The moult and migration strategies of Lesser Sand Plover, Greater Sand Plover and Terek Sandpiper

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Plagiarism declaration

I know the meaning of plagiarism and declare that all of the work in this thesis, save for that which is properly acknowledged, is my own.

Signature:___Signed by candidate___ Signature Removed

Date:________14th March 2017______

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"Even the stork in the sky
knows her appointed seasons,
and the dove, the swift and the thrush
observe the time of their migration."

Jeremiah 8:7

Abstract

Moult in birds is a critical yet often underrated component of a birds' annual life cycle together with breeding and migration. A good understanding of the moult strategy of a species is important for its conservation because key moulting grounds must be protected to allow this component of the life cycle to be undertaken. Lesser Sand Plovers, Greater Sand Plovers and Terek Sandpipers are among the least known of the commonly encountered long-distance migrant waders in Africa and Australasia. This is particularly true for the populations which spend the non-breeding season on the East African coast.

This study aims to describe the primary moult strategies for the three species from five locations at different latitudes: south-eastern India, Kenya, South Africa, north-western Australia and south-eastern Australia. Differences in moult strategy between species, age and latitude are highlighted and explanations are proposed for the differences in the light of the breeding behaviour, migration time and routes, food availability and local climatic conditions. Results from this study are combined with other moult studies on migrant waders to present hitherto undescribed patterns in wader moult strategies at a global scale. A synthesis is presented of published and available unpublished information about the different populations for the three study species, their distribution, status and migration strategies with a focus on those visiting the East African coast.

The three species follow a similar basic moult strategy in adults where primaries are moulted soon after arriving on the non-breeding grounds. Immature moult strategies are more complex and differ between species and latitude. In general adults in all three species at the more northern non-breeding sites start moult earlier than those travelling farther south probably as a result of greater proximity to breeding grounds. Lesser Sand Plovers have a relatively long duration of moult (152–154 days) across all locations where data were sufficient; Greater Sand Plovers have a short duration (80 days) in India and similar, comparatively longer durations (132–134 days) at the other latitudes. The Indian site is used mainly by this species as a site to stopover and moult while on migration to more southerly non-breeding grounds. Terek Sandpipers in Kenya have a relatively short duration of moult (99 days) when compared to India and Australia (121–130 days) and tend to have a rapid start to moult which then slows down after the first few primaries are moulted.

Young Lesser Sand Plovers in India mostly undergo a complete primary moult while in Kenya and Australia birds generally do not moult in their first year. First year Greater Sand Plovers mostly all undergo a complete primary moult irrespective of latitude. Terek Sandpipers in their first year do not moult in India in the north, mostly undergo a partial moult of outer primaries in Kenya on the

equator, and do a complete moult in south-eastern Australia. The north-west Australian population was divided into two almost equal groups: those that undergo a complete primary moult, and those that only moult a few outer primaries. A difference in winglength between these two groups suggests that there may be two distinct populations involved, most likely originating from distinct breeding grounds. In-depth study is needed to confirm this.

The overarching picture of moult in adult migrant waders is that at high latitudes moult starts early and is kept short. With decreasing latitude, the timing of moult is delayed with increasing distance from breeding grounds. In the tropics the lack of constraints of approaching harsh winter weather and long distances from breeding grounds allow species to adapt a wide range of moult strategies. As birds migrate farther south before they moult, constraints on time available to moult due to large distances travelled mean duration is reduced in order to fit it in. An upper limit in duration of moult in migrant waders irrespective of the size of the bird appears to be set at c. 160 days. Small birds have a wide variation in duration while as body size increases over 100 g, moult duration is necessarily longer. With harsh winters in the north, large waders are forced to migrate south in order to moult. This study suggests that irrespective of body size the 'gold standard' for duration of moult is around 120 days (four months).

