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S24-1 Progress with the statistical analysis of primary molt

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Abstract This paper considers two extensions to the statistical analysis of primary molt. The first extension relates to the development of statistical models that allow the simultaneous estimation of molt parameters for diverse groups of birds. Parameter estimation uses the method of maximum likelihood and the EM algorithm. The likelihood ratio criterion is applied in statistical hypothesis-testing for equality of sets of parameters, and the Akaike Information Criterion is used to guide model selection. This extension is illustrated using primary molt data for willow warblers (*Pylloscopus trochilus*) over 11 years. The second extension is the realization that important insights into the way that primary molt is incorporated into the annual cycle of birds can be obtained by investigating the parameters of molt of individual primary feathers. This extension is illustrated using six data sets from four species of waders, Charadriiformes.

Key words Primary molt, Statistical models, Waders, *Phylloscopus trochilus*

1 Introduction

The basic model developed by Underhill and Zucchini (1988) to estimate the parameters of primary molt adopted a particular approach. First, it assumed that all birds sampled were subject to the same basic trio of parameters describing primary molt, i.e. that birds molting at a given site have a single mean starting date, duration of molt, and standard deviation from starting date. The latter measures the spread of starting dates for individual birds, i.e. the extent to which molt is synchronized. Secondly, it interpreted primary feathers as arising from a single feather tract. This paper extends both assumptions. The first assumption, or extension, requires the development of statistical models, with associated likelihood equations and the mathematical tools to solve them. The second extension takes up the original model and applies it in a novel way.

2 Extension 1: molt models to enable comparisons between groups of birds

The basic model did not facilitate comparisons between groups of birds, between sexes, sites and years. The extended model allows these comparisons and enables sensible model fitting, with significance tests for parameters. Brandao (1997) produced the mathematical statistics to accomplish this for her as yet unpublished PhD thesis. She developed the likelihood equations, and used the method of maximum likelihood and the EM algorithm to estimate molt parameters. She then applied the likelihood ratio criterion to test for equality of parameters, and made use of the Akaike Information Criterion to guide model selection (Akaike, 1973; Linhart and Zucchini, 1986).

The value of the extended model is illustrated by a dataset for the willow warbler (*Phylloscopus trochilus*), for which we have primary molt protocols for 678 birds over 11 years at Lake Ladoga near St. Petersburg, Russia. Under the original version of the Underhill-Zucchini molt model, the only way to examine inter-year differences would have been to estimate the three molt parameters for each year, for a total estimate of 33 parameters. Theory developed by Brandao (1997) enables us to examine first whether the standard deviation parameters were the same for each year, immediately reducing the parameters to 23. Then followed a test of whether moult durations were the same for each year, such that only mean starting dates differed. It yielding just 13 parameters: 11 starting dates, a common duration, and a common standard deviation.

The next step tested which years had the same mean starting dates, few of which were unique due to exceptional conditions. At the end, the statistically most parsimonious model combining data for males and females suggested one mean starting date (12 July) for all except four years, a common duration of 45 days for all years, and a common standard deviation of 11 days for all years. The four exceptions to mean starting date were: 1979 (3 days early), 1980 (7 days late), 1985 (9 days late), and 1989 (6 days early). We have no auxiliary data to help explain the biological meaningfulness of this model.

The extensions developed by Brandao (1997) effectively enable analyses to be performed with a single "grouping" variable, analogous to one-way analysis of variance. The next step is to develop extensions that would simultaneously model more than one variable, such as year and sex, and the interactions between them. There is also a need for models which incorporate continuously explanatory variables. In the example above, it would be useful to be able to test whether the starting date of molt depends on factors such as mean temperature in June, and to be able to fit models of the form:

starting date in year i = a + b (temperature in year i)

where a and b would be two parameters to be estimated by the model, along with duration and standard deviation.

3 Extension 2: the parameters of molt of individual primary feathers

3.1 Duration data

Prior to Serra (2000), studies of primary molt focused on primary feathers as a single unit, considered as a tract of nine or ten feathers (e.g., Prater, 1981). Serra (2000) initiated the investigation of the parameters of molt of individual primary feathers. His analysis for the grey plover (*Pluvialis squatarola*) showed interesting differences between the strategies used by populations molting under differing climatic conditions. These differences hinted that further such research on other species might yield significant results. The first step was taken by Underhill (2002).

