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PERSPECTIVE

Application of a global age-coding system ("WRP"), based on molts and plumages, for use in demographic and other studies of birds

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ABSTRACT

Determination of a bird's age or cohort is critical for studies on avian demography, occurrence patterns, behavior, and conservation management. Age designations have largely been developed in north-temperate regions and utilize calendar-based or seasonally based codes; however, in tropical regions and in the southern hemisphere, these coding systems have limited utility at best. To address these issues, we had previously devised the "WRP system," based on the nomenclature of Humphrey and Parkes (H–P) and Howell et al., which defines molts in an evolutionary context applicable to birds globally. Here we refine and build upon core concepts and definitions of the WRP coding system, resolving key limitations that were identified during its first decade of use. The WRP system employs a three-letter alpha code in which each letter describes a different aspect of H–P terminology: the molt cycle (which informs a bird's age) and molt and plumage status within the cycle (each of which can also inform age). Here we recommend the continued use of most of the original ("core") WRP coding while augmenting the system with an optional adjunct-code entry for comprehensiveness, clarity, and flexibility, and we clarify a few additional codes to cover less common molting and plumage strategies. For most users, from 7 to 13 core and 1 adjunct WRP code will be sufficient to describe all plumages and provide molt status and ages for demographic studies or other purposes. The revised WRP system is flexible enough to be adapted to the specific goals of programs while also providing core codes that can facilitate the comparison of avian age, molt, and plumage status on a global basis. We anticipate that our revised and standardized version of the WRP system will be easily adopted and could eventually replace calendar-based and seasonally based coding.

Keywords: age code, molt cycle, plumage, reproductive success, terminology

LAY SUMMARY

- Age determination of birds is critical for studies on avian demography and conservation.
- Several age-designation systems currently in use are applicable to the temperate northern hemisphere but cannot be used in tropical regions or the southern hemisphere.
- The "WRP" coding system was thus designed for global use in demographic and other studies examining the ages and cohorts of birds.
- WRP coding is based on a rigidly defined molt terminology that designates molt cycle along with molt and plumage status, each of which informs age.
- Here we make recommendations to enhance and stabilize the core WRP system, providing clarified coding that can be adapted to individual programs while also being comparable on a global basis.

Aplicación de un sistema global de codificación de edad de las aves basado en mudas y plumajes para su uso en estudios demográficos y de otro tipo

RESUMEN

La determinación de la edad o de la cohorte de un ave es fundamental para los estudios sobre demografía aviar, patrones de ocurrencia, comportamiento y conservación. Las designaciones de edad se han desarrollado en gran medida en las regiones templadas del norte y utilizan códigos basados en el calendario o en las estaciones; sin embargo, en las regiones

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tropicales y en el hemisferio sur, estos sistemas de codificación tienen una utilidad limitada en el mejor de los casos. Para abordar estos problemas, nosotras teníamos previamente diseñaron el "sistema WRP", basado en la nomenclatura de Humphrey y Parkes (H–P) y Howell et al., que define las mudas en un contexto evolutivo aplicable a las aves a nivel mundial. Aquí refinamos y avanzamos sobre los conceptos y definiciones centrales del sistema de codificación WRP, resolviendo limitaciones clave que fueron identificadas durante su primera década de uso. El sistema WRP emplea un código alfa de tres letras en el que cada letra describe un aspecto diferente de la terminología H–P: el ciclo de la muda (que describe la edad de un ave) y el estado de la muda y del plumaje dentro del ciclo (cada uno de los cuales también puede describir la edad). Aquí, recomendamos continuar con el uso de la mayoría de la codificación WRP original ("núcleo"), al tiempo que ampliamos el sistema con una entrada opcional de código adjunto para mayor integralidad, claridad y flexibilidad, y aclaramos algunos códigos adicionales para cubrir las estrategias de muda y de plumaje menos comunes. Para la mayoría de los usuarios, de 7 a 13 núcleos y 1 código WRP adjunto serán suficientes para describir todos los plumajes y proporcionar el estado de la muda y las edades para estudios demográficos u otros fines. El sistema WRP revisado es lo suficientemente flexible como para adaptarse a los objetivos específicos de los programas y, al mismo tiempo, proporciona códigos básicos que pueden facilitar la comparación de la edad de las aves, la muda y el estado del plumaje a nivel mundial. Anticipamos que nuestra versión revisada y estandarizada del sistema WRP se adoptará fácilmente y eventualmente podría reemplazar la codificación basada en el calendario y en las estaciones.

Palabras clave: ciclo de muda, código de edad, éxito reproductivo, plumaje, terminología.

INTRODUCTION

Determination of a bird's age or cohort is critical for studies of avian demography, occurrence patterns, behavior, and conservation management. Historically, such designations and applicable coding for age have largely been developed in north-temperate regions, utilizing either calendar-based (e.g., Gustafson et al. 1997, Pyle 1997, 2008, Redfern and Clark 2001, van Noordwijk et al. 2003) or seasonally based (Cramp and Simmons 1977, Svennson 1992, Shirihai and Sevnsson 2018, Norevik et al. 2020, Jenni and Winkler 2020) coding systems. However, in tropical regions these systems have limited utility at best, due to a lack of breeding seasonality by many species (Wolfe et al. 2010, Johnson et al. 2012, Pyle et al. 2016, Johnson and Wolfe 2017). In the southern hemisphere, furthermore, opposite seasonality to that of the northern hemisphere leads to conflicting use of seasonally based codes for trans-equatorial migrants and, as many resident species in the southern hemisphere breed across December and January, calendar-based systems are also rendered inoperable (Lowe 1989, de Beer et al. 2001, Jackson 2005, Melville 2011, Pyle et al. 2015). To address these issues, Wolfe et al. (2010) devised an age-coding system based on the molt-cycle nomenclature of Humphrey and Parkes (1959) and Howell et al. (2003). Since 2010, this molt-cycle aging system has been increasingly used by banders and ornithologists throughout the Americas and in some other parts of the world (Wolfe et al. 2012, Pyle et al. 2015, 2016, 2017, Smith et al. 2015, Tórrez and Arendt 2016, Johnson and Wolfe 2017, Diaz et al. 2021), and it has subsequently become known as the "WRP system" after the authors of Wolfe et al. (2010). For continuity, we retain the "WRP" acronym to refer to this system, although we also suggest "Molt-cycle Ageing System (MCAS)" as an alternative designation.

