

# Does timing of breeding affect breeding plumage acquisition in shorebirds?

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The retention of winter feathers in breeding plumage is a trait exhibited by many species of shorebirds (Charadrii). Variation between populations in the degree of winter feather retention is thought to be due to either hybridisation when formerly allopatric populations mix, matching of plumage to breeding habitat, or differences in the timing of breeding. The timing of breeding hypothesis postulates that when breeding is early the pre-nuptial moulting process is curtailed so that the resources necessary for breeding are not compromised by the demands of moult. Hence, early breeding birds retain more winter feathers in their breeding plumage than later breeding birds. The timing of breeding hypothesis was supported by a test that showed that Redshanks *Tringa totanus* in Iceland nested earlier and had more retained winter feathers in their plumage in the 1980s than before 1977. By contrast, there was no evidence of a shift in the breeding season of Red-necked Phalaropes *Phalaropus lobatus* in Iceland, and no evidence of a change in the degree of winter feather retention. It is unlikely that “hybridisation” and “habitat matching” hypotheses can explain these effects. The results suggest that the acquisition of breeding plumage in shorebirds may be under natural selection for the timing of breeding but also under conflicting sexual selection for communication.

## INTRODUCTION

The plumage of many species of shorebirds (Charadrii) when breeding is a mixture of old, retained winter feathers and fresh, breeding feathers acquired during the pre-nuptial moult. Variation in the degree of winter feather retention occurs between individuals, but is most obvious between populations. It is particularly obvious in species where there is a marked contrast between bright breeding feathers and dull winter feathers, such as the Eurasian Golden Plover *Pluvialis apricaria*. Plumage differences between breeding populations of this species led to two subspecies being proposed: the “northern” *P.a. altifrons* and the “southern” *P.a. apricaria* (see, for example, Byrkjedal & Thompson 1998). “Southern” birds possess a lighter, white-yellow coloured feather that is not found in “northern” birds (Jukema 1989). “Southern” birds also retain more winter feathers than “northern” birds (Byrkjedal 1978). These traits show continuous variation that is not markedly related to northern and southern breeding areas, however, and current consensus tends not to make a subspecific distinction between populations (Wynne-Edwards 1957, Cramp & Simmons 1983, Byrkjedal & Thompson 1998).

Explanations of the variation in winter plumage retention in breeding shorebirds are several. One hypothesis is that it is the by-product of subspecies or population “hybridisation” (Hale 1971, Byrkjedal 1978). When populations formerly separated during glacial events have later come in to contact with each other in post-glacial periods the resulting “hybrid” population displays retention of winter feathers in breeding plumage. Presumably the hypothesis requires that formerly separated populations have some form of genetic incompatibility that is expressed by a disruption to the normal moulting process when the “parent” populations inter-breed.

This hypothesis suggests that retention of non-breeding feathers is non-adaptive and many observations fail to support it. For example, “parent” populations, as well as purported “hybrid” breeding populations, also show winter feather retention. Winter feather retention also occurs in species where “hybridisation” between populations is unlikely to have occurred (Cramp & Simmons 1983).

Two alternative adaptive hypotheses are more favoured. The first is that differences in winter feather retention represent cryptic matching of breeding plumage to breeding habitat (Byrkjedal 1978, Byrkjedal & Thompson 1998). The strong contrasts of a plumage predominantly composed of breeding feathers is more cryptic on heterogeneous habitat with strong visual contrasts in composition, whilst duller plumage with more retained winter feathers is more cryptic against homogeneous habitat with few visual contrasts in composition. The second hypothesis is that variation in winter feather retention represents energetic consequences of differences in the timing of breeding (Fjeldså pers. comm., in Byrkjedal 1978, Hale pers. comm., in Byrkjedal & Thompson 1998, Engelmoer & Roselaar 1998). Birds that breed early have less time to complete the pre-nuptial moult before the onset of the energy demands of breeding than do later breeding birds and so retain more winter feathers in their breeding plumage.

