JOURNAL OF
AVIAN BIOLOGY

Viewpoint article

Moult terminology: envisioning an evolutionary approach

Peter Pyle[1], **Steve N. G. Howell**[2], **Danny I. Rogers**[3] **and Chris Corben**[4]

[1]The Institute for Bird Populations, Petaluma, CA, USA
[2]Bolinas, CA, USA
[3]Department of Energy, Environment and Climate Action, Arthur Rylah Institute for Environmental Research, Heidelberg, Vic, Australia
[4]Columbia, MO, USA

Correspondence: Peter Pyle (ppyle@birdpop.org)

Journal of Avian Biology
2024: e03169
doi: 10.1111/jav.03169

Subject Editor: Lu Dong
Editor-in-Chief: Staffan Bensch
Accepted 17 November 2023

Keywords: bird, evolution, nomenclature, reptile, terminology

The study of avian moult has been inhibited not only by its complexity but by convoluted and often conflicting terminologies that have combined to cloud the subject. Over time, two nomenclatures have emerged with differing bases of definition. The 'life-cycle' system is used widely in the European literature (Cramp 1988, Jenni and Winkler 2020) and defines moult terms based on timing relative to current-day life-history events, primarily breeding. Conversely, the Humphrey–Parkes or 'H–P' system (Humphrey and Parkes 1959, as modified by Howell et al. 2003), is used more widely in the New World and Australia (Higgins and Davies 1996, Johnson and Wolfe 2018, Pyle 2008, 2022a, Howell 2010), and defines terms based on the principle of how moults have evolved along avian lineages (Howell and Pyle 2015, Pyle 2022b).

Recently, Kiat (2023) proposed that moult terminology be simplified, and advocated use of the life-cycle approach as a more understandable system to those not familiar with moult terminology. We appreciate Kiat's (2023) plea for a simpler moult terminology, and we empathize with the frustration that comes from learning an unfamiliar system, but we disagree with his primary conclusion. We argue that if one intends moult to be a subject for study, then a standardized and globally applicable terminology based on the best scientific evidence is preferable to a system that, while perhaps more widely understood among ornithologists and the general public for most passerines in boreal regions, is often imprecise or ambiguous and is difficult to apply to the majority of avian taxa on a global basis (Higgins and Davies 1996, Howell et al. 2004, Johnson and Wolfe 2018, Kiat 2023, Pyle 2022b).

The debate over the best moult and plumage terminology to use has persisted since the H–P system was proposed by Humphrey and Parkes (1959) over 60 years ago (c.f. Howell et al. 2003, 2004, Jenni and Winkler 2004, 2020, Kiat 2023, Pyle 2022b). At this point, certain opinions on which system should be favoured are calcified, and we do not wish to belabour the details yet again. In our experience, however, newer students grasp the H–P system quickly, whereas older ornithologists – including ourselves – who first learned life-cycle moult terminology, often have initial difficulty

NORDIC SOCIETY OIKOS

www.avianbiology.org

envisioning the H–P system's evolutionary approach. Our goal with this perspective is to propose and illustrate how moults may have evolved from basal to current lineages in birds, with the hope that it will assist future ornithologists to envision and appreciate the H–P system.

Adhering to the evolutionary (H–P) approach, we propose considering the prebasic moult (often regarded as similar to the post-breeding moult in life-cycle terminology), and perhaps the preformative moult (often regarded as similar to the post-juvenile moult in life-cycle terminology), as ancestral to all modern bird lineages, having evolved from reptiles (Howell and Pyle 2015, Kiat et al. 2020, 2021, Pyle 2022b, Fig. 1, Box 1). The complete or near-complete prebasic moult occurs in all current-day avian taxa and, rather than being simply a replacement of feathers, appears to be part of an endogenous restoration of body tissues (Voitkevich 1966, Murphy 1996, Kuenzel 2003) that may be ancestral to all vertebrates (King 1972). Considering the prebasic moult as homologous among modern birds is thus a parsimonious hypothesis, providing a robust nomenclatural framework that can be applied to all bird moults and plumages. The preformative moult also appears to be present in most if not all modern bird lineages, and here we further hypothesise that it may have evolved in reptiles as body size developed quickly in the first year of life; if not, it may have evolved early in avian evolution as it is found in most or all basal lineages (Fig. 1, Box 1). Assuming these hypotheses and homology among all modern bird taxa, the prebasic and preformative moults can provide the framework for defining all subsequently evolved moults within the H–P system. Additional inserted moults, including prealternate and presupplemental moults (not adequately defined under life-cycle terminology; c.f. Pyle 2022b), can evolve (both appearing and disappearing) along bird lineages such that, unlike prebasic and preformative moults, they should not be considered homologous across all birds. Instead, they may be regarded as homologous once they have evolved within a lineage (Howell et al. 2003, Johnson and Wolfe 2018, Pyle 2022a,b).

