The flexibility of primary moult in relation to migration in Palaearctic waders – an overview

Magdalena Remisiewicz[1,2]

[1]*Avian Ecophysiology Unit, Department of Vertebrate Ecology and Zoology, University of Gdańsk, al. Legionów 9, 80-441 Gdańsk, Poland. biomr@univ.gda.pl*
[2]*Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, South Africa*

Remisiewicz, M. 2011. The flexibility of primary moult in relation to migration in Palaearctic waders – an overview. *Wader Study Group Bull.* 118(3): 141–152.

Keywords: waders, primary moult, moult flexibility, habitats, Palaearctic

This paper presents an overview of patterns in the primary moult of waders using the Eurasian–African migration system and updates earlier summaries with results obtained from the Underhill–Zucchini moult models (1988, 1990). Recent applications of these models allow researchers to examine moult timing down to the progress of an individual feather in a tract and to determine the effects of environmental factors on moult. Waders present a wide variety of inter- and intra-specific strategies for their primary moult, an energy-costly activity they must fit in with breeding and migration, the other main energy-demanding events in their life cycle. Here I present the moult strategies of waders in the context of their age, size, sex and annual variation in breeding success, seasonal food abundance, the latitude where they moult, the distance they migrate, the habitats they use, and the rainfall patterns and temperatures at their moulting grounds. I also discuss how moult is adjusted to these factors. This overview emphasises the flexibility of many waders' moult strategies as an adaptation to the unpredictable food supply provided by ephemeral inland wetlands and compares these strategies with those of populations that use predictable coastal habitats. Discovering the mechanisms that allow waders to adjust their genetically controlled and hormonally regulated moult to proximate factors is suggested as one of the challenges in further studies of moult.

INTRODUCTION

Many waders journey annually within the Eurasian–African migration system. Among them we distinguish short- and medium-distance migrants that travel between their breeding grounds in the northern Palaearctic and their non-breeding grounds further south in Europe and in northern Africa from the long-distance migrants that seasonally fly as far south as southern Africa. Two ecological groups are distinguished in the Scolopacidae (sandpipers, snipes and phalaropes) and the Charadriidae (plovers) families (Piersma *et al.* 1996, Piersma & Wiersma 1996): those that breed in the high Arctic tundra and migrate to saltwater coastal habitats, and those that breed in the taiga and migrate to freshwater habitats (Piersma 1997, 2003, 2007). Costal mudflats and estuaries all over the world, such as the vast tidal areas of the Wadden Sea, the Gulf of Guinea and the west coast of South Africa, provide hundreds of thousands of migrant waders with rich and predictable invertebrate food during their stopovers and at their non-breeding grounds (e.g. Boere 1976, Hockey *et al.* 1992, Piersma 1997, 2003, van de Kam *et al.* 2004, Zwarts *et al.* 1990). Inland freshwater wetlands are also widespread and provide waders with temporarily rich but unpredictable food resources that depend on irregular rainfall (e.g. Allan *et al.* 1997, Colwell 2010, Minias *et al.* 2010, Piersma 1997, 2003). Different life histories have been suggested for waders using coastal habitats and for those that exploit freshwater habitats, with consequential contrasting patterns in their migration distance, the timing of migratory flights, genetic variability and immunocompetence (Colwell 2010, Kraaijeveld 2008, Piersma 1997, 2003, 2007).

Moult patterns have been studied mostly in species that migrate to coastal habitats, such as Curlew Sandpiper *Calidris ferruginea* (Elliott *et al.* 1976, Underhill 2006), Dunlin *C. alpina* (e.g. Holmes 1966, 1971), Sanderling *C. alba* (Summers *et al.* 1987, Underhill 2003), Purple Sandpiper *C. maritima* (Morrison 1976, Summers *et al.* 2004), Red Knot *C. canutus* (Summers *et al.* 2010), Terek Sandpiper *Xenus cinereus* (Waltner & Sinclair 1981), Ruddy Turnstone *Arenaria interpres* (Summers *et al.* 1989) and Grey Plover *Pluvialis squatarola* (e.g. Pearson & Serra 2002, Serra 2001a, Serra & Underhill 2006, Serra *et al.* 1999, 2006). Fewer studies have been undertaken on the moult of waders at inland wetlands, probably because the birds are more dispersed over many sites when using this habitat and are more difficult to catch in high numbers than waders in coastal areas (Tree 1979). Moult at African inland habitats has been investigated for: Little Stint *C. minuta* (Dean 1977, Pearson 1984), Common Sandpiper *Actitis hypoleucos* (Pearson 1977, Tree 2008), Ruff *Philomachus pugnax* (Pearson 1981, Schmitt & Whitehouse 1976) and Common Greenshank *Tringa nebularia* (Tree 1979). Most reviews summarising patterns of wader moult in the Eurasian–African migration system have therefore had a "coastal bias", with few references to the moult of inland waders (Ginn & Melville 1983, Pearson 1974, Prater 1981, Prater *et al.* 1977, Stresemann & Stresemann 1966, Tree 1974, Underhill 2003). Moult patterns of Nearctic waders moving between North America and South America or Australasia have been summarised by Pyle (2008) and Howell (2010). These reviews emphasise migration distance and non-breeding latitude as the main factors that influence the strategy

these waders choose for their moult. Potential differences in the moult strategies of coastal and inland ecological groups of waders have not been explored. I chose Wood Sandpiper *Tringa glareola* as a model of wader species that exclusively use freshwater inland habitats during migration and moult (Remisiewicz *et al.* 2009, 2010a, b), and Curlew Sandpiper as a model for waders that use both coastal and inland habitats (Barshep *et al.* 2011).

This paper discusses recent developments in the application of the Underhill–Zucchini models (Underhill & Zucchini 1988, Underhill *et al.* 1990; hereafter referred to as "the UZ models") to investigations of primary moult and presents the progression of knowledge about moult patterns of Palaearctic migrant waders since the publication of previous reviews, referring to patterns observed throughout the world. I present an account of wader moult strategies in the context of the birds' age and size, seasonal food abundance, migration distance, latitude of moult, rainfall at the moulting grounds, sex and annual variation in breeding success. I emphasise how waders adjust their moult to the timing of their migrations and how their flexible moult strategies allow them to adapt to the different wetland habitats they use in the non-breeding season.

TERMINOLOGY

Wing moult begins with the primaries, so the date that primary moult starts is often used as a reference in describing the process (e.g. Barta *et al.* 2006, Ginn & Melville 1983, Prater *et al.* 1977). I also focus on patterns of primary moult and when I refer to moult without further description I mean the moult of the primary feathers. Here I ignore the rudimentary outermost 11th primary and discuss only the moult of the remaining 10, a convention used in the main reviews on moult (e.g. Ginn & Melville 1983, Howell 2010, Prater 1981, Prater *et al.* 1977, Pyle 2008, Underhill 2003). I use the same terminology for moult sequences as Ginn & Melville (1983), who derived it from the system proposed by Dwight (1900) and Cramp & Simmons (1983). Individual primaries are described according to the order in which they normally moult; therefore the innermost primary is P1 and the outermost is P10. When discussing a wader's age I refer to the year of its life, not to the calendar year often used by ringers. Estimates of the timing and duration of moult were all derived from the UZ models, unless stated otherwise.

TIMING AND LOCATION OF MOULT, MIGRATION AND BREEDING IN RELATION TO FOOD ABUNDANCE

Moult, especially of large flight feathers, is an energy-intensive activity (e.g. Hoye & Buttemer 2011, Lindström *et al.* 1993, Murphy & King 1992) that is critical for migrants because they need high-quality flight feathers to complete their journeys (e.g. Serra 2001b, Videler 2005). Birds rarely undertake migration with a large gap in the wing caused by dropped feathers, which increases the energetic costs of flight (Hedenström & Sunada 1999). Active wing moult also impedes the accumulation of energy reserves for migration because energy is diverted to feather growth; moreover flight with a wing-gap is energetically more expensive than with a complete wing (Lindström *et al.* 1993, Murphy & King 1992). Birds tend to avoid overlapping moult with breeding or migration, the other energy-expensive activities in their lives, unless food is so abundant that they can conduct two of these activities simultaneously. They adopt many different strategies to schedule these events separately (Ginn & Melville 1983, Newton 2009, Stresemann & Stresemann 1966, Zwarts *et al.* 1990).

The time when, and the location where, waders moult their primaries depend largely on the availability of food (e.g. Barta *et al.* 2006, Ginn & Melville 1983, Newton 2009, Prater 1981). Moult takes place at or close to the northern breeding grounds if the species' prey peaks there in the northern summer. But moult takes place on the southern non-breeding grounds if food abundance peaks only briefly in the north and is followed by a more extended period of abundance in the south (Barta *et al.* 2006, Prater 1981). Two main life strategies have been identified among migrant waders, based on the way they schedule their life events between locations that support seasonally abundant food: the B-strategy and the S-strategy (Alerstam & Högstedt 1982, Alerstam & Lindström 1990, Holmes 1966, 1971, Meltofte 1996). B-strategy species spend most of their year at the breeding grounds where they find rich food resources that they exploit as long as possible. These birds usually moult all or most of their primaries on the breeding grounds. They are usually short- and medium-distance migrants to non-breeding grounds in the northern hemisphere (Alerstam & Högstedt 1982, Alerstam & Lindström 1990, Holmes 1971, Meltofte 1996). Abundant food at the breeding grounds might even allow these waders to overlap breeding and moult, as the east Siberian and Alaskan populations of Dunlin *Calidris alpina* do (Holmes 1971, Holmgren *et al.* 1993, 2001). Other waders might migrate first to sites rich in food, moult there and only then leave for their final non-breeding grounds, as Wilson's Phalarope *Phalaropus tricolor* do in North America (Jehl 1987). Moult might overlap with migration when stopover sites provide abundant food during post-breeding migration, as in Ruff migrating through the Netherlands (Koopman 1985). S-strategy species find abundant food at their southern "non-breeding survival grounds", where they usually spend more time than on their breeding grounds. These species are mostly long-distance migrants and usually delay moult until they reach productive non-breeding grounds in the southern hemisphere (Alerstam & Högstedt 1982, Alerstam & Lindström 1990). Prominent examples are the waders that breed in the Arctic or Eurasia's boreal zone and migrate to southern Africa, where they spend about six months of each year, such as Sanderling (Summers *et al.* 1987), Ruddy Turnstone (Summers *et al.* 1989), Curlew Sandpiper (Barshep 2011, Elliott *et al.* 1976) and Wood Sandpiper (Remisiewicz *et al.* 2009, 2010a,b).