Testing these two hypotheses is difficult. Measuring habitat heterogeneity to test the “habitat matching” hypothesis is exceedingly complex without resorting to some degree of subjectivity. A simple test of the “timing of breeding” hypothesis is to compare individuals, populations or taxa and relate a measure of the timing of breeding, such as first egg date, to the degree of winter feather retention. A positive relationship between the extent of breeding feathers (or negative for winter feathers) and timing of breeding would indi-



**Table 1.** Mean first egg dates for Redshanks and Red-necked Phalaropes in Iceland before and after 1977.

Species	Year	First egg date days after 1 May: (mean $\pm$ sd (n))	Source
Redshank	Pre-1977	25.1 $\pm$ 9.3 (45)	Väisänen (1977)
Redshank	1981	11.1 $\pm$ 2.5 (27)	Summers & Underhill (1991)
Redshank	1987	13.6 $\pm$ 4.1 (41)	This study
Red-necked Phalarope	Pre-1977	41.8 $\pm$ 7.2 (227)	Väisänen (1977)
Red-necked Phalarope	1986–1987	41.0 $\pm$ 7.6 (29)	This study

cate support for the hypothesis but does not imply a relationship between the two as they may co-vary with other factors.

Under this hypothesis, breeding plumage differences in the retention of winter feathers can be viewed as outcomes of differences in the availability of energy resources to moulting birds, but timing of breeding is just one of several possible influences that can affect energy availability. Within a population some inter-individual variation in plumage could be related to differences between individuals in their ability to gather food during the pre-nuptial moult, so that “higher quality” birds have more breeding plumage (Piersma & Jukema 1993). Such an influence may tend to obscure any differences due to timing of breeding, so that a simple correlative test of the timing of breeding hypothesis is possibly safer above the level of the individual. Even a test at a higher demographic level may encounter problems, however. Breeding groups or populations in different geographic regions frequently differ in their timing of breeding (Väisänen 1977). But populations may also experience differences in the timing or abundance of pre-breeding food supplies and in their migration strategy or other requirements that may compete with moulting energy demands (e.g. late winter survival).

Two recent studies have demonstrated that several shorebird species in western Europe are now breeding earlier than in the past, either through changing agricultural practices (Beintema *et al.* 1985) or climatic warming (Crick *et al.* 1997). In the Netherlands increased agricultural mechanisation has led to progressively earlier hay cutting that kills late broods of chicks, selecting for earlier breeding (Beintema *et al.* 1985). Such shifts in the breeding season provide the opportunity for a more satisfactory test of the timing of breeding hypothesis, which predicts that shorebirds that are now breeding earlier than in the past should have more retained winter feathers in their breeding plumage than in the past. Climate change may select for changes in both the onset of moult and the onset of breeding, and so may not result in changes in plumage. An agent, such as a change in agricultural practice, that acts only on the breeding grounds (and so de-couples the timing of breeding from the timing of moult) should be more likely to select for plumage change.

This paper describes a test in which the plumage of Redshanks *Tringa totanus* and Red-necked Phalaropes *Phalaropus lobatus* breeding in Iceland in the 1980s is compared with the plumage of birds prior to 1977. Breeding in the Redshank, a species strongly associated with hay meadows, became earlier over this period, but by contrast there was no change in the timing of breeding in Red-necked Phalaropes, a species not associated with agricultural land.

## METHODS

The Redshank was selected as an “experimental” species due to data availability and, given its frequent association

with agricultural habitats (hay and grazing meadows), it was a likely candidate to have shifted its breeding season (Beintema *et al.* 1985). The Red-necked Phalarope was selected as a “control” species, also because of data availability, and because it is not usually associated with agricultural habitats.

## Timing of breeding

Data presented for Iceland by Väisänen (1977) were used to determine the timing of breeding before 1977 for both the Redshank and the Red-necked Phalarope. More contemporary estimates of breeding seasons were obtained from Summers & Underhill (1991) for the Redshank (1981), and from fieldwork on Melrakaslétta, northeast Iceland for both Redshank and Red-necked Phalarope (1986, 1987). Whitfield (1990) gives a description of the study area and presents details of field methods used to estimate egg-laying dates. These methods involved direct observation of laying dates in incomplete clutches, estimates of the stage of incubation or hatch date from complete clutches, estimates of chick age from biometrics, and records of the onset of chick-caring behaviour in breeding adults. Timing of breeding is presented as first egg dates, in days after 1 May.

## Plumage

Plumage was examined in both a series of skins in the Icelandic Museum of Natural History, Reykjavík, and in live birds in the hand, captured whilst incubating or caring for young chicks, at the field site in northeast Iceland. Plumage was scored as the percentage of breeding feathers (as opposed to retained winter feathers) in each of three body regions: head and breast, “back” (mantle and scapulars), and “wing” (wing coverts and tertials), to the nearest 5%. Therefore, the maximum summer plumage score in each body region was 100. Belly plumage was not scored as in both species winter feathers are the same as or similar in colour to breeding feathers, diminishing confidence in being able to discriminate between the two feather types. In other body regions, breeding feathers were distinguished from retained winter feathers on the basis of colour, pattern, and degree of fading and abrasion (the latter feature was used as birds can occasionally acquire fresh winter-type feathers during the pre-nuptial moult). Feathers intermediate between the two main types (Jukema & Piersma 1987) were not noted in either species.

