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6 **COMMENTARY**

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8 **EXPANDING THE TRADITIONAL DEFINITION OF MOLT-MIGRATION**

9 Christopher M. Tonra^{1*} and Matthew W. Reudink²

10 ¹School of Environment and Natural Resources, The Ohio State University, 2021 Coffey Road,
11 210 Kottman Hall, Columbus, OH 43210, USA.

12 ²Department of Biological Sciences, Thompson Rivers University, 805 TRU Way, Kamloops,
13 BC V2C 0C8, Canada

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23 *Corresponding author: tonra.1@osu.edu

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 1960’s. 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, two-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

OVERVIEW

Migratory birds must balance three 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 molting 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 migrating 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 two 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 breath of strategies whereby these two life history stages overlap and interact. Ramenofsky and Wingfield (2005) 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.

1 **EXAMPLES OF MOLT-MIGRATION STRATEGIES, AS TRADITIONALLY DEFINED**

2 *Flight-feather molt occurring entirely on migratory stopover*

3 Perhaps the first use of the term “molt-migration” was by Salomonsen (1968) in describing
4 waterfowl post-breeding movements. Specifically, the term was applied to the movements of
5 many ducks, and later other Anseriformes (e.g., geese; Ogilve 1978), to secluded marshes in
6 order to complete flight-feather replacement during their definitive prebasic molt, including a
7 period of flightlessness. This phenomenon, which has been detailed in many species of
8 waterfowl since Salomonsen (e.g., Hohman et al. 1992, Robert et al. 2002, Dickson et al. 2012),
9 revealed a critical component of the habitat needs specific to molt in waterfowl, separate from
10 wintering and breeding. In addition, several species of grebe (Family Podicipedidae) have a
11 similar molt-migration as waterfowl (e.g., Storer and Jehl 1985, Piersma 1988). For example,
12 Eared Grebes (*Podiceps nigricollis*) halt migration at hypersaline lakes in the western U.S. to
13 complete flight-feather molt (e.g., Mono Lake, Great Salt Lake; Storer and Jehl 1985). These
14 grebes also endure a flightless period during this stopover as they molt all of their flight feathers.
15 Some shorebirds migrate to staging areas during fall migration and replace flight feathers, such
16 as Wilson’s Phalaropes (*Phalaropus tricolor*), which partially replace their primaries while
17 stopping over at many of the same lakes utilized by Eared Grebes (Jehl 1987).

18 In the arid regions of western North America, temperatures soar and resources become
19 increasingly limited by late summer, at which time birds are faced with the prospect of
20 completing their definitive prebasic molt with limited food resources in a harsh, demanding
21 environment. Several western migrants have developed an effective strategy for dealing with
22 limited resources for molt during the post breeding period (*summarized in* Rohwer et al. 2005,
23 Pyle et al. 2009). By flying south post-breeding and stopping *en-route* (to wintering grounds) to

1 molt, these species are able to temporally separate energetically demanding events. As an
2 example, at the end of the breeding season, Bullock's Orioles (*Icterus bullockii*) migrate to
3 northwest Mexico/southwest United States (Pillar et al. 2016), where they take advantage of the
4 high insect and fruit abundance that coincides with late summer rainstorms in this region
5 (Rohwer and Manning 1990). As the current increase in tracking studies using geolocators and
6 miniaturized GPS devices continues (e.g., Black-headed Grosbeak *P. melanocephalus*; Siegel et
7 al. 2016), it is quite likely we will discover additional species using this strategy. Though molt in
8 the Mexican monsoon region is strongly biased towards western migratory birds, geolocators
9 revealed that Painted Buntings breeding in Oklahoma, USA travel westward several hundred
10 kilometers to the Mexican monsoon region to molt prior to traveling southeast to overwinter in
11 southern Mexico (Contina et al. 2013). A similar system appears to occur in Trans-Saharan
12 migrants, whereby flight-feather molt is delayed until arrival at stopover sights south of the
13 Saharra, and birds arrive in freshly molted plumage at overwintering sites (e.g., European reed
14 warbler *Acrocephalus scirpaceus*, Dowsett-Lemaire and Dowsett 1986; great reed warbler
15 *Acrocephalus arundinaceus*, Hedenström et al. 1993).

