FEATURED PHOTO

STAFFELMAUSER AND OTHER ADAPTIVE STRATEGIES FOR WING MOLT IN LARGER BIRDS

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The remiges (primaries and secondaries) of birds take a relatively long time to develop. Growth rates of primaries, for example, can vary from 3.2 mm per day in smaller birds to 6.3 mm per day in larger birds, but the summed lengths of all primaries can be as much as ten times greater in larger birds than in smaller birds (Rohwer 1999). Most passerines and other smaller birds replace all primaries sequentially from the innermost (p1) to the outermost (p9 or p10) and maintain the ability to fly, but most larger birds lack the time (between periods of breeding and migration) to follow this sequence within a single molt and have evolved alternative strategies.

Some large birds that can forage and avoid predation without flying replace all of their remiges synchronously. They become flightless during the prebasic molt but, by doing so, substantially reduce the time it would take to replace each feather sequentially. Loons, grebes, anhingas, some sea ducks, and some alcids follow this strategy, diving underwater when flightless to feed and avoid predation. Other waterfowl and flamingos store nutrients and congregate at remote locations, such as the middle of large lakes or marshes, to complete rapid synchronous wing molts within two to three weeks. Rails, coots, and some cranes find impenetrable areas, and adult Bristle-thighed Curlews (*Numenius tahitiensis*) migrate to predator-free islands to undergo synchronous remigial molts.

However, many large birds that lack the time for a sequential replacement of remiges cannot afford to become flightless. Because of constraints on feather-growth rates, the replacement of two or three adjacent remiges in quick succession can leave large gaps in the wings, inhibiting flight (Tucker 1991, Hederström and Sunada 1999), so simply accelerating the rate at which feathers are molted may not provide a solution. Rather, most of these species have evolved strategies in which remiges at disjunct locations are replaced at the same time, producing multiple smaller gaps while maintaining the wing's surface integrity and the bird's ability to fly.

One such strategy involves "multiple molt series," including both proximal (inward or centripetal) and distal (outward or centrifugal) replacement from one or more focal points within the remiges. In falcons, for example, the primaries and secondaries are each replaced "inside out" from foci at p4/p5 and s4/s5 (Miller 1941), resulting in four small gaps during remigial molt and enabling the replacement of all remiges within a single prebasic molt (Pyle 2005). Other birds that molt in multiple series in all or part of the remiges include albatrosses (Langston and Rohwer 1995, Howell 2006), parrots (Dickey and van Rossem 1938), some cuckoos (Pyle 1997a), owls (Pyle 1997b), some kingfishers (Hanmer 1980), and puffbirds (Dickey and van Rossem 1938). This strategy adjusts the frequency of feather replacement to the rate of feather wear, so that all feathers are replaced when needed, resulting in relatively even amounts of wear among multiple feather tracts (Rohwer 1999).

