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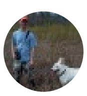

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USING MOLT AND PLUMAGE CYCLES TO AGE TROPICAL: UPDATES AND RECENT ADVANCES

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Resumen. – Utilizando ciclos de muda y plumajes para estimar la edad de aves tropicales: actualización y avances recientess. – Wolf *et al.* (2010) propusieron un sistema modificado para asignar edades a aves tropicales denominado sistema basado en ciclos, a partir del ciclo anual de muda y plumaje. Johnson *et al.* (2011) continuaron refinando el sistema de nomenclatura haciéndolo aplicable a todas las especies de aves sin importar si estas presentan muda prebásica prolongada y/o incompleta, incluyendo incluso patrones como Staffelmauser. A continuación sintetizamos ambas nomenclaturas de Wolf *et al.* (2010) y Johnson *et al.* (2011) en un solo marco lógico, a la ve que se realiza una recopilación de la teoría de muda contemporánea y se muestra aplicación global del sistema basado en ciclos utilizando ejemplos reales. El sistema basado en ciclos es una propuesta basada en información biológica de discriminación de cohortes que promueve un mejor entendimiento del ciclo de vida de las aves. Recomendamos a los ornitólogos empezar a usar este sistema para poder estudiar y monitorear con mayor precisión las poblaciones de aves tropicales.

Abstract. – Wolfe *et al.* (2010) proposed a transformative system of ageing tropical birds, called the cycle-based system, based on the annual molt and plumage cycle. Johnson *et al.* (2011) further refined the system by formulating nomenclature that broadens applicability to all bird species irrespective of prolonged and/or incomplete prebasic molts, including Staffelmauser patterns. Here, we synthesize Wolfe *et al.* (2010) and Johnson *et al.* (2011) into a practical framework provide a brief review of contemporary molt theory and demonstrate the universal applicability of the cycle-based system using real-world examples. The cycle-based system is a biologically-centric model of cohort discrimination that promotes a deeper understanding of the avian life-cycle. We recommend ornithologists begin using the system to more accurately monitor and study tropical bird populations.

Key words: molt, cycle-based system, age categorization, life cycle, cohort discrimination, neotropical bird monitoring

INTRODUCTION

Discriminating cohorts is an essential facet of demographic studies (Mason & Fienberg 1982, Sandercock *et al.* 2005). Identifying bird cohort, or age categorization, is classified in North America using a calendar-year system where all birds advance in age-class on 1 January. For example, if an individual bird has not yet surpassed its first new year, it is classified as a 'hatching year' (HY), and after crossing the 1 January threshold, HY individuals advance to 'second year' (SY) classification, then 'after-second year' (ASY), and so on. The calendar-year system becomes ineffectual when bird populations breed across 1 January because practitioners lose the ability to discriminate HY from SY individuals, and after-hatching year (AHY) from ASY individuals (Wolfe *et al.* 2010). Despite inherent flaws within the calendar-year system, it works well in the Northern hemisphere because most species adhere to discreet breeding seasons that typically occur during spring and summer months (for exceptions *see* Pyle 1997). Conversely, tropical landbirds exhibit more variance in breeding phenology resulting in a diversity of nesting seasonalities, such as: annual bimodal, irruptive, and/or prolonged breeding seasons (Diamond 1974, Snow & Snow 1964, Wolfe *et al.* 2009). For example, based on long term banding data, ten families of commonly captured understory birds were found to be breeding during every month of the year in the Central Amazon (P. Stouffer per. com.). The calendar-year system is impractical for many tropical bird communities due to variable breeding seasonality.

Because of incompatibilities between the calendar-year system and tropical bird communities, Wolfe *et al.* (2010) proposed a transformative system of age-categorization for tropical birds (called the cycle-based system) which relies on molt and plumage cycles, along with associated age-brackets. Johnson *et al.* (2011) further refined the cycle-based system with the addition of specific nomenclature that broadened applicability to species that exhibit prolonged and/or incomplete prebasic molts, including Staffelmauser patterns (Pyle 2008). Here we provide a brief review of contemporary molt theory, a synthesis of Wolfe *et al.* (2010) and Johnson *et al.* (2011), and illustrate the broad functionality of the system using real-world examples.