16 As noted above, food limitation likely plays a critical role in determining when and
17 where molt occurs (Jenni and Winkler 1994). Thus, in addition to moving latitudinally to a
18 stopover site to molt, movement may also involve changing elevations post-breeding, most
19 commonly in the form of upslope movements to, cooler, moister habitat to complete molt. This
20 appears to be the case for migrants in western North America, including Orange-crowned
21 Warbler (*Vermivora celata*; Steele and McCormick 1995), Townsend's Warbler (*Setophaga*
22 *townsendi*; Leu and Thompson 2002), Hermit Warbler (*S. occidentalis*; Pearson 1997), Cassin's
23 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 moult may have negative impacts on flight performance (e.g. Hedenström and Sunada 1999). Yet, despite the apparent risks/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*, Swainson’s Thrush *C. ustulatus*, Red-eyed Vireo *Vireo olivaceus*, Yellow Warbler, Rose-breasted Grosbeak *Pheucticus ludovicianus*, American Redstart *S.ruticilla* [but see Reudink et al. 2009]; Table 2 in Leu and Thompson 2002) may molt flight feathers during active migration, combining two highly energy-intensive events. If food resources are limited post-breeding, but flight feather

1 replacement is critical for flight performance during migration (e.g., crossing the Gulf of Mexico
2 or long-distance flights over the Atlantic Ocean), selection may favor a strategy whereby
3 individuals molt throughout migration. Furthermore, extremely protracted molts may
4 necessitate/facilitate molting during active migration. Such appears to be the case in Families
5 Accipitridae and Falconidae, where flight-feather molt can take as long as 4-8 months (e.g.,
6 Peregrine Falcon *Falco peregrinus* White et al 2002; Sharp-shinned Hawk *Accipiter striatus*
7 Bildstein and Meyer 2000).

8 We wish to highlight here that the distinction between suspended and continuous molt
9 bridging migration is a difficult one to document in many cases. For instance, Swainson's Hawk
10 (*Buteo swainsoni*) had been assumed to molt flight feathers continuously during migration (e.g.,
11 Palmer 1988). However, surveys of large capacity roost sites on the migration route failed to find
12 evidence of this in the form of dropped feathers (Smith 1980; Bechard and Weidensaul 2005),
13 and thus there appears to be support for a suspended molt (Bechard et al. 2010). Tree swallows
14 appear to begin molt following departure from breeding areas and complete molt late in
15 migration, but are assumed to molt continuously, as opposed suspending molt until arrival
16 stopover sites, without direct evidence (Stutchbury and Rowher 1990). Further, although stable
17 isotopes present a valuable technique to examine the distinction between continuous and
18 stopover moult, the coarse nature of isoscapes is problematic. For instance, in Loggerhead Shrike
19 intermediate stable-hydrogen isotope ratios provided evidence that some individuals continued to
20 molt on migration. Yet, for those shrikes that suspended molt, the isotope values for feathers
21 molted south of breeding areas overlapped both possible stopover sites and wintering areas
22 (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 which 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 subspecies of 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

1 and time, such that birds minimize feather age and wear during mate acquisition on arrival to the
2 breeding grounds. Furthermore, in addition to the long recognized molt-migration during the
3 prebasic remex molt in waterfowl (Salomonsen 1968), many species are known to molt contour
4 feathers during migration in both spring and fall (Pyle 2005). This includes both the autumnal
5 portion of the prebasic molt into colorful nuptial plumages, and the prealternate molt of some
6 females into cryptic breeding season plumage (based on updated terminology; Pyle 2005). For
7 instance, Northern Shoveler (*Anas clypeata*) males initiate the contour feather portion of their
8 prebasic molt while at post-breeding molting grounds, but either continue this complete contour
9 feather molt during fall migration or suspend it until after migration is completed, with some
10 birds still molting as late as November (DuBowy 1980 & 1986). Northern Pintail (*A. acuta*)
11 follow a similar pattern, with most of the contour feather molt delayed until after flight-feather
12 replacement peaking in October and continuing into the winter in some cases (Clark et al. 2014)
13 and Long-tailed Ducks (*Clangula hyemalis*) also appear to continuously molt during migration
14 (Payne et al. 2015).