Once an evolutionary basis is appreciated, moult strategies become substantially easier to compare across all species and geographic latitudes. For example, the four underlying strategies identified by Howell et al. (2003), which are defined by the number of moults that occur within the first and later moult cycles, can be provisionally placed in an evolutionary context (see Fig. 1 and Box 1 for details). Although it is likely that inserted moults may have disappeared without trace along some bird lineages, envisioning how these four strategies may have evolved for modern-day taxa has the potential to help inform a greater appreciation for the adaptive causes of inserted moults (Fig. 1).

We contend that an evolutionary (H–P) system is more applicable on a global basis for studying avian moult than is the life-cycle system, and we thus encourage those who use the life-cycle system to also attempt visualizing an evolutionary approach to moult terminology, rather than trying to simply synonymize H–P terms with life-cycle terms. We suggest first determining the prebasic moult cycle, then whether or not inserted moults occur in the first and/or later cycles, and lastly using an evolutionary approach to infer the correct designation of each inserted moult. Once envisioned, learned, and appreciated, the nomenclatural approach proposed by Humphrey and Parkes (1959), as modified by Howell et al. (2003), is scientifically more precise, allows the recognition of all inserted moults, and is easier to apply consistently to all taxa and by all parties interested in the study of moult in birds.

Acknowledgements – We thank Lauren Helton of the Institute for Bird Populations for preparing the figure with the phylogenetic tree (Figure 1).

Funding – Peter Pyle is generally supported by The Institute for Bird Populations but not specifically for this project. The same can be stated for the three co-authors regarding their institutions.

Author contributions

Peter Pyle: Conceptualization (equal); Investigation (equal); Visualization (equal); Writing – original draft (equal). **Steve N. G. Howell:** Investigation (supporting); Writing – review and editing (supporting). **Danny I. Rogers:** Investigation (supporting); Writing – review and editing (supporting). **Chris Corben:** Investigation (supporting); Writing – review and editing (supporting).

Transparent peer review

The peer review history for this article is available at https://publons.com/publon/10.1111/jav.03169.

Data availability statement

This article contains no additional data.

Supporting information

The Supporting information associated with this article is available with the online version.

References

Chandler, R. M., Pyle, P., Flannery, M. E., Long, D. J. and Howell, S. N. G. 2010. Flight feather molt of Turkey Vultures. – Wilson J. Ornithol. 122: 354–360.

Cramp, S. 1988. The birds of the western Palearctic, vol. 5. – Oxford Univ. Press.

Cramp, S. and Simmons, K. E. L. 1977. The birds of the western Palearctic, vol. 1. – Oxford Univ. Press.

Davies, S. 2002. Ratites and tinamous. – Oxford Univ. Press.

del Hoyo, J. and Collar, N. 2014. Illustrated checklist of the birds of the world, vol. 1. – Lynx Ediciones.

del Hoyo, J. and Collar, N. 2016. Illustrated checklist of the birds of the world, vol. 2. – Lynx Ediciones.

Forsman, D. 1999. The raptors of Europe and the Middle East. – T and AD Poyser.

Guallar, S. X., Rueda-Hernández, R. and Pyle, P. 2021. Evolution of the preformative molt in Cardinalidae correlates with transitions from forest to open habitats. – Ornithology 138: 1–14.

