Anas* have inserted presupplemental molts during their spring migration (Pyle 2013b).

Preformative Molt. In addition to the definitive molts discussed above, juvenile birds can undergo partial preformative molts during their first fall migration. This has especially been observed in songbirds stopping over in the Mexican monsoon region (e.g., Butler et al. 2002, Pyle et al. 2009). These molts can include eccentric flight-feather molts, such as those in Western Kingbirds (*Tyrannus verticalis*), where juveniles will replace some primaries, but delay this molt until stopover (Barry et al. 2009). Many of these molts, however, are contour feather–

only molts, such as those completed by first-year Warbling Vireos (*Vireo gilvus*), Western Tanagers (*Piranga ludoviciana*), and other species (Pyle et al. 2009). Preformative molts on stopover have also been observed in Europe in the European Starling (*Sturnus vulgaris*), where juveniles, but not adults, delay molt until migration (Svardson 1953, Kosarev 1999).

A Call for Standardizing the Classification of Molt-Migration Across Ornithology

We argue that the diversity of systems in which molt occurs during migration discussed above should all be classified as "molt-migration." However, in addition to our broadened definition of the overall phenomenon, this diversity in the timing and extent of the molts involved requires a more specific system of terminology to describe each case that is broadly applicable across systems. We could utilize an entirely spatial system, based on where molt begins and where it ends, relative to stationary phases of the annual cycle. However this would produce a complex system with numerous permutations, even without also including further classification levels for describing which feather tracts are involved. Further, a system based on the type of migration system may be useful (e.g., boreal, austral, altitudinal), however we sought to generate a system that would be broadly applicable across all types of migration. Thus, we propose a relatively simple, 2-tiered system that classifies (1) when/where molt commences relative to migration, and (2) what type of molt is involved. We expect that although not every single one of the diverse molt strategies globally will fit these definitions, this typology can be applied to the vast majority of variants on the theme of molt-migration in birds. For this classification, we consider the migration stage to have begun once an individual leaves its breeding or stationary nonbreeding site, moving to a new landscape (i.e. change in latitude, longitude, altitude). However, we exclude post-breeding movements within the same landscape as the stationary life history stage (e.g., post-fledging movements into adjacent habitats; Vitz and Rodewald 2010). In the first tier of our typology, we classify the following 2 categories based on when/where molt commences relative to migration:

1. **Continuous molt-migration.** Molt that is initiated on the breeding or stationary nonbreeding grounds then continues during migration until stopover or arrival at breeding or stationary nonbreeding grounds.
2. **Suspended molt-migration.** Molt that is initiated on the breeding or stationary nonbreeding grounds then is interrupted following migratory departure until stopover or arrival at breeding/stationary nonbreeding grounds.

TABLE 1. Example applications of proposed typology to classify forms of molt migration across avian taxa. Note that, as in the case of Red Knot, the typology is still useful even when data are not available to classify in both tiers.

Classification	Species example	Molt-migration description
Adult: Continuous prebasic molt-migration **First-year:** Continuous preformative molt migration	Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	Eastern populations initiate complete prebasic molt and partial preformative molts on breeding grounds, stopover on the northern Gulf of Mexico and complete molt before continuing across the gulf. However, some juveniles appear to continue molting flight feathers during trans-gulf migration (Yuri and Rohwer 1997).
Adult: Stopover prebasic molt-migration **First-year:** Stopover preformative molt migration	Western Kingbird (*Tyrannus verticalis*)	Adults undergo a complete prebasic molt during stopover in Mexican monsoon region/montane southwestern USA. Juveniles also appear to delay both their preformative body feather molt and eccentric flight-feather molt until they partially complete their fall migration, and prior to arrival at wintering areas (Barry et al. 2009).
Continuous or suspended prealternate molt-migration	Rufa Red Knot (*Calidris canutus rufa*)	Birds begin molting into alternate plumage on wintering grounds in Tiera del Fuego in February, continue to molt during migration, completing molt during stopover in eastern USA (Bueler and Piersma 2008). It is not currently clear if molts are suspended or continuous.
Suspended prebasic molt-migration	Swainson's Hawk (*Buteo swainsoni*)	Birds begin molting flight feathers at breeding sites, apparently pause molt during migration and complete molt at stationary nonbreeding sites (Smith 1980, Bechard and Weidensaul 2005).

3. **Stopover molt-migration**. Molt that is delayed until arrival at specific molting grounds (e.g., high-elevation or stopover site; Salomonsen 1968, Leu and Thompson 2002) and completed prior to further progression of migration or at the migration endpoint.