While timing of migration is relatively well-known for the three species in Australia, it was hitherto unknown that juvenile Lesser Sand Plovers do not reach Australia until February or March in contrast to all other migrant wader species where first years arrive in September/October. It is unknown where they stop en route or indeed why they delay in this way. All three species in Kenya peak at a maximum population in November and early December after which numbers reduce as birds start to depart for the breeding grounds. Resightings of colour-flagged Lesser and Greater Sand Plovers confirmed the north-western coast of India as an important stopover site for migrants heading to western China and Mongolian breeding grounds from Kenya.

A review of country population estimates for the three species suggested non-breeding populations in Africa of 200,000 Lesser Sand Plovers, 25,000–35,000 Greater Sand Plovers and 115,000–200,000 Terek Sandpipers. Mida Creek is shown to be a key stronghold for non-breeding waders in Kenya and its importance for their continued conservation is thus confirmed.

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Wildlife Service Watamu has always given the go ahead for carrying out the ringing within the Watamu Marine Reserve on Mida Creek and some staff have joined in the ringing and been a great help to have along.

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"The earth is the LORD's and everything in it"

A typical wader ringing night at Mida Creek

Chapter 1

Introduction

Introduction

Charadriiformes – the waders

The order Charadriiformes is a large and varied order of birds containing approximately 365 species of the more well-known waders or shorebirds as well as those as diverse and unique as thick-knees (Burhinidae), sheathbills (Chionidae), auks (Alicidae), skuas (Stercorariidae), buttonquails (Turnicidae) and the Ibisbill (Ibidorhynchidae) (del Hoyo et al. 1996). Within the broader grouping of 'waders', two families contain the majority of taxa, the plovers, Charadriidae (71 species), and the sandpipers, Scolopacidae (91 species) (Hayman et al. 1986). Both of these families include species which are long distance migrants. Most of the sandpipers breed in the high latitudes of the northern hemisphere; in the non-breeding season they spread out across broad latitudinal zones, with many migrating south of the Tropic of Cancer to exploit warm tropical conditions along the equator, and the austral summer farther south (Piersma and Bonan 2016a, 2016b). The Purple Sandpiper *Calidris maritima* is the northernmost species in the northern winter, spending the non-breeding season inside the Arctic Circle in northern Norway (Summers et al. 1990). Plovers breed much more widely than sandpipers, some inside the Arctic Circle (e.g. Common Ringed Plover *Charadrius hiaticula*) and others which are resident or make smaller non-breeding movements in the tropics such as Three-banded Plover *C. tricollaris* (Hayman et al. 1986).

Waders (or shorebirds as they are known in the USA and Australia) are classified as wetland birds with most species being strongly associated with permanent or seasonal wetlands ranging from marine habitats, alkaline lakes, to freshwater swamps, pools, rivers and artificial wetlands such as sewage works. Indeed, the name 'wader' derives from the foraging behaviour of many species which wade in shallow water in search of food. A number of species are highly specialised and thus restricted in their preference of wetland habitat, e.g. the East African race *venustus* of Chestnut-banded Plover *Charadrius pallidus* is restricted to a narrow fringe of highly saline beaches on the alkaline lakes of the Rift Valley (Zimmerman et al. 1996). Some are only found in freshwater habitats (e.g. Green Sandpiper *Tringa ochropus*) or marine habitats (e.g. Crab-plover *Dromas ardeola*) while others are more catholic in their preference for water salinity (e.g. Curlew Sandpiper *Calidris ferruginea*). A few, despite still be classified as 'waders' or 'shorebirds', are in fact rarely associated with wetlands being found in arid bushland, grasslands and deserts (e.g. the coursers such as Cream-coloured Courser *Cursorius cursor*). Yet others spend the breeding season in one habitat and the non-breeding season on the other side of the world in a totally different habitat (e.g. Lesser Sand Plover *Charadrius mongolus* which breeds in arid montane valleys in Central Asia far from a coastline but spends the non-breeding season almost exclusively on coastal sandflats and beaches) (Cramp and Simmons 1983, Hayman et al. 1986, del Hoyo et al. 1996).