Staffelmauser

Along with synchronous molt, the most common strategy for replacing remiges among large birds is "*Staffelmauser*," a German word meaning "staggered molt" introduced by German ornithologists Stresemann and Stresemann (1966). It is also known as "stepwise" or "serial" molt. *Staffelmauser* typically begins with an incomplete second prebasic molt, during which primary replacement proceeds distally from
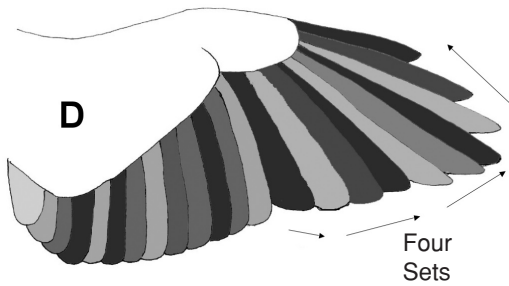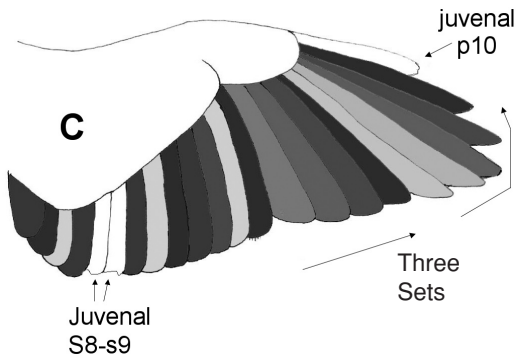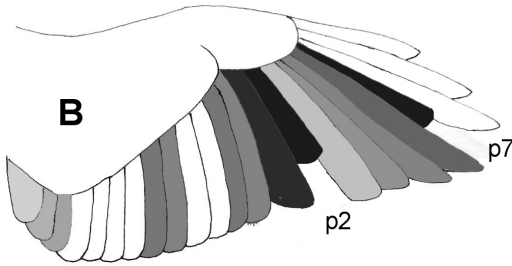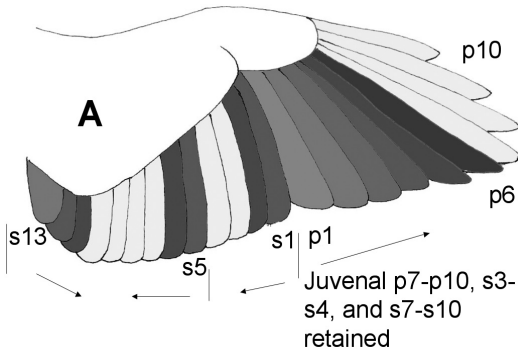
p1 (Figure 1), as in smaller birds, but then arrests before all feathers are replaced (Figure 1A). The bird thus retains its juvenal outer primaries for another molt cycle, which equates to an additional year in most North American species. The next prebasic molt begins where the previous molt left off the year before, while another sequence commences again from p1, thus resulting in two "waves" of simultaneous primary replacement (Figure 1B). Often, especially in the largest of birds, this molt still does not result in all ten juvenal primaries being replaced. The outermost wave may, for example, stop at p9 (Figure 1C), such that the next molt begins with three waves, commencing at p1, the point after which the proximal molt was arrested (p5 in the example shown in Figure 1C), and p10. As long as fewer than all ten primaries are replaced during each molt, this strategy eventually results in multiple waves of molt (and generations of feathers) within the primaries (Figure 1D).

The top photograph on this issue's back cover shows *Staffelmauser* among the remiges of a Swainson's Hawk (*Buteo swainsoni*) captured for banding near Raymondville, Texas, in March 2003. Among the ten primaries, the most recent molt included p2–p3 and p5–p8, leaving p1, p4, and p9–p10 as older and more worn feathers of a previous generation; once multiple waves have been established, p1 may or may not be replaced every year. This hawk thus displayed three feather "sets" between waves of distally oriented molts: p1–p3, p4–p8, and p9–p10. Within each set, outer feathers are sequentially fresher than inner feathers, even though the sets represent more than one cycle of molt. Provided that (1) no more than ten primaries are replaced during a single molt, (2) each primary is molted only once per year, and (3) the first replacement of primaries takes place during the second prebasic molt, the minimum age of birds following *Staffelmauser* is reflected by the number of molt sets in the primaries (Pyle 2005). Thus this Swainson's Hawk is at least three years old. Most species of *Buteo* can show three sets, and some individuals can show four (e.g., Figure 1D) or even five sets of primaries, allowing the determination of minimum age of birds up to five years old (Pyle 2005). At the same time, however, waves can "catch up" to each other, and under favorable circumstances some individuals may undergo a complete annual molt, obscuring *Staffelmauser* patterns and reducing our ability to determine minimum ages. For example, the Great Blue Heron (*Ardea herodias*) featured on the back cover, photographed at Jasper Ridge, California, 18 April 1988, shows just two sets of nonjuvenal feathers among the primaries, p1–p2 and p3–p10. Thus it is at least two years old, even though it is probably older (see below).

Whereas *Staffelmauser* among primaries has been studied in many species, concurrent patterns of replacement among secondaries are poorly documented. Unlike primaries, which molt in only one repeated series (p1 to p10), secondaries molt in as many as three series, which commence at three foci and proceed in different

Figure 1. Examples of *Staffelmauser* molt patterns in large birds. Darker shading indicates more recently replaced feathers; whiter shading indicates older feathers. *Staffelmauser* usually begins with an incomplete second prebasic molt, in which some secondaries and outer primaries are retained (A). During the third prebasic molt, replacement of remiges continues in sequence and at the same time begins anew, resulting in two "waves" of primary molt (B). In large birds this third prebasic molt may still not result in all juvenal primaries and secondaries being replaced (C), resulting in three waves of primary molt at the commencement of the fourth prebasic molt. After definitive prebasic molts, up to four or five "sets" (blocks of feathers between waves) can be identified between waves of molt (D), with the number of sets reflecting the minimum age of the bird. Because molts are protracted, a gradation from fresher feathers basally to more worn feathers distally can be identified within each set. Molt of secondaries shows multiple replacement series, commencing at foci at s1, s5, and the tertials (see text).