Serra (1998) showed that grey plovers molting in Britain completed molt in about 90 days (Table 1), whereas those molting in the south (southern India, Kenya, southern Africa and Australia) completed molt in about 130 days (Table 2), regardless of the time available. By estimating the parameters of molt for each of the 10 primaries, abbreviated here to P1 (innermost) to P10 (outermost), Serra (2000) examined the strategy employed by grey plovers to speed up molt in the north (Tables 1 and 2). Essentially, the innermost primary feathers (P1 and P2) were shed at the same pace in both environments. However, the outermost primary feathers (P8 to P10) were shed at short intervals and grown rapidly with the impending approach of freezing winter weather.

Underhill (2002) repeated this approach on four data sets: ruddy turnstones (*Arenaria interpres*) in southern Africa and Scotland (data from Summers et al., 1989, in which primaries were considered as a tract), reported in Tables 3 and 4; sanderlings (*Calidris alba*) in southern Africa (from Summers et al., 1987, in which primary molt data were not analyzed), reported in Table 5; and red knots (*Calidris canutus*) in southern Africa, from a previously unanalyzed dataset reported in Table 6.

The durations of primary molt in ruddy turnstones in southern Africa and Scotland were estimated to be 119 days and 94 days, respectively (Tables 3 and 4). Primary molt commenced early in August and ended early in November in western Europe; in southern Africa, it started in the second week of October and ended near the start of February. The durations of molt from P1 to P6 in southern Africa increased steadily from 10 days to a maximum of 27 days; and durations for P7 to P10 were fairly constant, varying between 24 and 27 days (Table 3). In contrast, the durations of molt of P1 to P5 in Scotland were fairly constant, varying

Table 1 Estimates of the key molt parameters of individual primaries in grey plovers (*Pluvialis squatarola*) in Britain Overall estimates are also shown (from Serra, 2000).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	*SD*	M	*SD*	S	*SD*
P1	28.4	1.2	37.9	1.0	24.3	0.9
P2	28.9	1.1	41.1	0.9	22.2	0.8
P3	31.2	0.9	46.3	0.6	18.0	0.5
P4	30.6	0.8	51.1	0.5	16.0	0.4
P5	29.7	0.8	58.1	0.4	15.0	0.4
P6	26.8	0.7	68.3	0.4	13.6	0.3
P7	25.6	0.8	79.8	0.4	11.8	0.3
P8	22.6	0.9	92.1	0.6	12.4	0.3
P9	18.4	1.0	105.3	0.8	14.0	0.5
P10	16.7	1.1	117.4	0.9	16.5	0.8
P1–10	89.5	1.0	49.9	0.4	13.8	0.2

Table 2 Estimates of the key molt parameters of individual primaries in grey plover (*Pluvialis squatarola*) populations in warm southern latitudes Overall estimates are also shown (from Serra, 2000).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	*SD*	M	*SD*	S	*SD*
P1	30.6	3.6	15.7	4.0	29.7	2.8
P2	28.5	3.4	20.0	3.4	25.1	2.4
P3	25.2	2.9	29.7	2.8	24.9	2.2
P4	26.3	2.6	40.5	2.3	24.5	1.8
P5	25.1	2.5	51.5	2.1	24.1	1.6
P6	26.6	2.4	61.2	1.9	21.6	1.3
P7	23.9	2.3	77.9	2.0	21.5	1.2
P8	30.3	2.5	92.3	2.2	24.4	1.3
P9	27.1	2.5	111.8	2.3	27.8	1.5
P10	33.4	2.7	129.0	2.4	30.2	1.5
P1–10	136.4	3.0	26.2	2.0	25.6	0.9