For museum specimens, collection date and sex were recorded from attached collection labels. In the field, Red-necked Phalaropes were sexed on the basis of breeding plumage coloration differences and behaviour, and Redshanks were sexed on the basis of behaviour.



**Table 2.** Median breeding plumage scores for Red-necked Phalaropes. H+B = head and breast, Back = mantle and scapulars, T+C = tertials and wing coverts, Overall = combined breeding plumage score.

	Male					Female				
	<i>n</i>	H+B	Back	T+C	Overall	<i>n</i>	H+B	Back	T+C	Overall
Pre 1977	31	90	90	0	180	30	95	95	0	190
Post 1977	12	95	90	0	185	10	97.5	95	0	192.5

## Data analysis

First egg dates and plumage scores were divided in to two time periods for the purposes of temporal comparisons: pre-1977 and post-1977. This split was dictated by the availability of historic data on first egg dates (Väisänen 1977). The timing of breeding hypothesis makes specific directional predictions about plumage differences and change, so one-tailed tests were used in tests involving plumage change and are noted where appropriate. All other tests were two-tailed. Frequency distributions of first egg dates did not significantly differ from normality (one sample Kolmogorov-Smirnov tests against expected normal distributions), allowing parametric tests of timing of breeding data. Non-parametric tests were used to compare plumage score data.

## RESULTS

### Timing of breeding

Descriptive statistics for estimates of timing of breeding for Redshanks and Red-necked Phalaropes are presented in Table 1. For the Red-necked Phalarope, comparing first egg dates from before 1977 with dates after 1977, variances were equal (F-test:  $F = 1.11$ ,  $n = 227$  and  $29$ ), and there was less than one day difference between mean first egg dates ( $t = 0.537$ , n.s.). For the Redshank, comparing first egg dates from before 1977 with dates after 1977, variances were unequal (F-test:  $F = 5.196$ ,  $n = 45$  and  $68$ ), and so Welch's approximate t-test was used to test the equality of means (Sokal & Rohlf 1995). Mean first egg date for Redshanks after 1977 was nearly two weeks earlier than mean first egg date before 1977 ( $t\text{-test} = 8.492$ ,  $P < 0.001$ ).

### Plumage

Within species, temporal sample availability for each sex was similar. For the Redshank, most samples of plumage scores were drawn from two periods: the 1950s and 1979 to 1987. For the Red-necked Phalarope, there were three main sampling periods: the mid-1950s, the late 1960s/early 1970s, and 1987.

No Red-necked Phalarope had breeding plumage feathers in the wing coverts and tertials (Table 2). Plumage scores for the other two body regions (head and breast, and "back")

were summed to give an overall score (maximum score 200). There was little difference in plumage scores between birds scored before 1977 and birds scored after 1977, for either females (Mann-Whitney  $U = 131.5$ ,  $P = 0.285$ , one-tailed) or males ( $U = 131$ ,  $P = 0.071$ , one-tailed). As there was no temporal difference in breeding plumage, data for both time categories were combined for each sex. Females had significantly higher breeding plumage scores than males ( $U = 347.5$ ,  $P < 0.001$ ) (Table 2).

Male Redshanks had more overall breeding plumage than females in both time periods that were considered, although the difference was much less marked before 1977 (before 1977: Mann-Whitney  $U = 89$ ,  $P = 0.155$ ; after 1977:  $U = 84.5$ ,  $P = 0.038$ ) (Table 3). Combined plumage scores were less from before 1977 than from after 1977 for both sexes of Redshanks, but the difference was statistically significant for females only (females:  $U = 28.5$ ,  $P = 0.018$ ; males:  $U = 39$ ,  $P = 0.141$ , one-tailed) (Table 3).

Combined plumage scores, however, obscured plumage differences between body regions. Redshanks had the most breeding plumage on the head and breast and there were few apparent sexual and temporal differences in this body region (Table 3). Back plumage (mantle and scapulars), on the other hand, had markedly fewer breeding feathers after 1977 than before 1977 for both sexes (female:  $U = 30.5$ ,  $P = 0.014$ ; male:  $U = 30$ ,  $P = 0.043$ ; one-tailed tests).