15 Recently, there are indications that this phenomenon occurs in other families as well.
16 Most studies of passerine prealternate molt have documented, or assume, that this molt occurs on
17 the wintering grounds, prior to departure for spring migration (e.g., Boone et al. 2010, Mowbray
18 1997, Mazerolle et al. 2005, Bulluck et al. 2016). However, few studies have directly addressed
19 questions about the spatial variation in prealternate songbird molt. At least one recent study
20 documented an obligate partial prealternate molt, completed during spring stopover, in Rusty
21 Blackbirds (*Euphagus carolinus*; Wright et al. 2018). In that case, much like many shorebirds,
22 individuals begin prealternate molt prior to leaving wintering grounds (Mettke-Hoffman et al.
23 2010), 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 complete 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 Parks 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 (*Philomachus pugnax*; Jukema & 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 Anas ducks 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, two-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 their breeding or stationary non-breeding 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 two categories based on when/where molt commences relative to migration:

a. Continuous molt-migration - Molt that is initiated on the breeding or stationary non-breeding grounds then continues during migration until stopover or arrival at breeding or stationary non-breeding grounds.

b. Suspended molt-migration - Molt that is initiated on the breeding or stationary non-breeding grounds then is interrupted following migratory departure until stopover or arrival at breeding/stationary non-breeding grounds.

c. 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 three categories based on the type of molt:

1 a. Prebasic molt-migration - Definitive molt, involving sequential, simultaneous, or staged
2 replacement of all primaries and contour feathers, occurring in an area distinct in latitude,
3 longitude, and/or elevation from the breeding or stationary non-breeding site.

4 b. Prealternate or presupplemental molt-migration - Definitive partial molts, involving
5 contour feathers, prior to or during (e.g., male waterfowl) the breeding season occurring in
6 an area distinct in latitude, longitude, and/or elevation from the breeding or stationary non-
7 breeding site. These may include replacement of basic or formative feathers (prealternate
8 molt), or replacement of alternate feathers (presupplemental molt).

9 c. Preformative molt-migration - Molts that may be complete, contour feather only, or
10 include eccentric flight-feather molt, occurring post-juvenile dispersal in an area distinct
11 in latitude, longitude and/or elevation from the natal site.

12
13 In Table 1, we provide multiple examples of the application of this typology. It should be noted
14 that, in some cases, a researcher may not have enough information to classify a system at both
15 levels. For instance, one may know a molt observed at a stopover site is “preformative molt-
16 migration”, but may not have clear evidence for whether the molt began prior to departure from a
17 breeding site, or initiated during migration. In these cases we advocate for a partial application of
18 our typology (i.e. simply, preformative molt-migration).

20 **IMPLICATIONS OF MOLT-MIGRATION AND FUTURE DIRECTIONS**

21 Although not exhaustive, the above examples highlight the prevalence of overlap between the
22 molt and migratory life history stages (Ramenofsky and Wingfield 2006), and thus the need to
23 synthesize different systems to elucidate evolutionary and ecological implications. A clear

1 understanding of the ecology of migratory birds is dependent on a full annual cycle approach
2 (Marra et al. 2015), which is currently limited by a lack of knowledge about the spatiotemporal
3 aspects of many stages. Molt is primary among these life history stages, though the studies
4 highlighted above exhibit an increasing appreciation for variation among species, and
5 individuals, in where and when molt is completed. As recognized in previous reviews and
6 syntheses on molt-migration (e.g., Jehl 1990, Leu and Thompson 2002, Pyle et al. 2009), without
7 a clear understanding of where and when molt is completed we cannot understand how this
8 critical life history stage is limited. For instance, in terms of flight performance, determining
9 what resources limit flight feather growth rate and feather quality (e.g., de la Hera et al. 2009).
10 Here, we have sought to expand this critical point to include all stages and types of molt in order
11 to move towards a comprehensive understanding of the ecological and evolutionary implications
12 of overlap with the migratory life history stage. This includes determining, in terms of contour
13 feather molts, where critical pigments in intraspecific interactions (e.g., Sparrow et al. 2017) and
14 ectoparasite resistance (e.g., Gunderson et al. 2008) are acquired. With a more comprehensive
15 typology, which can be utilized across all avian taxa, researchers can now classify molt-
16 migration strategies in a common language. The vast array of different molt (Howell et al. 2003)
17 and migration (Salewski and Bruderer 2007) strategies in birds appear to have evolved many
18 times independently, suggesting that common ecological or life history characteristics may drive
19 the evolution of molt strategies, including molt-migration. Phylogenies for birds (e.g., Prum et al.
20 2015) will be instrumental for conducting large-scale phylogenetic reconstructions of molt
21 strategies and phylogenetically-controlled analyses aimed at understanding which ecological,
22 behavioral, or life history traits promote the evolution of different molt strategies. In a
23 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 two 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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LITERATURE CITED