Breeding

The majority of waders nest on the ground in a simple shallow hollow or scrape, often with no lining but some species line the scrape with grass or vegetation (e.g. Purple Sandpiper) (Cramp and Simmons 1983, del Hoyo et al. 1996, Rae et al. 2011). Others have more unusual nesting habits such as Crab-plovers which nest in burrows a metre or more underground on sandy beaches and Green Sandpipers and Wood Sandpipers *Tringa glareola* which commonly nest in trees (del Hoyo et al. 1996). Two to four eggs are usually laid and in many species the eggs are cryptically coloured and patterned to camouflage them on the open ground thus making some of the most beautiful eggs of any bird (Cramp and Simmons 1983, Hayman et al. 1986, Hockey et al. 2005). While most waders are monogamous in their breeding strategy with both male and female playing a role in raising chicks, three other strategies may be found (Szekely and Reynolds 1995): polygynous species where the male mates with several females each of whom then is solely responsible for incubating their eggs and rearing the chicks (e.g. Ruff *Philomachus pugnax*); polyandrous species where the roles are reversed and females are the more brightly coloured of the pair, compete for males and attempt to mate with several in succession while the males incubate the eggs and rear the young (e.g. phalaropes *Phalaropus sp.* and African Jacana *Actophilornis africanus*); and double-clutch breeding where a female will lay two clutches of eggs in quick succession, the first being incubated and raised by the male and the second by the female e.g. Temminck's Stint *Calidris temminckii*, Sanderling *C. alba* and Little Stint *C. minuta*.

Foraging behaviour and adaptations

Waders are characterised as birds with generally long legs and long bills to aid in their foraging in water, demonstrated best by the stilts with a leg length to body size ratio only exceeded by flamingos (The Cornell Lab of Ornithology 2017). Leg length and bill shape are key features for aiding in identification of many species of wader and are closely linked to the foraging behaviour for that species (Hayman et al. 1986, Peacock 2017). Plovers tend to have short, strong bills that are good for picking prey items from the surface of sand or mud and have larger eyes set in larger heads (e.g. Grey Plover *Pluvialis squatarola*) than sandpipers which have longer bills with often soft tips designed for probing in mud and feeling for prey items that are out of sight under the surface (e.g. African Snipe *Gallinago nigripennis*). As a result, sandpipers tend to have relatively smaller heads and smaller eyes (del Hoyo et al. 1996, Peacock 2017). Feeding behaviour is also different as a result. Plovers tend to have a 'stop-start' foraging action in which the bird stops to look for a prey item and then makes a rapid run to peck at it. Many sandpipers, on the other hand, are constantly on the move and probing in the mud in a 'sewing machine' action. The difference is so marked that it is possible to differentiate a foraging plover from a sandpiper from its tracks in the mud.

Migration and movements

The majority of sandpiper and plover species breed in the Arctic or sub-Arctic and northern temperate zones and migrate south during the boreal winter to either milder temperate zones such as western and southern Europe or travel the long distances to tropical or southern temperate regions of Australia, Africa and South America (Cramp and Simmons 1983). Fewer species breed in the tropics and southern temperate regions. Of these many are resident (e.g. Chestnut-banded Plover) while a few undertake local movements probably in response to rainfall conditions (e.g. Kittlitz's Plover *Charadrius pecuarius*) though much is yet to be understood about such movements (del Hoyo et al. 1996, Zimmerman et al. 1996, Hockey et al. 2005). Given that many species breed in the high arctic and spend the non-breeding season south of the Tropic of Capricorn, waders undergo some of the most impressive migrations of any birds (Newton 2010). Recent developments in tracking technology such as satellite transmitters and geolocators have revealed hitherto unimagined feats in long distance travel and sustained flight. One of the most extreme is the migration of Bar-tailed Godwits *Limosa lapponica* which fly non-stop from Alaskan breeding grounds to non-breeding grounds in New Zealand, a distance of 11,690 km, the longest non-stop direct migratory flight documented for any bird (Battley et al. 2012).