A

p10

p6

s13

s1 p1

s5

Juvenal p7-p10, s3-s4, and s7-s10 retained

B

p7

p2

C

juvenal p10

Juvenal S8-s9

Three Sets

D

Four Sets

directions. This complicates analysis of feather replacement, especially after one or two molts have taken place. To understand strategies of secondary replacement, I examined hundreds of specimens showing *Staffelmauser* and was able to identify rules consistent across families.

The secondaries of most large birds are replaced sequentially, proximally from the outermost feather (s1), proximally from s5, and distally from the tertials (Figure 1A), no matter the number of secondaries (*cf*. Edwards and Rohwer 2005). The focus at s5 may relate to "dyastataxy," the evolutionary "loss" of a feather at this position, which is widespread in large species of birds (Miller 1941, Bostwick and Brady 2002). Thus, after the second prebasic molt, the last juvenal feathers in this sequence are often retained, among s3–s4, and among s8–s15 in species (including many large birds) that have 12–21 secondaries (Figure 1A). As with the primaries, subsequent molts of secondaries begin where the preceding molt arrested, while at the same time new waves begin, although not always commencing at all three foci every year. After two or more molts, variation in the number of secondaries replaced, combined with the complex sequence of replacement, can produce a variable array of possible patterns (Figure 1C–D), often interpreted as random (Siegfried 1971, Prevost 1983, Schreiber et al. 1989), even though the above rules and series appear to remain intact.

Thus, even though the Swainson's Hawk on the back cover is at least three years old, its pattern of feather wear implies proximally replaced sets of secondaries at s1–s2, s3–s4, and s5–s8, and a distally replaced set that includes at least s12–s10. It appears that among s1–s4 all four feathers were replaced during the preceding molt, but that s3 was replaced before s2, marking the resumption of a wave at s3, while another wave commenced at s1 and "caught up" to the set at s3–s4. By contrast, s5–s6 and s9 were retained during the previous molt, s9 representing the convergence between distal and proximal waves. On the Great Blue Heron's left wing, proximal sets can be identified at s1–s2, s3–s4, and s5–s6, and distal sets can be identified at s16–s12 and s11–s10. The right wing is similar except that the distal sets appear to be at s16–s13 and s12–s10, indicating that s12 had been replaced on the right wing but not on the left during the previous molt. On both wings, s7–s9, located at the convergence between the proximal and distal waves, had been retained during the previous molt. S8 on the right wing had likely been lost accidentally (Great Blue Herons should not be molting in April; Pyle and Howell 2004), although its unseasonal regrowth may influence subsequent patterns of feather replacement. (Strong asymmetry between the wings occurs at times and may indicate previous adventitious loss that disrupted the sequence in one wing.) This pattern, with several sets of nonjuvenal feathers among the secondaries, probably indicates an individual at least three or four years old, but more study is needed to document this.

Molt Terminology

Staffelmauser has presented a challenge to those attempting to apply the Humphrey and Parkes (1959) molt terminology (e.g., Schreiber et al. 1989, Filardi and Rohwer 2001). In species with prealternate molts, replacement of remiges can be protracted and overlap both the prebasic and prealternate body molts. In species lacking prealternate molts, replacement of feathers retained during previous molts can be considered either as part of the ongoing prebasic molt or as part of a protracted version of the prebasic molt in which other feathers of the same generation were replaced. For example, replacement of the juvenal p10 in Figure 1C might be considered either part of the second prebasic molt, in which three years were needed to complete replacement of all juvenal remiges, or part of the fourth prebasic molt, underway in the contour feathers at the time this primary is replaced.

