

INFLUENCES OF MORPHOLOGY AND BEHAVIOR ON WING-MOLT STRATEGIES IN SEABIRDS

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SUMMARY

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This review formally tests several widely held assumptions regarding the evolution of molting strategies. I performed an extensive literature review of molt in seabirds, extracting information on the pattern, duration and timing (relative to breeding and migration) of molt for 236 species of seabirds in three orders: Procellariiformes, Pelecaniformes, and Charadriiformes. I used these data to test three hypotheses relating to the evolution of wing-molt strategies in seabirds: (1) that complex molt patterns are more likely to occur in large birds; (2) that wing size is an important determinant of the duration of molt; (3) that non-migratory species are more likely to overlap breeding and molt. By applying traditional and phylogenetic comparative techniques to these data, I found support for all three hypotheses in at least one major seabird group. I hope that this review will serve as a guidepost for future molt-related studies of seabirds.

Key words: Molt, moult, life history, tradeoff, comparative studies, breeding, migration, seabirds

INTRODUCTION

A basic determinant of fitness entails the allocation of resources among various activities involved in survival and reproduction. Competition among these activities for limited resources such as time or energy gives rise to life-history tradeoffs, wherein investment in one activity occurs only at the expense of another. Two such activities that play an important role in all avian life histories are breeding and molt. Migration may introduce a third factor into this basic model of the avian life cycle. Interspecific variation in characteristics such as clutch size, migratory distance and molt strategy reflects different ways of negotiating these major life-history trade-offs. In this study, I review the literature available on molt for several major groups of seabirds to examine certain life-history and morphologic characteristics that appear to influence the evolution of the pattern, duration and timing of molt.

I consider the evolution of wing-molt strategies in seabirds from the perspective of balancing the demands of molt, breeding and migration. Seabirds are a particularly interesting group for studies of wing molt, because they face relatively severe constraints in replacing their feathers that result from their distinctive morphologies and life histories. Seabirds are generally larger than terrestrial birds, with larger wings and flight feathers. This increase in wing size introduces several constraints associated with the increased time, energy and nutrients required to replace longer feathers (King 1974, King 1980, Rohwer *et al.* 1992). Also, wing molt often introduces large gaps in a wing, resulting in reduced flight efficiency (Tucker 1991, Hedenström & Sunada 1999, Bridge 2003) and maneuverability (Swaddle & Witter 1997). These effects may be especially detrimental to seabirds that rely heavily on flight for capturing prey and for tracking ephemeral sources of food (Ashmole 1971). Thus, among seabirds we see a wide variety of wing-molt strategies, which have presumably evolved to mediate the costs of molt in the context of unique and often complex life histories.

Wing-molt strategies can be considered as a combination of three variables: (1) pattern: the sequence in which feathers are replaced; (2) duration: the rapidity or synchrony with which feathers are lost and regrown; and (3) timing: the occurrence of molt relative to breeding activity or seasonal cues. In this paper, I test three generalizations regarding how each of these molt-strategy components has evolved in response to other important life-history phenomena.

Notably, little interspecific variation is seen in the growth rate of individual feathers, and most seabirds grow all of their feathers at an approximate rate of 6 mm daily, regardless of the size or quantity of fully-grown feathers (Prevost 1983, Langston & Rohwer 1996, Rohwer 1999). This relatively uniform growth rate is probably attributable to a physiological constraint on the rate at which proteins diffuse through the collar of cells surrounding a developing feather (Langston & Rohwer 1996). This uniform growth rate is an important consideration when molting strategies are being compared between birds of different sizes, because it means that larger feathers will necessarily take more time to replace.

Most birds replace their primaries in a single molt series that begins with the innermost primary, p1, and progresses distally until the outermost primary, usually p10, is replaced (Ginn & Melville 1983). This wing-molt pattern is also prevalent among seabirds (Table 1), yet many seabird species have evolved more complex molting patterns. It has been suggested that these complex molting patterns arise in association with large wings, and that this association is attributable to increased time and energy demands associated with replacing large feathers (Langston & Rohwer 1996, Rohwer 1999, Edwards & Rohwer 2005). As Rohwer (1999) points out, large birds may be unable to replace all of their primaries in less than a year if they practice a simple wing-molt strategy. Because feathers require so much time to grow, a large bird with a descendent molt would have to shed many adjacent feathers in rapid succession, giving rise

to sizable gaps among the flight feathers that would probably reduce flight performance (Hedenström 2002). Hence, the first hypothesis addressed here is that complex molting patterns tend to occur in birds with large wings.

The second, somewhat related, generality addressed is the notion that the duration of wing molt is determined by wing size. Renewal of all the flight feathers can require as long as three years in some albatrosses (Prince *et al.* 1993, Langston & Rohwer 1995) to one or two months in alcids (Thompson *et al.* 1998, Bridge 2004, Thompson & Kitaysky 2004). The time required to replace all of the primaries is probably determined primarily by the intensity of molt (i.e. the rate at which feathers are shed) and the summed length of the primaries that must be replaced during wing molt (Rohwer 1999). Because all feathers grow at roughly the same rate, larger birds would be expected to require more time to grow their exceptionally long flight feathers (Prevost 1983, Langston & Rohwer 1996, Prum & Williamson 2001, Dawson 2003). I used phylogenetic comparative techniques to determine whether molt duration is correlated with wing size.

Finally, I examined an unusual tendency for some seabirds to overlap molting and breeding. Many authors have noted that temporal separation of molt and breeding is the norm (Payne 1972, King 1974, Murton & Westwood 1977, Ginn & Melville 1983, Hunter 1984), presumably because the energetic and nutritional

demands of these two activities are so great that most birds cannot reliably acquire resources at a rate sufficient to sustain both molt and breeding at the same time (King 1974, 1980).

However, there are several exceptions to this generality among seabirds. Molt–breeding overlap is common in species that have prolonged breeding seasons such as frigatebirds, which often provision their young away from the nest for up to a year (Nelson 1975, De Korte & De Vries 1978). Several studies have also noted that molt–breeding overlap tends to occur in conjunction with a sedentary or dispersive annual cycle as opposed to a migratory one (Ainley *et al.* 1976, Hunter 1984, Warham 1996). These studies offer reasonable explanations for their conclusions (such as limited food availability outside the nesting season favoring simultaneous molt and breeding), but they do not attempt a comparative examination that addresses the occurrence of molt–breeding overlap in a range of seabird species (e.g. Hunter 1984). Thus, I used data from the literature and current phylogenetic-comparative techniques to test whether molt–breeding overlap is equally likely to occur in sedentary/dispersive seabirds and in migratory species.

METHODS

Data compilation

I evaluated molt and life history information for 314 species belonging to the orders Procellariiformes, Charadriiformes, and Pelecaniformes.