Critical to the conservation of long-distance migratory waders is a proper understanding of the routes taken, the stopover sites used both for fattening for the onward journey and in some species for moult, together with the times of year that these sites are most important for the long-distance travellers (Evans et al. 1991, Davidson and Stroud 1996, Davidson et al. 1998, Piersma and Lindström 2004). An overall picture of general migration patterns has emerged from results of extensive ringing studies together with other tracking methods that has led to the description of 'flyways' for migrants (Davidson et al. 1998). These are broad corridors or routes that are followed by the majority of birds in particular breeding populations as they migrate south to regular non-breeding grounds (Delany et al. 2009).

A number of wader species have been well-studied and much is understood about their breeding biology, population dynamics, migration, moult, etc. and this is particularly true for species in the East Atlantic Flyway and East Asia/Australasia Flyway (Minton et al. 2011, 2013b) e.g. Red Knot *Calidris canutus* (Barter et al. 1988, Piersma et al. 1992, Balachandran 1998), Curlew Sandpiper (Elliott et al. 1976, Barshep 2011), Ruddy Turnstone *Arenaria interpres* (Summers et al. 1989, Davidson and Gill 2008) and Grey Plover (Branson and Minton 1976, Serra 2001). Large numbers of waders from a wide distribution across the Palearctic region migrate south to spend the non-breeding season in Africa with many passing along and using the eastern African coastline (Moreau 1952, Underhill et al. 1999, Delany et al. 2009). Despite this, observers are few and far between and thus little is known for even most of the common migrant wader species on the West Asia-Africa Flyway regarding origins, migration routes, timing and reliable population estimates (Davidson et al. 1998, Serra et al. 2001, Boere et al. 2006, Delany et al. 2009).

Moult in waders

Moult is an unavoidable event that every bird must undergo during its annual life cycle (Ginn and Melville 1983). It is one of three key energetically-expensive events that migrants in particular need to fit into an annual schedule of breeding, migrating and moult (Ginn and Melville 1983, Zenatello et al. 2002, Barta et al. 2008, Flinks et al. 2008, Newton 2009). As a result, many different moult strategies have evolved for migrant waders. For a minority of long-distance migrant waders moult starts on the breeding grounds such as Eurasian Golden Plover *Pluvialis apricaria* which exceptionally starts moult before completing breeding (Jukema and Wiersma 2014) and Dunlin *Calidris alpina* in Alaska (Holmes 1966) which complete moult prior to migration, and even moult during incubation (Kania 2003). However, most species separate the three activities of breeding, migration and moult such that there is little or no overlap between them (Pearson 1974, Prater et al. 1977, Hemborg and Lundberg 1998, Newton 2009, Remisiewicz et al. 2009, Remisiewicz 2011). Moult not only requires significant energy for generating new feather material which equals approximately 25% of dry body mass (Newton 1968), but the loss of flight feathers in particular creates a gap in the wing and a reduction in flight efficiency (Chai 1997, Hoye and Buttemer 2011). It is therefore crucial for the birds' survival that moult occurs in a place and at a time where the energetic impacts of feather loss and replacement can be controlled in relation to available resources. In long-distance migrant waders which breed in northern temperate regions and spend the non-breeding season in the tropics or further south, the norm is for birds to moult on the non-breeding grounds where they have time and resources to be able to put the required additional energy into feather growth (Pearson 1973, Ginn and Melville 1983, Kjellén 1994, Newton 2010). However even within species there are marked differences in moult strategies between populations (Holmes 1971, Serra 2000, Barshep et al. 2013). Obtaining a good understanding of these is important for contributing to their effective conservation (Evans et al. 1991). Moult has generally been studied far less than breeding or migration and thus there are still large gaps in our knowledge of when and how birds moult and the impact on their annual lifecycle (Newton 2009).