THE ANNUAL MOLT CYCLE OF PASSERINES

Heuristically, all passerines undergo an annual complete to nearly complete molt called the prebasic molt; the first prebasic molt initiates in the nest and is more commonly referred to as the prejuvenal molt (*sensu* Howell *et al.* 2003); thus, the prejuvenal and first prebasic molts are synonymous. We recommend using 'prejuvenal' instead of 'first prebasic' as established by Howell *et al.* (2003). Shortly after the completion of the prejuvenal molt all passerines go through a preformative molt, which is unique in that it occurs once in the life of a bird. The preformative molt is often incomplete or partial; however, some temperate and tropical passerines undergo complete preformative molts that are often indistinguishable from later basic plumages (e.g. Hirundinidae and many species in Formicaridae, *see* Ryder & Wolfe 2009). Because the preformative molt is often partial or incomplete, the formative plumage can be easily recognized by the presence of two generations of feathers among flight feathers and/or coverts; the boundaries between these two generations of feathers, formative and juvenal, within or between feather tracts, are called molt limits. Many migratory passerines undergo another partial to incomplete molt, called the prealternate molt, after the preformative molt but prior to a bird's first breeding season. Finally, after a bird's first breeding season (at about 1 year of age) birds will undergo a complete molt called the second prebasic molt. In most passerines the complete nature of the second prebasic molt typically results in a plumage indistinguishable from subsequent basic plumages and is, therefore, referred to as 'definitive.' Prebasic molts are used to define molt cycles, which are often approximately twelve months in length. For example, the period from the initiation of the prejuvenal molt (e.g. first prebasic molt) until the initiation of the second prebasic molt is referred to as the first molt cycle. Similarly, the period from the initiation of the second prebasic molt until the initiation of the third prebasic molt is known as the second molt cycle, and so on. Wolfe *et al.* (2010) defined the symmetrical shedding of P1 (or other primaries during certain molts in larger birds) as an unambiguous marker of molt-cycle succession. Most resident tropical passerines adhere to the Complex Basic Strategy (CBS; *see* Howell *et al.* 2003), where individuals will continue to undergo a single definitive prebasic molt during each cycle for the duration of their life. In contrast, most migratory passerines adhere to the Complex Alternate Strategy (CAS; *see* Howell *et al.* 2003) where individuals will continue to undergo definitive prealternate molts prior to the breeding season, and definitive prebasic molts following breeding during each cycle for the duration of their lives.

USING THE CYCLE-BASED SYSTEM TO CATEGORIZE BIRD AGE

The cycle-based system uses a three-position coding system. A finite number of letters are associated with each position, which in their entirety, represent the diversity of avian molt and plumage phenology (Fig 1).

First position. The first position represents the molt-cycle as defined by Howell *et al.* (2003). In the first position of the cycle-based system, 'F' represents first, 'S' second and 'T' for third molt cycle. After the fourth prebasic molt, cycles can be recorded using numbers (e.g. 4th, 5th cycle and so on) to reduce redundancy (Table 1). Definitive molt cycles (producing a plumage not distinguishable from subsequent plumages) are represented by 'D'. Finally, 'U' is used for unknown molt cycle.

Second position. The second position represents stasis (not molting), molting or after a given plumage. More specifically, if the molt cycle (as coded above) is known and the bird is not actively replacing feathers use 'C' for cycle. If the bird is actively molting (not adventitiously replacing feathers) use 'P' for pre, as in prejuvenal, prebasic, preformative or prealternate molt. Finally, if the bird is older than a known cycle and plumage (see below)