Battley, P.F., D.I. Rogers, and C.J. Hassell (2006). Prebreeding moult, plumage and evidence for a presupplemental moult in the Great Knot *Calidris tenuirostris*. Ibis 148:27-38.

Barry, J.H., L.K. Butler, S. Rohwer, and V.G. Rohwer (2009). Documenting molt-migration in Western Kingbird (*Tyrannus verticalis*) using two measures of collecting effort. The Auk 126:260-267.

Bechard, M.J. and Weidensaul, C.S., 2005. Feather molt by Swainson's hawks (*Buteo swainsoni*) on the Austral grounds of Argentina. Ornitología Neotropical, 16, pp.267-270.

Bechard, M. J., C. S. Houston, J. H. Saransola and A. Sidney-England. 2010. Swainson's Hawk (*Buteo swainsoni*). In The Birds of North America (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bna.265>

Bildstein, K. L. and K. D. Meyer (2000). Sharp-shinned Hawk (*Accipiter striatus*). In The Birds of North America (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bna.482>

1 Boone, A. T., P. G. Rodewald, and L. W. DeGroot (2010). Neotropical winter habitat of the
2 magnolia warbler: effects on molt, energetic condition, migration timing, and
3 hematozoan infection during spring migration. *The Condor* 112:115-122.

4 Bulluck, L. P., M. J. Foster, S. Kay, D. E. Cox, C. Viverette, and S. Huber (2016). Feather
5 carotenoid content is correlated with reproductive success and provisioning rate in female
6 Prothonotary Warblers. *The Auk* 134:229-239.

7 Butler, L.K., M.G. Donahue, and S. Rohwer (2002). Molt-migration in Western Tanagers
8 (*Piranga ludoviciana*): Age effects, aerodynamics, and conservation implications. *The*
9 *Auk* 119:1010-1023.

10 Buehler, D.M. and T. Piersma (2008). Travelling on a budget: predictions and ecological
11 evidence for bottlenecks in the annual cycle of long-distance migrants. *Philosophical*
12 *Transactions of the Royal Society of London B: Biological Sciences* 363:247-266.

13 Clark, R.G., J.P. Fleskes, K.L. Guyn, D. A. Haukos, J. E. Austin and M.R. Miller (2014).
14 Northern Pintail (*Anas acuta*). In *The Birds of North America* (P. G. Rodewald, Ed.).
15 Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bna.163

16 Contina, A., E.S. Bridge, N.E. Seavy, J.M. Duckles, and J.F. Kelly (2013). Using geologgers to
17 investigate bimodal isotope patterns in Painted Buntings (*Passerina ciris*). *The Auk*
18 130:265-272.

19 de la Hera, I., J. Perez-Tris, and J.L. Telleria (2009). Migratory behaviour affects the trade-off
20 between feather growth rate and feather quality in a passerine bird. *Biological Journal of*
21 *the Linnean Society* 97:98-105.

22 Dietz, M. W., S. Daan, and D. Masman (1992). Energy requirements for molt in the kestrel
23 *Falco tinnunculus*. *Physiological Zoology* 65:1217-1235.

