COMMENTARY

MIND THE GAPS: WHAT'S MISSING IN OUR UNDERSTANDING OF FEATHER MOLT

ELI S. BRIDGE[1]

University of Oklahoma, Center for Spatial Analysis, 101 David L. Boren Blvd., Norman, OK 73019

The life histories of all birds feature two major events, reproduction and molt, and many species of the temperate and polar zones add migration as a third major energetic and scheduling demand to their annual cycle. Although we are far from a complete understand of any of these phenomena, it seems that for a given species basic molt data are most often lacking. Open almost any field guide and you will find information on the timing and location of breeding and migration for almost all species included. For information on molt one must resort to more detailed species descriptions such as the *Birds of North America* series or the works of Pyle (1997, 2008), and even these species accounts may lack adequate data. If your species of interest is not included in a series that has descriptions of molt, you will probably find that there are no data at all. A few years ago I reviewed molt strategies in seabirds and found no information on molt for 25% of the 314 species I wanted to include in the review (Bridge 2007). The situation for terrestrial species is similar (Ryder and Wolfe 2009).

Birds demonstrate a bewildering array of molting strategies. The diversity of avian molts is such that an active debate over molt terminology continues more than 100 years after the first systematic studies of feather replacement (Dwight 1900, Howell et al. 2003, Thompson 2004, Willoughby 2004, Pyle 2005). For almost every rule we try to impose on the patterns or timing of molt, there are invariably several exceptions. However, one rule that does appear to apply to all species is that there is a physiological limit on the rate at which feathers can grow (Rohwer et al. 2009). All of the raw materials used to synthesize a feather must be conducted through a collar of cells that surrounds the base of the feather follicle (Lucas and Stettenheim 1972). Presumably, this bottleneck limits the rate of individual feathers' growth regardless of their size when fully grown. If we look across species ranging in mass from a few grams to several kilograms, there is little difference in the rate at which feathers are grown (Rohwer et al. 2009). For instance, a 27-g House Sparrow (*Passer domesticus*) grows its feathers at a rate of 2.7 mm per day, whereas a

9000-g Whooper Swan (*Cygnus cygnus*) grows 9 mm of feather per day (Prevost 1983). In other words, we see a 300-fold increase in body mass but only a 3-fold increase in feather-growth rate. This constraint on feather growth is evident when birds are pressured to accelerate molt. Across several taxa, speeding up molt results in feathers of low quality according to several metrics, including mass (Dawson 2004), integrity (Dawson et al. 2000, Serra 2001), and coloration (Serra et al. 2007, Griggio et al. 2009). The effect of rapidly grown plumage has been linked to decreased survival (Nilsson and Svensson 1996, Morales et al. 2007).

The limit on feather growth gives rise to some interesting life-history tradeoffs as birds balance the various costs of molt and other activities (e.g., breeding and migration). We often see the most complex molt strategies in large birds, in which the time constraints associated with growing large feathers are most pronounced. For large birds like albatrosses that must not only molt long feathers but maintain their ability to fly over vast distances, molt imposes a heavy toll, which is likely to affect other aspects of their annual cycle, such as breeding. More specifically, one might presume that large, aerial foragers should be forced to reduce their molting effort to breed successfully and vice versa. However, it has been difficult to conclusively identify a clear link between variation in molt and breeding success in large birds. The first study to do so appears in this issue of the *Condor*. Rohwer et al. (2011) found that Black-footed Albatrosses (*Phoebastria nigripes*) with more worn feathers are more likely to be unsuccessful in their attempts to breed.

The problem for the Black-footed Albatross is that there is insufficient time in its annual cycle for it to both breed and molt enough feathers to offset accumulated feather wear, and as a result some individuals accrue a molt debt that eventually erodes their ability to breed successfully. Hence, periodically birds skip breeding altogether to devote more time to growing feathers and paying off their molt debt. In the Black-footed Albatross, the molt debt is usually borne out in primaries 6 and 7 (P6 and P7). These feathers may be molted just prior to the outermost three primaries, or they may remain unmolted for several years, presumably as a means of reducing the time devoted to molt (Langston and Rohwer 1996; Fig. 1). A key finding in Rohwer et al. (2011) is that if P6 and P7 accumulate 2 or more years of wear, the birds are less capable of rearing offspring.