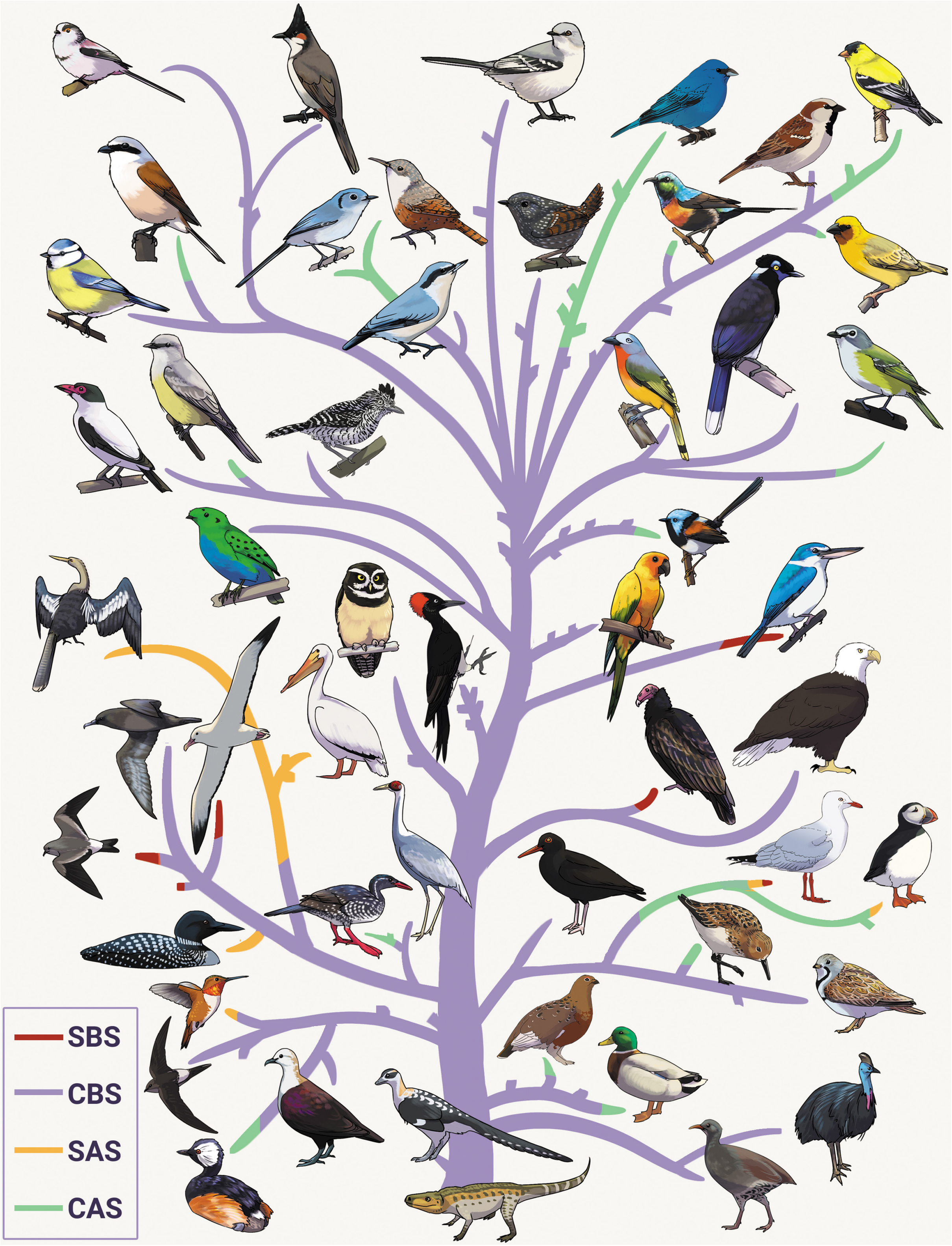

Figure 1. A theoretical evolutionary approach to moult in birds from reptiles, using the four moult strategies defined by Howell et al. (2003; see also Howell 2010). See Box 1 for details.

Higgins, P. J. and Davies, S. J. J. F. 1996. Handbook of Australian, New Zealand, and Antarctic birds, vol. 2. – Oxford Univ. Press.

Howell, S. N. G. 2001a. Molt of the ivory Gull. – Waterbirds 24: 438–442.

Howell, S. N. G. 2001b. A new look at moult in gulls. – Alula 7: 2–11.

Howell, S. N. G. 2010. Peterson reference guide to molt in North American birds. – Houghton Mifflin Harcourt.

Howell, S. N. G. 2012. Petrels, albatrosses, and storm-petrels of North America. – Princeton Univ. Press.