Unless remiges are replaced twice during a molt cycle, by definition all replacement should be considered part of a prebasic rather than a prealternate molt (Humphrey and Parkes 1959). *Staffelmauser* in species with and without a prealternate molt

is parallel, suggesting that it evolved from a common ancestor and thus should be presumed homologous with a prebasic rather than a prealternate molt (see below). Furthermore, because it appears that fewer than all remiges are typically replaced during *Staffelmauser* (Pyle 2005), I propose that all replacement of remiges be considered part of the "incomplete" prebasic molt occurring at the time of replacement. Thus replacement of p10 in Figure 1C would be considered part of an incomplete fourth prebasic molt, rather than part of a complete but protracted second prebasic molt. This interpretation yields a clearer definition of each feather's generation than does the alternative nomenclature, because determining the number of times a feather has molted is not possible once all juvenal feathers have been replaced. Difficulties in this interpretation may arise only in species that can replace remiges more than once during a single prebasic molt, as appears to be the case during the second prebasic molt in New-World vultures (M. Flannery pers. comm.) and perhaps the White-tailed Hawk (*Buteo albicaudatus*; W. S. Clark pers. comm.).

Evolution and Adaptive Benefits of *Staffelmauser*

Staffelmauser occurs in a wide diversity of North American birds, including tropicbirds (pers. obs.), boobies (e.g., Dorward 1962), pelicans (e.g., Schreiber et al. 1989), cormorants (e.g., Filardi and Rohwer 2001), frigatebirds (pers. obs.), bitterns (pers. obs.), most herons and egrets (e.g., Siegfried 1971, Shugart and Rohwer 1996), storks (Sutter 1984 in Rohwer 1999, pers. obs.), condors (Snyder et al.1987), ospreys (Prevost 1983), hawks and eagles (e.g., Bloom and Clark 2001, Clark 2004, Pyle 2005), chachalacas (pers. obs.), some cranes (see below), and some tropical terns (Dorward and Ashmole 1963, Ashmole 1968). In other tern species, the two or three additional, arrested waves of primary replacement, which can occur *within* a single molt cycle (*cf.* Ward et al. 2004), may represent a derived strategy of incomplete replacement, evolved from the *Staffelmauser* of ancestral tropical species (S. N. G. Howell). More difficult to explain, evolutionarily, is the molt pattern of the Limpkin (*Aramus guarauna*), which appears to undergo *Staffelmauser* but in the direction opposite that of other species (pers. obs. of specimens in U.S. National Museum), the primaries being replaced proximally from p10 to p1 and the secondaries being replaced distally from s5 and both proximally and distally from a focus among s8–s12!

Not all species of all of these groups exhibit *Staffelmauser*, and even within species the proportion of individuals following this strategy can vary (*cf.* Pyle 2005). Most intriguing are the molt strategies of the Sandhill Crane (*Grus canadensis*), in which resident southern subspecies follow *Staffelmauser* but most individuals of migratory boreal subspecies undergo synchronous molt of remiges (Nesbitt 1987, Nesbitt and Schwickert 2005, pers. obs.). In addition, *Staffelmauser* can occur occasionally in species that do not typically employ this strategy, such as in a White-tipped Dove (*Leptotila verrauxi*) I examined during banding at Tepotzlán, Mexico, in May 2004 and some Common Poorwills (*Phalaenoptilus nuttallii*) at high elevations (S. Rohwer pers. comm.). Unlike multiple replacement series, *Staffelmauser* thus appears not to be an independently derived strategy but rather an adaptive adjustment to the ancestral complete prebasic molt based on environmental constraints.

Two adaptive mechanisms have been proposed to explain *Staffelmauser*, the "time-constraints hypothesis" (Shugart and Rohwer 1996), in which *Staffelmauser* results simply from a lack of time to replace all feathers, and the "aerodynamic hypothesis" (Stresemann and Stresemann 1966, Tucker 1991, Hederström and Sunada 1999), in which it has evolved to replace as many feathers as possible without inhibiting flight efficiency. These two explanations are not necessarily mutually exclusive: time constraints may have provided the proximate cause for the evolution of *Staffelmauser*, whereas flight efficiency is an ultimate adaptive benefit (Pyle 2005). In other words, the ultimate result of *Staffelmauser*, multiple small gaps in the wing,

may have reduced pressure to adapt a strategy that includes multiple molt series, a greater departure from ancestral strategies and thus less likely to evolve. An argument against *Staffelmauser*, that the more exposed outer primaries are replaced less often, seems to have been compensated by the addition of increased melanin to these feathers, creating a feather more durable than the inner primaries and perhaps explaining the subtly darker wing tips often observed in species that have adopted *Staffelmauser*. To confirm such hypotheses and investigate other evolutionary pathways of molt it would be interesting to perform parsimony analysis of molt strategies relative to proposed phylogenies, as done by Bostwick and Brady (2002) to investigate the evolution of diastataxy.

ACKNOWLEDGMENTS

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