IS THE TIMING OF MOULT ALTERED BY MIGRATION? EVIDENCE FROM A COMPARISON OF AGE AND RESIDENCY CLASSES OF WESTERN SANDPIPERS *CALIDRIS MAURI* IN PANAMÁ

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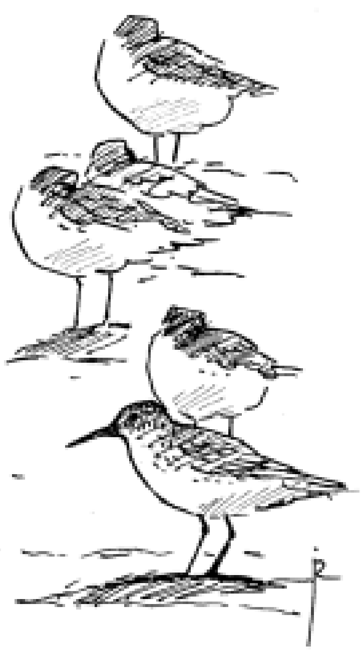

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Resident species typically undergo post-nuptial moult directly following breeding, whereas long-distance migrant species usually do so after arrival at staging or non-breeding (‘wintering’) grounds. It has been suggested that moult and migration are mutually exclusive activities. If so, one will displace the other in time. We contrasted the moult timing of migrant versus non-migrant Western Sandpipers *Calidris mauri*, taking advantage of the fact that in Panamá, most yearling birds (11-22 months of age), and some adults, were non-migratory summer residents. Yearling birds and other summer residents completed primary moult approximately 3-4 weeks earlier than adults returning from the breeding grounds. The same general pattern occurs with contour moult. Some adults of unknown migratory status also have moult patterns similar to summer residents. We interpret these patterns as indicating that earlier moult is advantageous, partially compensating residents for not migrating and breeding that year. We consider potential mechanisms that may favour an earlier moult, and discuss how moult schedules may influence Western Sandpiper migratory and life history strategies.

Key words: *Calidris mauri* - non-breeding - oversummering - migration - age-dependence - moult - annual cycle - timing - shorebirds

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INTRODUCTION

In birds, selection has typically favoured the non-overlap of demanding annual cycle events, such as moult, migration and breeding. Experimentally increased overlap between post-nuptial moult and breeding resulted in either reduced current reproductive effort or compromised survivorship (Blue Tits *Parus caeruleus*, Nilsson & Svensson 1996; Svensson & Nilsson 1997; Pied Flycatchers *Ficedula hypoleuca*, Slagsvold & Dale 1996; Hemborg & Lundberg 1998). Thus selection may have favoured delaying moult until after breeding. Since some migratory species breed in areas with short summer seasons, wing feather moult would be severely time-constrained if it occurred on the breeding grounds. In these species, wing moult typically occurs after they have left breeding areas (Norman 1997; Hemborg *et al.* 1998; Svensson & Hedenström 1999; see Hayman *et al.* 1986 for a review of shorebird species and Jenni & Winkler 1994 for a review of passerine species). This suggests that migration as well as breeding can displace moult timing until later in the annual cycle.

In many species of waders, young individuals spend their first boreal summer on the non-breed-

Table 1. Age category assignments. Most birds hatch in June, and the onset of spring migration is taken as April.

Age category	Definition	Age in months	Assignment criteria
Juvenile	Fledging to onset of spring migration period	0-10 (Jun–Apr)	Plumage characteristics
Yearling	Onset of spring migration period in the year following hatch to onset of next spring migration	10-22 (Apr–Apr)	Caught as juveniles during the previous winter
Adult	Onset of spring migration period in second year following hatch	>22	1995-96: Ring record only (i.e. ringed in 1993-94 or earlier) 1996-97: Ring record or if characterised as non-juvenile plumage during 1995-96.

ing grounds, delaying northward migration and breeding until at least their second year (Hayman *et al*. 1986). A few studies have reported that these young summer residents undergo post-nuptial moult earlier than migrants, which generally moult following their return (e.g. Paton & Wykes 1978; Johnson & Johnson 1983). Some proportion of older individuals may also fail to migrate north (Johnson 1973; Van Dijk *et al*. 1990; McNeil *et al*. 1994), but we know of no studies documenting the moult timing of summer resident adults. If moult timing is displaced by migration and breeding, then differences in moult timing ought to be related to summer residency, and not age *per se*.