GENERAL PATTERNS OF PRIMARY MOULT IN DIFFERENT AGE GROUPS

Adults

Adult migrant waders undergo a complete post-breeding moult in which they usually change their body feathers from breeding to non-breeding plumage and replace their flight feathers (Ginn & Melville 1983, Prater 1981, Prater *et al.* 1977). Most waders replace all of their primaries in this moult (Fig. 1) (Ginn & Melville 1983, Prater 1981, Prater *et al.* 1977). Primary moult usually starts from the innermost primary P1 and continues outwards to P10 (Fig. 2) (Ginn & Melville 1983, Prater 1981, Prater *et al.* 1977). The sequence usually continues uninterrupted in most waders. For those birds that do interrupt this moult, Prater *et al.* (1977) suggest using the term "suspension" for an interruption of moult of up to a few months that then resumes and is completed at the usual time for the population. Large waders, e.g. Eurasian Oystercatcher *Haematopus ostralegus*, might interrupt

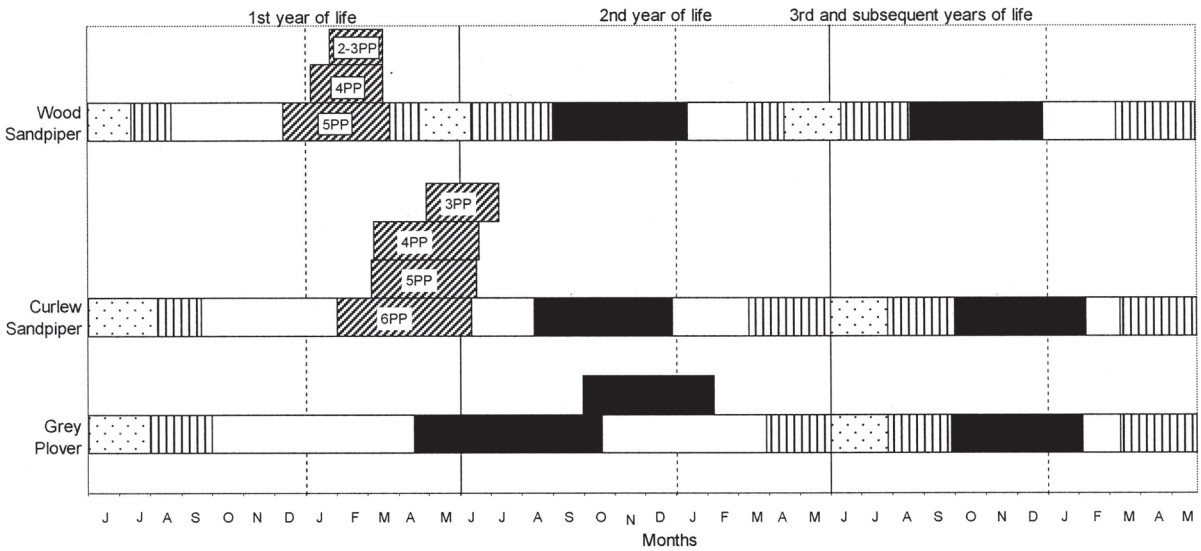

Fig. 1. Primary moult schedules and the other main events in the first three, and subsequent, years of Wood Sandpipers, Curlew Sandpipers and Grey Plovers that spend their non-breeding seasons in South Africa. Dotted bars = breeding, vertical hatched bars = migration, white bars = periods of "rest" when energy-costly events are reduced, diagonal hatched bars = partial moult with labels that denote how many outer primaries different groups replace, black bars = complete moult of all primaries. Some Grey Plovers undertake two cycles of complete moult on the non-breeding grounds (see text). Dashed vertical lines = end of calendar year, solid vertical lines = end of birds' year of life. Data for Grey Plovers after Serra *et al.* 1999, for Curlew Sandpipers after Barshep 2011, for Wood Sandpipers after Remisiewicz *et al.* 2009, 2010a, b.

primary moult for longer, up to eight or nine months, and might not even complete the moult sequence. This pattern is defined as "arrested" moult (Prater 1981, Prater *et al.* 1977). Small waders, such as Little Stint, might re-moult a few outer or inner primaries shortly before leaving the non-breeding grounds (Pearson 1974, 1984).

First-year birds

Between July and September, a few months after they hatch, Eurasian migrant waders undergo a partial post-juvenile moult into a body plumage similar to that of non-breeding adults. But they do not replace their flight feathers at this time and use the juvenile generation of primaries (those they grew as chicks) for at least their first migration (Ginn & Melville 1983, Prater 1981). Later in the non-breeding season, first-year birds, especially in long-distance migrant populations, might undertake a partial moult of their primaries (Fig. 1) (Pearson 1974, Prater 1981, Tree 1974). Small species, such as Little Stint, might replace all 10 primaries, but larger waders tend to replace only a few outer primaries, usually beginning from one of the middle primaries such as P6 or P7 and continuing outwards to P10 (Pearson 1974, 1977, Prater 1981, Prater *et al.* 1977, Schmitt & Whitehouse 1976, Tree 1974, 1979). Some populations might show more individually varied partial moult, including the replacement of a few inner or middle primaries, as in Red Knots moulting in South Africa (Summers *et al*. 2010). The mechanisms that determine at which primary this moult will start remain unknown in waders (Pearson 1974, Prater 1981). In the European Starling *Sturnus vulgaris* testosterone levels affect the number of outer primaries replaced in the pre-breeding moult (Dawson 1994).

Waders that usually migrate back to the breeding grounds in their first year undertake a partial primary moult between October and May, before they leave the non-breeding grounds, as in Wood Sandpiper (Fig. 1) (Remisiewicz *et al.* 2010a). Waders that remain at the non-breeding grounds until they are two years old, such as Curlew Sandpiper, Red Knot and Ruddy Turnstone, undergo this partial primary moult between April and August, at the end of their first year and the beginning of their second year of life (Fig. 1), or might forgo it (e.g. Barshep 2011, Elliott *et al.* 1976, Prater 1981, Summers *et al.* 1989, 2010). Many populations of species that migrate short or medium distances do not undertake this partial moult.

Second-year birds

Most second-year waders of species that remain at the non-breeding grounds until they are two years old undertake their first complete moult of all primaries just before they depart to the breeding grounds (Prater 1981). This moult resembles the post-breeding moult of adults, except that second-year birds usually start moulting earlier, before the adults arrive from the breeding grounds, and the moult proceeds more slowly (Fig. 1) (Pearson 1974, Prater 1981, Tree 1974). First-year Grey Plovers overstaying in South Africa do not undertake a partial moult, but replace all 10 primaries in their first cycle of primary moult, which begins on average in April and extends over 194 days, and so is completed when the birds are in their second year of life (Fig. 1). Adult Grey Plovers replace their primaries over 131 days starting on average in September (Fig. 1) (Serra *et al.* 1999). About 35% of second-year Grey Plovers undertake a second complete primary moult before their first departure from South Africa. This moult has a similar timing to that of the adults (Fig. 1) (Serra *et al.* 1999). In Curlew Sandpiper and Ruddy Turnstone in South Africa and Australia a partial moult of the primaries is followed by the complete replacement of all the primaries (Fig. 1), and this new sequence might begin before the partial moult is finished (Minton *et al.* 2006, Summers *et al.* 1989, Underhill 2006).

Waders that migrate to the breeding grounds in the first year of life do not experience this overlap because the two moult sequences are divided by migration, as in Wood Sandpiper (Remisiewicz *et al.* 2010b). In this species the first complete primary moult takes place after the birds' second arrival on the southern non-breeding grounds (Fig. 1). But a small proportion of Wood Sandpipers spend their first boreal summer in the south and these birds undertake this first

Fig. 2. Adult Wood Sandpiper *Tringla glareola* with six fully grown new inner primaries (P1–P6), P7 actively growing and three old primaries (P8–P10), and with a fully grown new outer secondary (S1) and actively growing S2; Turov, Belarus, 7 Aug 2002. (Photo: Pavel Pinchuk.)

complete primary moult at the end of their stay. Second-year Wood Sandpipers grow all 10 primaries at the same rate as the adults, but start two weeks later (Fig. 1) (Remisiewicz *et al.* 2010b). This delay could be caused by the slightly later arrival of the second-year birds, which are less experienced than the adults and probably migrate more slowly, as they do during their first southward migration (Remisiewicz *et al.* 2010b, Wichmann *et al.* 2004)

METHODS OF ANALYSING PRIMARY MOULT

The standard method of describing the state of a bird's primary moult involves recording the stage of development of each feather as a moult formula, a string of 10 digits, one for each primary, where a score of 0 indicates an old feather, 5 a fully-grown new feather and 1–4 describes intermediate stages of growth (Ashmole 1962, Ginn & Melville 1983). Many studies of primary moult in waders present its temporal progression as the sum of the scores for the 10 primaries, ranging from 0 (all old primaries, moult not started) to 50 (all new primaries, moult completed); values between 0 and 50 indicate moult in progress. The distribution of primary moult scores of a population is not linear over the moult season, which restricts analysis by linear regression (Newton 2009, Summers *et al.* 1983). Despite this shortcoming, studies have used regression analysis (e.g. Boere 1976, Dean 1977, Elliott *et al.* 1976, Pienkowski *et al.* 1976), or the fit a moult curve by eye to the medians of primary moult score plotted against date (e.g. Appleton & Minton 1978, Morrison 1976, Pearson 1984, Schmitt & Whitehouse 1976). An index of the proportion of feather mass grown (PFMG) was suggested as a means to transform the distribution of primary moult scores to a linear form (Summers 1980, Summers *et al.* 1983), using the moult score and relative mass of each primary (Underhill & Joubert 1995, Underhill & Summers 1993). This provides a moult index that has values from 0 (all 10 primaries are old, moult not yet started) to 1 (the whole of the mass of all 10 primaries is fully grown) (Underhill & Summers 1993). Based on the assumption that primary feather tissue is deposited at a uniform rate throughout the moult period, this transformation provides the moult index used in the models developed by Underhill & Zucchini (1988) and Underhill *et al.* (1990). These models estimate a population's moult starting date, the standard deviation of the starting date and the duration of moult for the primaries or any other tract of feathers. An extension to the models has also been developed that allows users to estimate the moult starting date for each feather separately and to compare different groups of moulting birds (Underhill *et al.* 2006).