TABLE 1
Seabird groups ranked according to wingspan measurements from Harrison (1983) and del Hoyo *et al.* (1996)^a

Group	Order	Molt pattern	Wing-molt duration	Median wingspan (cm)
Pelicans	Pelecaniformes	Complex (stepwise or multiple series)	Unknown, probably exceeds 1 year	274
Albatrosses	Procellariiformes	Complex (multiple series and biannual patterns)	2–3 Years	221
Frigatebirds	Pelecaniformes	Complex (stepwise)	Unknown	218
Sulids	Pelecaniformes	Complex (stepwise)	10–14 Months	152
Skuas	Charadriiformes	Simple (descendent)	4–6 Months	124
Gulls	Charadriiformes	Simple (descendent)	3–4 Months	122
Fulmar-petrels	Procellariiformes	Simple (descendent or variant ^b)	2–4 Months	107
Skimmers	Charadriiformes	Simple (descendent)	7–9 Months	106
Cormorants	Pelecaniformes	Complex (stepwise)	5–10 Months	105
Tropicbirds	Pelecaniformes	Complex (stepwise)	4–6 Months (not clear)	104
Shearwaters	Procellariiformes	Simple (descendent or variant ^b)	3–5 Months	98
Gadfly petrels	Procellariiformes	Simple (descendent)	3–4 Months	90
Terns	Charadriiformes	Complex (repeated molt, stepwise, or descendent)	6–9 Months	78
Prions	Procellariiformes	Simple (descendent)	2–4 Months	61
Alcids	Charadriiformes	Simple (synchronous or descendent)	1–3 Months	57
Northern Storm-Petrels	Procellariiformes	Simple (descendent)	3–5 Months	47
Southern Storm-petrels	Procellariiformes	Simple (descendent)	3–5 Months	42
Diving petrels	Procellariiformes	Simple (synchronous or descendent)	2–4 Months	33

^aSee text for group definitions and descriptions of molt patterns. Data are compiled from sources listed in Table A (online).

^bThe primary molt series may begin at p2 and proceed proximally and distally.

Individual literature searches for each species generally began with standard ornithological references such as *The Handbook of the Birds of the Western Palearctic* series (Cramp 1977, Cramp 1983, Cramp 1985), the *Handbook of the Birds of Australia and New Zealand* (Marchant & Higgins 1990, Higgins & Davies 1996) and the recently completed *Birds of North America* species accounts. I then sought further sources using bibliographies and electronic searches. In some cases, molt data were generated from museum specimens or published photographs. The data from this review, as well as a complete bibliography, can be downloaded from the *Marine Ornithology* Web site and are also available from the author upon request. Henceforth, I refer to this data matrix as Table A.

For each species, I first tried to categorize the pattern of primary molt as either a single series of descendent molt, a synchronous molt (all feathers lost almost simultaneously), or a complex molting pattern (stepwise or multiple molt series). Information about secondary molt was rare and could not be effectively incorporated into the study. Intensity of wing molt was recorded as the number of primaries grown simultaneously and the approximate duration of molt (i.e. the time required to renew all of the flight feathers). Species were considered to exhibit molt–breeding overlap if wing molt occurred while they incubated eggs or provisioned dependent young.

The migratory habits of each species were assigned to one or more of three categories: sedentary, dispersive, and migratory. Birds that remain at their breeding grounds throughout the year were categorized as sedentary. Birds that leave the breeding area after fledging chicks but that spend the non-breeding period in the general area or region of the breeding site were considered dispersive. Birds that travel long distances to traditional wintering grounds after breeding were classified as migratory. Species in which different populations exhibit different migratory behaviors were assigned to more than one movement category (e.g. dispersive and migratory).

Finally, I incorporated wingspans into the data set for almost all species. I preferred this measure to the more conventional wing-length measurement, because wingspans were available for a wider array of seabird species. In most cases I used Harrison's (1983) wingspan measurements, which were the most comprehensive set of measurements I found for seabirds. In some cases where wingspans were absent from Harrison (1983), I used measurements from del Hoyo *et al.* (1996).

In deciding which groups of species to include in this review, I adhered to a traditional definition of seabirds by including taxonomic groups in which there are a substantial number of species with pelagic phases in their life history. I excluded several taxonomic groups that have marine-associated species, such as sea ducks (Aythyinae), loons (Gaviidae), and grebes (Podicipedidae), but included some groups that spend little time away from the shore (e.g. pelicans). I also excluded most Charadriiformes (i.e. all members of the suborders Charadrii and Pterocli), because they are primarily shorebirds or terrestrial species. Finally, I excluded the anhingas and darters (Anhingidae) from all formal analyses because they are not strongly associated with marine habitats. However, molt in this family is discussed in relation to that of its allies.

In several of the analyses presented below I lumped species into groups of close relatives using published phylogenies or traditional taxonomy. Within the Procellariiformes, these groupings were based on distinct clades within the Adams-consensus supertree in

Kennedy & Page (2002), which was generated from independently derived phylogenies using matrix reconstruction with parsimony. These procellariiform groups included two distinct clades of storm-petrels (a northern clade [*Oceanodroma* and *Hydrobates*] and a southern clade [*Garrodia*, *Fregatta*, *Pelagodroma* and *Oceanites*]), the albatrosses (Diomedidae), the fulmarine petrels (*Fulmarus*, *Thalassoica*, *Daption*, *Pagodroma* and *Macronectes*), the shearwaters (*Puffinus*, *Procellaria*, *Bulweria*, *Pseudobulweria* and *Calonectris*), the gadfly petrels (*Pterodroma*), the diving petrels (Pelecanoididae) and the prions (*Pachyptila* and *Halobaena*). The Kerguelen Petrel (*Lugensa brevirostris*) was not classified within any of these groups because of its uncertain position in the procellariiform supertree.

For Pelecaniformes, I defined groups based on traditionally recognized families. These were the cormorants (Phalacrocoracidae), the sulids (Sulidae—gannets and boobies), the pelicans (Pelecanidae), the frigatebirds (Fregatidae) and the tropicbirds (Phaethontidae).

Within Charadriiformes I included the larids (Laridae—gulls and terns), the skimmers (Rhyncopidae), the alcids (Alcidae) and the skuas (Stercorariidae), which together comprise a distinct clade in a recent charadriiform phylogeny (Paton *et al.* 2003). For this review, I subdivided the larids to recognize the gulls (Larini) and the terns (Sternini) as distinct groups. Species names followed Sibley & Monroe (1990), with the exceptions of Newell's Shearwater *Puffinus newelli*, Macquarie Shag *Phalacrocorax purpurascens*, Heard Shag *Phalacrocorax nivalis*, Long-billed Murrelet *Brachyramphus perdix*, Cayenne Tern *Sterna eurygnatha*, and Thayer's Gull *Larus thayeri*, to which those authors did not give species status.

Throughout this work, I refer to specific primary feathers using a commonly employed letter and number code. Primaries are indicated by a lowercase "p" followed by a number that indicates the feather's relative position among the primaries, counting from the innermost primary, p1, to the most distal.