Adult Western Sandpipers *Calidris mauri* undergo wing moult after they arrive on the non-breeding grounds and, as far as we know, yearling birds (see Table1 for age classifications) do not moult their wing feathers until their second summer or early autumn. Juvenile Western Sandpipers wintering in Panamá do not fatten and moult in their first spring into a complete alternate breeding plumage in preparation for northward migration and breeding (O'Hara 2002), suggesting that most spend their first boreal summer in Panamá. In this study, we assess the timing of primary flight feather and contour moult of Western Sandpipers for two age classes (yearlings and adults) and migratory statuses (returning migrants versus summer residents), with the objective of correlating age and migratory status with the timing of moult completion. If moult timing is displaced from a more favourable time by migration and breeding, then the timing of both wing and contour feather moult should be different for summer residents than for migrants, regardless of age. Alternatively, if residents moult concurrently with returning migrants, we cannot assert that such a displacement occurs. We then discuss how differential moult timing affects age-classes differently, and how it may influence selection for migratory versus summer residency behaviour in young and old birds.

MATERIALS AND METHODS

We studied Western Sandpipers at two beaches near Chitré, province of Herrera, Panama (08°00'N, 80°50'W), where the species has been ringed for 14 years. Data for this study were collected from 1 September 1995 to 31 March 1997. Birds were captured during tidal ebb in mistnets positioned over shallow water 30-150 m from the high-tide beach as they flew from roosting sites behind mangroves towards freshly exposed mudflats. Captured Western Sandpipers were categorised as juvenile, yearling, or adult (see Table 1 for definitions of age categories). Categorisation was based on plumage (Page *et al*. 1972; Prater *et al*.

Table 2. Capture dates and samples used in age analyses.

Age category	Year	Capture date	Sample size		
			Primary score = 9	Primary score	Contour score
Yearling	1996	15 Aug - 1 Apr	9	181	181
Adult	1995	1 Sep - 1 Apr	11	353	325
Adult	1996	15 Aug - 1 Apr	30	842	843

Table 3. Capture dates and samples used in summer residency analyses. Mean primary flight feather and contour feather moult scores and standard errors for summer residents and birds of unknown summer residency status.

Age category	Summer residency[1]	Captured during active post-nuptial moult?[2]	*n*	Primary moult score mean ± SE	Rufous in contour moult score mean ± SE
Non-juvenile	Confirmed	Yes	11	9.18 ± 0.26	1.27 ± 0.19
Yearling	Confirmed	Yes	3	9.67 ± 0.33	1.0 ± 0
Yearling	Unknown	Yes	13	9.38 ± 0.14	1.08 ± 0.08
Adult 1996	Confirmed	No	52		
Adult 1996	Unknown	Yes	71	6.63 ± 0.27	2.25 ± 0.12

[1] Captured between 1 May and 1 August 1996
[2] Captured between 15 August and 1 October 1996

1977) and/or ringing history. Individuals identified as juveniles in 1995-96 were categorised as yearlings the following year. A sample of unringed birds caught in summer of 1996 are referred to as ‘non-juveniles’ (i.e. a mixture of adults and yearlings of unknown proportions). We assigned gender based on exposed culmen length (Page & Fearis 1971: males < 24.3 mm, females > 24.7 mm), but since sex had no significant effect on moult score distributions ($P > 0.1$), we present results from analyses using pooled score data from all birds.