- Dickson, R.D., D. Esler, J.W. Hupp, E.M. Anderson, J.R. Evenson, and J. Barrett (2012). Phenology and duration of remigial molt in Surf Scoters (*Melanitta perspicillata*) and White-winged Scoters (*Melanitta fusca*) on the Pacific coast of North America. Canadian Journal of Zoology 90:932-944.
- Dowsett-Lemaire, F. and Dowsett, R.J. (1987). European Reed and Marsh Warblers in Africa: migration patterns, moult and habitat. Ostrich, 58:65-85.
- DuBowy, P. J. (1980). Optimal foraging and adaptive strategies of postbreeding male Blue-winged Teal and Northern Shovelers. Master's Thesis, Univ. of N. Dakota, Grand Forks.
- Dubowy, Paul J. (1996). Northern Shoveler (*Anas clypeata*). In The Birds of North America (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bna.217
- Froehlich, D.R., S. Rohwer, and B. J. Stutchbury (2005). Spring molt constraints versus winter territoriality. Pages 321-335 in Birds of Two Worlds: The Ecology and Evolution of Migration (R. Greenberg and P.P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.
- Gunderson, A. R., A. M. Frame, J. P. Swaddle, and M. H. Forsyth (2008). Resistance of melanized feathers to bacterial degradation: is it really so black and white? Journal of Avian Biology 39:539-545.
- Harrison, X.A., J.D. Blount, R. Inger, D.R. Norris, and S. Bearhop (2011). Carry-over effects as drivers of fitness differences in animals. Journal of Animal Ecology 80:4-18.
- Hedenström, A., S. Bensch, D. Hasselquist, M. Lockwood, and U. Ottosson (1993). Migration, stopover and moult of the great reed warbler *Acrocephalus arundinaceus* in Ghana, West Africa. Ibis, 135:177-180.

1 Hedenström, A., and Sunada (1999). On the aerodynamics of moult gaps in birds. *Journal of*
2 *Experimental Biology* 202:67-76.

3 Hill, G. E. (2006). Female mate choice for ornamental coloration in birds. In: *Bird Coloration:*
4 *Function and Evolution*. Hill, G.E. and K. J. McGraw (eds). Harvard University Press
5 University Press, Cambridge, MA.

6 Hohman, W.L., C.D. Ankney, and D.H. Gordon (1992). Ecology and management of
7 postbreeding waterfowl. Pages 128-189 in *Ecology and Management of Breeding*
8 *Waterfowl* (B.D.J. Batt, et al., Eds.). University of Minnesota Press, Minneapolis, MN.

9 Howell, S.N.G., C. Corben, P. Pyle, and D. I. Rogers. (2003). The first basic problem: a review
10 of molt and plumage homologies. *The Condor* 105:635-653.

11 Humphrey, P. S., and K. C. Parkes. (1959). An approach to the study of molts and plumages. *The*
12 *Auk* 76:1-31.

13 Jehl Jr., J. R. (1987). Molt and moult migration in a transequatorially migrating shorebird:
14 Wilson's Phalarope. *Ornis Scandinavica*:173-178.

15 Jehl Jr., J. R., (1990). Aspects of the molt migration. Pages 102-113 in *Bird Migration*. Springer,
16 Berlin, Heidelberg.

17 Jenni, L. and W. Winkler (1994). Molt and ageing European Passerines. Academic Press,
18 London, UK.

19 Jukema, J. and T. Piersma (2000). Contour feather moult of Ruffs *Philomachus pugnax* during
20 northward migration, with notes on homology of nuptial plumages in scolopacid waders.
21 *Ibis* 142:289-296.

22 Kosarev, V. (1999). Summer movements of starlings *Sturnus vulgaris* on the Courish Spit of the
23 Baltic Sea. *Avian Ecology and Behaviour* 30:99-109.

1 Leu, M. and C.W. Thompson (2002). The potential importance of migratory stopover sites as
2 flight-feather molt staging areas: a review for Neotropical migrants. *Biological*
3 *Conservation* 106:45-56.

4 Lourenço, P.M. and T. Piersma (2015). Migration distance and breeding latitude correlate with
5 the scheduling of pre-alternate body moult: a comparison among migratory waders.
6 *Journal of Ornithology* 156:657-665.

7 Marra, P.P., Hobson, K.A. and Holmes, R.T. (1998). Linking winter and summer events in a
8 migratory bird by using stable-carbon isotopes. *Science* 282:1884-1886.