In the second tier of our typology, we classify the following 3 categories based on the type of molt:

1. **Prebasic molt-migration.** Definitive molt, involving sequential, simultaneous, or staged replacement of all primaries and contour feathers, occurring in an area distinct in latitude, longitude, and/or elevation from the breeding or stationary nonbreeding site.
2. **Prealternate or presupplemental molt-migration.** Definitive partial molts, involving contour feathers, prior to or during (e.g., male waterfowl) the breeding season occurring in an area distinct in latitude, longitude, and/or elevation from the breeding or stationary nonbreeding site. These may include re-placement of basic or formative feathers (prealternate molt), or replacement of alternate feathers (presupplemental molt).
3. **Preformative molt-migration.** Molts that may be complete, contour feather only, or include eccentric flight-feather molt, occurring post–juvenile dispersal in an area distinct in latitude, longitude, and/or elevation from the natal site.

We provide multiple examples of the application of this typology (Table 1). It should be noted that, in some cases, a researcher may not have enough information to classify a system at both levels. For instance, one may know a molt observed at a stopover site is "preformative molt-migration," but may not have clear evidence for whether the molt began prior to departure from a breeding site or was initiated during migration. In these cases we advocate for a partial application of our typology (i.e. simply, preformative molt-migration).

Implications of Molt-Migration and Future Directions

Although not exhaustive, the above examples highlight the prevalence of overlap between the molt and migratory life history stages (Ramenofsky and Wingfield 2006), and thus the need to synthesize different systems to elucidate evolutionary and ecological implications. A clear understanding of the ecology of migratory birds is dependent on a full annual cycle approach (Marra et al. 2015), which is currently limited by a lack of knowledge about the spatiotemporal aspects of many stages. Molt is primary among these life history stages, though the studies highlighted above exhibit an increasing appreciation for variation among species, and individuals, in where and when molt is completed. As recognized in previous reviews and syntheses on molt-migration (e.g., Jehl 1990, Leu and Thompson 2002, Pyle et al. 2009), without a clear understanding of where and when molt is completed we cannot understand how this critical life history stage is limited. For instance, in terms of flight performance, determining what resources limit flight feather growth rate and feather quality (e.g., de la Hera et al. 2009). Here, we have sought to expand this critical point to include all stages and types of molt in order to move toward a comprehensive understanding of the ecological and evolutionary implications of overlap with the migratory life history stage. This includes determining, in terms of contour feather molts, where critical pigments in intraspecific interactions (e.g., Sparrow et al. 2017) and ectoparasite resistance (e.g., Gunderson et al. 2008) are acquired. With a more comprehensive typology, which can be utilized across all avian taxa, researchers can now classify molt-migration strategies in a common language. The vast array of different molt (Howell et al. 2003) and migration (Salewski and Bruderer 2007) strategies in birds appear to have evolved many times independently, suggesting that common ecological or life history characteristics may drive the evolution of molt strategies, including molt-migration. Phylogenies for birds (e.g., Prum et al. 2015) will be instrumental for conducting large-scale phylogenetic reconstructions of molt strategies and phylogenetically controlled analyses aimed at understanding which ecological, behavioral, or life history traits promote the evolution of different molt strategies. In a conservation sense, whereas molting and staging areas have long received attention as critical habitat (reviewed in Jehl 1990, Leu and Thompson 2002), increasing documentation of molt-migration in its myriad forms will require a similar recognition in other migratory taxa.

In conclusion, the focus on molt-migration is likely to continue growing, and we hope to see many exciting avenues of research explored to understand these systems. Important questions, recognized by other researchers on this topic (e.g., Leu and Thompson 2002), still remain and are critical to unraveling how molt-migration arises and is maintained as a strategy. For instance, although energetics is likely a driver of many strategies, the nutritional advantages of molting on migration or stopover are not well described for most species. This is likely of great importance, particularly in understanding individual variation in the spatiotemporal aspects of molt (Piersma et al. 2001, Tonra et al. 2015, Nordell et al. 2016). Equally important is understanding the proximal physiological mechanisms regulating the overlap in molt and migration stages. This is especially true given apparent physiological conflicts between these 2 energetically expensive and physically challenging states that involve substantial physiological changes (Williams 2012). In order to reach the increasingly prevalent goal of unravelling the full annual cycle ecology of species (Marra et al. 2015), we must continue to explore phenomena such as molt-migration and other seasonal interactions (Marra et al. 1998, Harrison et al. 2011). This will require a comprehensive focus on the stages of the annual cycle involved and describing them in the same terms across avian systems.

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