Although Rohwer et al. (2011) have made an important contribution to the ornithological literature, their work also makes evident some of the gaps in our knowledge of feather molt. Why should something as obvious as a molt/breeding tradeoff only now find empirical support? One reason is that, for many species, we lack comprehensive information about feather molt. Without documentation of basic molt data such as timing, location, sequence, intensity, completeness (for species with incomplete molts), and degree of individual variation, comparative studies aimed at describing the origin and maintenance of molt strategies
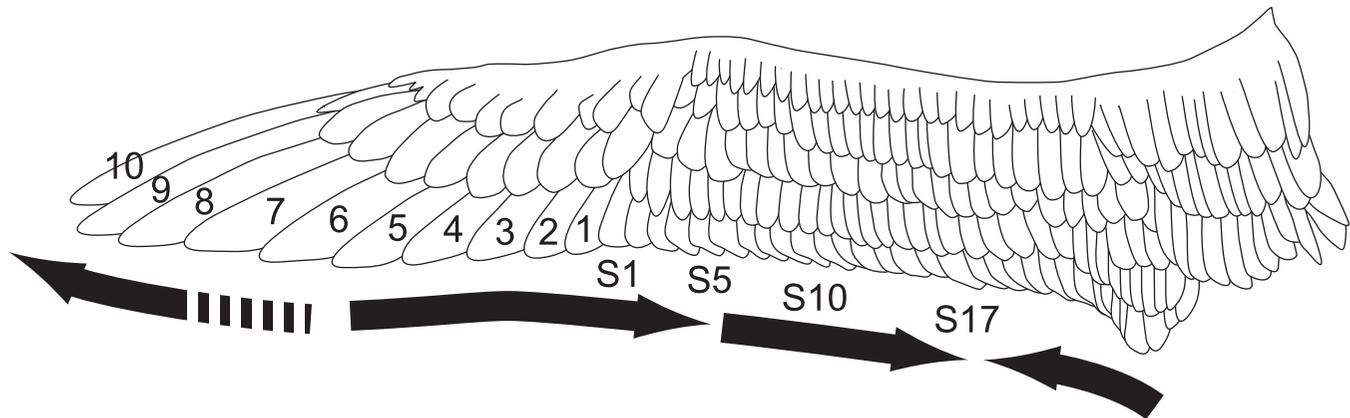
FIGURE 1. Tracing of a Black-footed Albatross wing illustrating a simplification of the molt pattern first described by Langston and Rohwer (1996) and later revised by Edwards and Rohwer (2005). Arrows indicate initiation points and direction of four series of molt of the primaries (numbered 1 through 10) and secondaries (some labeled S1, S5, etc.). According to Rohwer et al. (2011), birds with limited time to molt may skip primaries 6 and 7 and begin the distal molt series at P8.

are plagued by gaps in the data (e.g., Figuerola 2001, Bridge et al. 2007, de la Hera et al. 2009).

Lack of molt data is also a hindrance to studies that use stable-isotope ratios in feathers to address feeding habits and biogeography. We have the capability to infer food sources and to localize breeding and wintering areas for many bird populations simply by plucking and analyzing one or two feathers (Hobson and Wassenaar 2008). However, these techniques are useful only when clear and comprehensive molt data are available. A recent paper by Rocque et al. (2006) illustrates this point. Rocque et al. collected primaries and back feathers from Northern Wheatears (*Oenanthe oenanthe*) under the assumption that the primaries should have stable-isotope signatures reflecting the breeding range (central Alaska), whereas the body feathers should indicate the winter range (sub-Saharan Africa). Unfortunately, the isotopic signatures of the two feather types were nearly identical. Although Rocque et al. interpreted this finding as a failure of the stable-isotope technique, it is quite likely that ambiguity in the molt descriptions in the literature led to the downfall of this study. As Larson and Hobson (2009) pointed out, the real discovery of Roque et al. (2006) was that their Northern Wheatears molted their back feathers in Alaska. Stable isotopes have subsequently been used on Northern Wheatears with greater success (Delingat et al., in press).

