

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 &

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

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 *Falco*

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 slagpenruï als regel aan het einde van het broedseizoen of kort daarna. Trekvogels ruïen deze pennen in veel gevallen pas als ze in de overwinteringsgebieden zijn aangekomen. Ruïen en trekken worden meestal beschouwd als activiteiten die niet goed samengaan en die op verschillende tijdstippen moeten plaatsvinden, edTf 9.93.60 zikevaen mt ijdstmwadehefT* 0.0134 32 [(]. ijdals het ken)Tj ijdlaa