Examination of molt patterns

Most modern studies of wing molt describe patterns of feather replacement in terms of molt series (e.g. Langston & Rohwer 1995, Shugart & Rohwer 1996, Voelker & Rohwer 1998, Filardi & Rohwer 2001). A molt series is a group of adjacent feathers that molt together according to a single set of rules that define the order of feather replacement and the timing of the molt series activation with respect to seasonal events or other molt series (Langston & Rohwer 1996, Edwards & Rohwer 2005). Because such detailed descriptions were available for only a few species, molting patterns were merely classified as simple or complex. Simple molting patterns included patterns with only one molt series among the primaries (e.g. descendent molt) and synchronous molt (nearly simultaneous loss of all of the primaries). Complex molt patterns generally involved multiple concurrent molt series, such as stepwise molt (see "Discussion" for descriptions of complex patterns).

With the exception of the terns, classifications of molt patterns as complex or simple were essentially uniform in most of the major groups of seabirds (Table A, online). Hence, I did not examine molt patterns at the species level. Rather, I ranked groups of seabirds according to median wingspan, and noted whether complex or simple molt patterns were dominant in the group (Table 1). For a species-level examination of variation in molt patterns among the terns, see Bridge *et al.* (in press).

Examination of molt duration

Because molt duration depends on the pattern of feather replacement, the relationship between molt duration and wing size is best examined within related groups of birds that exhibit the same general molt pattern. The most speciose groups that meet these criteria are the gulls (Larini) and a large clade of procellariiform seabirds comprising the gadfly petrels, the fulmarine petrels, the prions, the shearwaters, and the Kerguelen Petrel (Kennedy & Page 2002). With a few exceptions, all members of these groups undergo a single annual bout of descendent molt that replaces all of the primaries. Thus, for these groups of seabirds, I used the molt duration data compiled in Table A (online) together with measurements of wing size to test whether longer wings are associated with an increase in the molting period. Generating discrete values for molt duration was problematic, because most reports in the literature merely give approximate date ranges for the initiation and completion of wing molt. In most cases I used the difference between the midpoints of these initiation and completion date ranges rounded to the nearest 0.5 month as a rough estimate of molt duration. I used published estimates of molt duration (also rounded to the nearest 0.5 month) based on studies of individual birds or monitoring of populations when these were available, although many of the studies overestimate the duration of molt because they incorrectly apply linear regression models (Pimm 1976).

I first tested for a relationship between wingspan and molt duration using simple linear regression, with separate tests performed for each species group. However, because data from closely related species are not statistically independent, I referenced published phylogenies of the gulls and Procellariiformes to calculate Felsenstein's (1985) independent contrasts using the PDAP module (Midford *et al.* 2003) in Mesquite v1.0 (Maddison & Maddison 2003). For the gulls, I used the phylogeny from Crochet & Desmarais (2000), which was generated using maximum likelihood (ML) techniques on 660 bp of mtDNA from the control region and 275 bp of mtDNA in the cytochrome *b* gene. ML branch lengths for this tree (P.A. Crochet pers. comm.) were uneven, and so I subjected them to Sanderson's (1997) nonparametric rate-smoothing method in the program r8s v1.50 (Sanderson 2002). The resulting tree was then pruned to remove all taxa for which data were missing before using that tree to generate independent contrasts of wingspan and molt duration.

For the procellariiform group, independent contrasts were examined using the consensus of four ML trees generated by Nunn & Stanley (1998) from 90 complete cytochrome *b* sequences. Branch lengths for this tree were produced by downloading the mtDNA data matrix from TreeBASE (www.treebase.org) and using PAUP v4.0b2a (Swofford 1999) to calculate Tamura–Nei distances. The resulting branch lengths were uniform and did not require smoothing. As described above for the analysis of gulls, the tree was pruned to remove taxa with missing data before being used to generate independent contrasts. For both species groups, I tested for a relationship between molt duration and size by performing a regression of the independent contrasts for these variables through the axis as prescribed by Garland *et al.* (1992).

Examination of molt–breeding overlap

To test the hypothesis that molt–breeding overlap tends to occur in conjunction with non-migratory life histories, I first employed a simple contingency-table approach, wherein the presence or absence of molt–breeding overlap and the presence or absence of migratory behavior were coded as binary data. I excluded from this analysis species that are reported to have both migratory and

sedentary populations, such as the Wedge-tailed Shearwater *Puffinus pacificus* and the Broad-billed Prion *Pachyptila vittata*. Likewise, I excluded species wherein the presence of molt–breeding overlap was questionable or unknown. Only species with pronounced molt–breeding overlap were coded as having this characteristic. If wing molt and breeding only occasionally co-occur or if molt–breeding overlap occurs only very late in the chick-rearing period, then the species was coded as not having molt–breeding overlap. If co-occurrence of molt and breeding is highly variable then the species was excluded from the analysis. Species were coded as migratory as described above, and sedentary and dispersive species were both regarded as non-migratory.

In the one group that exhibited a significant association between sedentary behavior and molt–breeding overlap (i.e. Procellariiformes, see “Results”), I further examined the relationship by using the phylogeny of Kennedy & Page (2002) to perform a contingency states test (Sillén-Tullberg 1993). The contingency states test compiles the number of times that a character undergoes a particular transition (gain or loss), together with the number of times the state of the character is maintained among the available internodes in a phylogenetic tree. These transitions and retentions are then compared with the states of the second character to determine if the first character changes its state in response to the second.

The contingency states test cannot make use of taxa with missing character data. Thus, I pruned from the tree species that lacked data for either molt–breeding overlap or migratory behavior. I generated reconstructions of ancestral states for both the independent and dependent variables using MacClade v4.05 (Maddison & Maddison 2002), with equivocal branches assigned to states based on the MAXSTATE criterion. I then performed the contingency states test using the program CoSta v1.03 (Lindenfors 1999).

RESULTS

Of the 314 species examined, I found some form of molt-related data for 236. I found no molt data for 78 species—roughly 25% of the seabirds. Many of these species are Asian or South American birds, which lack inclusion in a set of detailed species accounts such as *The Birds of North America* series.

Molt pattern complexity

Table 1 lists the major groups of seabirds (defined in “Methods”) in order of decreasing median wingspan. Topping the list with the longest wings are the pelicans, followed by the albatrosses, the frigatebirds, and the sulids. All four of these groups feature molt strategies that depart from the standard descendent-molt pattern by adopting forms of stepwise or multiple-series wing-molt patterns. Complex molting patterns are also seen among the cormorants, the tropicbirds, and the terns. The remaining groups have simple molting patterns and are reported to practice either a simple descendent molt or a synchronous molt. A simple Wilcoxon rank-sum test indicated that this concentration of complex molting patterns among large birds is probably not due to random chance ($n = 18$, $Z = -2.17$, $P = 0.03$)

It should be noted that a recent study of Sooty Shearwaters *Puffinus griseus* and Northern Fulmars *Fulmarus glacialis*, which concluded that primary molt is initiated at p2 and proceeds both proximally and distally, raises the possibility that certain aspects of molt in Procellariiformes have been overlooked (Thompson

et al. 2000). However, barring any gross oversights in this group (e.g. the presence of multiple molt series among the primaries), their classification would be unaltered in this study.