In addition to basic descriptive data, there are other important gaps in our knowledge of molt. In particular, the physiology of molt is poorly understood, especially with regard to the mechanisms that control the sequence of feather molt in an individual bird. Although there are numerous studies of the extrinsic and intrinsic factors that regulate the onset of feather molt (reviewed by Dawson 2006, 2008), we know little about the signaling pathways that control and organize the growth of specific feather follicles. The organization of simple descendent molt patterns, in which the feathers of a molt series are consistently replaced in proximal or distal waves, has long been attributed to the follicles differing in their sensitivity to a systemically released hormone (Ashmole 1968) or to a "chain reaction" of sequential stimulation by adjacent follicles (Miller 1941), but decades after these ideas were proposed, we still lack empirical tests of their validity.

Moreover, these simple mechanisms for explaining serial descendent molt cannot account for the complexity of molt patterns in many large large birds, such as the stepwise molts (i.e.,

Staffelmauser) that are common to many species (see Bridge 2007) or the biennial cycles of albatrosses (Furness 1988, Prince et al. 1993, Edwards and Rohwer 2005). Other mechanisms such as fluctuations in hormone receptors within follicles and/or some form of "tissue memory" must come into play. Rohwer et al. (2011) proposed that birds may be able to sense turbulence associated with worn feathers, citing documentation of extensive innervation of feather follicles (Brown and Fedde 1993). They interpret this observation as evidence of a neurophysiological mechanism that might allow the central nervous system to control molt directly. Although I disagree with this view on the grounds that we know of no means by which the central nervous system can direct the growth of individual feather follicles, the idea of birds somehow selecting which feathers to replace is intriguing. Such discriminating feather replacement might be effected by birds tugging on worn feathers to remove them physically or to stimulate follicle growth mechanically. As Rohwer et al. (2011) state, experimentation in this area is needed.

The tools for studying molt physiology are in place for the most part. Nearly 20 years ago, Péczely (1992) quantified hormone receptors in feather follicles by using a simple radio-immunoassay technique. Immunocytochemistry has also been used to examine hormone receptors in skin and feather follicles of poultry (Herremans et al. 1993). Although these exploratory studies would seem to pave the way for more directed research into molt regulation at the level of the feather follicle, there have been no efforts in this direction. Indeed, these two papers have been cited a total of nine times since their publication.