## DISCUSSION

With a caveat of limited data in mind, these results support the timing of breeding hypothesis as an explanation for the retention of winter feathers in the breeding plumage of shorebirds. It seems most unlikely that the change in Redshank plumage is due to a change in the heterogeneity of their breeding habitat. While there have been no measures of habitat heterogeneity, Icelandic Redshanks continue to breed in the same habitats that they always appear to have bred in: hay meadows, wet pasture and low-lying marshes.

A hybridisation hypothesis also appears to be an unlikely explanation. Under the hybridisation hypothesis, for the plumage of Icelandic Redshanks to change there must have been an influx of birds from another population, presumably northern Britain. British Redshanks are smaller than Icelandic Redshanks (Hale 1971, 1980, Engelmoer & Roselaar

**Table 3.** Median breeding plumage scores for Redshanks. H+B = head and breast, Back = mantle and scapulars, T+C = tertials and wing coverts, Overall = combined breeding plumage score.

	Male					Female				
	<i>n</i>	H+B	Back	T+C	Overall	<i>n</i>	H+B	Back	T+C	Overall
Pre 1977	11	95	70	5	175	12	85	52.5	2.5	135
Post 1977	10	90	52.5	5	142.5	11	80	30	0	105



1998) and an influx of British Redshanks to Iceland should have led to a reduction in the size of Icelandic Redshanks as well as a change in their plumage. This prediction is not supported by the results of Summers & Underhill (1991). Engelmoer & Roselaar (1998) also point out that the broad geographic patterns of winter feather retention in British and Icelandic Redshanks, attributed to degrees of population mixing by Hale (1971, 1980), are also consistent with differences in the timing of breeding. Parsimony and the weight of evidence suggest, therefore, that the plumage of Icelandic Redshanks has changed because of a selection process acting on Icelandic Redshanks rather than an influx of birds from another population.

It is not known why Icelandic Redshanks are now breeding earlier than in the past, but the apparent lack of a change in the breeding season for species not associated with agricultural habitats (this study, Whitfield unpublished) implicates a change in agricultural practices. Progressively earlier hay-cutting, as in The Netherlands (Beintema *et al.* 1985), would seem to be a likely candidate. Alternatively, although perhaps less likely, the change may be due to selection on the wintering grounds in Britain. Overwintering Redshanks are highly vulnerable to depredation by Sparrowhawks *Accipiter nisus* (Whitfield 1985, Cresswell & Whitfield 1994). Most Sparrowhawk depredation on juvenile Redshanks falls on individuals that fledge late as these individuals that arrive late on the wintering grounds are forced to feed in habitats where they are vulnerable to Sparrowhawk attack (Whitfield unpublished). The progressive recent recovery of the British Sparrowhawk population from the effects of pesticide contamination (Newton & Haas 1984) could have led to increased selection for early breeding in Icelandic Redshanks.

Individual shorebirds tend to retain the same amount of winter feathers in their breeding plumage from year to year (Parr 1980, Whitfield unpublished data) so the change in Redshank plumage was probably due to natural selection on genotypes rather than progressive changes in phenotypic responses. While the retention of winter feathers would appear to be under natural selection it is also under sexual selection, judging by sexual differences in a range of species (e.g. Parr 1980, Piersma & Jukema 1993, Byrkjedal & Thompson 1998, this study). It also appears likely that the pressures on winter feather retention from natural selection and sexual selection are in conflict.

Natural selection favours birds that migrate to the breeding areas and start breeding as early as environmental conditions allow because, for example, this can allow adoption of the best breeding sites and produce young birds that (as appears to be the case for Redshanks) have a competitive edge over later fledged birds. While there may be counteracting selection against arriving too early when, for example, there may be insufficient food supplies, natural selection for early breeding should favour birds that truncate the pre-nuptial moult and acquire less breeding plumage. However, under sexual selection, birds with more breeding plumage may be favoured (Piersma & Jukema 1993). Under these conflicting selection pressures it might be expected that shorebirds should prioritise the acquisition of breeding plumage in the body areas most important in communication between conspecifics when breeding. This was confirmed in the present study for Redshanks as the head and breast area showed the highest proportion of acquired breeding feathers and the highest temporal stability. Judging by the direction

of sexual differences, sexual selection probably acts strongest on male Redshanks whereas natural selection for early breeding may be strongest in females (Summers & Underhill 1991). It would be predicted, therefore, that when natural selection for early breeding increases, a change in breeding plumage should be most evident in females. While sample sizes were too small to confirm this statistically, this appeared to have occurred in Icelandic Redshanks.

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