Molt duration and size

Simple regression of molt duration on wingspan showed significant positive correlations for both the procellariiform group [n = 25, $r^2 = 0.41$, $P < 0.001$; Fig. 1(a)] and the gulls [n = 29, $r^2 = 0.32$, $P = 0.001$; Fig. 1(c)]. Regression of the standardized contrasts of these variables in the gulls indicated that the relationship between wingspan and molt duration is significant after controlling for shared ancestry [n = 23, $r^2 = 0.33$, $P = 0.003$; Fig. 1(b)]. Similarly, regression of independent contrasts indicated that the positive correlation between wingspan and molt duration in the procellariiform group is not an artifact of phylogeny [n = 23, $r^2 = 0.36$, $P = 0.002$; Fig. 1(d)]. However, it is important to point out that the relationship between

wingspan and molt duration in the procellariiform group appears to be driven by the two species of giant petrel (*Macronectes*), both of which have relatively large wings and an extended wing-molt period [Fig. 1(c)]. With these two species removed, the simple regression of molt duration on wingspan and the regression of independent contrasts are both nonsignificant (simple regression: n = 23, $r^2 = 0.07$, $P = 0.22$; independent contrasts: n = 21, $r^2 = 0.05$, $P = 0.31$).

Molt–breeding overlap

The results for all species and for the Pelecaniformes and the Charadriiformes separately indicated that molt–breeding overlap was not significantly more common in non-migratory species [all species: $P = 0.08$, Table 2(a); Pelecaniformes: $P = 0.26$, Table 2(b); Charadriiformes: $P = 0.12$, Table 2(c)]. However, among Procellariiformes, molt–breeding overlap occurred more frequently than expected among non-migratory species [one-tailed

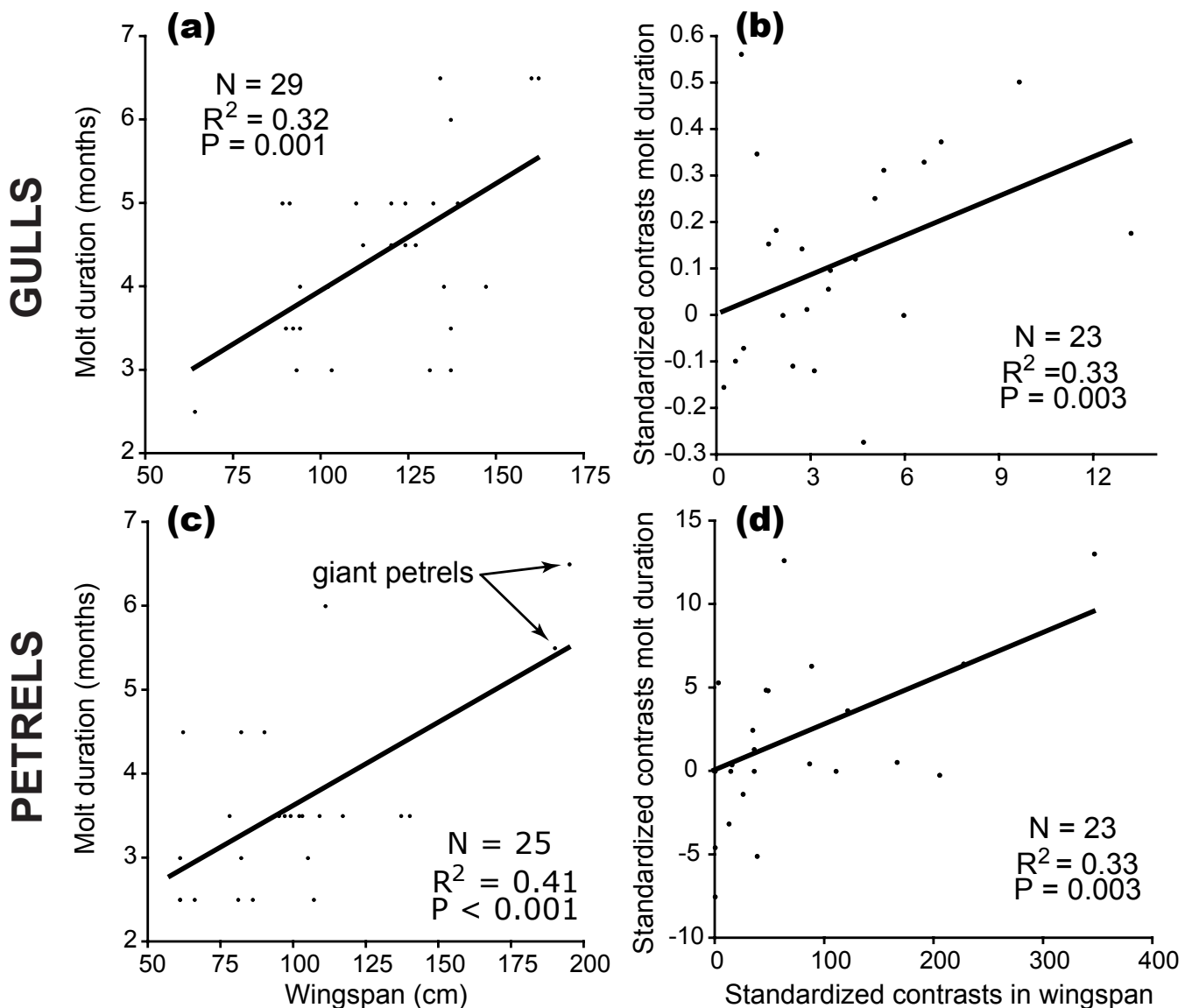


Fig. 1. Relationship between wingspan and molt duration in the gulls (upper panels) and the procellariiform clade (petrels) described in the text (lower panels). Panels on the left (a and c) show simple linear regressions of molt duration on wingspan using data from Table A (online). Panels on the right (b,d) illustrate linear regressions through the origin, based on standardized contrasts in wing span and published phylogenies of the gulls (Crochet & Desmarais 2000) and the Procellariiformes (Kennedy & Page 2002).

Fisher exact test: $P = 0.002$; Table 2(d)]. A contingency states test (Sillén-Tullberg 1993) further indicated that molt–breeding overlap is significantly more likely to arise in sedentary or dispersive procellariiform species than in migratory ones (Fisher exact test: $P = 0.035$; Table 3; Fig. 2).

TABLE 2
Contingency tables examining the association between migratory behavior and molt–breeding overlap using data listed in Table A (online)

	Molt–breeding overlap		Total
	Absent	Present	
(a) All available data ($P = 0.08^a$)			
Sedentary	37	27	64
Migratory	69	30	100
Total	106	57	163
(b) Selected groups within the Pelecaniformes ($P = 0.26^a$)			
Sedentary	5	10	15
Migratory	0	4	4
Total	5	14	19
(c) Selected groups within the Charadriiformes ($P = 0.12^a$)			
Sedentary	22	9	31
Migratory	27	22	49
Total	49	31	80
(d) Procellariiformes ($P = 0.002^a$ [a two-tailed test gives the same P value])			
Sedentary	10	8	18
Migratory	42	4	46
Total	52	12	64

^a Indicates the probability that the *positive* association between molt–breeding overlap and migratory behavior is attributable to chance alone (one-tailed Fisher exact test).