Perhaps one of the most obvious lines of inquiry with regard to molt relates to the aerodynamic implications of replacing flight feathers. There are a few experimental studies that have attempted to quantify the effects of molt on flight ability and/or efficiency (e.g., Tucker 1991, Chai 1997, Swaddle et al. 1999, Bridge 2003), but they do not attempt to make inferences about molt across species. We have yet to see an empirical, comparative study that takes into account how factors such as wing shape and flight mode might interact with different wing-molt patterns or the intensity of molt. Harkening back to Rohwer et al. (2011), it would also be of great interest to know how the aerodynamic effects of molt compare to those of feather wear. Do a few worn primaries really create an aerodynamic impediment severe enough to affect foraging ability and breeding success? Some
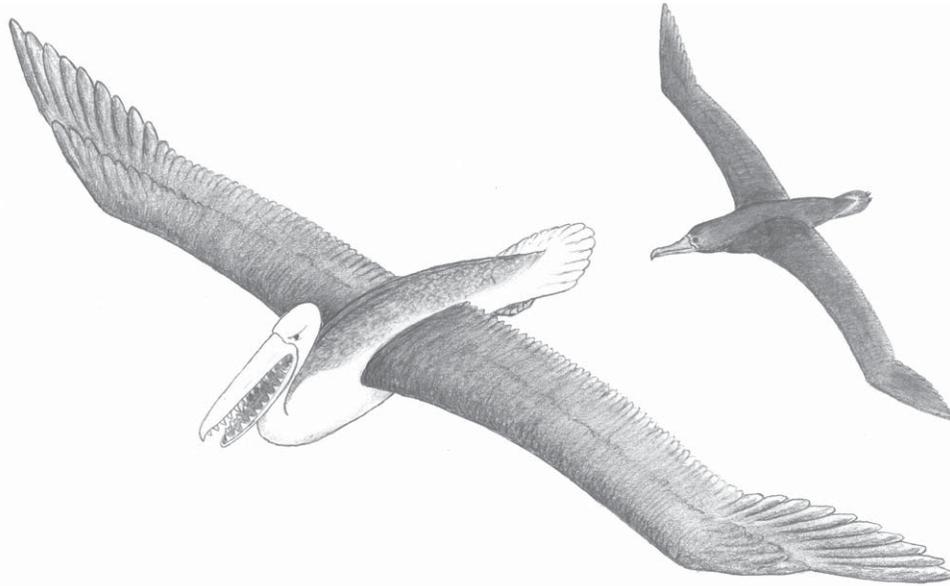
FIGURE 2.   Hypothesized appearance of *Osteodontornis orri* in comparison to a Black-footed Albatross. Birds are drawn to the same relative scale. In a single molt cycle, *O. orri* would likely have replaced more than 100 large flight feathers (primaries and secondaries). Drawing by Don P. Bridge.

preliminary studies suggest that feather wear can create considerable drag (Bridge 2009), but feather-abrasion experiments on live birds would be a welcome addition to the scientific record.

Rohwer et al. (2011) make it clear that albatrosses face considerable challenges as a result of their need to grow large feathers, but their problems likely pale in comparison to those of several groups of extinct birds with even larger feathers. For example, *Osteodontornis orri* and perhaps other relatives of this extinct "tooth-billed" seabird probably featured wingspans of 6.5 m—double that of most albatross species (Fig. 2)—and they probably practiced dynamic soaring and aerial foraging similar to what we see in many extant long-winged seabirds. We can only wonder how these birds managed to molt 10 primaries and an estimated 44 secondaries (extrapolated from albatrosses) on each wing, while balancing the demands of feeding themselves and raising young. If the molt cycles of most extant birds are any indication of the constraints faced by *Osteodontornis* then it is very unlikely that such a species could reproduce on a yearly basis. Indeed, contemplating the molt of *Osteodontornis* gives credence to the notion put forth by Rohwer et al. (2009) that constraints associated with molt (as opposed to weight limits relating to powered flight) could be the principal limitation on body size in flying birds.

Feathers are the unifying characteristic of all birds, yet our understanding of molts and plumages lags behind that of other major life-history phenomena. Clearly, we need to work toward a more complete compilation of basic life-history data. However, publishing these data offers little in terms of prestige and can be difficult because of how journals prioritize submissions. Fortunately, online data sharing and widespread data collection by amateur scientists may prove to be the next great archive of molt data. The molt-card program initiated in the early 1960s by the British Trust for Ornithology (Snow 1967) has already provided a rich source of molt data, not to mention grist for many field guides and publications (e.g., Ginn and Melville 1983). Although a equivalent program is lacking in the New World, the explosive success of the e-Bird initiative (Sullivan et al. 2009), which now comprises about 70 000 birders, is evidence of the potential for cyberinfrastructure and citizen science to advance avian biology. Although e-Bird does not provide molt data, new sources of basic bird data are emerging. For example, the widespread use of digital cameras and photo-sharing websites has put a wealth of bird images at our fingertips. I have occasionally used photographs from the Internet as documentation of molt phenomena (Bridge 2004), but much more extensive use of photographic information is possible. With the "information age" upon us, I hope that we can progress rapidly toward a more complete account of every species of bird.

LITERATURE CITED

ASHMOLE, N. P. 1968. Breeding and molt in the White Tern (*Gygis alba*) on Christmas Island, Pacific Ocean. Condor 70:35–55.