The WRP system uses molt and plumage terminology originally proposed by Humphrey and Parkes (H–P), which is based upon how molts evolved along ancestral or in some cases recent bird lineages, rather than on contemporary and often plastic factors such as their seasonal timing, location, or extent (Pyle 2013a, Wolfe et al. 2014, Howell and Pyle 2015). Unlike traditional molt and plumage nomenclatures, the WRP system is equally applicable to birds in both temperate and tropical regions, irrespective of the timing and location of molts relative to those of breeding. However, the WRP system has also undergone some revisions (e.g., Johnson et al. 2011, Pyle et al. 2016, Johnson and Wolfe 2017), and users have applied differing definitions to WRP codes, depending on their project goals or target species. Although flexibility of definitions can be useful, it has also caused some confusion that has hindered the widespread and consistent adoption of the WRP system.

Universal applicability is a key advantage of the WRP system, as it provides a single global framework that facilitates international collaboration (Wolfe et al. 2010, Johnson and Wolfe 2017). Additional benefits over traditional systems are that plumages and molts within a cycle are also designated, that the coding is based on consistent progressions of molts and plumages rather than arbitrary changes in calendar years or seasonal regimes, and that alpha-code age designations are more intuitive and easily remembered than numeric designations assigned or required by some programs. Currently, several large North American programs such as the North American Bird Banding Program, The Institute for Bird Populations' MAPS and MoSI Programs, Environment and Climate Change Canada (Piranga), and the Cornell Lab of Ornithology's eBird program, Birds of the World accounts, and Macaulay Library are considering adopting the WRP

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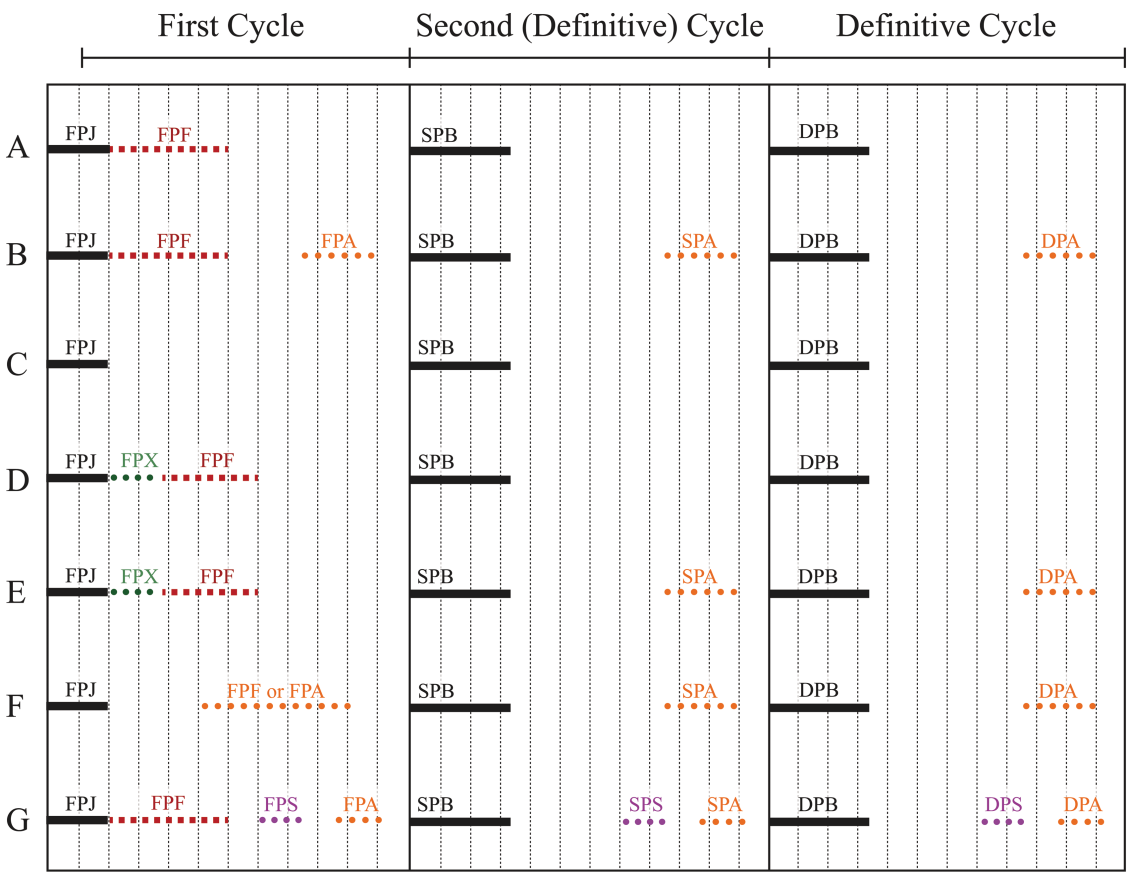

FIGURE 1. Molt strategies in birds with cycle-based terminology defined by Humphrey and Parkes (1959) and Howell et al. (2003) and using WRP molt codes. Vertical lines represent months assuming that molt cycles are approximately annual for an individual bird (although the first cycle can be temporally longer than a year). Molts are abbreviated as FPJ (first prebasic or prejuvenile), FPX (auxiliary preformative), FPF (preformative), FPS (first presupplemental), FPA (first prealternate), SPB (second prebasic), SPS (second presupplemental), SPA (second prealternate), DPB (definitive prebasic), DPS (definitive presupplemental), and DPA (definitive prealternate). Solid lines indicate molts that are usually complete, dashed lines indicate molts that can be complete or less than complete, and dotted lines indicate molts that are typically less than complete. Common molt strategies are represented by **A** and **B**, less common strategies by **C–G**. See text for more details and further explanation.

system. Revisions to such works as those of Pyle (1997, 2008) will also include WRP-system codes.