The assumption of a constant rate of primary growth has been shown to hold true for many populations of moulting waders analysed using these models, including adult Ruddy Turnstones and Red Knots moulting in Scotland and South Africa (Summers *et al.* 1989, 2004), Purple Sandpipers moulting in Iceland, Norway and Great Britain (Summers *et al.* 2004), Grey Plovers and Wood Sandpipers moulting in South Africa (Serra *et al.* 1999, Remisiewicz *et al.* 2009, respectively), and Curlew Sandpipers moulting in South Africa and NW Australia (Barshep 2011, Barshep *et al.* 2011). But it did not prove true for Redshanks moulting in Scotland (Summers *et al.* 1983, Underhill *et al.* 1990), Grey Plovers moulting in Great Britain (Serra 2001a, Serra *et al.* 2006), and Curlew Sandpipers moulting in SE Australia, Kenya and India (Barshep 2011). Summers *et al.* (1983) and Underhill *et al.* (1990) suggested a power transformation of the PFMG indices to a linear form in such cases, allowing them to be applied in the moult models (Underhill & Zucchini 1988, Underhill *et al.* 1990).

A linear rate of feather growth has been shown for separate primaries in waders and in passerines (e.g. Dawson 2003, Dawson & Newton 2004, Newton 1967, Sach 1968, Serra & Underhill 2006). Therefore the UZ moult models can be applied to estimate the timing of the moult of each primary and thus the daily mass production rate for each feather (Serra 2001a, Serra & Underhill 2006, Serra *et al.* 2006, Underhill 2003). Having these daily rates for each primary, and con-

sidering the overlapping growth of neighbouring primaries, we can model the rate at which primary feather material is deposited over the season (Remisiewicz *et al.* 2009).

Individual variation in the number of primaries that first-year waders replace had impeded analyses of the timing of their partial moult. But the recent application of the UZ models to estimate moult timing of single primaries has enabled users to analyse the course of partial moult (Remisiewicz *et al.* 2010a). The course of the first complete moult in second-year waders can also be analysed by the UZ moult models when all primaries from the preceding moult sequences are treated as old feathers and only the progress of the new moult cycle is analysed (Remisiewicz *et al.* 2010b). Analysing the effects of different external factors on moult – such as year, sex, predation pressure, temperature and rainfall – has been enabled by including covariates in the moult models, using the package Moult (Barshep 2011, Barshep *et al.* 2011, Erni *et al.* in press). These methods can be extended to analyse the course of moult for all the main feather tracts if their moult scores and the relative mass of each feather are available (Salewski *et al.* 2004). These moult models have already been applied in more than 40 studies of waders and other taxa, and have also been used to estimate the timing of events in the life cycle of organisms as far apart as birds and bryophytes (van der Valk 2011).

The software developed by Walter Zucchini (Underhill & Zucchini 1988) and Anabela Brandão (Brandão 1998, Underhill *et al.* 2006) to apply the UZ models to moult data had a limited number of trained users, which hampered the wide use of this method. Birgit Erni helped to overcome this difficulty by developing the application Moult based on the UZ models (Erni *et al.* in press). The package works under R, a freeware programming and software environment for statistical analysis, which allows skilled users to supplement the package by coding any procedures they might require for their analyses (R Development Core Team 2009). The Moult package is available at: *http://cran.r-project.org/package=moult*.

Apart from the three main parameters that describe the timing of moult (start date, its standard deviation, and moult duration), other parameters can be valuable in understanding primary moult strategies. These include the number of replaced primaries, the number of primaries growing simultaneously and the intervals at which subsequent primaries are dropped (e.g. Prater 1981, Serra 2001a, Serra & Underhill 2006, Underhill 2003, Underhill & Zucchini 1988, Underhill *et al.* 1990). The size of the gap in the wing caused by shed and growing feathers has been described by a "raggedness score" which is derived from the moult scores (Bensch & Grahn 1993, Haukioja 1971). The raggedness score tends to be higher in the earlier stages of moult, when waders grow more primaries simultaneously, and to decrease non-linearly when larger primaries are grown (Holmgren *et al.* 1993, 2001, Serra *et al.* 2006). However, the raggedness score can be refined by assessing the wing gap as the proportion of feather mass missing (PFMM) in relation to the mass of all 10 primaries (Ward *et al.* in press). This approach is compatible with the concept of PFMG used in the UZ models. A few studies have assessed the size of the wing gap in waders. Dunlins moulting rapidly in Siberia that grow up to five inner primaries simultaneously have raggedness scores of 3 to 20 (Holmgren *et al.* 1993, 2001), similar to Dunlins moulting on the non-breeding grounds in Italy (Serra *et al.* 1998). This amounts to 7–26% of the mass of all primaries when recalculated as PFMM. But Wood Sandpipers moulting in southern Africa show a wing gap that averages 8–11% of the mass of all primaries, small enough that they probably retain sufficient flight ability for local movements between the ephemeral wetlands they use (Remisiewicz *et al.* 2009, 2010a, b).

FACTORS AFFECTING MOULT PATTERNS IN WADERS OF DIFFERENT AGE GROUPS

Wing length and the patterns and duration of moult

Prater (1981) suggests that at similar geographical latitudes wader species with longer wings extend their primary moult over longer periods. He relates this to the greater mass of flight feathers that longer-winged birds must produce compared with shorter-winged species. This tendency holds true for populations that breed and moult within the northern hemisphere, but breaks down for those that cross the equator, probably because of the variability of the climate and the food supply (Prater 1981). Remisiewicz *et al.* (2009) show that the relationship between wing length and moult duration holds true among waders that moult in the southern hemisphere, specifically in southern Africa, when different habitat conditions are accounted for. To partly correct for this relationship I used the ratio of a population's estimated moult duration to wing length in comparing the timing of the moult of different-sized waders at northern and southern latitudes (Fig. 3).

In first-year waders, the shorter-winged the species or the population and the further they migrate, the more primaries they tend to replace, at least within the genera *Calidris* and *Tringa* (Prater 1981). Among small waders, such as Little Stint, Common Sandpiper and Ringed Plover, most birds ending their migration in Kenya or southern Africa replace all 10 primaries in the first-year moult (Middlemiss 1961, Pearson 1974, 1977, 1984, Tree 1974). Some individuals undertake an additional moult of these feathers before they depart for the breeding grounds. This complete moult might overlap the unfinished sequence of the earlier partial moult (Pearson 1974, Prater 1981). Mid-size and large waders replace fewer primaries during partial moult. In Kenya and in southern Africa, Curlew Sandpipers usually replace four to six outer primaries, but the larger Common Greenshanks and Ruffs usually replace only one or two outer primaries (Barshep 2011, Elliott *et al.* 1976, Pearson 1974, Prater 1981, Schmitt & Whitehouse 1976, Tree 1979).

Geographical latitude and moult strategies

Three main moult strategies have been identified that appear to be related to the latitude and location at which migrant waders moult: in the northern hemisphere at the breeding grounds, in the northern hemisphere at the non-breeding grounds and in the southern hemisphere at the non-breeding grounds (Holmes 1966, 1971, Howell 2010, Prater 1981, Pyle 2008, Underhill 2003). Howell (2010) presents a classification of American sandpipers based on these moult strategies.

Populations of Purple Sandpiper *Calidris maritima* that breed in Iceland and moult there just after they raise their chicks exemplify Palearctic waders that moult at their northern hemisphere breeding grounds (Fig. 3) (Morrison 1976, Summers *et al.* 2004). Other populations of the same species begin primary moult on the breeding grounds, suspend it for migration and complete the process at the final northern hemisphere non-breeding grounds, such as the Purple Sandpipers from Russia that complete their moult in N Norway (Fig. 3) (Summers *et al.* 2004). Long-distance migrants that spend their non-breeding season in the southern hemisphere usually moult there to take advantage of warm weather and

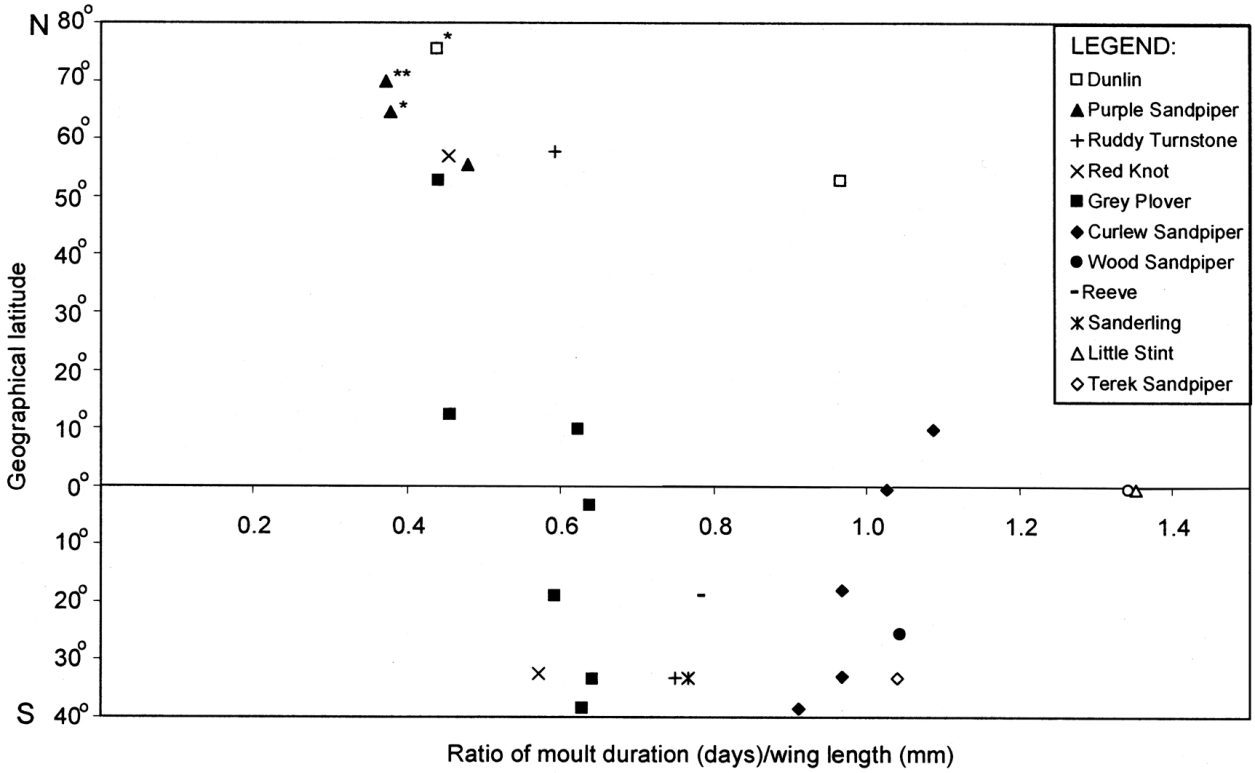

Fig. 3. Ratio of the duration of complete primary moult in adult waders to their wing length, at northern and southern latitudes. * = moult at the breeding grounds, ** = moult begun at the breeding grounds completed at the non-breeding grounds, all the remaining populations moult at the non-breeding grounds. Open symbols = moult duration estimated by non-UZ method. See the text for sources that provide the moult durations and wing lengths used in this figure.