Western Sandpipers moult into non-nuptial (dull non-breeding) contour plumage on the non-breeding grounds between August and December, and into nuptial (bright breeding) contour plumage between February and May. The bright alternate plumage includes variable numbers of rufous-centred or rufous-edged contour feathers (crown, cheeks, mantle, upper scapulars, and tertials) and coverts (Prater *et al.* 1977; Hayman *et al.* 1986). We scored the extent of non-nuptial body plumage during post-nuptial moult in the autumn, as follows: 1 = no rufous anywhere; 2 = trace of rufous on any tract such as the mantle, upper scapulars, tertials, or crown; 3 = traces of rufous on more than one tract; 4 = presence of rufous in three or four tracts; 5 = rufous on lower scapulars and other tracts; 6 = full alternate plumage, with rufous throughout all previously mentioned tracts. For consistency with previous work at this site, we scored primary moult as follows: ‘10’ = primary moult completed, all 10 primaries new; ‘9’ = 9 new primaries, 10th still growing or missing; ‘8’ = 8 new and 2 old (or 1 old and 1 missing) primaries; through to ‘0’ = no new primaries. We scored only the right wing, and thus have no measure of moult symmetry.

Birds captured between 1 May and 1 August were classed as non-breeding ‘summer residents’. Local population size increased dramatically after 15 August, as ‘migrants’ returned. We classified the period prior to 1 October as the (minimum) period of active moult, because the earliest record of completed body moult is 1 October.

Statistical analyses

To examine the effect of age on moult timing, we compared distributions of dates of primary and body moult scores between yearling and adult birds. We also compared the capture dates of yearlings and adults whose primary moult score was 9, since those with a score of 10 could have completed moult at any preceding time. Sample sizes for these comparisons are given in Table 2. Plumage scores were treated as ordinal response variables and analysed using logistic regression models (Wald χ^2, two-tailed $\alpha = 0.05$) with a cumulative logit link function (PROC LOGISTIC; SAS Institute 1999). Distributions of dates for birds scored with a primary moult score of 9 were compared using a Wilcoxon Rank Sum Test for two samples (PROC NPAR1WAY with two-tailed $\alpha = 0.05$: SAS Institute 1999). We examined the effect of summer residency on moult timing by comparing the moult scores among samples of birds that varied in their summer residency status (Table 3). We did not compare these samples statistically because of low sample sizes.

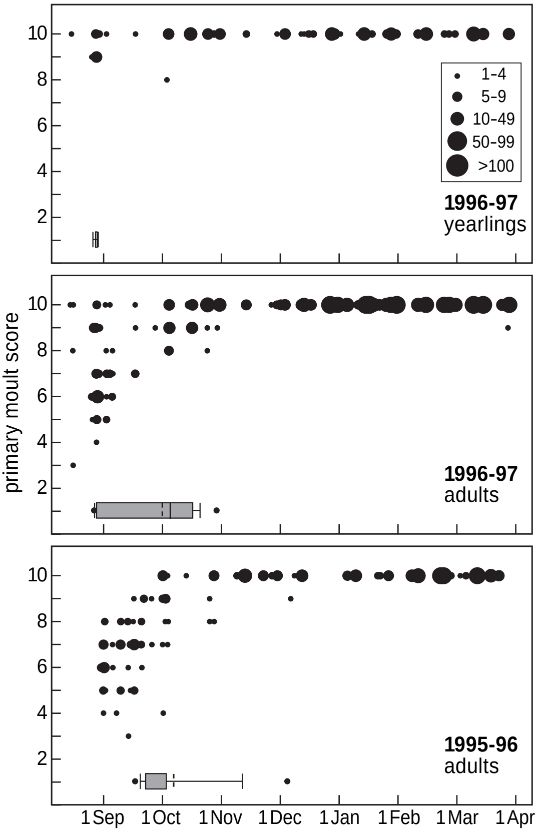

Fig. 1. Phenology of primary moult scores (see Materials and Methods for score assignments). Area of circles represent sample size category as described in the legend. Distribution of dates that individuals were scored with a primary feather replacement score of 9 (9 new primaries) are displayed at the bottom of each panel with a box and whisker plot (solid line = median; dashed line = means; percentiles: boxes = 25-75, whiskers = 10-90, and dots = 5-95). Timing of moult differed significantly between yearlings and adults from both years (1995 $Z_{9,11}$= 3.76, $P < 0.001$; 1996 $Z_{9,30}$ = 2.56, $P = 0.01$). Timing of moult also differed among years within adult birds ($Z_{11,30}$ = 4.86 $P <$ 0.001).