A reexamination of the WRP system is therefore needed to ensure stabilization of code definition and consistency of application for users throughout the world. Here we refine and build upon the core definitions of the WRP system (Wolfe et al. 2010, Johnson et al. 2011), resolving key limitations that were identified during its first decade of use. We emphasize that our revised WRP system provides the flexibility to be adapted to specific needs of programs while also providing codes that can be compared on a global basis.

HUMPHREY–PARKES TERMINOLOGY

Effective application of WRP coding requires familiarity with the cycle-based molts and plumages defined by Humphrey and Parkes (1959) as modified by Howell et al. (2003). All birds have a well-defined annual (or nearly annual) molting episode that involves growth or replacement of all or nearly all feathers, termed the prebasic molt (Humprey and Parkes 1959, Howell et al. 2003; Figure 1). This molt appears to have evolved from reptiles (Howell and Pyle 2015, Kiat et al. 2020) and reflects an ancestral physical-restoration process (Murphy 1996, Kuenzel 2003) that has been maintained through all bird lineages. The prebasic molt forms the foundation for H–P terminology (Howell et al. 2003, Pyle 2013b, Howell and Pyle 2015). It often occurs continuously at one location, but can also be suspended within molt cycles during the breeding season or for migrations (Pyle 1997, 2008, Tonra and Reudink 2018, Carnes et al. 2021).

Molt cycles are defined as the periods between prebasic molts, typically between the first molting of a primary during these molts (Figure 1). The first complete growth of body and flight feathers that typically occurs in the nest or at the natal site of birds is now considered the first prebasic

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molt (Howell et al. 2003), a synonym of the *prejuvenile molt*, which is a familiar traditional term maintained for practicality in WRP coding. The prejuvenile molt initiates the *first molt cycle*, which extends until commencement of the *second prebasic molt*, often at about one year of age. This molt initiates the *second molt cycle*, followed about a year later by the *third prebasic molt* initiating the *third molt cycle*, and so on. Typically, the second or subsequent molt cycles are also referred to as *definitive molt cycles*. Once an individual bird's plumage reaches a mature appearance following the first cycle, it is considered to be in its *definitive plumage*, represented by *definitive prebasic molts* followed by *definitive basic plumages*. For most passerines and many other small birds, the second prebasic molt results in definitive basic plumage, whereas in larger birds or other species with delayed plumage maturation, definitive appearance may not be reached until the third, fourth, or later basic plumages.

Along ancestral avian lineages additional molts have evolved between annual prebasic molts, considered "inserted molts" under H–P nomenclature. Within definitive cycles, the first inserted molt to evolve along an ancestral lineage is termed the *definitive prealternate molt* and a second inserted molt to evolve is termed the *definitive presupplemental molt* (cf. Pyle 2007; Figure 1). Note that, unlike prebasic molts, prealternate molts are not necessarily homologous across all bird taxa (Howell et al. 2003), just those along an extant bird's lineage back to the point in which the prealternate molt first evolved; prealternate molts have evolved independently within many bird lineages. Prealternate molts occur more regularly in species that migrate, likely due in part to more solar exposure experienced throughout the course of an annual cycle (Pyle 2008, Terrill et al. 2020), and are therefore more common in temperate than in tropical regions, where fewer species undertake migrations. Definitive presupplemental molts are rare.

The first molt cycle differs from the definitive cycle in that one or two, unique, extra inserted molts have evolved (Howell et al. 2003). Because the first molt cycle can be temporally longer than subsequent molt cycles, an extra replacement of weaker juvenile feathers is often needed. Most if not all birds have evolved a separate molt unique to the first cycle, now termed the *preformative molt* (Howell et al. 2003). This molt may be an ancestral molt, also evolved from dinosaurs, as it appears to occur in most or all bird lineages. Preformative molts are often less than complete, although they can be complete in at least some temperate and tropical species or individuals within species. In rare cases a second additional first-cycle molt has evolved, termed the auxiliary preformative molt (Howell et al. 2003, Pyle 2008), previously referred to as the "first presupplemental molt" (Thompson and Leu 1994). Auxiliary preformative molts are uncommon, poorly understood, and appear to be limited, usually involving body feathers only (Figure 1).

Most but not all bird species that have definitive prealternate molts also have paralogous *first prealternate molts* within the first molt cycle, and at least some species with definitive presupplemental molts also have paralogous *first presupplemental molts*. First prealternate and presupplemental molts are nearly always less than complete (Figure 1). Most of the world's bird species have a single inserted molt within the first cycle, the preformative molt, whereas most of those with definitive prealternate molts have two inserted molts, the preformative, and first prealternate molts. Other first-cycle molting strategies, including those with no inserted molt in the first cycle or more than two inserted molts in the first or later cycles, are rare (Figure 1). Despite this variation and complexity, however, we have thus far found no bird species with molt strategies that cannot be comfortably defined within the H–P nomenclatural framework.

H–P nomenclature is based upon molts and how they evolved. Plumages are strictly defined as those following molts. Thus, for example, the prejuvenile molt results in *juvenile plumage*, the preformative molt results in *formative plumage*, the first prealternate molt results in *first alternate plumage*, a definitive prebasic molt results in *definitive basic plumage*, and the definitive prealternate molt results in *definitive alternate plumage*. Following a complete molt, a plumage will have only one feather generation. After less-than-complete molts, a plumage will be comprised of two or more feather generations, and these multi-generational plumages include boundaries between feather generations or "molt limits," which are frequently used to identify a bird's age and/or its plumage.