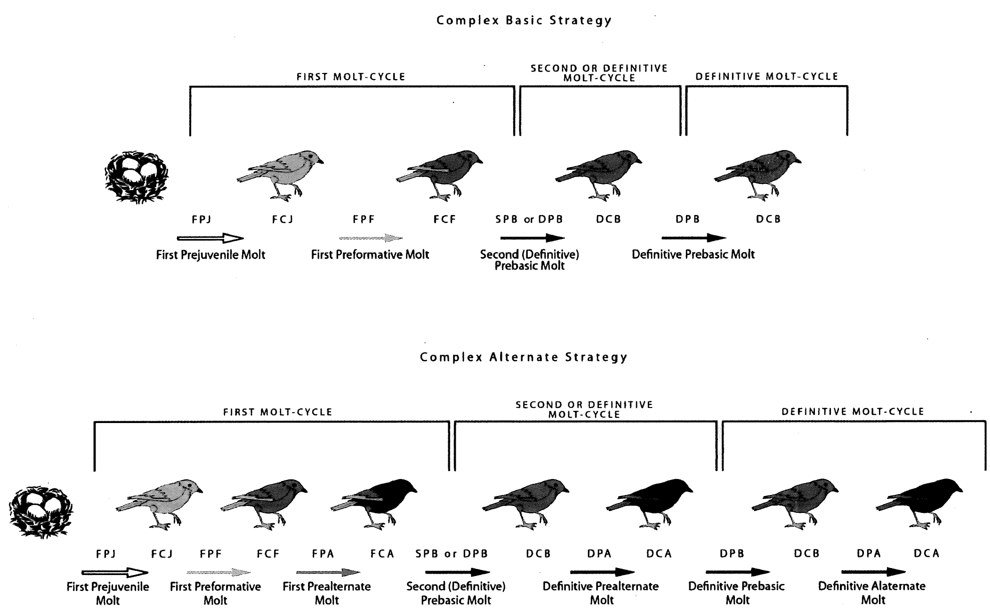

FIG. 1. Molt and plumage cycles for the complex basic and complex alternate strategies (CBS and CAS; see Howell *et al.* 2003). Cycle-based codes are associated with each molt and plumage to show the association between life-cycle phenology and the cycle-based system.

but age is not precisely known, then use 'A' for after a given plumage.

Third position. The third position represents plumage within a given molt cycle. Possible codes include 'J' for juvenal, 'F' for formative, 'S' for supplemental, 'B' for basic and 'A' for alternate. If the plumage within a molt cycle is not known, 'U' for unknown can be used.

The cycle-based system's three positions and their associated finite number of codes facilitate repeatable and accurate age categorization (Table 1). Banding data and molt cards can be used to create age brackets associated with cycle-code classification. For example, most First-Cycle Juvenal (FCJ) passerines will typically have associated age brackets between 0 and 2 months. Upon the initiation of the First-Preformative Molt (FPF) many passerine species will be associated with age brackets between 1 and 4 months of age. Family, genus and species-specific age brackets will continually be refined as plumage and molt phenology data are collected.

REAL-WORLD EXAMPLES

In July 2011, a single *Myrmotherula longipennis* was captured 80km north of Manaus, Brazil. The *M. longipennis* had outer greater coverts, primary coverts and remiges which were juvenal, more brown and worn relative to fresher and darker, formative inner greater coverts. Because the individual was not molting and had recognizable molt-limits within the greater coverts, it was determined that the bird had not initiated the second prebasic molt, and was, therefore in the first molt cycle (first position 'F'). Because the *M. longipennis* was not molting the second position received a 'C' for cycle, or stasis. Finally, the *M. longipennis* had molt limits (indicative of a partial preformative molt) and was, therefore determined to be in formative plumage (third position 'F'). In conclusion, the bird's age was categorized as FCF (First-Cycle Formative).

TABLE 1. Complete list of codes used in the cycle-based system.

1st Position	1st Position Definition	2nd Position	2nd Position Definition	3rd Position	3rd Position Definition
U	Unknown Molt Cycle	C	Not Molting ('C' for cycle)	U	Unknown Plumage
D	Definitive Molt Cycle	P	Molting ('P' for pre)	J	Juvenal Plumage
F	First Molt Cycle	A	After a Given Plumage	S	Supplemental Plumage
S	Second Molt Cycle			F	Formative Plumage
T	Third Molt Cycle			B	Basic Plumage
4	Fourth Molt Cycle			A	Alternate Plumage

In November 2011, a *Xiphorhynchus guttatus* was captured in the Madre de Dios region of Eastern Peru. The bird had an unossified skull and was symmetrically replacing the second and third primary (P2 and P3). Because most Woodcreepers undergo complete preformative molts, birds symmetrically replacing flight feathers may be in their first-cycle (undergoing a complete preformative molt) or in later cycles (undergoing complete definitive prebasic molts). To differentiate the two, outer primaries (older feathers) have to be assessed to determine if they are juvenal (in which case the individual would be undergoing a complete preformative molt) or post-juvenal (in which case the individual would be undergoing a definitive prebasic molt). In this particular individual, the outer primaries were tapered, indicative of juvenal remiges being replaced during the preformative molt; thus, the first position was recorded as 'F' for first molt-cycle. Because the bird was undergoing the preformative molt, the second position was recorded as 'P' for pre or molting. Because the condition of the outer primaries and the unossified skull eliminated the possibility of the bird undergoing a definitive prebasic molt, the third position was recorded as 'F' for formative. In conclusion, the bird's age was categorized as FPF (First Pre-Formative).