abundant food in the austral summer. Examples include the populations of Red Knot, Ruddy Turnstone, Sanderling and Wood Sandpiper that migrate to southern Africa (Fig. 2) (Remisiewicz *et al.* 2009, Summers *et al.* 1987, 1989, 2010).

Populations that moult in the northern hemisphere undergo earlier, shorter and more synchronous moult than their conspecifics in the southern hemisphere (Fig. 3), because the approaching winter in the north limits the time these waders have available for moult (Prater 1981, Underhill 2003). In the Arctic, the invertebrate food supply available to waders peaks in June or July (van de Kam *et al.* 2004); but in European wetlands the invertebrate food supply is abundant between May and September, and then diminishes as the weather deteriorates (van de Kam *et al.* 2004, Prater 1981). These conditions compel a rapid moult in the waders that exploit these resources (Fig. 3). For species that moult in the southern hemisphere, their time of arrival on the non-breeding grounds, between late July and October, and their departure from them between mid-February and May, set limits to the beginning and the duration of moult (Fig. 3) (e.g. Ginn & Melville 1983, Harrison *et al.* 1997, Pearson 1974, Tree 1974). This leaves these long-distance migrants up to six months to complete their moult, so it can take place more slowly, later and less synchronously than in conspecifics that winter in the north (Prater 1981).

Different populations of a wide-ranging species might schedule their moult between the breeding and the non-breeding grounds differently. Dunlins that breed in N Alaska around 71°N start primary moult during egg laying and replace all their flight feathers, including secondaries and tertials, over about 70 days. But Dunlins that breed in W Alaska around 61°N, where summer is longer, begin to moult their flight feathers when their chicks have hatched and complete the process in about 96 days (non-UZ estimates; Holmes 1971). Dunlin populations breeding in Siberia east of the Yamal Peninsula moult their primaries in about 48–50 days (non-UZ estimates), starting during incubation (Fig. 3). Populations breeding west of the Yamal Peninsula start their moult on the breeding grounds, but leave before it is completed. Some suspend moult, others continue their moult during migration. Other populations breeding in Scandinavia and in NW Russia moult all their primaries on the non-breeding grounds in Britain in *c.*100 days (non-UZ estimate, Fig. 3) (Gromadzka 1986, Holmgren *et al.* 1993, 2001, Johnson & Minton 1980, Kania 1990).

The Grey Plover shows a transition between northern and southern hemisphere strategies (Fig. 3). Some populations begin their moult at their breeding grounds in Siberia, suspend, and then resume at stopover sites or at their final non-breeding grounds in Europe (Gromadzka & Serra 1998, Krupa & Krupa 2002). Most Siberian populations of Grey Plover that moult entirely in Great Britain or Italy show the northern hemisphere strategy, on average replacing their primaries over 90–93 days between August and November (Fig. 3) (Serra & Rusticali 1998, Serra *et al.* 2006). The constraint that winter imposes on moult was demonstrated by the 38% of adult Grey Plovers that had not completed primary moult in Great Britain by November; these birds suspended moult during December–February, and then resumed, completing moult in March–April (Serra *et al.* 2006). Grey Plover populations from the same breeding range that migrate long-distances to India, Kenya, South Africa or Australia, use the southern hemisphere strategy. They take 127–131 days to moult their primaries and on average finish the process between 5 January and 8 February (Figs 1 & 3) (Balachandran *et al.* 2000, Minton & Serra 2001, Pearson & Serra 2002, Serra 2001a). Adult Wood Sandpipers that moult in southern Africa use the typical southern hemisphere strategy: they begin dropping

their primaries only after they arrive on the non-breeding grounds and on average extend their primary moult to 131 days, completing it in the last 10 days of December (Figs 1 & 3) (Remisiewicz *et al.* 2009).

Migration distance and moult

Effect of migration distance on moult timing in adults

For adult waders that moult entirely on their non-breeding grounds, the further they fly, the longer their migration takes, and the later primary moult starts. At most sites in the southern hemisphere, adults are reported to start moult within about two weeks of arrival (e.g. Barshep 2011, Minton *et al.* 2006, Pearson 1974, 1984, Pearson & Serra 2002, Remisiewicz *et al.* 2009, Serra 2001a, Serra *et al.* 1999); for example, adult Wood Sandpipers arrive in southern Africa from the end of July and generally begin their primary moult in the third week of August (Remisiewicz *et al.* 2009).

Differences in timing of moult in relation to migration distance are most evident when different populations of the same species are compared (Fig. 3). In Scotland, Red Knots and Ruddy Turnstones begin moulting their primaries at the end of July, and average primary moult duration is 77 and 94 days respectively. But the populations of the same species that migrate to the coasts of South Africa do not begin their moult until they land there in September–October. There, average primary moult duration of Red Knots is 95 days and Ruddy Turnstones 119 days (Summers *et al.* 1989, 2010, Underhill 2003).

Different populations of Grey Plovers illustrate how the mean date at which moult starts is delayed in relation to migration distance. In Great Britain and Italy, moult begins around 18–19 Aug (Serra & Rusticali 1998, 2006), but in southern locations ranging from tropical India to SE Australia average start date becomes progressively later (ranging from 1 Sep to 5 Oct) as migration distance (differing by up to 6,000 km) increases. At all these southern locations estimated moult duration is similar, ranging from 127 to 131 days, despite differing migration distance (Fig. 3) (Balachandran *et al.* 2000, Minton & Serra 2001, Pearson & Serra 2002, Serra 2001a, Serra *et al.* 1999). This means that the different populations of Grey Plovers have from about two weeks to two months for premigratory fattening between completing primary moult and departure for the breeding grounds. Departure dates range from February to April, depending on the latitude at which they moult (Fig. 1) (Serra 2001a).

On average adult Curlew Sandpipers begin their moult in South Africa and in NE Australia in the second half of September (Fig. 1). But those moulting farther south in SE Australia (and about 3,000 km further from the breeding grounds) start their moult 22–38 days later, moult faster and complete the process in eight fewer days on average than the birds at the two locations further north (Fig. 3) (Barshep 2011, Barshep *et al.* 2011).

Effect of migration distance on the primary moult of first-year waders

First-year waders in populations that migrate to the southern tropics and sub-tropics are more likely to undertake a partial moult of their primaries at their non-breeding grounds than those that remain in the northern hemisphere (Pearson 1974, Pienkowski *et al.* 1976, Prater 1981, Stresemann & Stresemann 1966, Tree 1974). Partial moult of the outer primaries occurs more frequently and more extensively among long-distance migrants. The hypotheses put forward to explain this are that the juvenile feathers are of poor quality and abrade faster under the harsh sun in southern tropical latitudes than in the north (Ginn & Melville 1983, Pearson 1974, Prater 1981). For example, first-year Common Greenshanks in the Dutch Wadden Sea or in Kenya occasionally moult one or two outer primaries (Boere 1976, Pearson 1974). In southern Africa 16% of first-year Common Greenshanks replace one to five outer primaries, most often (54% of moulters) three, in their partial moult (Tree 1979, A.J. Tree unpubl. data). In Kenya 40–50% of first-year Wood Sandpipers show partial moult, but in southern Africa 98% do (Pearson 1974, Remisiewicz *et al.* 2010a). This suggests that the hypothesis that feathers deteriorate faster under a harsh sun does not explain the partial moult very well, because in the southern African sub-tropics the sun is weaker than in tropical Kenya, yet the proportion of first-year waders that undertake this moult is higher.

The tendency to replace outer primaries might be population-specific and be related to the birds' migration distance. Outer primaries wear faster than inner ones but are crucial for efficient flight (Videler 2005). Therefore replacing them before a migratory flight might have an adaptive value in a population migrating over a long distance. But in a population that migrates over a shorter distance, saving the energy needed to replace these feathers might be more advantageous. The individuals that do not undertake this partial moult are probably able to complete two more migrations, to and from the breeding grounds, on their juvenile primaries. Wood Sandpipers and Ruffs observed in Kenya with extremely worn primaries tend to be in poor condition (Pearson 1974). These birds, on their post-breeding migration in the second year of life, might be compelled to replace their worn primaries before they reach the non-breeding grounds because of the additional energy cost of flight with damaged primaries (Videler 2005). This probably explains the widespread but infrequent observations of Wood Sandpipers in primary moult in Europe during their southward migration (Fig. 2) (Pinchuk *et al.* 2008).