DISCUSSION

Molt patterns

Deviations from a simple descendent molt pattern may be attributable to the fact that speeding up a descendent molt can occur only by increasing the number of adjacent primaries that are grown simultaneously (Rohwer 1999). A rapid descendent molt would give rise to large gaps among the primaries, which may impair flight ability (Hedenström & Sunada 1999). Thus, in response to evolutionary pressures to molt quickly and to avoid large, molt-induced gaps among the flight feathers, some birds appear to have evolved complex molting strategies, which allow several feathers to be replaced simultaneously while spreading out the locations of missing feathers on the wing and effectively minimizing the molt-induced loss of wing area.

The fact that the four largest groups of seabirds have complex molt strategies suggests that their large flight feathers favor the evolution of complex patterns of feather replacement. However, this comparative approach does not attempt to decouple the relationship between size and functional ecology, and some aspects of the life histories of large seabirds may favor both large size and complex molt. For instance, soaring flight as practiced by albatrosses may depend on large size for momentum and on minimization of molt gaps via a complex molt pattern. Interestingly, if each group with complex molt patterns is examined separately, it can be seen that they achieve complexity in different ways.

Pelecanidae

The largest seabirds, the pelicans, are very poorly studied with respect to molt, with the exception of the Brown Pelican *Pelecanus occidentalis*, whose molts and plumages were the subject of a monograph by Schreiber *et al.* (1989). This monograph describes a multiple-series primary molt in adults, wherein two waves of proximal to distal feather replacement begin respectively at p1 and p5 or p6 and proceed distally [Fig. 3(a)]. However, the patterns of new, old and growing feathers described are also consistent with a stepwise molt, and the data are insufficient to distinguish between these two patterns. Thus, little can be concluded about wing-molt patterns in pelicans other than that they have a complex, multi-wave molt as opposed to a descendent molt.

Diomedidae

The albatrosses have the highest aspect ratios of any group of birds and spend many months each year at sea, mostly on the wing (Tickell

TABLE 3
Hypotheses and results for contingency-states test examining the relationship between molt–breeding overlap and non-migratory behavior in Procellariiformes

Null hypothesis	Transitions	Seasonal movements		P Value ^a
		Migratory	Non-migratory	
Molt–breeding overlap equally likely to arise in migratory and non-migratory species	Molt–breeding overlap gained	3	5	0.035
	Absence of molt–breeding overlap maintained	73	24	
Molt–breeding overlap equally likely to be lost in migratory and non-migratory species	Molt–breeding overlap lost	2	0	0.47
	Molt–breeding overlap maintained	5	3	

^a Fisher exact test.

2000). Given their long feathers and their heavy reliance on flight, it is likely that albatrosses face severe time constraints with regard to wing molt. They have developed unique molting strategies for meeting that challenge—strategies that often involve multiple molt series and that may require three years for a complete replacement of the primaries (Prince *et al.* 1993, Langston & Rohwer 1995, Langston & Rohwer 1996, Edwards & Rohwer 2005).

Fregatidae and Sulidae

Ranking just below the albatrosses in wingspan are the frigatebirds, followed by the sulids. Available molt data indicate that all members of these two groups have a stepwise molt. As mentioned

previously, a stepwise molt allows large birds to minimize molt gaps by spreading wing molt across the wing. A second interesting feature of the stepwise molt is that it is commonly paused for a short period—perhaps for a breeding attempt—and then resumed where it left off. Such a flexible molt strategy might be advantageous to frigatebirds and sulids because, in addition to relatively large wings, these two groups are characterized by highly irregular breeding seasons (Nelson 1975, 1978). However, it is also possible for molt series to be temporarily suspended in birds with a simple descendent molt (Snow 1967, Cannell *et al.* 1983). Hence, both wing size and life-history are likely to have influenced the evolution of the complex molt patterns that occur in frigatebirds.