The final example was taken from Johnson *et al.* (2011) where in October 2009, a *Campephilus guatemalensis* was captured in Tortuguero, Costa Rica, with three distinct generations of feathers, none of which were juvenal. Because *C. guatemalensis* can exhibit incomplete definitive prebasic molts, it was determined that the woodpecker had at least surpassed the second and third prebasic molt (J. D. Wolfe, unpubl. data). When an individual bird has knowingly surpassed a given plumage, we can use the second position 'A' code for after a given plumage. Therefore, the first position was recorded as 'S' for second cycle. The second position was recorded as 'A' for after a given plumage and the third position was recorded as 'B' for definitive basic. Thus, the bird's age was categorized as SAB (After Second-cycle Basic).

DISCUSSION

The cycle-based system is universally applicable to all species, including such complicated strategies as southern and northern hemisphere breeding raptors and Pelicaniformes that exhibit Staffelmauser, to Amazonian Thamnophilids with partial preformative molts, and species that exhibit delayed-plumage maturation, irrespective of breeding seasonality. The cycle-based system is biologically centric: it uses the life-cycle of birds to differentiate cohorts, not an arbitrary calendar date that has no relevance when considering avian natural history. The cycle-based system also promotes a deeper understanding of molt phenology because the practitioner's knowledge of the avian life-cycle facilitates more-accurate and precise age classification. Finally, the cycle-based system has the capacity to retain information that is typically lost when using the calendar-year system by strategically implementing 'U' or unknown codes in the first and third positions. For example, if the molt-cycle of a particular migrant warbler is not known, but the phase or plumage is (e.g. alternate plumage), practitioners can record the bird as 'Unknown-Cycle Alternate' or UCA. Conversely, if the molt cycle is known (e.g. identified in the first cycle by an incomplete skull) but the plumage or phase is not (e.g. Woodcreepers with similar juvenal and formative plumages), practitioners can record the bird as 'First-Cycle Unknown' or FCU.

Despite significant advances provided by the cycle-based system, one cautionary note is warranted. Bird populations with prolonged breeding seasons coupled with rapid preformative molts can cause the system to lump cohorts. For example, *Catharus guttatus* has prolonged breeding seasons where formative plumaged breeding birds can finish nesting prior to molting while earlier fledged birds have already completed the preformative molt. The result: formative plumaged birds that are two months of age and breeding individuals over a year old can be lumped into the same cohort, First-Cycle Formative (FCF). The latter scenario maybe rare and we believe the benefits afforded by the cycle-based system out-weigh this confounding factor. To mitigate potentially lumping cohorts, we recommend using both the cycle-based and calendar-based system in unison when appropriate (e.g. *not* in equatorial regions) to provide extremely robust measures of cohort differentiation.

In conclusion, the cycle-based system provides a universally applicable framework that promotes a deeper understanding of natural history and retains more information relative to the calendar-year system. We recommend ornithologists consider using the cycle-based system to improve their capacity to differentiate bird cohorts in tropical latitudes.

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LITERATURE CITED

Diamond, A. W. 1974. Annual cycles in Jamaican forest birds. J. of Zoo. 173: 277–301.

Mason, W. M., & S. E. Fienberg. 1982. Cohort analysis in social research. Springer-Verlag, New York, New York, USA.

Howell, S. N. G., C. Corben, P. Pyle, & D. I. Rogers. 2003. The first basic problem: a review of molt and plumage homologies. Condor 105: 635–653.

Johnson, E. I., J. D. Wolfe, T. B. Ryder and P. Pyle. 2011. Modifications to a molt-based ageing system

proposed by Wolfe *et al.* (2010). J. Field Ornithol. 82: 422–424.

Pyle, P. 1997. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA.

Pyle, P. 2008. Identification guide to North American birds. Part 2. Slate Creek Press, Bolinas, CA.

Ryder, T. B., & J. D. Wolfe. 2009. The current state of knowledge on molt and plumage sequences in selected Neotropical bird families: a review. Ornitol. Neotrop. 20: 1–18.

Sandercock, B. K., K. Martin, & S. J. Hannon. 2005. Life history strategies in extreme environments: comparative demography of arctic and alpine ptarmigan. Ecology 86: 2176–2186.

Snow, D. W., & B. K. Snow. 1964. Breeding seasons and annual cycles of Trinidad landbirds. Zoologica 49: 1–39.

Wolfe, J. D., P. Pyle, & C. J. Ralph. 2009. Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. Wilson J. Ornithol. 121: 556–567

Wolfe, J. D., T. B. Ryder, & P. Pyle. 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. J Field Ornithol. 81: 186–194