The timing of the partial moult is related to a species' propensity to return to its breeding grounds in the first year of life. Small species, such as Little Stint and Common Sandpiper, mostly breed in their first year of life, as do some mid-size waders, such as Wood Sandpiper and Marsh Sandpiper. But other mid-sized waders, including Sanderling and Curlew Sandpiper, and most larger waders, such as Ruddy Turnstone, Grey Plover, Eurasian Curlew and Common Whimbrel, usually remain in their southern non-breeding grounds for the austral winter, and do not migrate north until they are two years old (Ginn & Melville 1983, Hockey *et al.* 1998, Pearson 1974, 1977, Prater 1981, Summers *et al.* 1995, Underhill 2006). If waders leave the non-breeding grounds in their first year of life, usually between February and May, any partial moult of primaries takes place before their departure, and the fewer primaries they replace the later they start the process (Fig. 1) (Ginn & Melville 1983, Prater 1981, Prater *et al.* 1977). First-year Wood Sandpipers in southern Africa replace 2–6 outer primaries between December and late March (Fig. 1) (Remisiewicz *et al.* 2010a). There is large inter-specific variation in this partial moult, but little is known about the factors that influence the strategy that an individual chooses (Ginn & Melville 1983, Pearson 1974, Prater 1981).

Timing of departure from non-breeding grounds sets a constraint on moult

Long-distance migrants at non-breeding sites must carefully schedule their moult and the energy-intensive period of pre-migratory fattening before they depart for the breeding grounds (e.g. Ginn & Melville 1983, Newton 2009, Prater 1981, Stresemann & Stresemann 1966). In Africa waders usually begin their pre-migratory fattening four weeks (range: 2–6 weeks) before departing between mid-February and May (e.g. Serra *et al.* 1999, Tree 1979, Zwarts *et al.* 1990). In these areas, adult waders usually finish primary moult between December and February (e.g. Pearson 1984, Pearson & Serra 2002, Remisiewicz *et al.* 2009, Serra *et al.* 1999, Summers *et al.* 1989, Underhill 2003). This leaves them several weeks between the end of primary moult and the start of pre-migratory fattening during which period they might finish moulting any remaining flight feathers and body feathers. Therefore the departure time is probably not a severe constraint to the moult of these adults (e.g. Ginn & Melville 1983, Pearson 1984, Remisiewicz *et al.* 2009, Serra 2001a).

However for first-year birds that migrate north, the date of departure from the non-breeding grounds sets a limit to partial moult. Curlew Sandpipers, which replace 2–6 outer primaries but stay in the south for the benign austral winter, undertake a partial moult starting in April and finishing around the end of June (Fig. 1) (Barshep 2011, Elliott *et al.* 1976, Minton *et al.* 2006, Underhill 2006). Similar-sized Wood Sandpipers, which depart for the breeding grounds in March–April of their first year, replace a similar number of primaries in southern Africa but do so between December and March, 2–5 months earlier than the Curlew Sandpipers (Fig. 1) (Remisiewicz *et al.* 2010a).

That departure date constrains partial moult in first-year birds that migrate north can be demonstrated among first-year Wood Sandpipers that apply different strategies to their partial moult in southern Africa. Regardless of the number of primaries they replace, whether they begin their moult in December or in January, and whether they choose a slow, intermediate or rapid moult, almost all finish in the last 10 days of March (Fig. 1) (Remisiewicz *et al.* 2010a). Northward migration of Wood Sandpipers through Europe is rapid and is concentrated over a short period (Remisiewicz *et al.* 2007), which could be an effect of this synchronised end to moult by the first-year birds, timed to allow them to depart with the adults (Fig. 1) (Remisiewicz *et al.* 2010a). First-year Wood Sandpipers finish moulting just before they depart. The process overlaps with, and probably impedes, their pre-migratory fattening, in contrast with the adults that have a few months between the end of primary moult and departure (Fig. 1) (Remisiewicz *et al.* 2009, 2010a). Some first-year birds accumulate lower fat reserves for migration than adults (M. Remisiewicz & A.J. Tree, unpubl. data). This might explain why first-year males arrive at stopover sites near the breeding grounds a few days after the adult males (Remisiewicz & Wennerberg 2006). The delay is probably caused by the younger birds' greater need to their replenish energy reserves en route than adults. Female Wood Sandpipers of both age classes occur at these stopover sites at about the same time, and later than males that arrive first at the breeding grounds to establish territories (Remisiewicz & Wennerberg 2006). This suggests that the sexes have different strategies for their return migration to the breeding grounds, and probably for the preceding moult of flight and body feathers (Meissner *et al.* in press), as demonstrated in Bar-tailed Godwits (Piersma & Jukema 1993).

Annual differences in the timing of primary moult in waders

Annual differences in the timing of moult have been observed among waders at stopover sites during southward migration and on their non-breeding grounds (e.g. Barshep *et al.* 2011, Boere 1976, Holmgren *et al.* 1993). These might be related to annual variation in breeding success, as demonstrated in Curlew Sandpiper (Barshep *et al.* 2011). In years of poor breeding success in Siberia, failed breeders of both sexes leave the breeding grounds earlier (Schekkerman *et al.* 1998, Summers *et al.* 1998). Thus they arrive on their non-breeding grounds in Australia earlier and on average begin to moult 9–10 days earlier than in good breeding years (Barshep *et al.* 2011). Year-to-year differences in the timing of moult might also be affected by variations in the conditions that waders encounter on their moulting grounds. This is suggested by the varying proportion of Little Stints caught with suspended moult in different years at variable ephemeral wetlands in the interior of southern Africa (M. Remisiewicz & A. J. Tree unpubl. data). This topic has not yet been well explored because of methodical difficulties, but the Moult package opens new opportunities to investigate it (Barshep *et al.* 2011, Erni *et al.* in press).

Effect of sexual roles on the timing of primary moult in waders

In some species male and female adult waders start primary moult at different times, which is attributed to their different roles in parental care (Boere 1976, Ginn & Melville 1983, Stresemann & Stresemann 1966). The sex that provides parental care for less time usually leaves the breeding grounds as soon as the eggs are laid or the chicks hatch. These adults arrive at the non-breeding grounds and begin to moult earlier than their mates that stayed to raise the chicks. In Purple Sandpipers breeding in Iceland, females usually desert the brood at hatching and start to moult several days ahead of their mates (Morrison 1976, Summers *et al.* 2004). Barshep *et al.* (2011) showed that annual differences in the onset of primary moult in Curlew Sandpipers at their non-breeding grounds are sex-dependent. Females incubate the eggs and rear the chicks in Curlew Sandpipers that breed in Siberia (Holmes & Pitelka 1964). In years of low breeding success, males begin to moult in Australia around five days earlier than in good breeding years. But females begin their primary moult about 11 days earlier in poor years than in good years, when most stay in Siberia to raise the chicks (Barshep *et al.* 2011). In good breeding years, females begin their moult in Australia about nine days later than males (Barshep *et al.* 2011). Studies showing the relation between sex and the timing of primary moult are lacking for monomorphic waders. A combination of molecular sexing techniques (e.g. Remisiewicz & Wennerberg 2006, Wennerberg *et al.* 1999; overview in Dos Remedios *et al.* 2010) and the recently developed statistical tools for analysing moult now allow researchers to link the mating systems of migrant waders and their parental care strategy with variation in primary moult patterns or those of other feather tracts (Meissner *et al.* in press).

Coastal and inland habitats affect moult patterns in waders differently

Different life histories have been suggested for long-distance migrant waders that spend the non-breeding season at inland

freshwater sites and those that spend it at coastal habitats (Colwell 2010, Kraaijeveld 2008, Piersma 1997, 2003). Coastal habitats, mostly intertidal mudflats with a patchy distribution worldwide, provide waders with a rich and highly predictable food supply of marine invertebrates (e.g. Boere 1976, Colwell 2010, Hockey *et al.* 1992, Piersma 1997, 2003, 2007, van de Kam *et al.* 2004, Zwarts *et al.* 1990). In contrast, inland wetlands are widespread in all continents but often occur irregularly. Ephemeral inland wetlands provide a rich, but often temporary and unpredictable, food supply that depends mainly on varying rainfall, especially in arid areas (Allan *et al.* 1997, Kraaijeveld 2008, Piersma 1997, 2003, Roshier *et al.* 2002, van de Kam *et al.* 2004). The use of spatially and temporarily variable resources at freshwater wetlands selects waders for more flexible movement patterns than at predictable coastal habitats (Colwell 2010, Kraaijeveld 2008, Piersma 1997, 2003, Roshier *et al.* 2002, Skagen *et al.* 2008, van de Kam *et al.* 2004). The patterns of flight feather moult, which requires a rich food supply and is a part of a population's migration strategy, also tend to differ between species using inland and coastal habitats. These patterns are particularly flexible among waders that use freshwater inland wetlands (Remisiewicz *et al.* 2009, 2010a). Adults of several long-distance migrant waders at inland wetlands in southern Africa take on average 26 days longer to moult than similar-sized species using coastal habitats (Remisiewicz *et al.* 2009). The Wood Sandpiper, which uses inland habitats exclusively outside the breeding period, extends its moult over one of the longest periods among the eight migrant wader species that moult in southern Africa between 15°S and 35°S with which it was compared (Fig. 3). This extended and consequentially slow moult by waders at inland habitats is probably an adaptation to their use of ephemeral wetlands in the interior of Africa (Remisiewicz *et al.* 2009). Prolonged moult reduces daily energy costs, which is beneficial for species that use unpredictable resources during this process, as shown in the White-plumed Honeyeater *Lichenostomus penicillatus* in an arid zone of Australia (Hoye & Buttemer 2011).

First-year Wood Sandpipers in southern Africa show a range of strategies for their first-year partial moult: a slow moult of 5–6 outer primaries, beginning on average during 8–16 Dec (29% of first-year birds), an intermediate-rate moult of four primaries starting on average on 6 Jan (63%), or a fast moult of 2–3 primaries starting on 24 Jan (7%) (Fig. 1) (Remisiewicz *et al.* 2010a). The individual's choice of moult strategy is related to its body mass and date. Heavier birds are more likely to start moulting than lighter birds, but this is more pronounced in Nov–Jan, early in the season they spend in the south. In later months almost all remaining first-year Wood Sandpipers start to moult regardless of their body mass (Remisiewicz *et al.* 2010a). Whatever their strategy, most of these birds complete their moult in the second half of March, when most adults and first-years depart from southern Africa (Fig. 1) (Remisiewicz *et al.* 2010a). About 6% of first-year birds caught in March–April are still moulting or have skipped the partial moult and these individuals probably remain in their southern Africa non-breeding grounds for the austral winter (Remisiewicz *et al.* 2010a, Underhill 1997). After good summer rains, southern Africa's transitory inland wetlands support swarms of invertebrates, which attract an abundance of birds. But these resources might not last long and the wetlands might soon dry out (Allan *et al.* 1997). Flexibility in the choice of a suitable moult strategy might allow first-year Wood Sandpipers to adjust their energy-intensive moult to the variable conditions provided by these inland wetlands (Remisiewicz *et al.* 2010a). Adult Dunlins in Great Britain also show flexible moult strategies: birds that start moult in mid-August moult more quickly than those that start in July, so that all have finished by October (non-UZ estimates; Johnson & Minton 1980).