BRIDGE, E. S. 2003. Effects of simulated primary molt on pigeon flight. Ornis Fennica 80:121–129.

BRIDGE, E. S. 2004. Wing-molt strategies in seabirds. Ph. D. dissertation, University of Minnesota, St. Paul, MN.

BRIDGE, E. S. 2007. Influences of morphology and behavior on wing-molt strategies in seabirds. Marine Ornithology 34:7–19.

BRIDGE, E. S. 2009. How does imping affect wing performance? Journal of Wildlife Rehabilitation 29:4–9.

BRIDGE, E. S., G. VOELKER, C. W. THOMPSON, A. W. JONES, AND A. J. BAKER. 2007. Effects of size and migratory behavior on the evolution of wing molt in terns (Sterninae): a phylogenetic-comparative study. Auk 124:841–856.

BROWN, R. E., AND M. R. FEDDE. 1993. Airflow sensors in the avian wing. Journal of Experimental Biology 179:13–30.

CHAI, P. 1997. Hummingbird hovering energetics during molt of primary flight feathers. Journal of Experimental Biology 200:1527–1536.

DAWSON, A. 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. Ibis 146:493–500.

DAWSON, A. 2006. Control of molt in birds: association with prolactin and gonadal regression in starlings. General and Comparative Endocrinology 147:314–322.

DAWSON, A. 2008. Control of the annual cycle in birds: endocrine constraints and plasticity in response to ecological variability. Philosophical Transactions of the Royal Society B 363:1621–1633.

DAWSON, A., S. A. HINSLEY, P. N. FERNS, R. H. C. BONSER, AND L. ECCLESTON. 2000. Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival. Proceedings of the Royal Society of London B 267:2093–2098.

DE LA HERA, I., J. A. DIAZ, J. PEREZ-TRIS, AND J. L. TELLERIA. 2009. A comparative study of migratory behaviour and body mass as determinants of moult duration in passerines. Journal of Avian Biology 40:461–465.

DELINGAT, J., K. A. HOBSON, V. DIERSCHKE, H. SCHMALJOHANN, AND F. BAIRLEIN. In press. Morphometrics and stable isotopes differentiate populations of Northern Wheatears (*Oenanthe oenanthe*). Journal of Ornithology.

DWIGHT, J., JR. 1900. The sequence of plumages and moults of the passerine birds of New York. Annals of the New York Academy of Sciences 13:73–260.

EDWARDS, A. E., AND S. ROHWER. 2005. Large-scale patterns of molt activation in the flight feathers of two albatross species. Condor 107:835–848.

FIGUEROLA, J. 2001. Ecological correlates of feather mite prevalence in passerines. Journal of Avian Biology 31:489–494.

FURNESS, R. W. 1988. Influences of status and recent breeding experience on the moult strategy of the Yellow-nosed Albatross *Diomedea chlororhynchos*. Journal of Zoology London 215:719–727.

GINN, H. B., AND D. S. MELVILLE. 1983. Moult in birds. British Trust for Ornithology, Tring, UK.

GRIGGIO, M., L. SERRA, D. LICHERI, C. CAMPOMORI, AND A. PILASTRO. 2009. Moult speed affects structural feather ornaments in the Blue Tit. Journal of Evolutionary Biology 22:782–792.

HERREMANS, M., L. BERGHMAN, E. DECUYPERE, AND F. VANDESANDE. 1993. Immunocytochemical demonstration of progesterone and estrogen receptors in feathers and skin of adult hens. Acta Biologica Hungarica 44:353–366.

HOBSON, K. A., AND L. I. WASSENAAR. 2008. Tracking animal migration with stable isotopes. Elsevier, New York.

HOWELL, S. N. G., C. CORBIN, P. PYLE, AND D. I. ROGERS. 2003. The first basic problem: a review of molt and plumage homologies. Condor 105:635–653.

LANGSTON, N. E., AND S. ROHWER. 1996. Molt–breeding tradeoffs in albatrosses: life history implications for big birds. Oikos 76:498–510.