Moult studies—a quantitative description

To undertake a study of the full moult of all feather tracts in a bird is a major undertaking and fraught with challenges of obtaining data from moult observations of body and covert feathers that are measureable and comparable. However, moult of other feather tracts is frequently completed within the period of primary moult (Ashmole 1962, Spaans 1976, Pearson 1981, Ginn and Melville 1983). Thus, consideration of primary moult timing and duration provides a good indication of overall moult for a species. Furthermore, there are tried and tested methods of recording and analysing moult in order to estimate timing and duration, the key parameters in moult, which are widely used such that making comparisons between species, populations and locality are possible (Newton 2009, Remisiewicz 2011).

Moult scores were taken for this study following the standard method by (Ashmole 1962) and (Ginn and Melville 1983): primary feathers are numbered descendently, namely the inner primary that is often first to moult is ‘P1’ and the outer primary, P10; an old, unmoulted feather is scored '0', a new fully-grown feather is scored '5' and the stages in between are scored 1-4. Each stage is clearly defined making comparison between observers possible. However, as the inner primaries are considerably smaller in size than the outer, feather mass between primaries is therefore considerably different. Thus, using the basic moult score, whereby each feather is scored according to how far grown it is and the sum of the scores of the primaries is then plotted against date, does not allow for accurate estimation of start date and duration of primary moult (Summers 1976, Ginn and Melville 1983). A better measure is that of the percentage of feather mass grown (PFMG) (Summers et al. 1983, Underhill and Zucchini 1988). The PFMG is calculated by transforming the basic moult score into a moult index following Underhill and Summers (1993). The moult index runs from a score of zero, not yet moulted, then becomes a continuous variable from zero to one (exclusive) indicating the progress through moult, to a final score of one, indicating that moult is complete. The moult index is assumed to increase linearly through time. From this moult index, it is possible to estimate start date and duration of moult using the Underhill-Zucchini moult model (Underhill and Zucchini 1988). While this model dealt with the challenges of moult analysis and allowed comparison across a wide range of localities (e.g. Underhill et al. 1992), for many years it remained a major challenge to utilise by most researchers because it was programmed in FORTRAN, and required substantial experience and knowledge of the iterative algorithm to ensure that the result converged correctly (Oschadleus 2005). With the advance of the open source program 'R', Erni et al. (2013) developed a package to run the analysis easily. As a result, the number of studies on moult has greatly increased (e.g. Rohwer and Rohwer 2013, Bonnevie and Craig 2014, Jukema and Wiersma 2014, Dietz et al. 2015).

Typically, the Underhill-Zucchini moult model has been applied to the whole primary tract of the wing, taking into account all ten of the large primaries (the eleventh, outermost primary of waders is so small as to be excluded from analyses) (Underhill et al. 1990, Pearson and Serra 2002, Summers et al. 2004, Round et al. 2012). However, Serra (2000) and Underhill (2003) applied the moult model to individual primary feathers so as to investigate the detail of wader moult strategy. In this way it is possible to describe the detail of timing and duration for each primary relative to each other thus revealing interesting differences in strategy between populations as a result of local environmental conditions. This approach to describing the pattern of moult is referred to in this thesis as the "per primary analysis". A data type 2 analysis was performed on each individual primary to obtain the parameters of moult for each (Serra 2000, Underhill 2003) where the dataset was large enough to allow this.

The Underhill-Zucchini moult model requires the relative feather masses of the primaries; these can be taken from any similar-sized species within the same family without greatly affecting the results obtained from the Underhill-Zucchini moult model analysis (Underhill and Summers 1993). Relative primary masses for this study were obtained from Terek Sandpipers and Greater Sand Plovers in Australia (C.D.T. Minton unpubl. data) following the methods of Summers et al. (1983) and Underhill and Joubert (1995). The relative feather masses for the Greater Sand Plover were used for the moult analyses of both Greater Sand Plover and Lesser Sand Plover.