Erratic rains in southern latitudes favour adaptability in moult patterns

Erratic rains in the southern hemisphere influence the timing of wader moult because water levels at inland wetlands determine the availability of food (Barshep 2011, Lipshutz *et al.* 2011, Prater 1981). Kittlitz's Plover *Charadrius pecuarius* shows flexibility in adjusting its moult to different rainfall patterns and consequential feeding conditions at inland wetlands in Africa (Lipshutz *et al.* 2011). Throughout its sub-Saharan breeding range, most populations of this species are intra-African migrants that move southwest of their breeding areas after heavy rainfall, but the populations in the eastern interior and along the coasts of southern Africa are mostly sedentary (Dodman & Parker 2009). Two populations occur at one wetland in the interior of South Africa (Lipshutz *et al.* 2011). The local sedentary birds moult their primaries at the end of the breeding season, so in March–April they are in moult or have fresh primaries. But at the same time an itinerant population, probably immigrants from more northern areas, have mostly worn primaries that are at least a few months old (Lipshutz *et al.* 2011). Barshep (2011) shows that in tropical and subtropical climates the patterns of wader primary moult are adjusted to local rainfall and food abundance. In coastal regions of India, adult Curlew Sandpipers begin primary moult soon after arrival in mid-August; moult duration averages 107 days so it is completed in mid-December (Barshep 2011). The first half of their primary moult takes place rapidly during the monsoon season between July and September, when invertebrate food is abundant. But the rate of feather growth slows down during the drier post-monsoon period that follows. In contrast, adult Curlew Sandpipers moulting at similar latitudes around the inland lakes of the Great Rift Valley in Kenya arrive in August but do not begin their moult until October (Barshep 2011). The average duration of their primary moult is 128 days, three weeks longer than in India, so it is not completed until February. In Kenya, the moulting period mostly coincides with the "short rains" that occur between October and December (Barshep 2011).

Flexibility in the timing and rate of moult

Different populations of each species adjust their moult schedules to conditions at different geographical locations (Fig. 3). The rate of primary moult is regulated by the intervals at which consecutive primaries are shed (inter-shedding intervals), the number of primaries growing simultaneously and the rate of growth of each primary (Barshep 2011, Prater 1981, Remisiewicz *et al.* 2009, 2010a,b, Serra 2001a, Serra & Underhill 2006, Underhill 2003). Whole populations or single individuals might use different combinations of these regulatory mechanisms. Adult Ruddy Turnstones in Scotland conduct a rapid moult (Fig. 3) replacing the inner five primaries almost simultaneously. But they drop the outer primaries at longer intervals and grow them faster than the inner primaries (Underhill 2003). Fast-moulting Grey Plovers and Red Knots in the northern hemisphere show a similar "northern strategy" for their moult (Summers *et al.* 2010, Underhill 2003). But adult Ruddy Turnstones that moult slowly in South Africa grow only their innermost three primaries simultaneously; they drop the remaining primaries at longer intervals and

grow them at a slower rate than Ruddy Turnstones moulting in Scotland (Fig. 3) (Summers *et al.* 1998, Underhill 2003). A similar "southern strategy" is applied by Sanderlings and Red Knots moulting in South Africa (Underhill 2003). Adult and second-year Wood Sandpipers in southern Africa moult their innermost three primaries in quick succession, but they shed the remaining primaries at longer intervals and grow them at an even slower rate than southern-moulting Ruddy Turnstones (Remisiewicz *et al.* 2009, 2010a, Underhill *et al.* 2003). In this way Wood Sandpipers extend their moult over about 4.5 months, a long period for their wing length (Fig. 3) (Remisiewicz *et al.* 2009). The flexibility with which waders are able to control the rate of primary moult at an intra-population level can also demonstrated in relation to first-year Wood Sandpipers in southern Africa (Fig. 1) (Remisiewicz *et al.* 2010a). Those that moult rapidly shed 2–3 outer primaries almost simultaneously and grow these feathers at a faster rate than the individuals that replace 4–6 primaries over a longer period (Remisiewicz *et al.* 2010a).

Suspending moult for a short time at the non-breeding grounds might be an additional mechanism that waders use to adapt to temporary food scarcity (Pearson 1974, Prater 1981, Prater *et al.* 1977, Tree 1974). Moult suspension is most common among small waders with wings shorter than 200 mm, but larger species also occasionally suspend moult (Prater 1981). Suspension might be site-specific, depending on the resources provided by a wetland, and might allow passage migrants to undertake short-distance movements in search of more plentiful food (Prater 1981, Remisiewicz *et al.* 2009, M. Remisiewicz & A.J. Tree unpubl. data).

CONCLUSION

Waders display a wide variety of moult strategies, complicating the search for common patterns. The overlapping effects of different factors on the course of moult – ranging from a species' breeding biology, through migration distance and the habitats that they use, to the weather and the availability of food on the moulting grounds – make it difficult to discern general patterns. The general timing and patterns of moult in waders have a genetic background and are regulated by a bird's internal clock adjusted to circadian rhythms (e.g. Piersma & Ramenofsky 1998, Zwarts *et al*. 1990). To a large extent moult is under hormonal control, which probably allows waders to adjust feather replacement to other events in their life cycle, such as breeding, as shown in passerines (e.g. Dawson 1994, 2006). But the annual variation in the timing of wader moult, the variety of moult patterns in a population and the flexible responses to individual and environmental conditions, which I have summarised, suggest that some physiological mechanisms allow waders to adjust their moult to the proximate conditions they face. Discovering these mechanisms is one of the challenges in further studies of moult. These mechanisms might be related to the hormonal mechanisms that allow migrant waders to assess their level of fat reserves at stopover sites (e.g. Kochan *et al.* 2006).

The UZ moult models and their extensions, and new user-friendly software (Erni *et al.* in press), provide tools that allow deep insights into the course of wader moult and its relation to environmental factors. In combination with environmental data and methods such as DNA and stable isotope analysis, detailed studies of moult patterns promise a deeper understanding of wader life history. Studies on moult can help to determine the extent of the intra-specific plasticity of waders in adapting to environmental changes, which is particularly important for conservation efforts in an era of global climate change. More comparative studies are required to determine the moult patterns of different populations in response to the conditions they encounter at different non-breeding grounds. I hope this overview encourages wader researchers to take a second look at their moult data and to collect new material, then to use the new tools to analyse these data and help to fill the many gaps in our knowledge of the biology of waders.

ACKNOWLEDGEMENTS

I am indebted to Les Underhill for setting me on track in the fascinating study of wader moult and for being an extraordinary mentor. Włodek Meissner introduced me to the world of waders about 20 years ago. Włodek Meissner, Lorenzo Serra, Ron Summers and Les Underhill kindly commented on an earlier version of this manuscript. I am grateful to Tony Tree who let me freely use his African wader moult data, which he has collected since the 1960s, as well as to the many other people who provided data or helped to collect it. Walter Zucchini and Anabela Brandão provided software for my earlier moult analyses. Birgit Erni developed the R Moult package that has facilitated moult analyses and she taught me how to use her software. Yahkat Barshep inspired me to dig deeper into the intricacies of wader moult. Joel Avni provided constant support and commented on this manuscript. Pavel Pinchuk kindly provided the photograph. I acknowledge a post-doctoral fellowship from the Claude Leon Foundation for my studies at the Animal Demography Unit of the University of Cape Town in 2008–2011.

REFERENCES

Alerstam, T. & Högstedt, G. 1982. Bird migration and reproduction in relation to habitats for reproduction and survival. *Ornis Svecica* 13: 25–37.

Alerstam, T. & Lindström, Å. 1990. Optimal bird migration: The relative importance of time, energy and safety. In: *Bird Migration: Physiology and Ecophysiology.* Gwinner E. (ed.). pp. 331–352. Springer Verlag, Wien-Heidelberg.

Allan, D.G., Harrison, J.A., Herremans, M., Navarro, R.A. & Underhill, L.G. 1997. Southern African geography: its relevance to birds. In: *The atlas of southern African birds. Vol. 1: Non-passerines*. Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V., Brown. C.J. (eds). BirdLife South Africa, Johannesburg, pp. lxv–ci.

Appleton, F.G. & Minton, C.D.T. 1978. The primary moult of the Lapwing. *Bird Study* 25: 253–256.

Ashmole, N.P. 1962. The Black Noddy, *Anous tenuirostris*, on Ascension Island. Part 1. General biology. *Ibis* 103b: 235–273.

Balachandran, S., Hussain, S.A. & Underhill, L.G. 2000. Primary moult, biometrics, mass and age composition of Grey Plover *Pluvialis squatarola* in southeastern India. *Bird Study* 47: 82–90.

Barshep, Y. 2011. *Migration and Moult Strategy of the Curlew Sandpiper*. Unpubl. Ph.D. thesis, Department of Zoology, University of Cape Town, Cape Town, South Africa.

Barshep Y., Minton C., Underhill L.G. & Remisiewicz M. 2011. The primary moult of Curlew Sandpipers *Calidris ferruginea* in north-western Australia shifts according to breeding success. *Ardea* 99: 43–51.

Barta, Z., Houston, A.I., McNamara, J.M., Welham, R.K., Hedenström, A., Weber, T.P. & Feró, O. 2006. Annual routines of non-migratory birds: optimal moult strategies. *Oikos* 112: 580–593.

Bensch, S. & Grahn, M. 1993. A new method for estimating individual speed of moult. *Condor* 95: 305–315.

Boere, G.C. 1976. Moulting waders in Dutch Waddensee. *Ardea* 64: 210–289.