THE WRP AGE-DESIGNATION SYSTEM

Core WRP Coding

The H–P nomenclature provides a clear and globally consistent chronological progression of molts and plumages to which the WRP age-designation system adheres. As detailed by Wolfe et al. (2010) and subsequent publications (Johnson et al. 2011, Wolfe et al. 2012, Pyle et al. 2015, 2016, 2017, Johnson and Wolfe 2017), the WRP system employs a three-letter alpha code in which each letter describes a different aspect of H–P terminology (Table 1). Here we recommend the continued use of most original coding. We also augment the system with an optional "adjunct code" for comprehensiveness and clarity, and we propose a few additional molt and plumage codes to cover all molt strategies found among the world's birds. In the majority of cases, "core" WRP codes and definitions will remain unchanged from original usage (Tables 1 and 2, Figures 1A–B and 2), while we also augment them with codes to increase flexibility and to cover less-frequent

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TABLE 1. Characters used for each position of WRP age-designation codes. Core WRP coding is indicated in bold. Table 2 and Figures 2 and 3 provide examples of WRP coding for species with core and less-frequently used codes, respectively

First position – cycle(age)	Second position – molt status	Third position – plumage
F – first	**C – cycle** (molt completed)	**J – juvenile**
S – second	**P – "pre"** (molt in progress)	**F – formative**
T – third	U – unknown	**A – alternate**
D – definitive		**B – basic**
4 to 9 – fourth to ninth		X – auxiliary formative
		S – supplemental
		U – unknown

molt strategies (e.g., Figures 1C–G and 3) that can be utilized as needed for certain species or research programs.

The letter in the first position of a WRP code designates the molt cycle and includes core codes **F** for first, **S** for second, **T** for third, and **D** for definitive cycles (Table 1). The letter in the second position represents molt status, with individuals in active molt (e.g., body and/or flight feathers being actively replaced during a molt episode) designated with **P** for "pre" (as in preformative or prebasic) and those between active molts by **C** for cycle (Table 1). In previous versions of the WRP system, A (for after) was also an option for the second position (Johnson et al. 2011), but to improve coding precision, consistency, and usability, we recommend eliminating this coding option and using an adjunct code instead (see below). The letter in the third position indicates the plumage, including core codes **J** for juvenile, **F** for formative, **B** for basic, and **A** for alternate (Table 1). If the molt cycle, molt status, and/or plumage cannot be determined, "unknown codes" (designated by U) and/or adjunct codes can be used and provide flexibility, as discussed in more detail below.

Many users (e.g., banders and ringers) will apply these codes primarily to passerines and other small birds that attain definitive appearance following the second or third prebasic molt. In such cases just 13 core WRP codes are needed: **FPJ** (undergoing the prejuvenile molt), **FCJ** (juvenile plumage), **FPF** (undergoing the preformative molt), **FCF** (formative plumage), **FPA** (undergoing the first prealternate molt), **FCA** (in first alternate plumage), **SPB** (undergoing the second prebasic molt), **SCB** (in second basic plumage), **TPB** (undergoing the third prebasic molt), **DCB** (in definitive basic plumage), **DPA** (undergoing the definitive prealternate molt), **DCA** (in definitive alternate plumage), and **DPB** (undergoing the definitive prebasic molt). In such programs, codes SCB and TPB would be needed only for woodpeckers and small raptors in which second basic plumage is easily recognized, and for species that lack prealternate molts, FPA, FCA, DPA, and DCA will not be needed. Thus, as few as 7 core codes (FPJ, FCJ, FPF, FCF, SPB, DCB, and DPB) will apply to most passerines and other small landbirds. As a primary focus of most studies on passerines is age (cycle) we believe that a reduction of choices for the first position to just 2 or 3 codes (F, S, or D) will simplify age-coding for such programs, irrespective of what codes are applied in the second and third positions, including unknown codes as described below. We anticipate that these core WRP codes (Tables 1 and 2, Figures 1A–B and 2) along with the occasional use of adjunct codes will cover the molt strategies of the vast majority of bird species. Examples of species with molts and plumages covered by core WRP codes include Barred Antshrike (*Thamnophilus doliatus*) with incomplete preformative, complete prebasic, and no prealternate molts (Figure 2A); Northern Wheatear (*Oenanthe oenanthe*) with partial preformative, complete prebasic, and partial prealternate molts (Figure 2B); and White-bellied Woodpecker (*Dryocopus javensis*) with incomplete preformative and prebasic molts and identifiable second (and occasionally third) basic plumages (Figure 2C).

The first letter indicating cycle is paramount when using the WRP system for age determination. No matter the state of molt or plumage, this letter will indicate a bird's age in terms of molt cycles which approximately equates to years. For example, "F" will indicate a bird in its first cycle (year) of life, "S" its second, and "T" its third, whereas "D" represents a minimum age, that cycle in which definitive appearance of a species is typically reached. The second (molt) and third (plumage) codes can be used to further refine a bird's age within each cycle. For example, FCJ will usually indicate a bird within the first one to a few months of its first year; FPF, FCF, FPA, and FCA a bird within specific months of the first year depending on the species; SPB usually a bird of 10–14 months of age depending on the species, and SCB a bird just following its first cycle, often between 11 and 24 months of age, again depending on the species. A cycle-based system is similar to the annual, age-based coding systems employed in the southern hemisphere (Lowe 1989, de Beer et al. 2001, Jackson 2005, Melville 2011), but our system provides much greater detail and refinement for defining molt cycles at the individual level. We stress that this level of refinement can be used to advantage by researchers familiar with the molt and plumage cycles of their study species and it can also be used to specify cohort in species that breed seasonally. In some species (e.g., among manakins; Johnson and Wolfe 2017), sexes may attain definitive appearance

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TABLE 2. Complete list of WRP codes. Bold indicates more commonly used (including core WRP) codes, for instance, those that will be primarily used for demographic studies of passerines, woodpeckers, and other small landbirds. Adjunct codes M (Minimum-aged plumage), H (Hatching season FCF), and A (After hatching season FCF) are indicated for WRP codes in which usage is anticipated. See text for the additional use of unknown codes