Howell, S. N. G. and Corben, C. 2000. A commentary on molt and plumage terminology: implications from the Western Gull. – W. Birds 31: 50–56.

Howell, S. N. G. and Dunn J. L. 2007. A reference guide to gulls of the Americas. – Houghton Mifflin, Boston.

Howell, S. N. G. and Pyle, P. 2005. Molt, age determination, and identification of puffins. – Birding 37: 412–418.

Howell, S. N. G. and Pyle, P. 2015. Use of 'definitive' and other terms in molt nomenclature: a response to Wolfe et al. (2014). – Auk 132: 365–369.

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

Howell, S. N. G., Corben, C., Pyle, P. and Rogers, D. I. 2004. The first basic problem revisited: reply to commentaries on Howell et al. (2003). – Condor 106: 206–210.

Humphrey, P. S. and Parkes, K. C. 1959. An approach to the study of molts and plumages. – Auk 76: 1–31.

Jenni, L. and Winkler, R. 2004. The problem of molt and plumage homologies and the first plumage cycle. – Condor 106: 187–190.

Jenni, L. and Winkler, R. 2020. Moult and ageing of European passerines, 2nd edn. – Bloomsbury Publishing.

Johnson, E. I. and Wolfe, J. D. 2018. Molt in Neotropical birds: life history and aging criteria. – CRC Press.

Kiat, Y. 2023. Moult terminology: let's make it simpler! – Ibis 165: 697–703.

Kiat, Y., Izhaki, I. and Sapir, N. 2019. The effects of long-distance migration on the evolution of moult strategies in Western-Palearctic passerines. – Biol. Rev. 94: 700–720.

Kiat, Y., Balaban, A., Sapir, N., O'Connor, J. K., Wang, M. and Xu, X. 2020. Sequential molt in a feathered dinosaur and implications for early paravian ecology and locomotion. – Curr. Biol. 30: 3633–3638.e2.

Kiat, Y. and Izhaki, I. 2021. Split moult: time constraints or endogenous strategy? – Ibis 163: 536–548.

Kiat, Y., Pyle, P., Balaban, A. and O'Connor, J. K. 2021. Reinterpretation of purported molting evidence in the Thermopolis Archaeopteryx. – Commun. Biol. 4: 837.

King, J. L. 1972. Adaptive functions of vertebrate molting cycles. – Am. Zool. 12: 77–93.

Kuenzel, W. J. 2003. Neurobiology of molt in avian species. – Poult. Sci. 82: 981–991.

Marchant, S. and Higgins, P. J. (eds). 1990. Handbook of Australian, New Zealand, and Antarctic birds, vol. 1, parts A & B. – Oxford Univ. Press.

Murphy, M. E. 1996. Energetics and nutrition of molt. – In: Carey, C. (ed.), Avian energetics and nutritional ecology. Chapman and Hall, pp. 158–198.

Pons, J. M., Hassanin, A. and Crochet, P. A. 2005. Phylogenetic relationships within the Laridae (Charadriiformes: Aves) inferred from mitochondrial markers. – Mol. Phylogenet. Evol. 37: 686–699.

Pyle, P. 1998. Eccentric first-year molts in certain Tyrannid flycatchers. – W. Birds 29: 29–35.

Pyle, P. 2005a. Molts and plumages of ducks. – Colonial Waterbirds 28: 207–218.

Pyle, P. 2005b. First-cycle molts in North American Falconiformes. – Raptor Res. 39: 378–385.

Pyle, P. 2007. Revision of molt and plumage terminology in ptarmigan (Phasianidae: *Lagopus* spp.) based on evolutionary considerations. – Auk 124: 508–514.

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

Pyle, P. 2013. Molt homologies in ducks and other birds: a response to Hawkins (2011) and further thoughts on molt terminology in ducks. – Waterbirds 36: 75–79.

Pyle, P. 2022a. Identification guide to North American birds, Part 1, 2nd edn. – Slate Creek Press.

Pyle, P. 2022b. Defining moults in migratory birds: a sequence-based approach. – J. Avian Biol. 2022: e02958.

Pyle, P. 2022c. Examination of digital images from Macaulay library to determine avian molt strategies: a case study on molts and plumages in eight species of North American hummingbirds. – Wilson J. Ornithol. 134: 52–65.