9 Marra, P.P., E. B. Cohen, S. R. Loss, J. E. Rutter and C. M. Tonra (2015). A call for full annual
10 cycle research in animal ecology. *Biology Letters* 11:20150552.

11 Mazerolle, D. F., K. A. Hobson, and L. I. Wassenaar (2005). Stable isotope and band-encounter
12 analyses delineate migratory patterns and catchment areas of white-throated sparrows at a
13 migration monitoring station. *Oecologia* 144:541-549.

14 Mettke-Hofmann, C., P. B. Hamel, G. Hofmann, T. J. Zenzal Jr., A. Pellegrini, J. Malpass, M.
15 Garfinkel, N. Schiff, and R. Greenberg. (2015) Competition and habitat quality influence
16 age and sex distribution in wintering rusty blackbirds. *PloS One* 10: e0123775.

17 Mowbray, T. B.(1997). Swamp Sparrow (*Melospiza georgiana*), In *The Birds of North America*
18 (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithica, NY, USA. doi:
19 10.2173/bna.279

20 Newton, I. (1966). The moult of the Bullfinch *Pyrrhula pyrrhula*. *Ibis* 108: 41-67.

21 Nordell, C.J., S. Haché, E.M. Bayne, P. Sólymos, K.R. Foster, C.M. Godwin, R. Krikun, P.P.
22 Pyle and K.A. Hobson (2016). Within-site variation in feather stable hydrogen isotope

($\delta^{2}\text{H}$) values of boreal songbirds: implications for assignment to molt origin. PloS One 11:e0163957.

Ogilvie, L.W. (1978) Wild Geese. Poyster, Berkhamsted, UK

Palmer, R. S. (1988). Handbook of North American birds. Volume 5: diurnal raptors (Part 2). Yale Univ. Press, New Haven, Connecticut.

Payne, A. M., M. L. Schummer, and S. A. Petrie (2015). Patterns of molt in Long-tailed Ducks (*Clangula hyemalis*) during autumn and winter in the Great Lakes Region, Canada. Waterbirds, 38:195-200.

Pearson, S.F. (2013). Hermit Warbler (*Setophaga occidentalis*). In The Birds of North America (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. doi: 10.2173/bna.303

Pérez, G.E. and K. A. Hobson (2006). Isotopic evaluation of interrupted molt in northern breeding populations of the Loggerhead Shrike. The Condor, 108:877-886.

Piersma, T. (1988). The annual moult cycle of Great Crested Grebes. Ardea 76:82-95.

Piersma, T., and J. Jukema (1993). Red breasts as honest signals of migratory quality in a long-distance migrant, the Bar-tailed Godwit. The Condor 95:163-177.

Piersma, T., L. Mendes, J. Hennekens, S. Ratiarison, S. Groenewold, and J. Jukema (2001). Breeding plumage honestly signals likelihood of tapeworm infestation in females of a long-distance migrating shorebird, the bar-tailed godwit. Zoology 104:41-48.

Pillar, A.G., P. P. Marra, N. J. Flood, and M. W. Reudink (2016). Molt migration in Bullock's Orioles (*Icterus bullockii*) confirmed by geolocators and stable isotope analysis. Journal of Ornithology 157:265-275.

1 Prum, R.O., J.S. Berv, A. Dornburg, D.J. Field, J.P. Townsend, E.M. Lemmon and A.R.
2 Lemmon (2015). A comprehensive phylogeny of birds (Aves) using targeted next-
3 generation DNA sequencing. *Nature* 526:569-573.

4 Pyle, P. (1997). Identification Guide to North American Birds, Part I. Slate Creek Press, Point
5 Reyes Station, California.

6 Pyle, P. (2005). Molts and plumages of ducks. *Waterbirds* 28: 208-219.

7 Pyle, P. (2013a). Evolutionary implications of synapomorphic wing-molt sequences among
8 falcons (Falconidae) and parrots (Psittaciformes). *Condor* 115:593-602.

9 Pyle, P. (2013b). Molt homologies in ducks and other birds: A response to Hawkins (2011) and
10 further thoughts on molt terminology in ducks. *Waterbirds*, 36:77-81.