Adjunct	Molt cycle (WRP) code	Designated condition
First cycle		
	FPJ	**Prejuvenile Molt**
	FCJ	**Juvenile Plumage**
	FPX	Auxiliary Preformative Molt
	FCX	Auxiliary Formative Plumage
(M)	**FPF**	**Preformative Molt**
(H, A, **M**)	**FCF**	**Formative Plumage**
(M)	**FPA**	**First Prealternate Molt**
(M)	**FCA**	**First Alternate Plumage**
(M)	FPS	First Presupplemental Molt
(M)	FCS	First Supplemental Plumage
Second cycle		
(M)	**SPB**	**Second Prebasic Molt**
(M)	**SCB**	**Second Basic Plumage**
(M)	SPA	Second Prealternate Molt
(M)	SCA	Second Alternate Plumage
(M)	SPS	Second Presupplemental Molt
(M)	SCS	Second Supplemental Plumage
Third cycle		
(M)	**TPB**	**Third Prebasic Molt**
(M)	TCB	Third Basic Plumage
	TPA	Third Prealternate Molt
	TCA	Third Alternate Plumage
Older predefinitive cycles		
(M)	4PB, 4CB	Fourth-cycle Codes
(M)	5PB, 5CB	Fifth-cycle Codes
(M)	6PB, 6CB	Sixth-cycle Codes
(M)	7PB, 7CB	Seventh-cycle Codes
(M)	8PB, 8CB	Eighth-cycle Codes
(M)	9PB, 9CB	Ninth-cycle Codes
Definitive cycle		
	DCB	**Definitive Basic Plumage**
	DPA	**Definitive Prealternate Molt**
	DCA	**Definitive Alternate Plumage**
	DPS	Definitive Presupplemental Molt
	DCS	Definitive Supplemental Plumage
	DPB	**Definitive Prebasic Molt**

during different cycles; thus, a DCB female may indicate a different age-designation or cohort-designation category than a DCB male. Note also that in some species completion of preformative or prebasic molts may overlap commencement of prealternate molts, for example, among shorebirds, terns, and tyrannid flycatchers (Pyle 2008, 2019, Carnes et al. 2021). In these cases, we recommend applying the code to the following molt, FPA or DPA in this case, to better indicate timing within molt cycles. Finally, some species have been reported to undergo molt cycles of less than or greater than 1 year. While this remains poorly documented at the individual level, even if such molt cycles exist, the WRP system can still be used to infer age, and can also be used to investigate cycle length.

Less-frequent (Non-core) Plumage and Molt Categories

A few larger bird species, including those among gulls, albatrosses, frigatebirds, condors, and eagles, can take from four to 10 or more years to acquire definitive plumage (Cramp and Simmons 1977, Marchant and Higgins 1990, Pyle 2008). Following Johnson et al. (2011), we recommend numeric codes 4–9 for use in the first position in such species (Tables 1 and 2). For example, Bald Eagles (*Haliaeetus leucocephalus*) of North America do not assume definitive plumage until their fourth or fifth cycle, resulting in use of codes TCB, 4PB, and 4CB (Figure 3A). Additionally, relatively few species show identifiable second or third alternate plumages, resulting in the infrequent use of the

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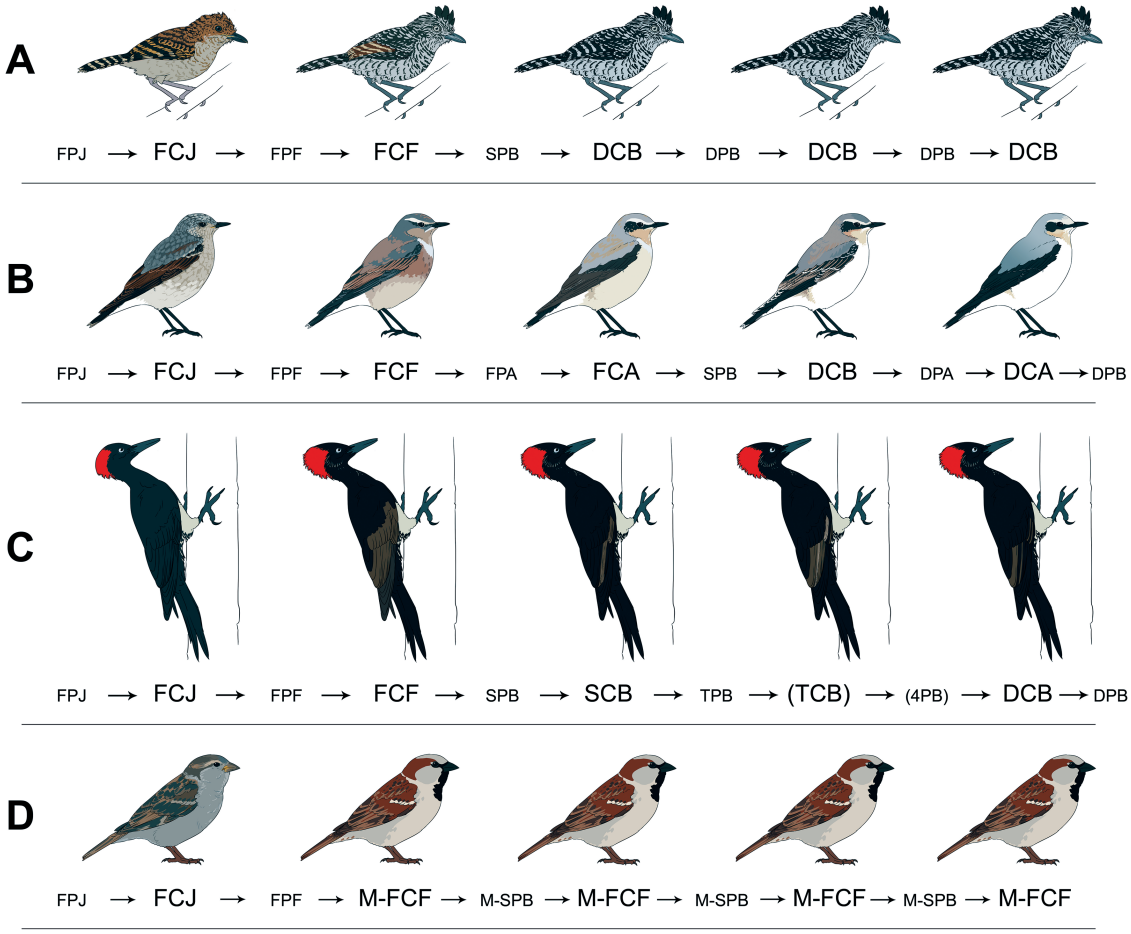