Pyle, P. and Reid, M. 2016. Molts and plumages in the Long-tailed and other jaegers: an alternate explanation for nonbreeding plumages? – West. Birds 47: 242–257.

Pyle, P., Tranquillo, K., Kayano, K. and Arcilla, N. 2016. Molt patterns, age criteria, and molt-breeding overlap in American Samoan landbirds. – Wilson J. Ornithol. 128: 56–69.

Sieburth, D. and Pyle, P. 2018. Evidence for a prealternate molt-migration in the Rufous hummingbird and its implications for the evolution of molts in Apodiformes. – Auk 135: 495–505.

Suh, A., Paus, M., Kiefmann, M., Churakov, G., Franke, F. A., Brosius, J., Kriegs, J. O. and Schmitz, J. 2011. Mesozoic retroposons reveal parrots as the closest living relatives of passerine birds. – Nat. Commun. 2: 443.

Terrill, R. S., Seeholzer, G. F. and Wolfe, J. D. 2020. Evolution of breeding plumages in birds: a multiple-step pathway to seasonal dichromatism in New World warblers (Aves: Parulidae). – Ecol. Evol. 10: 9223–9239.

Voitkevich, A. A. 1966. The feathers and plumage of birds (English translation). – October House Inc.

Willoughby, E. J. 1991. Molt of the genus *Spizella* (Passeriformes, Emberizidae) in relation to ecological factors affecting plumage wear. – Proc. W. Found. Vert. Zool. 4: 247–286.

Box 1.

A theoretical evolutionary approach to moult in birds from reptiles, using the four moult strategies defined by Howell et al. (2003, Howell 2010). The phylogenetic tree is based primarily on that of del Hoyo and Collar (2014, 2016), with a few exceptions (e.g. parrots and falcons are here placed basal to passerines; Suh et al. 2011). This phylogenetic concept of avian lineages has been and will continue to be revised as new data on systematics accumulate; however, we are confident that, for the purposes of our hypotheses, this tree serves as an adequate template to demonstrate an evolutionary approach to moults.

The four strategies are 'simple basic strategy' (SBS; no preformative or prealternate moults), 'complex basic strategy' (CBS; a preformative moult but no prealternate moults), 'simple alternate strategy' (SAS; a single moult in the first cycle and prealternate moults in later cycles), and 'complex alternate strategy' (CAS; a preformative moult in the first cycle and prealternate moults in all cycles); presupplemental moults may also occur within taxa exhibiting complex strategies. Note that current taxa at the end of each lineage can exhibit more than one strategy. In lineages (other than CBS) in which this occurs, we show SBS, SAS, and/or CAS if any one extant species exhibits or appears to exhibit this strategy. We wish to emphasize that, despite these strategies and accompanying H–P terms having unambiguous definitions based on the principles of evolution, our understanding of precisely how moults have evolved from basal to derived taxa is still progressing. The following syntheses should be regarded as our own interpretations of how moults may have evolved and can be considered as working hypotheses.

All birds have prebasic moults, which we consider an ancestral endogenous process that forms a structural framework to illustrate the evolutionary approach to moulting strategies using Humphrey–Parkes (H–P) nomenclature (Humphrey and Parkes 1959). Here we hypothesise that preformative moults may have also evolved from reptiles, as they are present in most bird taxa including basal lineages such as ratites (in Tinamiformes, at least; Davies 2002, Johnson and Wolfe 2018; and we suspect in Apterygiformes) as well as Galloanseres, Columbiformes, and Podicipediformes (Pyle 2005a, 2007, 2008, 2022a). Inserted preformative moults may have occurred in reptiles and vertebrates as body size developed quickly in the first year of life or, if not, they appear to have evolved during the basal stages of avian evolution. As such, we therefore provisionally hypothesise that the CBS is ancestral to all modern birds. Further study on the moults of reptiles and feathered dinosaurs (c.f. Kiat et al. 2020, 2021a,b), as well as the poorly known moulting strategies of ratites (Marchant and Higgins 1990, Davies 2002), could shed further light on this hypothesis.