RESULTS

Effect of age on moult timing

Yearlings and adults differed in their primary flight feather moult timing by approximately three to four weeks. Yearlings had replaced 9 or 10 primaries by 1 October or earlier, whereas most adults did not reach this stage until 1 November (1996-97: Fig. 1). Primary moult timing differed significantly between age categories (Wald $\chi^2_{843,181}$ = 231.5, $P < 0.001$). A comparison of capture dates of individuals with primary scores of 9 substantiates this conclusion (Fig. 1). The mean date for yearlings was 27 August, while that for adults was 29 September ($Z_{9,30}$ = 2.56, P = 0.010). In autumn, yearlings had lower contour moult scores than adults (e.g. through 1 December; Wald $\chi^2_{155,50}$ = 19.3, $P < 0.001$). Yearling birds showed little or no rufous colour (score of 2 or less) until the onset of pre-alternate moult around the beginning of January, while adults had higher contour moult scores (i.e. a score of 3 or

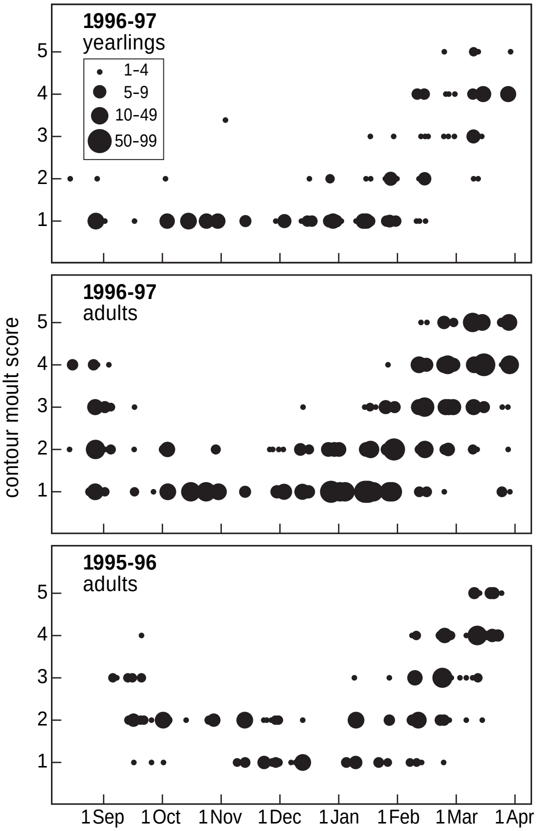

Fig. 2. Phenology of rufous colour in contour plumage (see Materials and Methods for score assignments). Area of circles represent sample size category as described in the legend.

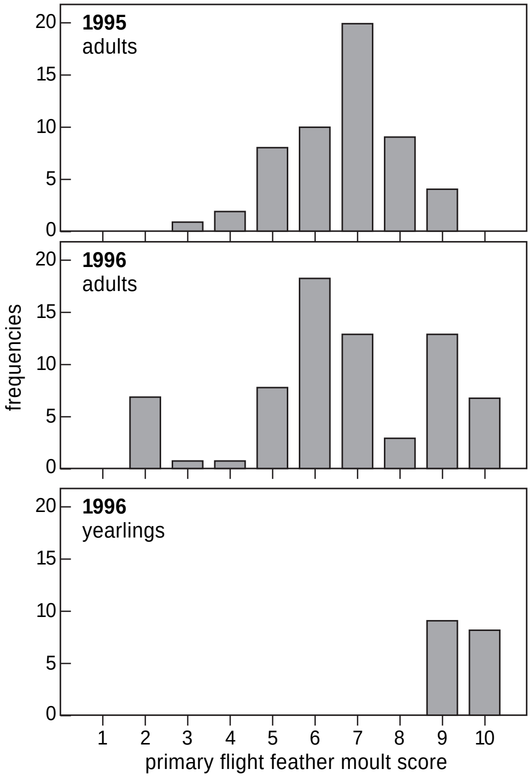

Fig. 3. Primary moult scores from August 15 to October 1 for adults in 1995 and 1996, and for yearlings in 1996.

higher) until 1 November in both 1995 and 1996 (Fig. 2). After 1 December, the two increased similarly (Wald $\chi^2_{688,132} = 3.26$, $P = 0.071$).