FIGURE 2. Examples of core WRP codes for (**A**) male Barred Antshrike (*Thamnophilus doliatus*), (**B**) male Northern Wheatear (*Oenanthe oenanthe*), (**C**) female White-bellied Woodpecker (*Dryocopus javensis*), and (**D**) male House Sparrow (*Passer domesticus*). Use of non-core codes TCB and 4PB can only be applied infrequently to woodpeckers, most birds in the third cycle being indeterminate and coded DCB and DPB, respectively (see text).

WRP codes SPA and SCA. Silver Gull (*Chroicocephalus novaehollandiae*) of Australia and New Zealand is an example of a species with identifiable second alternate plumages (Figure 3B), whereas in larger gulls and a few other bird species, WRP codes TPA and TCA can also be applied.

Uncommon molting strategies can also affect WRP interpretation. For example, some species such as ostriches, albatrosses, and American vultures may lack a preformative molt (Figure 1C). In these cases, FCJ (for juvenile plumage) can be used until the second prebasic molt commences and often indicates a bird that is from 1 to 10–14 months old. Thus far, auxiliary preformative molts have been identified only in a few North American passerines and one South American passerine (Pyle 1997, Johnson and Wolfe 2017), but could potentially occur in a wider range of taxa or in passerines throughout the world. Following Johnson and Wolfe (2017), we recommend the code **X** for the third position, to account for auxiliary formative molts (FPX) and plumages (FCX). Species that undergo these molts can either lack (Figure 1E) or undergo (Figure 1F) prealternate molts as well, an example of the latter being Indigo Bunting (*Passerina cyanea*) of North America (Figure 3C). Although the order in which the auxiliary preformative and preformative molts have evolved along ancestral lineages is not yet known (Pyle 2007), for the purposes of WRP coding we assume that the auxiliary preformative molt precedes the preformative molt, based on comparison of molts in related species within at least some avian families (Thompson and Leu 1994). In some species, completion of auxiliary preformative molts may overlap commencement of preformative molts (Pyle 1997); in these cases, we recommend applying the code FPF, as described above.

Likewise, only a few bird species undergo definitive presupplemental molts, including those among ptarmigan, shorebirds, terns, and possibly ducks (Battley et al. 2006, Pyle 2007, 2008, 2013b, 2019). Here we recommend the code **S** for the third position, to indicate definitive

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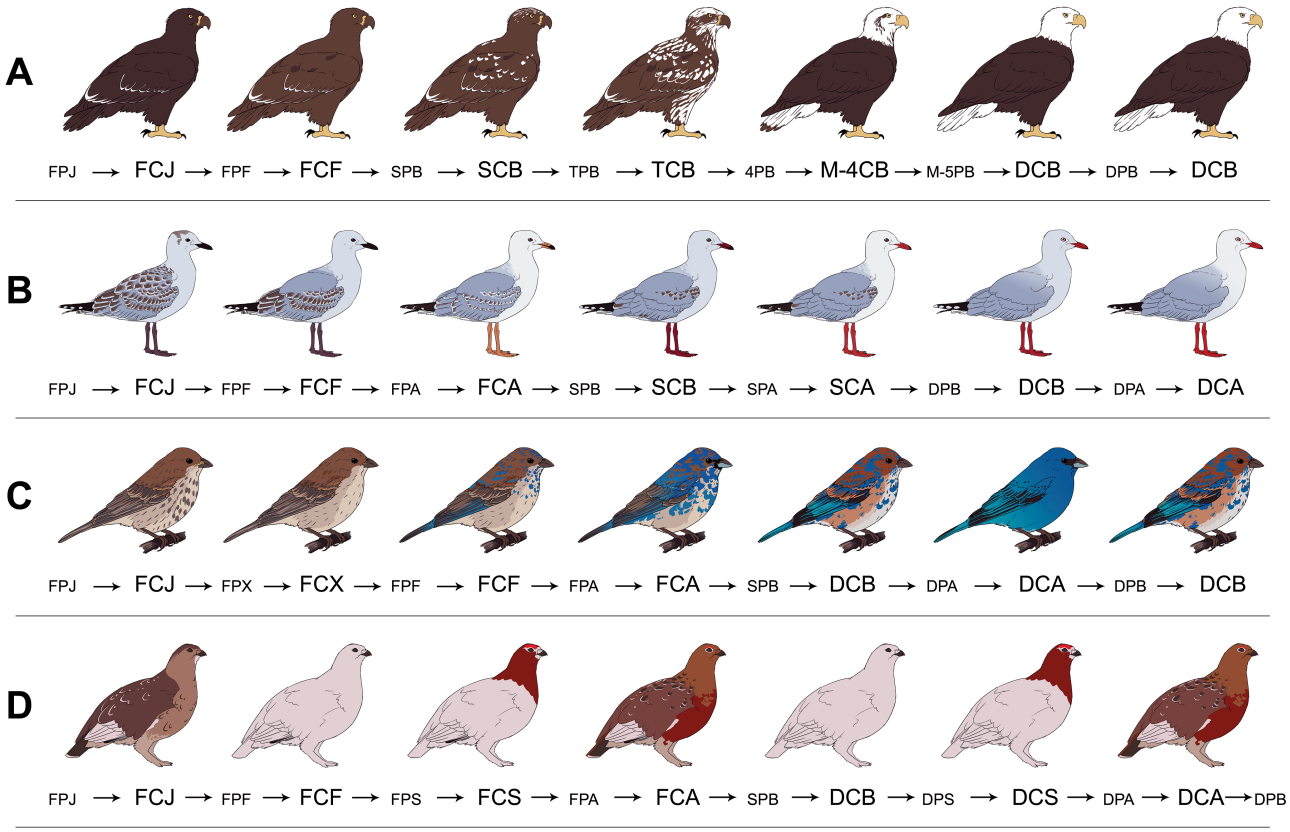