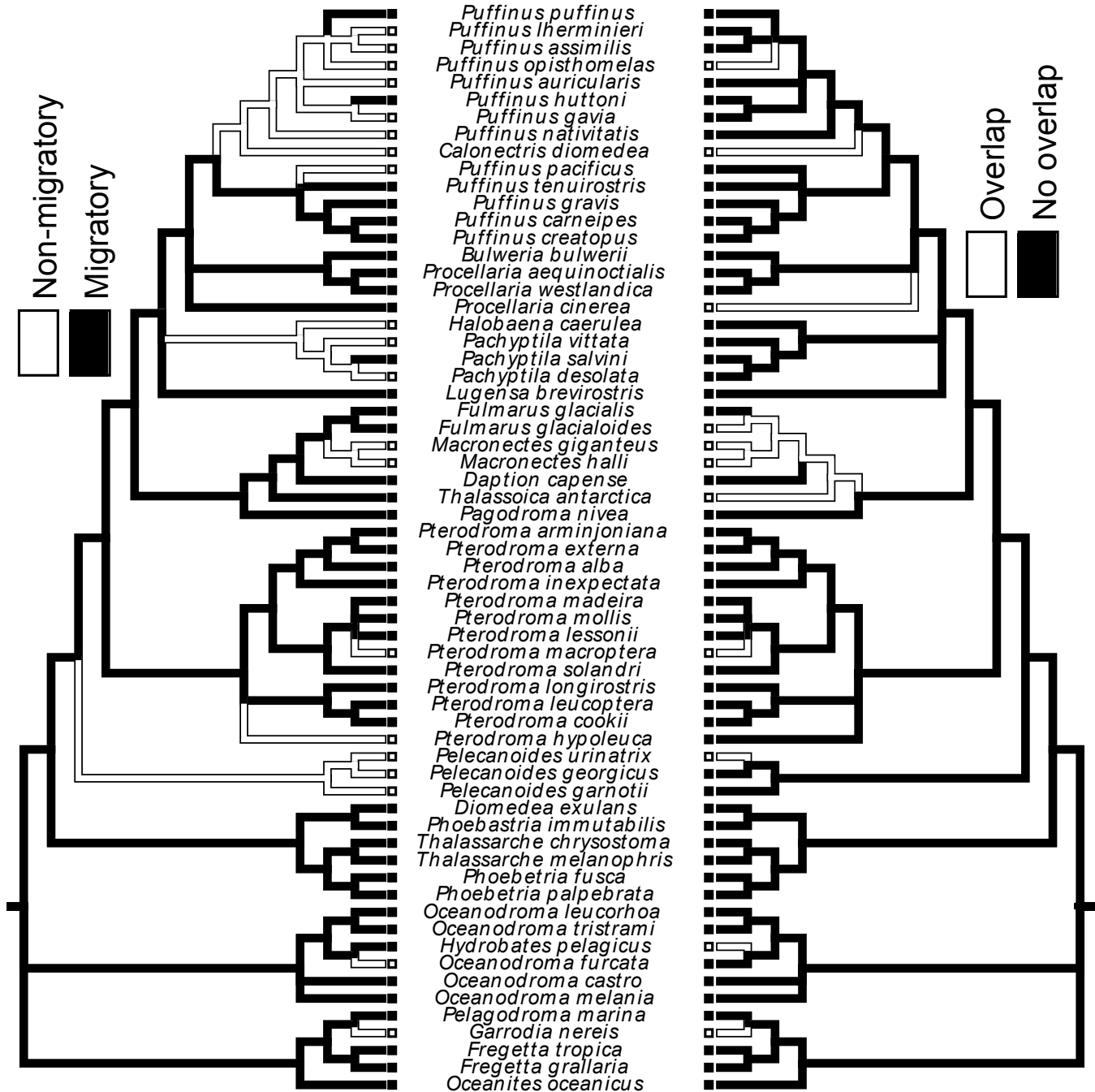


Fig. 2. Contingency states analysis of the presence or absence of molt–breeding overlap in comparison with migratory and non-migratory life histories. The mirrored phylogenies show the array of ancestral states associated with the independent character or variable (seasonal movements) on the left and the dependent variable (molt–breeding overlap) on the right.

Phaethontidae

Irregular breeding cycles are also characteristic of the tropicbirds and a few tern species (Ashmole 1968, Schreiber & Ashmole 1970, Gould *et al.* 1974). These species also exhibit molt patterns that differ from a simple descendent molt and may benefit from the flexibility afforded by more complex molt patterns. This link between irregular breeding and complex molt patterns may help explain why these groups constitute an exception to the general lack of complex molting strategies in small and medium-sized seabirds.

Phalacrocoracidae

Most cormorants also undergo a stepwise molt of the primaries (Potts 1971; Cramp 1977; Cooper 1985; Rasmussen 1987, 1988; Marchant & Higgins 1990, Filardi & Rohwer 2001), which is at first puzzling, given that these birds generally do not have particularly large wings and that they are not prone to irregular breeding cycles. Nevertheless, cormorants have been shown to retain worn feathers for one or two years, suggesting that, with regard to molt, they face serious time constraints similar to those faced by larger birds (Rasmussen 1988, Filardi & Rohwer 2001). Stepwise molt in cormorants may be related to the somewhat high wing loading in this group, exacerbated by the fact that the plumage often becomes

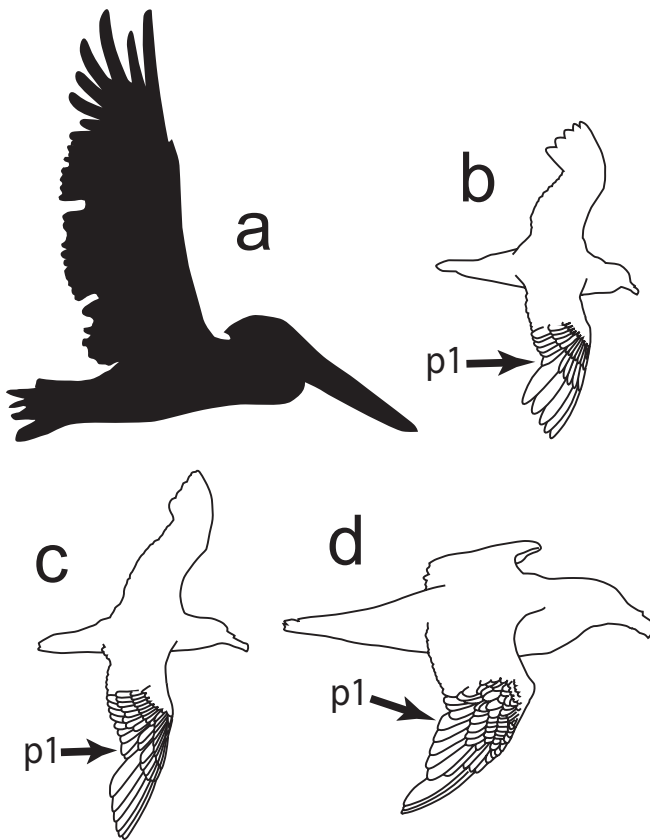


Fig. 3. Seabirds in molt. (a) Silhouette of a Brown Pelican. Note the multiple molt locations among the primaries and secondaries. (b) Tracing from a photograph of a Bermuda Petrel (*Pterodroma cahow*) molting five inner primaries: p1 is partially grown and visible, but p2 to p4 have yet to emerge from the coverts. Note the exaggerated spreading of the remaining feathers. (c) Tracing from a photograph of a Cory's Shearwater (*Calonectris diomedea*), which is molting its four innermost primaries. Primaries 1 and 2 are visible. (d) Tracing from a photograph of an Antarctic Giant Petrel molting p5 (almost fully grown) through p7 (not visible).

soaked with water. However, stepwise molt is the dominant pattern within the Pelecaniformes and may represent an ancestral characteristic. Thus, the cormorants may exhibit stepwise molt because of phylogenetic constraints, rather than natural selection for this characteristic.

Anhingidae

Although this review excluded anhingas and darters from all analyses, it is interesting to note that these species may be a possible exception to the prevalence of stepwise molt in Pelecaniformes. Anhingas and darters undergo a simultaneous molt that renders them flightless (Owre 1967, White 1975, Frederick & Siegel-Causey 2000). It is impossible to determine whether this molt strategy evolved in relation to a non-marine habitat, but it indicates the potential for evolutionary change with regard to molt patterns in the Pelecaniformes. Hence, phylogenetic constraint may not be a satisfactory explanation for the persistence of stepwise molt in cormorants, which are probably the sister family to Anhingidae (Siegel-Causey 1997).

Sternini

Molt patterns are unusually variable among the terns. Most *Sterna* terns exhibit a rare form of wing molt that involves repeated replacement of some inner primaries, whereas the outer primaries are replaced only once each year (Cramp 1983, Olsen & Larsson 1995, Higgins & Davies 1996). Although similar to a stepwise molt, repeated molt in terns is distinct because initiation of wing molt following breeding does not take up where incomplete waves left off. Rather, post-breeding wing molt always begins anew with a molt wave initiated at p1.

Among the terns that do not exhibit repeated molt are several species that practice what appears to be either a stepwise or a multi-series molt. In these species, two or more molt waves are initiated at different locations and proceed concurrently in a distal direction. Finally, a few terns practice a simple descendent molt. This array of molting strategies among the terns appears to be attributable to the emergence of varying migratory regimes or degrees of seasonality in the life histories of derived species (Bridge *et al.* in press). Additionally, some forms of wing molt in terns may have a role in sexual selection (Bridge & Nisbet 2004).

Other groups

The remaining species have either a descendent molt or a synchronous molt, and in most cases, their molt strategies differ more in the intensity with which feathers are shed than in the sequence of feather replacement. All of the groups displaying these patterns comprise species with relatively regular breeding schedules. Furthermore, wing size in species with descendent molt is generally small to intermediate, with a few notable exceptions, such as the giant petrels (*Macronectes*) and the skuas. Thus, there appears to be little evolutionary pressure for these groups to adopt complex molt strategies.