Age versus summer residency status

Of the 425 summer residents captured in 1996, 52 were adults (12.2%), based on ringing history, and the balance were unaged individuals. Summer resident adults would have been individuals that had either spent the entire summer in Panamá or failed breeders that had returned early enough to be detected between 1 May and 1 August. This is a minimum estimate of the true proportion of adults, since the unaged sample includes adults not previously captured. Is earlier moult a function of age *per se*, or might migratory/residency status also play a role? To properly answer this question, we would have had to have collected data during active moult from both known summer resident adults and migrant yearlings. Although we lack these complete data, we compare moult timing among sets of birds for which we have partial information regarding age and summer residency (Table 3). Among birds known to have spent the summer in Panama, yearlings had similar moult scores to our sample of non-juveniles, which consist of an unknown proportion of yearlings and adults. If adults moulted later, the non-juvenile sample should have had lower mean scores.

Among birds of unknown summer residency, but known age, yearlings moulted earlier than adults, in general (Fig. 1). However, the adult sample for 15 August to 1 October 1996 appears heterogeneous, including approximately 28% with primary moult scores of 9 or 10 (Fig. 3). The distribution for adults from 1995 was more normally distributed. Only 7% of adults were captured in 1995 with these scores, and some had completed their moults by as early as mid-August (Figs. 1, 2). The proportion of adults with 'advanced' moult varied between years for both primary flight feather (Wald $\chi^2_{353,842} = 9.25$, $P = 0.002$) and contour feather (Wald $\chi^2_{325,843} = 43.46$, $P < 0.001$) moult scores, with no early moulting adults detected in 1995. In summary, we have shown that some adults are summer residents in Panama, 'advanced' moult is not restricted to the yearling age-class, and the proportion of adults with advanced moult varies between years.

DISCUSSION

Yearling Western Sandpipers completed post-nuptial primary flight feather moult 3-4 weeks earlier than adults. This finding is consistent with studies showing age-dependent onset or progress of post-nuptial moult in other species of waders (Loftin 1962; Pienkowski & Minton 1973; Boere 1976; Paton & Wykes 1978; Johnson & Johnson 1983; Serra *et al.* 1999; Balachandran *et al.* 2000). Here, we highlight an age difference in the completion of this moult. Interpretation of age differences in contour scores in autumn was less straightforward than that for primary scores, because adults had higher contour scores prior to the onset of post-nuptial moult. While breeding adults would have had scores of 4 or 5 the previous April, juvenile birds ranged between 0–3 (O'Hara unpublished data; for examples in other species see; Loftin 1962; McNeil 1970; Johnson 1973). Nevertheless, the distributions of adult scores continued to change through the end of October, while that of the yearlings did not, as expected if the younger birds had completed moulting earlier.

Most, if not all, yearling birds spend their first boreal summer in Panama. Early moult completion for these individuals may be a function of age per se, and/or migratory status. To better separate the potential effects of these two factors would require active moult data (15 Aug-1 Oct) from (1) adults known to have spent the previous summer in Panama or failed breeders that returned early enough that migration did not displace moult timing and (2) yearlings that had migrated north in their first spring. We lack data from such adults, and have no way of assuring that yearlings we did not catch during the summer had in fact migrated. Nevertheless the moult scores of individuals for which we had partial information regarding age and migratory status (Table 3) are consistent with the hypothesis that moult timing is affected by the migratory/summer residency of an individual, regardless of its age. If this is so, we have also documented annual variation in the migratory versus residency propensities of adult Western Sandpipers (Fig. 3).