Statistical model fitting is both science and art. "Underhill's rule of thumb" for model-building is that a minimum of around seven data points are needed per parameter fitted (L.G. Underhill pers. comm.). Thus, to fit the three-parameter moult model, the minimum number of data points is about 20. These data points then need to be well scattered both through the moult period and through the value of the moult index. Larger samples are preferable. Being a parametric model, the Underhill-Zucchini moult model is sensitive to the presence of outliers, especially when the sample size is small. Thus, each model which is fitted needs to be assessed both qualitatively (do the fitted parameters make sense?) and quantitatively (given the estimated standard errors, are the estimates of the parameters useful?).

Underhill and Zucchini (1988) chose a particular parameterisation for their moult model. In essence, their model says that the starting date has a normal distribution with a mean and a standard deviation, and that each bird has the same moult duration. The mean measures the mid-date at which moult starts in the population, and the standard deviation provides a measure of how synchronized moult is. However, this is an asymmetric parameterisation, placing the emphasis on the start date, and downplaying the estimate of the end date (start date + duration). A symmetric parameterisation would have been to assume that the date at which the moult index reaches 0.5 (i.e. half way through moult) has a normal distribution with mean and standard deviation. The start date and the end date are then estimated symmetrically around the "mid-date" as mid-date minus 0.5×duration, mid-date plus 0.5×duration. In Chapter 9 of this thesis, it is sensible, for reasons explained there, to make use of the symmetric parameterisation.

Moult studies of waders around the Indian Ocean rim

Breeding populations of many species of wader are spread east-west across the Palearctic in an often continuous distribution (e.g. Whimbrel *Numenius phaeopus*, Common Greenshank *Tringa nebularia* (del Hoyo et al. 1996). In the non-breeding season, these birds move south and are divided east and west by the Indian Ocean, spreading out along the coastlines of eastern Africa, the Middle East, southern Asia, and Australasia. Thus, generally eastern-breeding populations migrate south into South East Asia and Australia and the western populations migrate south into the Middle East and Africa. The perimeter of the Indian Ocean basin, therefore, harbours distinct populations of migrant waders which face different challenges to find and reach their non-breeding sites, generating a range of different strategies for migration and moult.

The majority of published studies of moult in waders using the Underhill-Zucchini moult model has been at localities on the East Atlantic Flyway, along the western coastline of Europe and Africa (compiled in Table 1 of Chapter 9). The primary moult patterns of only two species have been described at several sites along the rim of the Indian Ocean: Serra (2001) did moult analyses for the Grey Plover *Pluvialis squatarola* in South Africa, Kenya, India and two sites in Australia and Barshep (2011) did similar analyses for the Curlew Sandpiper *Calidris ferruginea*. This thesis extends the studies to five species, adding Lesser Sand Plover, Greater Sand Plover and Terek Sandpiper. There were contrasting patterns between Grey Plover and Curlew Sandpiper. The Grey Plover showed a clear pattern of commencing moult later at localities farther south, whereas the Curlew Sandpiper showed a far more irregular pattern. One of the objectives of this thesis is to explore this comparison further.