Along bird lineages, preformative moults may be lost and prealternate moults can be gained through evolution. Although the absence of a preformative moult in a species can be difficult to confirm (c.f. Pyle 2005b, 2008), it appears not to occur in at least some lineages, which thus exhibit the SBS. These include albatrosses (Diomedidae; Pyle 2008), storm-petrels (Oceanitidae and Hydrobatidae; Cramp and Simmons 1977, Marchant and Higgins 1990, Pyle 2008, Howell 2010, 2012), penguins (Sphenisciformes; Marchant and Higgins 1990), New World vultures (Cathartidae; Pyle 2008, Chandler et al. 2010), some Halcyoninae kingfishers (Alcedinidae; Pyle et al. 2016), and the Ivory Gull *Pagophila eburnea* (Howell 2001a). Barn owls (Tytonidae) may also show a SBS depending on the interpretation of first-cycle moults (c.f. Howell 2010, Pyle 2022b). As these current-day taxa all occur along lineages that basally exhibit the CBS, we propose that the preformative moult has been lost evolutionarily along these lineages, rather than the SBS being ancestral.

Juvenile feathering in most bird taxa is weaker and less durable than that of later plumages, probably because there is a selective advantage to rapid growth of juvenile plumage, therefore shortening the period of high mortality rates in which birds are unable to fly. Preformative moults therefore appear to be necessary to replace juvenile plumage that is not durable enough to remain functional throughout the first cycle. In contrast, taxa exhibiting the SBS share the trait of having relatively protected and long natal stages, often in burrows or cavities, where chicks are at low risk from predation and are also fed protein-rich food. In such species, selection may favour slow growth of a durable juvenile plumage that will remain functional until the second cycle, precluding the need for a preformative moult (Howell 2010). Such traits are shared by diurnal raptors (Accipitridae and Falconidae) and petrels (Procellariidae), families previously thought to exhibit the SBS (Cramp and Simmons 1977, Marchant and Higgins 1990, Forsman 1999) but for which limited preformative moults have recently been identified in some or most taxa (Pyle 2005b, 2008). The preformative moults within these families may be vestigial carryovers from ancestral taxa exhibiting the CBS, and could be lost in the future, or perhaps they have redeveloped along lineages in which the preformative moult was lost. Derived lineages such as some cavity nesting passerines and woodpeckers also share the traits of relatively protected natal stages where chicks are at low risk from predation but continue to undergo preformative moults. It is possible that not enough time has elapsed for these species to lose the preformative moult evolutionarily, although note that some taxa of kingfishers do appear to have lost the preformative moult (Pyle et al. 2016).

Inserted prealternate moults have evolved independently along various bird lineages, including basal taxa such as ptarmigan (Galliformes, *Lagopus*; Pyle 2007), ducks (Anatidae; Pyle 2005a, 2013), grebes (Podicipediformes; Pyle 2008), and waders or shorebirds (Charadriidae and Scolopacidae), as well as derived taxa such as many passerines (Passeriformes). Prealternate moults, therefore, should not be considered homologous across all birds (Howell et al. 2004, Pyle 2022b).

Box 1 (continued).

These moults appear to have initially evolved to replace worn feathers, with some taxa later taking advantage of them for purposes of sexual selection or predation avoidance (Howell 2010, Pyle 2022a). In many species among various lineages (e.g. grebes, divers, waders or shorebirds, and several passerine branches), males or both sexes gain more colourful alternate feathering to better attract mates. In other taxa, such as ducks and perhaps skuas (jaegers), alternate feathering has become less colourful or more cryptic given surrounding habitat preferences, to better avoid predation (Pyle 2005a, Pyle and Reid 2016). Still in other species, alternate feathering resembles basic feathering in colour patterns. Despite subsequent selection for alternate feather colouration, the initial evolution of prealternate moults appears to have occurred independently along many lineages as behavioural changes, including migration strategies (below), resulted in the need to replace exposed feathers more than once on an annual basis. In some derived lineages (e.g. among waders and some passerines), different genera or even species within genera can have or lack prealternate moults. In such cases, further study may reveal whether or not prealternate moults have been recently gained among taxa that have alternate plumages, or recently lost in species that lack them.