How can moult timing affect migration-oversummering life history choices?

We suggest that earlier moult by summer residents is evolutionarily adaptive. If residents can moult at a more advantageous time than migrants, birds that opt out of migration and breeding for a year obtain a previously unrecognised compensatory benefit. Ultimately, the selection on migration/summer residency behaviour will balance a bird's expectation of successful migration and breeding in one year against the differential survival probabilities of remaining and deferring breeding until the following year. Below, we review current explanations for summer residency, as developed primarily to explain a predominance in yearling birds as summer residents, and explore how changes in moult timing may favour shifting the balance towards this life history alternative for birds of all ages.

Summers *et al.* (1995) argued that that the likelihood of summer residency by yearlings was positively related to both migration distance and longevity. In waders, breeding success of yearling birds is often lower than that of older birds (Oring *et al.* 1983; Gratto *et al.* 1983). Thus the potential reproductive payoff for yearling breeders may be low enough to select for summer residency, if the costs of migration increase sufficiently with distance. Hockey *et al.* (1998) suggested that lower foraging proficiency of young birds may result in either or both sufficiently higher risks of mortality, or delayed arrival on the breeding grounds and higher probability of breeding failure, thereby favouring residency. An alternative mechanism for poorer performance by yearling birds is that insufficient development of parasite resistance precludes adequate preparation for spring migration (McNeil *et al.* 1994).

We propose that flight feather moult considerations also contribute towards the shifting of the balance in favour of summer residency in younger birds for three reasons: (1) moulting during periods of reduced competition for resources, (2) moulting at times with reduced predation risk, and (3) reducing the risk incurred by undertaking migratory flights with worn feathers. We discuss all three hypotheses below.

(1) Summer resident Western Sandpipers moult during periods of reduced competition for resources necessary for feather growth. Competition has often been implicated as a chief mechanism explaining distribution patterns among habitats, and first year birds may be particularly sensitive to changes in population densities if they are competitively subordinate to older birds (e.g. Myers 1981, Gauthreaux 1982, Townshend 1985). By moulting during periods of reduced competition (Serra *et al.* 1999), individuals may achieve faster rates of moult, grow higher quality feathers, and through greater habitat choice, reduce risks taken to accrue the resources needed to grow new feathers. However, reduced competition fails to account for concurrent primary moult by yearling, non-migratory Grey Plovers *Pluvialis squatarola* in South Africa and pre-migratory mass gain of older migrants (Serra *et al.* 1999).

(2) Avian predation can have a major impact on non-breeding and migrating wader populations (Page & Whitacre 1975; Bijlsma 1990; Wilson 1994). Juvenile waders are more vulnerable to avian attacks than adults as they may be easily separated from wader flocks (e.g. Bijlsma 1990 and references therein). Flight performance, including predator evasion, is reduced by both primary flight feather abrasion (Hochbaum & Caswell 1991; Swaddle *et al.* 1996) and moult (Tucker 1991; Chai 1997), although birds may be able to compensate somewhat for missing feathers (Swaddle *et al.* 1999). Since yearling Western Sandpipers will be experiencing their first wing moult, they may be more vulnerable to predatory attacks if they moulted at the same time as adults. In Panama, the main wader predators are Peregrine Falcons *Falco peregrinus* and Merlins *F. columbarius*, which all but disappear during the boreal summer months (Ridgely & Gwynne 1993). Although wader densities also drop during the summer, we expect far lower risk of predation per individual, and less differential relative to older birds, making this a safer time to moult.