Table 3 Estimates of the parameters of molt of individual primaries in the ruddy turnstone (*Arenaria interpres*) in southern Africa Overall estimates are also shown (from Underhill, 2002).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	*SD*	M	*SD*	S	*SD*
P1	10.0	4.2	103.3	6.2	23.3	3.7
P2	13.4	4.6	103.8	5.9	22.4	3.4
P3	18.5	4.9	105.0	5.9	23.5	3.0
P4	16.9	4.3	113.2	5.9	25.9	3.0
P5	22.3	4.2	119.4	5.9	27.9	3.0
P6	27.2	4.0	128.4	5.2	29.1	2.9
P7	26.9	3.6	141.9	4.6	36.3	3.4
P8	25.6	3.1	162.6	3.3	35.2	2.8
P9	24.1	2.7	179.9	2.7	34.7	2.4
P10	26.2	2.7	191.7	2.5	34.6	2.1
P1–10	118.9	5.7	101.0	4.6	31.4	1.6

from 15 to 17 days; molt of P6 to P9 varied from 19 to 28 days, while P10 took 39 days to molt (Table 4).

The duration of primary molt in sanderlings in southern Africa was 98 days (Table 5). It commenced in early November and was complete by the middle of February. Molt from P1 to P6 increased in steady progression; P6 had the longest estimated molt duration of the ten primaries, and the molt durations of P7 to P10 were similar but slightly shorter (Table 5). The duration of primary molt for the knots in southern Africa was 95 days (Table 6). It commenced in late October, and was completed towards the end of January. Durations for individual primaries varied between 14 and 20 days, apart from P10 which took an estimated 24 days (Table 6).

3.2 Implications of molt duration data

What is remarkable about these results is their variability, not just the overall timing and duration of primary molt but particularly the patterns within the 10 primaries themselves. A striking example of the latter is the difference in molt strategies in ruddy turnstones and grey plovers in Britain. Both species completed primary molt in about 90 days (Tables 1 and 3), beginning in early August and finishing in early November prior to the advent of freezing conditions in late autumn and winter. Ruddy turnstones, however, molted P1 to P4 almost simultaneously and P5 four days later to complete molt of the first five primaries within about 20 days (Table 3). In contrast, molt of the same primaries took 50 days to complete in the grey plover (Table 1). Molt of the last five primaries (P6 to P10) in the ruddy turnstone took 79 days, and in the grey plover 66 days.

At northern sites, 20%–30% of grey plovers fail to complete molt prior to the onset of winter, and suspend molt until improved conditions occur in spring (Serra, 1998). Similar suspension does not occur in the ruddy turnstone which makes a rapid start to molt in August, when conditions are still favorable, and completes molt at a leisurely pace adapted to the increasing harsh conditions faced through autumn. In particular, P9 and P10 are estimated to take 28 days and 39 days (*SD* = 2 days in both) to grow, respectively (Table 3). Growth duration for these feathers is, with the exception of P1 and P2 in northern grey plovers, the longest of any in the six populations examined here (Tables 1–6). We conclude that molt strategy in the ruddy turnstone is better adapted to northern conditions than in the grey plover. This might reflect the recent colonization of northern latitudes by grey plovers, their numbers reaching Britain having increased six fold over the past three decades.

The duration of molt in the four species in southern Africa was remarkably variable: red knots took 92 days, sanderlings 100, ruddy turnstones 119 and grey plovers 131 (Tables 2, 4–6). The duration of primary molt in red knots there is similar to that in northern populations of ruddy turnstones and grey plovers, and to estimates of the duration of molt in red knots in Britain and the Netherlands (Boere, 1976; Ginn and Melville, 1983). This might indicate

Table 4 Estimates of the parameters of molt of individual primaries in the ruddy turnstone (*Arenaria interpres*) in Scotland Overall estimates are also shown (from Underhill, 2002).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	*SD*	M	*SD*	S	*SD*
P1	15.3	3.1	35.3	4.5	16.0	2.2
P2	15.7	3.1	35.3	4.5	16.0	2.2
P3	16.2	3.2	34.5	4.7	17.0	2.3
P4	16.7	3.2	34.6	4.7	17.8	2.3
P5	16.3	2.7	39.0	4.0	18.5	2.1
P6	19.4	2.3	48.5	2.6	16.5	1.4
P7	28.2	2.0	54.7	1.9	15.9	0.9
P8	23.2	1.7	70.2	1.5	17.6	1.0
P9	28.0	1.8	82.7	1.3	18.0	1.1
P10	38.8	2.2	89.0	1.3	19.1	1.0
P1–10	93.6	1.6	27.3	2.3	15.6	0.7