LARSON, K. W., AND K. A. HOBSON. 2009. Assignment to breeding and wintering grounds using stable isotopes: a comment on lessons learned by Rocque et al. Journal of Ornithology 150:709–712.

LUCAS, A. M., AND P. R. STETTENHEIM. 1972. Avian anatomy: integument. U.S. Agricultural Research Service, Washington, DC.

MILLER, A. H. 1941. The significance of molt centers among the secondary remiges in the Falconiformes. Condor 56:13–20.

MORALES, J., J. MORENO, S. MERINO, J. J. SANZ, G. TOMAS, E. ARRIERO, E. LOBATO, AND J. MARTINEZ-DE LA PUENTE. 2007. Early moult improves local survival and reduces reproductive output in female Pied Flycatchers. Ecoscience 14:31–39.

NILSSON, J. A., AND E. SVENSSON. 1996. The cost of reproduction: a new link between current reproductive effort and future reproductive success. Proceedings of the Royal Society of London B 263:711–714.

PÉCZELY, P. 1992. Hormonal regulation of feather development and moult on the level of feather follicles. Ornis Scandinavica 23:346–354.

PREVOST, Y. 1983. The moult of the Osprey *Pandion haliaetus*. Ardea 71:199–209.

PRINCE, P. A., S. RODWELL, M. JONES, AND P. ROTHERY. 1993. Moult in Black-browed and Grey-headed Albatrosses *Diomedea melanophris* and *D. melanphris*. Ibis 135:121–131.

PYLE, P. 1997. Identification guide to North American Birds, part I. Columbidae to Ploceidae. Slate Creek Press, Bolinas, CA.

PYLE, P. 2005. Molts and plumages of ducks (Anatinae). Waterbirds 28:208–219.

PYLE, P. 2008. Identification guide to North American Birds, part II. Anatidae to Alcidae. Slate Creek Press, Point Reyes Station, CA.

ROCQUE, D. A., M. BEN-DAVID, R. P. BARRY, AND K. WINKER. 2006. Assigning birds to wintering and breeding grounds using stable isotopes: lessons from two feather generations among three intercontinental migrants. Journal of Ornithology 147:395–404.

ROHWER, S., R. E. RICKLEFS, V. G. ROHWER, AND M. M. COPPLE [ONLINE]. 2009. Allometry of the duration of flight feather molt in birds. PLoS Biology 7(6): e1000132. doi:10.1371/journal.pbio.1000132.

ROHWER, S., A. VIGGIANO, AND J. M. MARZLUFF. 2011. Reciprocal tradeoffs between molt and breeding in albatrosses. Condor 113:61–70.

RYDER, T. B., AND J. D. WOLFE. 2009. The current state of knowledge on molt and plumage sequences in selected neotropical bird families: a review. Ornitología Neotropical 20:1–18.

SERRA, L. 2001. Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*. Journal of Avian Biology 32:377–380.

SERRA, L., M. GRIGGIO, D. LICHERI, AND A. PILASTRO. 2007. Moult speed constrains the expression of a carotenoid-based sexual ornament. Journal of Evolutionary Biology 20:2028–2034.

SNOW, D. W. 1967. A guide to moult in British birds. BTO Guide 11. British Trust for Ornithology, Tring, UK.

SULLIVAN, B. L., C. L. WOOD, M. J. ILIFF, R. E. BONNEY, D. FINK, AND S. KELLING. 2009. eBird: a citizen-based bird observation network in the biological sciences. Biological Conservation 142:2282–2292.

SWADDLE, J. P., E. V. WILLIAMS, AND J. M. V. RAYNER. 1999. The effect of simulated flight feather moult on escape take-off performance in starlings. Journal of Avian Biology 30:351–358.

THOMPSON, C. W. 2004. Determining evolutionary homologies of molts and plumages: a commentary on Howell et al. (2003). Condor 106:199–206.

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

WILLOUGHBY, E. J. 2004. Molt and plumage terminology of Howell et al. (2003) still may not reflect homologies. Condor 106:191–196.