(3) Western Sandpipers begin to moult their first set of flight feathers, grown as chicks on the breeding grounds, when they are 13-15 months old. If they migrated in their first spring, they would have to complete three migratory movements on these feathers. In contrast, adults make two migrations on each set of flight feathers. In many species of waders, particularly those with the most lengthy migratory flights, selection has favoured the evolution of a complete or partial wing moult of the outermost primaries (i.e. 'supplemental moult': Prater *et al.* 1977 or 'partial primary wing moult or PPW': Gratto & Morrison 1981; Gratto 1983; Serra *et al.* 1999). This replacement of juvenile primaries prior to northward migration may increase first winter survivorship and/or facilitate earlier breeding attempts. In either case, it probably reduces migratory risks for birds that migrate in their first spring. A supplemental moult has not been documented in Western Sandpipers, despite ample opportunity for it to have been detected, possibly making migratory distance an important correlate of migration/residency decisions in this species. In contrast to Panamá, only a small proportion of Western Sand-

pipers spending the non-breeding season in western Mexico and farther north remain as residents, and these birds have less wing wear than individuals wintering farther south (P.D. O'Hara & G. Fernandez unpublished data).

Feather wear considerations may help us to understand why resident birds do not moult their flight feathers even earlier (e.g., in May). A potential explanation is that birds would pay on the other end, during migratory seasons in the following year, since earlier moulted feathers would have more abrasion than those grown in August or September. This may explain why oversummering birds reduce the difference in timing relative to migrants to as little as a few weeks of 'extra' winter wear. Feather wear considerations also suggest an adaptive interpretation for an enigmatic pattern of two primary moults that occur in rapid succession (starting in March-April and in September-October), in 'first/second year' summer resident Grey Plovers in South Africa (Serra *et al.* 1999). In the absence of the second moult, these plovers would migrate north the following year and return to South Africa on feathers that were 4-5 months older. By undergoing the second moult, these birds match the feather wear schedules of adults.

Although, we have little information on what factors might result in over-summering by adults, we suggest that summer resident adults also shift to an earlier moult timing. Hypothesis (3) would be less important for adults, because unlike the juveniles, they grow new feathers following their southward migration, however; hypotheses (1) and (2) are applicable to all birds.

In summary, the evidence suggests that in the absence of migratory movements, post-nuptial moult occurs at a more advantageous time for birds of all ages. In addition, the effect of differential feather wear between age classes may help explain their different propensities to migrate versus remaining on the non-breeding grounds as summer residents. In concert with the previously suggested hypotheses, we recommend including the role that moult and moult timing plays in any consideration of the evolution of sandpiper migratory and life history strategies.

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SAMENVATTING

Standvogels beginnen hun slagpenrui als regel aan het einde van het broedseizoen of kort daarna. Trekvogels ruien deze pennen in veel gevallen pas als ze in de overwinteringsgebieden zijn aangekomen. Ruien en trekken worden meestal beschouwd als activiteiten die niet goed samengaan en die op verschillende tijdstippen moeten plaatsvinden. In dit artikel wordt de timing van de rui van trekkende en niet-trekkende Alaskastrandlopers *Calidris mauri* in Panama met elkaar vergeleken. Dit was mogelijk omdat vrijwel alle jonge vogels (11-22 maanden oud) en sommige volwassen vogels in Panama overzomeren. Zowel de jonge als de overzomerende oude vogels waren drie tot vier weken eerder met de slagpenrui klaar dan oude vogels die uit de broedgebieden terugkeerden. Hetzelfde verschijnsel deed zich voor met de rui van de lichaamsveren. De vroege rui heeft dus niets met leeftijd te maken maar met het al of niet volbrengen van de trektocht vanuit het broedgebied. Het verschil in timing tussen blijvers en trekkers wordt uitgelegd in het kader van de specifieke voordelen van een vroege rui. In de eerste plaats is het mogelijk dat de zomerrui zo vroeg plaatsvindt omdat in die tijd de intra-specifieke competitie voor voedselbronnen klein is. Ten tweede zijn er zomers geen valken in Panama en is ruien in die tijd waarschijnlijk veiliger dan later in het jaar als het predatierisico door de terugkeer van valken weer is toegenomen. Ten derde ontkomen sommige individuen misschien niet aan de vroege zomerrui vanwege de ernstige slijtage aan het verenpak (met name jonge vogels). Pas als de veren weer op orde zijn, kunnen zulke vogels met enige kans van slagen aan de trek deelnemen. (TP)

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