Table 5 Estimates of the parameters of molt of individual primaries in the sanderling (*Calidris alba*) in southern Africa Overall estimates are also shown (from Underhill, 2002).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	*SD*	M	*SD*	S	*SD*
P1	12.5	1.3	129.9	1.3	19.6	1.1
P2	12.7	1.3	132.1	1.3	19.3	1.1
P3	15.6	1.5	134.4	1.3	19.5	1.0
P4	19.0	1.6	139.1	1.4	20.6	1.0
P5	19.5	1.6	147.4	1.5	22.5	0.9
P6	22.8	1.7	156.4	1.5	23.3	0.9
P7	21.3	1.6	171.5	1.5	22.0	0.9
P8	19.7	1.4	186.5	1.4	20.8	0.8
P9	18.6	1.3	199.1	1.3	20.0	0.8
P10	21.3	1.3	208.5	1.2	19.0	0.7
P1–10	97.6	1.6	132.7	1.1	20.5	0.5

Table 6 Estimates of the parameters of molt of individual primaries in the red knot (*Calidris canutus*) in southern Africa Overall estimates are also shown (from Underhill, 2002).

Primary	Duration (days)		Mean (days since 1 July)		Standard deviation (days)	
	D	*SD*	M	*SD*	S	*SD*
P1	13.7	2.5	119.8	3.2	23.8	2.2
P2	14.1	2.4	120.3	3.2	23.4	2.1
P3	15.7	2.4	122.5	3.0	23.4	2.0
P4	18.6	2.5	128.2	2.8	23.9	1.9
P5	20.1	2.4	135.0	2.8	26.4	1.9
P6	16.8	2.2	146.4	2.6	27.7	2.0
P7	15.7	2.0	157.5	2.3	28.1	1.9
P8	16.5	2.0	168.2	2.3	29.9	1.9
P9	18.6	2.0	178.4	2.2	30.4	1.7
P10	23.5	2.1	188.5	2.2	32.4	1.6
P1–10	94.8	3.5	118.5	2.9	30.8	1.2

that red knots have not migrated to hot environments in the non-breeding season for long enough to adapt to the opportunity to extend molt through the period available for it.

On the other hand, populations of grey plovers that migrate sufficiently far south, so that harsh weather does not constrain the duration of primary molt, extend the molt period to about 130 days, regardless of the time available (Serra, 1998). Only P1 and P2 are molted in quick succession, four days apart, and grow slowly; the remaining feathers grow at a fairly constant rate. The average intervals between shedding of the smaller primaries P2 to P6 is 10 days; for the larger primaries P6 to P10, the average interval lengthens to 17 days (Table 2).

Although the overall durations of primary molt differed among red knots, sanderlings and ruddy turnstones, the sequences within the 10 primary feathers were similar. The three species molted P1 to P3 in quick succession, and then the remainder at a fairly constant rate.

Primary molt of grey plovers commences shortly after the completion of southwards migration, and extends over about 130 days (Serra, 1998); populations of grey plovers in the northern tropics therefore have long "slack" periods between the end of primary molt and preparation for migration, such as accumulation of fat reserves and acquisition of breeding plumage. This species appears to be adapted to molting in the tropics and subtropics, these environments probably providing the best conditions for it out of breeding.

In contrast to grey plovers, northern ruddy turnstones molt their inner five primaries extremely rapidly, a strategy which seems adapted to reducing stress in northern regions. The only trace of this "northern strategy" in southern Africa is the rapid molt of the first three primaries; the overall duration of primary molt in the ruddy turnstone in warm climates approaches that of the grey plover (Tables 2 and 3). We conclude that the ruddy turnstone is a species which is primarily adapted to molting in northern latitudes, but has modified this strategy to capitalizing better on the opportunity to extend molt in tropical and subtropical areas.

Waders are well known for the diversity of strategies used in their life cycles. We have demonstrated that this is also true for their patterns of primary molt. We now need to extend analyses of the kind used here to a broader range of species, beyond waders and migrants.

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