Brandão, A. 1998. *A Comparative Study of Stochastic Models in Biology.* Unpubl. Ph.D. thesis, University of Cape Town, Cape Town, South Africa.

Colwell, M.A. 2010. *Shorebird Ecology, Conservation, and Management*. University of California Press, Berkeley, Los Angeles, London.

Cramp, S. & Simmons, K.E.L. (eds). 1983. *The Birds of the Western Palearctic. Vol. 3.* Oxford University Press, Oxford.

Dawson, A. 1994. The effects of daylength and testosterone on the initiation

and progress of moult in Starlings *Sturnus vulgaris*. *Ibis* 136: 335–340.

Dawson, A. 2003. A detailed analysis of primary feather moult in the Common Starling *Sturnus vulgaris* – new feather mass increases at a constant rate. *Ibis* 145: E69–E76.

Dawson, A. 2006. Control of molt in birds: Association with prolactin and gonadal regression in starlings. *Gen. Compar. Endocr.* 147: 314–322.

Dawson, A. & Newton, I. 2004. Use and validation of a molt score index corrected for primary-feather mass. *Auk* 121(2): 372–379.

Dean, W.R.J. 1977. Moult of Little Stints in South Africa. *Ardea* 65: 73–79.

Dodman, T. & Parker, V. 2009. Kitlitz's Plover *Charadrius pecuarius*. In: *An Atlas of Wader Populations in Africa and Western Eurasia*. Delaney, S., Scott, D., Dodman. T. & Stroud, D. (eds). Wetlands International, Wageningen.

Dos Remedios, N., Lee, P.L.M., Székely, T., Dawson, D.A. & Küpper, C. 2010. Molecular sex-typing in shorebirds: a review of an essential method for research in evolution, ecology and conservation. *Wader Study Group Bull.* 117(2): 109–118.

Dwight J. 1900. The moult of North American shore birds (Limicolae). *Auk* 17: 368–385.

Elliott, C.C.H., Waltner, M., Underhill, L.G., Pringle, J.S. & Dick, W.J.A. 1976. The migration system of the Curlew Sandpiper *Calidris ferruginea* in Africa. *Ostrich* 47: 191–213.

Erni, B., Oschadleus, H.D., Bonnevie, B. Altwegg, R. & Underhill L.G. in press. An R package to analyse moult in birds. *Journal of Statistical Software*.

Ginn, H.B. & Melville, D.S. 1983. *Moult in Birds.* BTO Guide 19. British Trust for Ornithology, Tring, UK.

Gromadzka, J. 1986. Primary moult of adult Dunlins *Calidris alpina* of different age during autumn migration. *Vår Fågelv. Suppl.* 11: 51–56.

Gromadzka, J. & Serra, L. 1998. Differential migration of juvenile and adult Grey Plovers *Pluvialis squatarola* at the mouth of the Vistula River, Poland. *Ornis Fenn.* 75: 193–199.

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. & Brown, C.J. (eds). 1997. *The Atlas of Southern African Birds. Vol. 1: Non-passerines*. BirdLife South Africa, Johannesburg, South Africa.

Haukioja, E. 1971. Processing moult card data with reference to the Chaffinch *Fringilla coelebs*. *Ornis Fenn*. 48: 25–32.

Hedenström, A. & Sunada, S. 1999. On the aerodynamics of moult gaps in birds. *J. Exp. Biol.* 202: 67–76.

Hockey, P.A.R, Navarro, R.A., Kalejta, B. & Velásquez, C.R. 1992. The riddle of the sands: Why are shorebird densities so high in southern estuaries? *Am. Nat.* 140: 961–979.

Hockey, P.A.R, Turpie, J.K. & Velásquez, C.R. 1998. What selective pressures have driven the evolution of deferred northward migration by juvenile waders? *J. Avian. Biol.* 29: 325–330.

Holmes, R.T. 1966. Breeding ecology and annual cycle adaptations of the Red-Backed Sandpiper (*Calidris alpina*) in Northern Alaska. *Condor* 68: 3–46.

Holmes, R.T. 1971. Latitudinal differences in the breeding and molt schedules of Alaskan Red-backed Sandpipers (*Calidris alpina*). *Condor* 73: 93–99.

Holmes, R.T. & Pitelka, F.A. 1964. Breeding behaviour and taxonomic relationships of the Curlew Sandpipers. *Auk* 81: 362–376.

Holmgren, N., Ellegren, H. & Pettersson, J. 1993. The adaptation of moult pattern in migratory dunlins *Calidris alpina*. *Ornis Scandinavica* 24: 21–27.

Holmgren, N., Jonsson, P.E. & Wennerberg, L. 2001. Geographical variation in the timing of breeding and moult in dunlin *Calidris alpina* on the Palearctic tundra. *Polar Biology* 24: 369–377.

Howell, S.N.G. 2010. *Molt in North American birds*. Peterson Reference Guide Series. Houghtin, Mifflin, Harcourt, Boston, New York.

Hoye, B.J. & Buttermer, W.A. 2011 Inexplicable inefficiency of avian molt? Insights from an opportunistically breeding arid-zone species, *Lichenostomus penicillatus*. *PLoS ONE* 6(2): e16230.

Jehl, J.R., Jr. 1987. Moult and moult migration in a transequatorially migrating shorebird: Wilson's Phalarope. *Ornis Scand*. 18: 173–178.

Johnson, C. & Minton, C.D.T. 1980. The primary moult of the dunlin *Calidris alpina* at the Wash. *Ornis Scand*. 11: 190–195.

Kania, W. 1990. The primary moult of breeding dunlins *Calidris alpina* in the central Taymyr in 1989. *Wader Study Group Bull*. 60: 17–19.

Kochan, Z., Karbowska, J. & Meissner, W. 2006. Leptin is synthesized in the liver and adipose tissue of the Dunlin (*Calidris alpina*). *Gen. Compar. Endocr.* 148: 336–339.

Koopman, K. 1985. Primary moult and weight changes of ruffs in the Netherlands in relation to migration. *Ardea* 74: 69–77.

Kraaijeveld, K. 2008. Non-breeding habitat preference affects ecological speciation in migratory waders. *Naturwissenschaften* 95: 347–354.

Krupa, M. & Krupa, R. 2002. Biometrics and primary moult of the Grey Plover (*Pluvialis squatarola*) caught during autumn migration through the Puck Bay. *Ring* 24: 91–103.

Lank, D.B., Butler, R.W., Ireland, J. & Ydenberg, R.C. 2003. Effects of predation danger on migration strategies of sandpipers. *Oikos* 103: 303–319.

Lindström, Å., Visser, H. & Daan, S. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiol Zool* 66: 490–510.

Lipshutz, S., Remisiewicz, M., Underhill, L.G. & Avni, J. 2011. Seasonal fluctuations in population size and habitat segregation of Kittlitz's Plover *Charadrius pecuarius* at Barberspan Bird Sanctuary, North West province, South Africa. *Ostrich* 82: 207–215.

Meissner, W., Remisiewicz, M. & Gogga, P. in press. Sex and age differences in the development of breeding plumage in Wood Sandpiper *(Tringa glareola)* at the final stage of their spring migration in northeastern Poland. *Ornis Fennica.*

Meltofte, H. 1996. Are African wintering waders really forced south by competition from northerly wintering conspecifis? Benefits and constraints of northern versus southern wintering and breeding in waders. *Ardea* 84: 31–44.

Middlemiss, E. 1961. Biological aspects of *Calidris minuta* while wintering in south-west Cape. *Ostrich* 32: 107–121.

Minias, P., Kaczmarek, K., Włodarczyk, R., Janiszewski, T. & Bargiel, R. 2010. Feeding conditions determine return rates to stopover sites of inland waders on autumn migration. *Ibis* 152: 840–844.

Minton, C.D.T. & Serra, L. 2001. Biometrics and moult of Grey Plovers, *Pluvialis squatarola*, in Australia. *Emu* 101: 13–18.

Minton, C.D.T., Rogers, K.G., Jessop, R.E., Graham, D.M. & Lowther, A.D. 2006. Biometrics and moult of the Curlew Sandpiper *Calidris ferruginea* in Australia. *Int. Wader Stud.* 19: 195–204.

Morrison, R.I.G. 1976. Moult of the Purple Sandpiper *Calidris maritima* in Iceland. *Ibis* 118: 237–246.

Murphy, M.E. & King, J.R. 1992. Energy and nutrient use during moult by white-crowned sparrows *Zonotrichia leucophrys gambelli*. *Ornis Scand* 23: 304–313.

Newton, I. 1967. Feather growth and moult in some captive finches. *Bird Study* 14: 10–24.

Newton, I. 2009. Moult and plumage. *Ringing & Migration* 24: 220–226.

Pearson, D.J. 1974. The timing of wing moult in some Palaearctic waders wintering in East Africa. *Wader Study Group Bull*. 12: 10–17.

Pearson, D.J. 1977. The first year moult of the Common Sandpiper *Tringa hypoleucos* in Kenya. *Scopus* 1: 89–94.

Pearson, D.J. 1981. The wintering and moult of Ruffs *Philomachus pugnax* in the Kenyan Rift Valley. *Ibis* 123: 158–182.

Pearson, D.J. 1984. The moult of the Little Stint *Calidris minuta* in the Kenyan Rift Valley. *Ibis* 126: 1–15.

Pearson, D.J. & Serra, L. 2002. Biometrics, moult and migration of Grey Plovers at Mida Creek, Kenya. *Ostrich* 73: 143–146.

Pienkowski, M., Knight, P.J., Stanyard, D.J. & Argyle, F.B. 1976.The primary moult of waders on the Atlantic coast of Morocco. *Ibis* 118: 374–365.

Piersma, T. 1997. Do global patterns of habitat use and migration strategies co-evolve with relative investments in immunocompetence due to spatial variation in parasite pressure? *Oikos* 80: 623–631.

Piersma, T. 2003. "Coastal" versus "inland" shorebird species: interlinked fundamental dichotomies between their life- and demographic histories? *Wader Study Group Bull*. 100: 5–9.

Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology* 148, S1: 45–59.

Piersma, T. & Jukema, J. 1993. Red breasts as honest signals of migratory quality in a long-distance migrant, the Bar-tailed Godwit. *Condor* 95: 163–177.