11 Pyle, P., W. A. Leitner, L. Lozano-Angulo, F. Avilez-Teran, H. Swanson, E. G. Limón and M.
12 K. Chambers (2009). Temporal, spatial, and annual variation in the occurrence of molt-
13 migrant passerines in the Mexican monsoon region. *The Condor* 111:583-590.

14 Ramenofsky, M. and J.C. Wingfield (2006). Behavioral and physiological conflicts in migrants:
15 the transition between migration and breeding. *Journal of Ornithology*, 147:135-145.

16 Reudink, M.W., P.P. Marra, K.M. Langin, C.E. Studds, T.K. Kyser, and L.M. Ratcliffe (2008).
17 Molt-migration in the American Redstart (*Setophaga ruticilla*) revisited: explaining
18 variation in feather δD signatures. *The Auk* 125:744-748.

19 Robert, M., R. Benoit, and J.P.L. Savard (2002). Relationship among breeding, molting, and
20 wintering areas of male Barrow's Goldeneyes (*Bucephala islandica*) in eastern North
21 America. *The Auk* 119:676-684.

1 Rohwer, S. and J. Manning (1990). Differences in timing and number of molts for Baltimore and
2 Bullock's orioles: Implications to hybrid fitness and theories of delayed plumage
3 maturation. *The Condor* 92:125-140.

4 Rohwer, S., L. K. Butler, D. Froehlich (2005). Ecology and demography of east–west differences
5 in molt scheduling of neotropical migrant passerines" Pages 87-105 in *Birds of Two*
6 *Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P.P. Marra, Eds.).
7 Johns Hopkins University Press, Baltimore, Maryland.

8 Rohwer, V.G., S. Rohwer, and J.H. Barry (2008). Molt scheduling of western Neotropical
9 migrants and up-slope movement of Cassin's Vireo. *The Condor* 110:365-370.

10 Salewski, V., and B. Bruderer (2007). The evolution of bird migration—a synthesis.
11 *Naturwissenschaften*, 94:268-279.

12 Salomonsen, F. (1968). The moult migration. *Wildfowl* 19:5-24.

13 Senar, J.C. (2006). Bird colors as intrasexual signals of aggression and dominance. In: *Bird*
14 *Coloration: Function and Evolution*. Hill, G.E. and K. J. McGraw (eds). Harvard
15 University Press University Press, Cambridge, MA.

16 Sieburth, D., and P. Pyle. 2018. Evidence for a prealternate molt-migration in the Rufous
17 Hummingbird and its implications for the evolution of molts in Apodiformes. *The Auk:*
18 *Ornithological Advances* 135:495-505.

19 Siegel, R.B., R. Taylor, J. F. Saracco, L. Helton, and S. Stock (2016). GPS tracking reveals non-
20 breeding locations and apparent molt migration of a Black-headed Grosbeak. *Journal of*
21 *Field Ornithology* 87:196-203.

1 Smith, N. G. (1980). Hawk and vulture migrations in the Neotropics. Pages 51–65 in Migrant
2 birds in the Neotropics: ecology, behavior, distribution, and conservation (A. Keast and
3 E. S. Morton, Eds.). Smithsonian Institution Press, Washington, DC.

4 Sparrow, K.L., K.K. Donkor, N.J. Flood, P.P. Marra, A.G. Pillar and M.W. Reudink (2017).
5 Conditions on the Mexican moulting grounds influence feather colour and carotenoids in
6 Bullock's orioles (*Icterus bullockii*). Ecology and Evolution 7:2643-2651.

7 Steele, J. and McCormick, J. (1995). Partitioning of the summer grounds by Orange-crowned
8 Warblers into a breeding grounds, adult molting grounds and juvenile staging areas.
9 North American Bird Bander, 20:152.

10 Storer, R.W. and J.R. Jehl Jr. (1985). Moults patterns and moult migration in the Black-necked
11 Grebe *Podiceps nigricollis*. Ornis Scandinavica 16:253-260.