FIGURE 3. Examples of less-commonly used WRP codes for (**A**) Bald Eagle (*Haliaeetus leucocephalus*), (**B**) Silver Gull (*Chroicocephalus novaehollandiae*), (**C**) male Indigo Bunting (*Passerina cyanea*), and (**D**) male Willow Ptarmigan (*Lagopus lagopus*).

presupplemental molts (DPS) and plumages (DCS). Some of these species appear to undergo first presupplemental molts (FPS) followed by first supplemental plumages (FCS) (Figure 1G). Examples include small shorebirds and terns, and Willow Ptarmigan (*Lagopus lagopus*) of the Holarctic (Figure 3D), while a few species of terns may also have identifiable second presupplemental molts (SPS) and supplemental plumages (SCS). By contrast, in other species such as ducks, large terns, and large shorebirds, supplemental plumages appear to be restricted to definitive cycles. As with auxiliary preformative molts, presupplemental molts may either precede or follow prealternate molts chronologically within a cycle, depending on how each evolved (Pyle 2007). Additional study is needed on the evolution and sequence of these uncommonly occurring molts and plumages, which we hope to facilitate by providing applicable WRP codes for them.

Unknown Codes

"Unknown codes" provide flexibility within the WRP system and allow users to exclude individuals from data analyses. We recommend continued use of the code U for birds in which the molt cycle, molting status, and/or plumage were uncertain or indeterminable. Examples of unknown cycle codes include UCU, UPU, and UUU to indicate that the cycle (age) is indeterminate. Here we recommend replacing these largely with adjunct codes, but they can continue to be options to provide flexibility for certain specific cases (see below). Unknown plumage codes include FCU, SCU, and DCU for birds in which the cycle is known but the plumage is indeterminate. These codes can account for species in which prealternate molts are either absent or present and, following the period of the prealternate molt, plumage determination can be difficult. Unknown codes can also be used when molt status is unknown (e.g., FUF, FUA, DUB, or DUA), for birds in which neither molt nor plumage is known (e.g., FUU, SUU, or DUU), or for birds in which none of the three parameters are known (UUU). For most programs we anticipate that these unknown codes will be needed only infrequently, and we encourage attempted use of more informative molt and plumage designations, if possible, to further understand the molt and plumage dynamics in their target species.

Adjunct Codes

The WRP system as described above has led to an inability to designate cycle (age) in certain specific situations. To address this limitation, we introduce the use of an optional

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"adjunct code" before the WRP code for 3 reasons: (1) to enable cohort designation for birds in formative plumage; (2) to better designate a bird's minimum age, replacing the previously applied "after" designation; and (3) to provide users flexibility to add customized notations depending on their goals. For experienced users, we anticipate that adjunct codes will be needed for only a small proportion of birds (i.e. for the great majority of individuals the adjunct code can be left blank). For the purposes of describing adjuncts to WRP codes we recommend a hyphen (e.g., "M-FCF"; see below), but databases would employ only two fields of 1 and 3 characters for the adjunct and primary codes, respectively.

The separation of recently fledged ("hatching-year") birds from breeding adults is critical for estimating reproductive success in demographic studies (Peach et al. 1996, DeSante et al. 2001, 2005). The core WRP codes FCJ, FPF, and FCF allow for accurate identification of hatching-year birds of most species; however, for some species (including certain warblers, flycatchers, and orioles in the Americas), birds in fresh formative plumage (FCF) at 1–2 months of age can overlap those in worn formative plumage (FCF) that have not commenced their second prebasic molt by 11–12 months of age. In tropical species that undergo protracted or year-round breeding, there is an even greater need for a cohort designation to distinguish fresh from worn formative plumages (Pyle et al. 2016, 2017, Johnson and Wolfe 2017). For demographic studies, the subdivision of FCF into different cohort groupings will increase accuracy in estimating reproductive success. Therefore, we introduce the adjunct codes "**H**" for hatching season or "**A**" for after hatching season to distinguish post-fledging (H-FCF) from yearling (A-FCF) birds in formative plumage. In tropical species that undergo seasonally protracted or year-round breeding, we recommend that H-FCF designate a bird estimated to be <6 months old and A-FCF designate one estimated to be >6 months of age. We also recommend the use of "U-FCF" in cases where a bird cannot be confidently assigned to H-FCF or A-FCF based on such factors as plumage wear, eye color, degree of skull ossification, or recapture of a marked bird. However, for most species and projects, the core code FCF will be sufficient to unambiguously designate cohort as well as age, and the adjunct code can be left blank.

In some cases, it may not be possible to determine the molt cycle of an individual bird with certainty, but it is known to be at least of a certain age. Such designations can be important for studies, including those on reproductive success. For example, following a complete preformative molt, distinguishing a bird in formative plumage (FCF) from one in definitive basic plumage (DCB) may not be possible. In previous versions of the WRP system, the code "FAJ" could be applied in such cases. This and other "after-codes" (e.g., "SAB" and "TAB") provided exceptions to the WRP letter-position scheme, causing confusion to some users, while others used unknown codes UCU or UCB in these instances instead. These codes could also not be used in combination with the molting (P) code and could not be applied to birds in alternate plumages or those species that can be identified in fourth or later plumage cycles.