Molt duration in relation to wing size and molt intensity

Renewal of all the flight feathers can require from as long as three years in some albatrosses to one or two months in alcids (Table A, online). The time required to replace all of the primaries is probably determined primarily by the intensity of molt (i.e. the rate at which feathers are shed) and the lengths of the primaries that must be replaced (Rohwer 1999). My findings support this conclusion, given that I found significant correlations between wingspan and molt

duration in both of the seabird groups I examined. Additionally, examination of Table 1 indicates that the long-winged groups tend to require more time to renew all of their primaries.

Wing size explains some of the variation in molt duration, but other important influences obviously affect molt duration as well. In particular, the intensity of wing molt can do much to define the length of the molting period, regardless of the size of a bird's wings. Among groups with a molt, the slowest to replace the flight feathers is the skimmers. Birds in this group require approximately nine months to complete their simple descendent primary molt (Gochfeld & Burger 1994). Wing molt is so gradual in these birds that, to help explain observations of an extended wing-molt period, some authors have mistakenly reported that wing molt occurs twice annually (e.g. Bent 1921, Oberholser 1974).

Because the skimmers are intermediate in size (Table 1), it appears that low molt intensity rather than wing size is the best explanation for their protracted wing molt. I speculate that wing molt in skimmers is gradual because of their unique form of aerial foraging (i.e. flying fast and low with the lower mandible cutting the water's surface). Minimizing molt-gaps may be necessary for skimmers to maintain the high degree of power and control required for their fishing technique. The skimmers are an excellent example of how detailed empirical data, such as the precise numbers of feathers growing per wing through the duration of molt, could shed light on how molt interacts with other life-history phenomena.

A much more rapid form of descendent molt occurs in several groups of procellariiform seabirds, including the fulmarine petrels, the gadfly petrels and the shearwaters. These birds often initiate molt by shedding four to six inner primaries over just a few days, creating large gaps in the middle of the wing [Fig. 3(b,c)]. The effects of this intense wing molt on flight are largely unknown, but flightlessness has been reported in Greater Shearwaters *Puffinus gravis* and Southern Fulmars *Fulmarus glacialis* undergoing wing molt (Meinertzhagen 1956). The outer primaries are generally replaced at a slower rate, with rarely more than three feathers growing at once [Fig 3(d)].

In some of these species, accelerated wing molt appears to be an adaptation associated with demanding breeding and migration schedules. Marshall & Serventy (1956) pointed out that the transequatorial migrants among the petrels often delay wing molt until they reach their wintering quarters, which limits the time available for molting and requires that molt proceeds very rapidly. Alternatively, fast-molting procellariiform seabirds may schedule wing molt to coincide with brief seasonal increases in food availability, which would allow the birds to undertake the energetic burden of feather growth at a time when resources are abundant (Ainley *et al.* 1976, Hunter 1984, Warham 1996).

Synchronous wing molt occurs in two groups of seabirds, the alcid and the diving petrels. Common to both groups is notably high wing loading (Warham 1977). Widening the scope to consider other groups of aquatic birds, loons (Gaviidae), waterfowl (Anseriformes), grebes (Podicipediformes) and anhingas/darters (Anhingidae) are found also to conform to the pattern of high wing loading and synchronous molt (Thompson & Kitaysky 2004). One explanation for synchronous wing molt in most of these groups is that they have such high wing loading that almost any molt-induced reduction in wing area may render a bird flightless or nearly so (Thompson *et al.* 1998). Anhingas

and darters, which have relatively large wings, may weaken this explanation, although waterlogged plumage increases wing loading at times in these species. Thus, synchronous molt in most diving birds probably evolved as a means of both shortening the molting period and avoiding a prolonged molt-induced disruption of flight ability (Bridge 2004). Furthermore, for birds that can dive and forage effectively during a synchronous molt, the costs of flightlessness are significantly less than they are for species that rely heavily on flight for foraging. Hence, foraging modes almost certainly mediate the adaptive value of synchronous molt.

Molt–breeding overlap

Molt–breeding overlap was clearly associated with the absence of migratory behavior in the Procellariiformes. This trend is probably attributable to the fact that sedentary or dispersive species experience extreme seasonal fluctuations in food availability because they do not follow spatial shifts in prey species abundance, as migratory birds do. Thus, the more sedentary procellariiform seabirds probably undertake both molt and breeding simultaneously in concurrence with abundant food resources (Ainley *et al.* 1976, Hunter 1984, Furness 1987).

The relationship between molt–breeding overlap and sedentary behavior was found primarily among the storm-petrels, the fulmarine petrels and the gadfly petrels. Among the storm-petrels, molt–breeding overlap occurs only in the sedentary Grey-backed *Garrodia nereis* and Ashy *Oceanodroma homochroa* Storm-Petrels. Based on a small (260 bp) mtDNA sequence stored on GenBank, these two species do not appear to be closely related (pers. obs.). The Ashy Storm-Petrel probably is more closely related to Leach's Storm-Petrel (*Oceanodroma leucorhoa*) and Tristram's Storm-Petrel (*Oceanodroma tristrami*) than to the Grey-backed Petrel. Therefore, in all likelihood, these two species represent instances in which molt–breeding overlap arose independently in sedentary storm petrels.

At least four of the eight species of fulmarine petrels overlap molt and breeding, and among those four, a pair of sister species, the Antarctic Giant Petrel *Macronektes giganteus* and Hall's Giant Petrel *M. halli* are primarily dispersive and sometimes sedentary. Similarly, although data on molt–breeding overlap are few for the gadfly petrels (Table A, online), the only gadfly petrel for which I found reports of molt–breeding overlap was the Great-winged Petrel *Pterodroma macroptera*, which is a primarily sedentary (though sometimes dispersive) species among its relatively migratory allies (Fig. 2).

Overlap of molt and breeding schedules appears to be absent among well-studied albatross species, except for the Sooty Albatross *Phoebastria cauta* (Table A, online), although the documentation for this species is uncertain (Marchant & Higgins 1990). Albatrosses exhibit extremely demanding breeding behaviors, with incubation shifts lasting up to several weeks (Tickell 2000). Given the energetic cost of this activity, as well as foraging flights that can range for thousands of miles, albatrosses are probably unable to sustain molt and breeding efforts simultaneously.

All of the diving petrels are sedentary or dispersive (or both), and yet only one species, the Common Diving Petrel *Pelecanoides urinatrix* is known to overlap breeding and molt (Payne & Prince 1979, Marchant & Higgins 1990). However, the other three species of diving petrel probably undergo a synchronous molt (Watson 1968, Marchant & Higgins 1990), which would make breeding

impossible, because a flightless bird could not access its nest.

This variation in molt strategy among the diving petrels differs from that of the alcids, where large species with high wing loading molt synchronously, and smaller species molt gradually. Although wing loading measurements are not available for the diving petrels, the Common Diving Petrel is not smaller than its congeners. Hence, it is unlikely that size accounts for its gradual wing molt.