12 Stutchbury, B.J. and S. Rohwer (1990). Molt patterns in the Tree Swallow (*Tachycineta bicolor*).
13 Canadian Journal of Zoology, 68:1468-1472

14 Svardson, G. (1953) Visible migration within Fenno-Scandia. Ibis 95:181-211.

15 Swaddle, J.P., M.S. Witter, I.C. Cuthill, A. Budden, and P. McCowen (1996). Plumage condition
16 affects flight performance in common starlings: implications for developmental
17 homeostasis, abrasion and moult. Journal of Avian Biology 27:103-111.

18 Tonra, C.M., C. Both and P.P. Marra (2015). Incorporating site and year-specific deuterium
19 ratios ($\delta^2\text{H}$) from precipitation into geographic assignments of a migratory bird. Journal
20 of Avian Biology 46:266-274.

21 Tucker, V. A. (1991). The effect of molting on the gliding performance of a Harris' Hawk
22 (*Parabuteo unicinctus*). The Auk 108:108-113.

- Vézina, F., A. Gustowska, K. M. Jalvingh, O. Chastel, and T. Piersma (2009). Hormonal correlates and thermoregulatory consequences of molting on metabolic rate in a northerly wintering shorebird. *Physiological and Biochemical Zoology*, 82:129-142.
- Vitz, A.C. and A. D. Rodewald (2010). Movements of fledgling Ovenbirds (*Seiurus aurocapilla*) and Worm-eating Warblers (*Helmitheros vermivorum*) within and beyond the natal home range. *The Auk* 127:364-371.
- Warnock, N. (2010). Stopping vs. staging: the difference between a hop and a jump. *Journal of Avian Biology* 41:621–626.
- White, Clayton M., N. J. Clum, T. J. Cade and W. Grainger-Hunt (2002). Peregrine Falcon (*Falco peregrinus*), In the Birds of North America (P. G. Rodewald, Ed.). Cornell Lab of Ornithology, Ithica, NY, USA. <https://doi.org/10.2173/bna.660>
- Wiegardt, A.K., D.C. Barton, and J.D. Wolfe (2017a). Post-breeding population dynamics indicate upslope molt-migration by Wilson's Warblers. *Journal of Field Ornithology* 88:47-52.
- Wiegardt, A., J. Wolfe, C.J. Ralph, J.L. Stephens, and J. Alexander (2017b). Postbreeding elevational movements of western songbirds in Northern California and Southern Oregon. *Ecology and Evolution* doi:10.1002/ece3.3326
- Williams, T. D. (2012). Hormones, life-history, and phenotypic variation: opportunities in evolutionary avian endocrinology. *General and Comparative Endocrinology*, 176:286-295.
- Wingfield, J.C. (2008). Organization of vertebrate annual cycles: implications for control mechanisms. *Philisophical Transactions of the Royal Society: Biological Sciences* 363:425-441.

- 1 Wright, J. R., C. M. Tonra, and L. L. Powell (2018). Prealternate molt-migration in Rusty
2 Blackbirds and its implications for stopover biology. *Condor: Ornithological*
3 *Applications* 120:507-516.
- 4 Yuri, T. and S. Rohwer (1997). Molt and migration in the northern rough-winged swallow. *The*
5 *Auk* 114:249–262.

TABLES

Table 1. Examples and 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
<i>adult</i> - continuous prebasic molt-migration <i>first-year</i> - continuous preformative molt migration	Northern Rough-winged Swallow (<i>Stelgidopteryx ruficollis</i>)	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).
<i>adult</i> - stopover prebasic molt-migration <i>first-year</i> - stopover preformative molt migration	Western Kingbird (<i>Tyrannus verticalis</i>)	Adults undergo a complete prebasic molt during stopover in Mexican monsoon region/montane Southwestern U.S.A. 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 (<i>Calidris canutus rufa</i>)	Birds begin molting into alternate plumage on wintering grounds in Tierra del Fuego in February, continue to molt during migration, completing molt during stopover in eastern U.S.A. (Bueler and Piersma 2008). It is not currently clear if molts are suspended or continuous.
suspended prebasic molt-migration	Swainson's Hawk (<i>Buteo swainsoni</i>)	Birds begin molting flight-feathers at breeding sites, apparently pause molt during migratiuon and complete molt at stationary non-breeding sites (Smith 1980; Bechard and Weidensaul 2005)

FIGURE CAPTIONS

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.