To resolve these issues, we introduce the adjunct code "**M**" for "at a minimum," as a modifier indicating that the bird is at minimum the age of the associated WRP code. We advocate the use of adjunct-code M primarily to designate birds not known to be in their first or later cycle; for example, M-FCF indicates either FCF (at minimum in formative plumage) or a later cycle code (e.g., DCB), replacing prior use of the code FAJ. M-FCF will most commonly be used for species that undergo complete preformative molts such as the globally distributed House Sparrow (*Passer domesticus*) (Figure 2D). For those few species with complete preformative molts and alternate plumages, such as Little Stint (*Calidris minuta*), Grasshopper Sparrow (*Ammodramus savannarum*), and Fulvous Shrike-Tanager (*Lanio fulvus*), individuals undergoing the prealternate molt can be designated M-FPA, and those in alternate plumage can be designated M-FCA. More generally, the adjunct code M can be used for birds that cannot be aged precisely, e.g., M-FPF for a bird undergoing a complete preformative or prebasic molt, or M-SPB for one undergoing either the second or a later prebasic molt, which is often indistinguishable when completing growth of the last feather of a complete molt (Pyle 1997, 2008, Pyle et al. 2016). In many such cases, the use of M can supplant the use of an unknown code; however, the use of either can provide added flexibility for certain analyses. For example, M-FCF can designate a breeding adult (either A-FCF or DCB) whereas UCU can designate either a young bird or an adult (either H-FCF or DCB).

For woodpeckers and other species that are readily identified in their second cycle, M-SCB can be used to designate birds that could be in either second or later basic plumages, followed by M-TPB for such birds during the ensuing molt. Importantly, adjunct-code M should not be used in lieu of definitive-cycle codes (DCB, DPB). For example, M-FCF should not be used for second or later cycles in species for which definitive plumage is consistently achieved in the second cycle, including most passerines and many other small birds. When only a small proportion of birds can be determined to be in a given pre-definitive cycle, for example, some but not all woodpeckers in their third cycle (Siegel et al. 2016), we recommend that DCB include birds in that cycle as opposed to using codes M-TCB and M-4PB, while maintaining the use of TCB and 4PB as an option for those individuals (Figure 2C).

A less-frequent but particularly valuable application of the adjunct-code M can occur with birds in basic plumages in which precise cycle is unknown, but a minimum cycle can be

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recognized. Older birds of species that exhibit Staffelmauser (including arrested molts between cycles) might be identifiable as at minimum in second basic plumage (M-SCB), third basic plumage (M-TCB), or fourth basic plumage (M-4CB) based on patterns of replacement among remiges (Pyle 2005, 2008), and species among albatrosses, frigatebirds, or condors may not acquire definitive plumage until 10 years of age or older, but can be recognized as in a minimum pre-definitive plumage (Pyle 2008). For example, Bald Eagle can assume definitive plumage in either its fourth or fifth cycle, such that birds in certain pre-definitive plumages can be coded M-4CB indicating either 4CB or 5CB or as M-5PB during the ensuing molt, before acquiring definitive appearance and being coded DCB (Figure 3A). We emphasize that the use of M and U codes will only be needed in a small proportion of individuals, the 13 core codes being sufficient in most cases. As such, we invite users to develop their own protocols for the use of M and U codes but to adhere more strictly to the definition in the use of core codes.

Finally, we propose that additional adjunct codes can be defined for other specific purposes, as needed by individual researchers or projects. Other than the adjunct codes "H," "A," "U," and "M" specified above, almost any other alpha or numeric entry can be used and not interfere with the interpretation of age or molt and plumage status provided by the three-letter code. For example, some birds can temporarily suspend molts for various reasons. Suspended molts within molt cycles are common in tropical regions (Johnson et al. 2012, Pyle et al. 2016) but also can occur in north-temperate raptors for incubation (Pyle 2005) and for migrants during southbound migration (e.g., Pyle 2008, Barry et al. 2009, Tonra and Reudink 2018). Users of the traditional WRP system have had difficulty assigning codes indicating molts that have been temporarily suspended, primarily because it is unknown at the time of designation whether or not a molt has completed or is suspended and will resume later within the molt cycle. In such cases we recommend the use of the ensuing plumage code for now, for example, FCF as opposed to FPF for species that may have suspended the preformative molt for migration such as Western Kingbird (*Tyrannus verticalis*) (Barry et al. 2009); FCF presumes that the molt has completed and will not resume following migration. However, researchers may want to use an adjunct-code (for example, "S") for birds that they suspect have suspended the preformative (S-FPF) or prebasic (e.g., S-SPB, S-TPB, S-DPB) molts. There will likely be other specific uses of well-defined adjunct codes, and we emphasize that this extra column adds flexibility to the WRP system that otherwise provides rigidly defined core codes to facilitate comparison of avian age, molt, and plumage status on a global basis.

CONCLUSIONS

Here we present a full suite of WRP codes (Tables 1 and 2) that we believe will cover all cycles, molts, and plumages of birds globally. We anticipate that the WRP system can be used consistently to designate identifiable ages, molts, and plumages, allowing comparison of designations between programs while standardizing and clarifying previously used coding based on calendar years or seasons. For any given program, a restricted code-usage list can be constructed that will be applicable to the program for purposes of data verification, and can also designate temporal ranges within annual cycles in which given codes will be expected (cf. Pyle et al. 2017). Only 13 core WRP codes and the adjunct code M-FCF are sufficient to describe typical molts and plumages for most passerines and woodpeckers, whereas as few as 7 of these are applicable to passerines and other small birds that lack prealternate molts (Tables 1 and 2). We suspect that, for most users, these 7–13 core codes and the adjunct code "M" will be sufficient to describe all molts and plumages within their programs, although we also provide less-frequently used codes and propose flexibility with the use of additional unknown and adjunct codes, as needed, to cover all molt and plumage strategies globally.

We acknowledge that rare molt-plumage combinations among the world's birds may be discovered that will not be covered by our currently proposed WRP system, or that will require additional coding combinations than those provided here. But we hope that the application of WRP coding will lead to a further understanding of avian molt and plumage strategies, enhance the accuracy of molt and plumage designations for birds found throughout the world, and inform future demographic studies.

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