Among the shearwaters and prions, sedentary/dispersive life histories appear to be fairly common, yet only a few of these species overlap molt and breeding (Fig. 3; Table A, online). This fact helps to explain the failure of the contingency states test to reject the null hypothesis that molt–breeding overlap is equally likely to be lost in migratory and non-migratory species (Table 3). Also notable within these two groups is a violation of the apparent association between molt–breeding overlap and sedentary behavior by the Grey Petrel *Procellaria cinerea*, a migratory species that molts and breeds concurrently (Fig. 2). However, it is worth noting that the seasonal movements of this species are generally limited to circumpolar dispersal (between 60 degrees and 25 degrees south latitude) with birds present in breeding areas year-round. Its treatment as a migratory species in my analyses is the result of northward movements approaching the equator along the western coast of South America by some individuals (Harrison 1983, Marchant & Higgins 1990). Thus, migratory behavior appears to be limited in this species, which may favor a summer molt during part of the breeding season when local food availability is high.

The fact that molt–breeding overlap is so often associated with non-migratory life histories in the procellariiform seabirds begs the question of why this trend did not hold for the pelecaniform and the charadriiform seabirds despite the fact that molt–breeding overlap was fairly common in those groups [Tables 2(b,c)]. As mentioned earlier, molt–breeding overlap can result from extended breeding seasons or prolonged molting periods, or both. Thus, pelecaniform seabirds, such as the pelicans and the cormorants, which often undergo nearly continuous wing molt (Johnsgard 1993), and frigatebirds and sulids, which provision chicks and fledglings for extended periods (Nelson 1975, De Korte & De Vries 1978, Nelson 1978), may overlap breeding and molting as a consequence of protracted molting or breeding periods.

Among Charadriiformes, alcids are generally sedentary/dispersive species (Table A, online), and yet overlap of wing molt and nesting activity is not feasible for most because they become flightless during their synchronous molt (although some alcids provision recently fledged chicks during wing molt—Gaston & Jones 1998). Franklin's gull *Larus pipixcan* and most terns replace some or all wing feathers twice annually (Burger & Gochfeld 1994, Olsen & Larsson 1995). Thus, wing molt in these birds may begin during the latter part of the breeding season to allow time for a second molt before the next breeding season. Finally, the prevalence of molt–breeding overlap among the gulls may be related to their tendency toward a migratory life history and increased evolutionary pressure for early and efficient migration to the wintering grounds. Hence, molt–breeding overlap in the gulls during the late chick-provisioning period may be a consequence of pressure to complete wing molt before fall migration.

Guidance for future studies

Comparative studies of molt are limited by significant information gaps. A brief examination of Table A (online) reveals that, for many

species, basic molt parameters remain unknown. Although the present review shows some evidence of evolutionary trends, where molting strategies appear to be influenced by environmental and behavioral factors, such comparative investigations would be greatly improved by additional data. The information compiled for this review should indicate where additional research is most needed.

Not only are data scarce for many species, but detailed studies of molt are also exceedingly rare. Many descriptions of complex molt patterns assumed a stepwise molt whenever evidence showed alternation of old and new feathers. Such descriptions generally failed to examine actively molting birds, which would allow for a stepwise molt to be distinguished from a multi-series molt (e.g. Ashmole 1968, Cramp 1977, Higgins & Davies 1996). Even some of the more rigorous studies of molt, such as those by Rasmussen (1987, 1988) and Potts (1971) of stepwise molt in cormorants, present data that are insufficient to evaluate their conclusions regarding molt series and the rules followed.

A small but growing number of studies have adopted improved methods of describing molt patterns, and these methods have provided new insights into many complex molt patterns, achieving a level of sophistication that greatly increases the potential for hypothesis-testing regarding life-history tradeoffs in birds. For example, the study by Shugart and Rohwer (1996) of stepwise molt in Black-crowned Night-Herons *Nycticorax nycticorax* revealed the process by which an interrupted molt early in life serves to generate multiple waves of feather replacement within the same molt series. Other examples include work by Langston & Rohwer (1995) and Langston & Hillgarth (1995), which revealed the biannual nature of molt in some albatrosses, and by Yuri & Rohwer (1997), which linked ecological differences between two populations of Rough-winged Swallows *Stelgidopteryx serripennis* to differences in their molting schedules. In these papers, molt descriptions are based on well defined criteria for the identification of molt series and their associated rules regarding initiation, direction and consistency. These and similar studies should serve as examples for future descriptions of wing-molt patterns.

In almost all bird species, there is a need not only for improved descriptions of molt patterns, but also for improved estimates of molt duration. The duration of molt in most species is known only in terms of approximate dates of molt initiation or completion, derived from field sightings of birds in molt or with renewed plumage. Of the studies that estimate molt onset and duration from banding data or museum specimens, many are flawed in two ways. First, the traditional means of scoring molt ranks feathers on a scale from 0 (fully grown old feather) to 5 (fully grown new feather) with each non-zero value between 0 and 5 representing the length of a growing feather relative to its full length (Ginn & Melville 1983). In this scheme, p1 has the same contribution to molt score as p10, despite the fact that p10 may be double the length of p1 and thus take twice as long to replace. Improved methods of scoring molt take into account the individual lengths or weights of the feathers replaced during molt, such that shorter feathers contribute less to a molt score than do longer ones (e.g. Underhill & Zucchini 1988, Underhill *et al.* 1990, Dawson & Newton 2004).

The second problem is how molt scores are used to estimate molt parameters in a population (i.e. duration, initiation and variance). A common technique is simply to regress molt score on observation date (e.g. Ginn & Melville 1983). This technique overestimates

molt duration in individual birds, because the slope of the regression line reflects not only the relationship between molt score and time, but also the variability in the initiation of molt within the population (Pimm 1976, Underhill & Zucchini 1988). One solution to this problem involves reversing the dependent and independent variables such that date is regressed on molt score (Pimm 1976). This approach yields an estimate of molt duration for the average individual bird rather than an estimate of the average duration of molt for the population. A more advanced approach is presented by Underhill & Zucchini (1988) and Underhill *et al.* (1990), who offer statistically sound models for accurately estimating molt duration for various data-sampling schemes.

This paper provides some indication of the potential for comparative studies of seabird life histories to reveal important trends in ecology and evolution. Since the groundbreaking work of Ashmole (1971), which integrated molt strategies and other important life-history phenomena, evidence has been mounting that molt serves as a “currency” through which birds mediate major life-history tradeoffs. Field experiments have shown that depriving birds of this currency by manipulating the wing feathers or by causing molt to be delayed, induces marked reductions in survival or reproductive output, or both (Slagsvold & Dale 1996, Svensson & Nilsson 1997). Because molt is an important, yet poorly described, aspect of the avian life cycle, molt studies may be the most important limiting factor to furthering our understanding of life-history tradeoffs in birds (Thompson *et al.* 1998, Rohwer 1999, Filardi & Rohwer 2001, Leu & Thompson 2002).

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