Divers (loons; Gaviiformes), Pelecaniformes, some larger gulls (among Laridae), and some alcids (Alcididae) have evolved prealternate moults in the second and later basic cycles but apparently undergo only one moult in the first cycle (Pyle 2008, 2009; Howell 2001b, 2010), and thus exhibit the SAS. The SAS may have evolved in one of several ways (Howell and Pyle 2015). In one scenario, lineages that exhibited a CBS may have gained a prealternate moult in the second and later cycles but not in the first cycle. It is possible that such an evolutionary history has occurred for divers and Pelecaniformes, as well as ibises and spoonbills (Threskiornithidae). In these species, development of colourful plumages for mate selection may have resulted in the retention of an inserted prealternate moult in birds of breeding age but not those of pre-breeding ages. This may not be the case for those Procellariiformes and other species exhibiting the SBS, which may rely more on vocalizations (e.g. petrels, kingfishers) or dance and/or flight displays (e.g. albatrosses, New World vultures) for mate selection. Prealternate moults have recently been documented in a few migratory hummingbirds (Trochilidae) and, although H–P nomenclature has been debated for these species (Howell 2010, Pyle 2022a), it is possible that a prealternate moult evolved in the second and later cycles but not the first (Sieburth and Pyle 2018, Pyle 2022c). Another scenario leading to the SAS would be the loss of either the preformative moult or the first prealternate moult (or a merging of these two moults) along a lineage exhibiting the CAS. Such an evolutionary history may have occurred for some alcids, as proposed by Pyle (2009), as well as for larger gulls (Howell and Corben 2000) and for Gaviiformes and Pelicaniformes as mentioned above. Among gulls (Laridae), for example, basal taxa, such as those in genera *Chroicocephalus* and *Leucophaeus* (Pons et al. 2005), exhibit a CAS whereas the more derived white-headed gulls (genus *Larus*) exhibit the SAS (Howell and Dunn 2007, Pyle 2008). Having lost the first prealternate moult or having had it merge with the preformative moult in ancestral species was perhaps due to the increased energy and longer period needed to replace feathers in larger gulls. Likewise, among alcids (Alcidae), larger species such as those of genus *Fratercula* may have lost the prealternate moult or had it merge with the preformative moult during the first cycle (Howell and Pyle 2005, Pyle 2008, 2009). No non-passerine taxa among more derived lineages (e.g. Strigidae, Picidae and Psitaciiformes) and no species of passerine (Passeriformes) has been documented with either the SBS or the SAS.

The CAS, involving a preformative moult in the first cycle and prealternate moults in both first and later cycles, likely resulted primarily from the evolution of inserted prealternate moults into all cycles. All taxa in which the CAS is exhibited by at least some species, including those among Podicipediformes, Galloanseraes, Charadriiformes, and Gruiformes, appear to have evolved along lineages in which the CBS was basal and still occurs in many species within these groups. Passerines share a common ancestor which likely exhibited the CBS, given that it is shown by most passerines, and taxa immediately ancestral to passerines, such as parrots (Psittaciformes) and falcons (Falconidae). Moreover, basal passerine lineages such as New Zealand wrens (Acanthisittidae), broadbills (Calyptomenidae), pittas (Pittidae), antbirds (Thamnophilidae), ovenbirds (Furnariidae), tityras (Tityridae), and lyrebirds (Menuridae), all exhibit the CBS.

It appears that the CAS has evolved many times within Passeriformes, including along basal Passeriform lineages such as fairywrens (Maluridae), tyrannid flycatchers (Tyrannidae), and vireos (Vireonidae), as well as derived (including terminal) lineages such as cardinals (Cardinalidae), sunbirds (Nectariniidae), finches (Fringillidae), wood-warblers (Parulidae), and tanagers (Thraupidae). However, the CBS has also been maintained among terminal taxa, such as penduline-tits (Remizidae), bulbuls (Pycnonotidae), mockingbirds (Mimidae), and elachuras (Elachuridae), with no evidence that prealternate moults have evolved along their lineages. The CAS appears to have evolved more often in highly migratory than in resident (including most tropical) species of birds, perhaps due to the increased effects of solar radiation on exposed feathers on an annual basis, requiring feathers to be replaced more than once per cycle to maintain functionality (Pyle 1998, Howell 2010, Kiat et al. 2019, Terrill et al. 2020, Guallar et al. 2021, Kiat and Izhaki 2021). For similar reasons, it also appears to have evolved in some resident species found in harsher habitats such as saltmarshes, scrub, and thornforests, which can contribute to rapid feather wear (Willoughby 1991, Howell 2010, Pyle 2022a).