Piersma, T. & Ramenofsky, M. 1998. Long-term decreases of corticisterone in captive migrant shorebirds that maintain seasonal mass and moult cycles. *J. Avian Biol.* 29: 97–104.

Piersma, T. & Wiersma, P. 1996. Family *Charadriidae* (plovers). In: *Handbook of the Birds of the World. Vol. 3. Hoatzin to Auks*. pp. 384–442. Lynx Edicions, Barcelona.

Piersma, T., van Gils, J. & Wiersma, P. 1996. Family *Scolopaciade* (sandpipers, snipes and phalaropes). In: *Handbook of the Birds of the World. Vol. 3. Hoatzin to Auks.* pp. 444–533. Lynx Edicions, Barcelona.

Pinchuk, P., Remisiewicz, M., Włodarczyk, R. & Karlionova, N. 2008.

Observations of primary moult in adult Wood Sandpipers *Tringa glareola* on southward migration in east and central Europe. *Wader Study Group Bull*. 115: 24–28.

Prater, A.J. 1981. A review of the patterns of primary moult in Palearctic waders (Charadrii). In: *Proceedings of the Symposium on Birds of the Sea and Shore, 1979*. African Seabird Group, Cape Town. pp. 393–409.

Prater, A.J., Marchant, J.H. & Vuorinen, J. 1977. *Guide to the Identification and Ageing of Holarctic Waders*. BTO Guide 17. British Trust for Ornithology, Tring.

Pyle, P. 2008. *Identification Guide to North American Birds, Part 2.* Slate Creek Press, Bolinas, California. pp. 500–507.

R Development Core Team. 2009. *http://www.r-project.org/*

Remisiewicz, M. & Wennerberg, L. 2006. Differential migration strategies of Wood Sandpiper (*Tringa glareola*) – genetic analyses reveal sex differences in morphology and spring migration phenology. *Ornis Fennica* 83: 1–10.

Remisiewicz, M., Meissner, W., Pinchuk, P. & Ściborski, M. 2007. Phenology of spring migration of Wood Sandpiper *Tringa glareola* through Europe. *Ornis Svecica* 17: 3–14.

Remisiewicz, M., Tree, A.J., Underhill, L.G., Gustowska, A. & Taylor, P.B. 2009. Extended primary moult as an adaptation of adult Wood Sandpipers *Tringa glareola* to their use of freshwater habitats of southern Africa. *Ardea* 97(3): 271–280.

Remisiewicz, M., Tree, A.J., Underhill, L.G. & Taylor, P.B. 2010a. Rapid or slow moult? The choice of a primary moult strategy by immature Wood Sandpipers *Tringa glareola* in southern Africa. *J. Ornithol.* 151: 429–441.

Remisiewicz, M., Tree, A.J., Underhill, L.G. & Taylor, P.B. 2010b. The path to adult dress: primary moult in second-year Wood Sandpipers *Tringa glareola* in southern Africa. *Wader Study Group Bull*. 117: 35–40.

Roshier, D.A., Robertson, A.I. & Kingsford, R.T. 2002. Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. *Biological Conservation* 106: 399–411.

Sach, G. 1968. Die Mauser des grossen Brachvogels, *Numenius arquata*. *J. Ornithol*. 109: 485–511.

Salewski, V., Altwegg, R., Erni, B., Falk, K.H., Bairlein, F. & Leisler, B. 2004. Moult of three Palaearctic migrants in their West African winter quarters. *Journal of Ornithology* 145: 109–116.

Schekkerman, H., van Roomen, M.W.J. & Underhill, L.G. 1998. Growth, behaviour of broods and weather-related variation in breeding productivity of Curlew Sandpipers *Calidris ferruginea*. *Ardea* 86: 153–168.

Schmitt, M.B. & Whitehouse, P.J. 1976. Moult and mensural data on Ruff on the Witwatersrand. *Ostrich* 47: 179–190.

Serra, L. 1998. The adaptation of primary moult to migration and wintering in the Grey Plover (*Pluvialis squatarola*): a preliminary outlook. *Biologia e Conzervacione Fauna* 102: 123–127.

Serra, L. 2001a. Cold winters vs. long journeys: adaptations of primary moult and body mass to migration and wintering in the Grey Plover *Pluvialis squatarola*. Ph.D. thesis, University of Cape Town, Cape Town, South Africa.

Serra, L. 2001b. Duration of primary moult affects primary quality in Grey Plovers *Pluvialis squatarola*. *Journal of Avian Biology* 32: 377–380.

Serra, L. & Rusticali, R. 1998. Biometrics and moult of Grey Plovers (*Pluvialis squatarola*) wintering in northeastern Italy. *Vogelwarte* 39: 281–292.

Serra, L. & Underhill, L.G. 2006. The regulation of primary moult speed in the Grey Plover, *Pluvialis squatarola*. *Acta Zool. Sin.* 52 (Supplement): 451–455.

Serra, L., Baccetti, N., Cherubini, G. & Zenatello, M. 1998. Migration and moult of Dunlin *Calidris alpina* wintering in the central Mediterranean. *Bird Study* 45: 205–218.

Serra, L., Whitelaw, D.A., Tree, A.J. & Underhill, L.G. 1999. Moult, mass and migration of Grey Plovers *Pluvialis squatarola* wintering in South Africa. *Ardea* 87: 71–81.

Serra, L., Clark, N.A. & Clark, J.A. 2006. Primary moult, body mass and migration of Grey Plovers *Pluvialis squatarola* in Britain. *Ibis* 148: 292–301.

Skagen, S.K., Granfors, D.A. & Melcher, C.P. 2008. On determining the significance of ephemeral continental wetlands to North American migratory shorebirds. *Auk* 125: 20–29.

Stresemann, E. & Stresemann, V. 1966. Die Mauser der Vögel. *J. Ornithol.* 107.

Summers, R.W. 1980. On the rate of change of moult scores in waders. *Wader Study Group Bull* 28: 24.

Summers, R.W., Swann, R.L. & Nicoll, M. 1983. The effects of methods on estimates of primary moult duration in the Redshank *Tringa totanus*. *Bird Study* 30: 149–156.

Summers, R.W., Underhill, L.G., Waltner, M. & Whitelaw, D.A. 1987. Population, biometrics and movements of the Sanderling *Calidris alba* in southern Africa. *Ostrich* 58: 24–39.

Summers, R.W., Underhill, L.G. & Prŷs-Jones, R.P. 1995. Why do young waders in southern Africa delay their first return migration to the breeding grounds? *Ardea* 83: 351–357.

Summers, R.W., Underhill, L.G. & Syroechkovski, E.E., Jr. 1998. The breeding productivity of dark-bellied Brent Geese and Curlew Sandpipers in relation to changes in the numbers of arctic foxes and lemmings on the Taimyr Peninsula, Siberia. *Ecography* 21: 573–580.

Summers, R.W., Underhill, L.G., Nicoll, M., Strann, K-B. & Nilsen, S.Ø. 2004. Timing and duration of moult in three populations of Purple Sandpipers *Calidris maritima* with different moult/migration patterns. *Ibis* 146: 394–403.

Summers, R.W., Underhill, L.G., Waltner, M. & Swann, R.L. 2010. Differences in biometrics and moult of non-breeding Red Knots *Calidris canutus* in southern Africa and Scotland reflect contrasting climatic conditions. *Ibis* 152: 127–135.

Tree, A.J. 1974. The use of primary moult in ageing the 6–16 month age class of some Palearctic waders. *Safring News* 3(3): 21–24.

Tree, A.J. 1979. Biology of the Greenshank in southern Africa. *Ostrich* 50: 240–251.

Tree, A.J. 2008. The Common Sandpiper in Zimbabwe. *Honeyguide* 54: 40–51.

Underhill, L.G. 1997. Wood Sandpiper *Tringa glareola*. pp. 410–411. In: *The Atlas of Southern African Birds.* Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. & Brown, C.J. (eds). BirdLife South Africa, Johannesburg, South Africa.

Underhill, L.G. 2003. Within ten feathers: Primary moult strategies of migratory waders (*Charadrii*). pp. 187–197. In: *Avian Migration*. Berthold, P., Gwinner, E. & Sonnenschein, E. (eds). Springer-Verlag, Berlin Heidelberg.

Underhill, L.G. 2006. A preliminary overview of the life spiral of Curlew Sandpipers *Calidris ferruginea*. *Int. Wader Stud.* 19: 209–211.

Underhill, L.G. & Joubert, A. 1995. Relative masses of primary feathers. *Ringing & Migration* 16: 109–116.

Underhill, L.G. & Summers, R.W. 1993. Relative masses of primary feathers in waders. *Wader Study Group Bull.* 71: 29–31.

Underhill, L.G. & Zucchini, W. 1988. A model for avian primary moult. *Ibis* 130: 358–372.

Underhill, L.G., Serra, L. & Brandão, A. 2006. Progress with the statistical analysis of primary molt. *Acta Zool. Sin.* 52 (Supplement): 440–443.

van de Kam, J., Ens, B., Piersma, T. & Zwarts, L. 2004. *Shorebirds. An Illustrated Behavioural Ecology*. KNNV Publishers, Utrecht, The Netherlands.

van der Valk, R. 2011.On estimating the duration of phenological stages in bryophytes. *Lindbergia* 34: 44–50.

Videler, J. 2005. *Avian Flight*. Oxford University Press, Oxford.

Waltner, M. & Sinclair, J.C. 1981. Distribution, biometrics and moult of the Terek Sandpiper *Xenus cinereus* in southern Africa. In: Cooper, J. (ed.). *Proceedings of the Symposium on Birds of the Sea and Shore, 1979*. African Seabird Group, Cape Town.

Ward, V.L., Oschadleus, H.D. & Underhill, L.G. in press. Primary moult of the Kelp Gull *Larus dominicanus vetula* in the Western Cape, South Africa. *Acta Orn.*

Wennerberg, L., Holmgren, N.M.A., Jonsson, P.E. & von Schantz, T. 1999. Genetic and morphological variation in Dunlin *Calidris alpina* breeding in the Palearctic tundra. *Ibis* 141: 391–398.

Zwarts, L., Ens, B.J., Kersten, M. & Piersma, T. 1990. Moult, mass and flight range of waders ready to take off for long-distance migrations. *Ardea* 78: 339–364.