Study sites

This study looks at four populations of the three species of migrant wader, Lesser Sand Plover *Charadrius mongolus*, Greater Sand Plover *C. leschenaultii*, and Terek Sandpiper *Xenus cinereus* that occur around the Indian Ocean basin during the non-breeding season. An additional population of Terek Sandpipers in South Africa is also considered for comparison within that species (Fig. 1). The main non-breeding area considered was the Kenyan coast where birds were trapped at Mida Creek (3°20'S 39°58'E). Mida Creek is a tidal inlet c. 32 km^2 in size with c. 580 ha of intertidal muddy sand flats fringed by mangrove forest and which form rich feeding grounds for up to c. 10,000 migrant waders (Hockey et al. 1999, C. Jackson unpubl. data). The northernmost non-breeding area considered was south-east India where birds were trapped at two sites: Mandapam (9°17'N, 79°8'E) and the Great Vedaranyam Swamp (10°18'N, 79°51'E) 250 km to the north. Mandapam is a narrow strip of land stretching into the Palk Strait with Palk Bay to the north and the Laccadive Sea to the south. The Great Vedaranyam Swamp is an area of c. 350 km^2 consisting of mudflats, lagoon and salt marsh with extensive areas that are good foraging grounds for waders (Balachandran 1990). On the eastern boundary of the Indian Ocean, data were considered from Eighty Mile Beach (19°29'S 121°13'E), the major non-breeding grounds for waders that lies on the north-western Australia coastline between Broome and Port Hedland. The beach stretches for 220 km with extensive intertidal areas which are rich in invertebrates thus supporting large numbers of waders (c. 20% of migrant waders that spend the non-breeding season in Australia) (Minton et al. 2013a). The most southerly population studied was birds reaching the wetland complexes along the southern coastline of Victoria, south-eastern Australia (38°22'S 145°32'E). These wetlands hold up to 40,000 migratory waders during the austral summer and form an important refuge for these birds to moult (Minton et al. 2012). A fifth location, the Western Cape, South Africa (33°05'S 18°17'E), was considered for Terek Sandpiper data for comparison of moult strategy with both the other four locations and with the only other previous study undertaken on the study species from Africa by Walter and Sinclair (1981). Langebaan, the main study site, is also an area of extensive intertidal habitats that is rich in invertebrates that migrant waders feed on (Robertson and Cooper 1981).

Location and methods for moult data collection

Between 1976 and 2014 Lesser Sand Plovers, Greater Sand Plovers and Terek Sandpipers were trapped and ringed at the above locations using either mist nets (Kenya, South Africa, India) or cannon-netting (Australia). Indian birds were mostly ringed under the Bombay Natural History Society's Bird Migration Project (Balachandran 1990); in north-western Australia the Australasian

Wader Study Group undertake annual wader-ringing expeditions to capture, mark and measure waders as part of long-term studies of their migration and ecology. Data from south-eastern Australia were collected by the Victorian Wader Study Group which similarly undertakes regular wader ringing activities. Terek Sandpipers in South Africa were ringed through activities of the Western Cape Wader Study Group and data from Kenyan birds were collected by A Rocha Kenya from wader caught during regular wader-ringing activities. Birds were ringed with metal numbered rings from the ringing scheme of the region where the birds were caught. In Australia and from 2010 in Kenya colour flags were also attached above the tibio-tarsal joint in an attempt to increase recoveries from birds sighted along the flyway (Jackson 2016). The age of each bird was determined, where possible, to 'first year' and 'sub-adult', and 'adult' by plumage characteristics described by (Prater et al. 1977) and from personal observation (D.J. Pearson pers. comm., C. Jackson pers. obs.). An 'adult' bird was taken as one that was in its second year or more on the understanding that most birds appear to breed in their second year, albeit in the second half of that year (Prater et al. 1977). A bird that can be identified as at the start of its second year from the moult progression combined with feather condition (worn or unworn), is termed as 'sub-adult'. These birds very soon 'become adults' as the moult progresses and the plumage becomes indistinguishable from that of an older adult. Sub-adults, often termed 'second-year birds' in other studies e.g. (Serra et al. 1999, Summers et al. 2010), either have retained some juvenile plumage or show evidence of feathers moulted during a distinct first year moult that can be distinguished from adult feathers from the condition of the feather, particularly the tip. However, these features tend to be lost by October/November and thereafter all such birds are aged as 'adult'. Birds with plumage characteristics which left the age unclear were not aged and were omitted from analyses.

Primary moult scores were taken following the standard method by Ashmole (1962) and Ginn and Melville (1983) with the primaries numbered descendently, namely the inner primary that is often first to moult is P1 and the outer primary, P10 (Ginn and Melville 1983).

For the south-eastern Australia population, the dataset was small and was particularly poorly distributed for P1 to P3 when doing a per primary analysis (Chapter 2, Table 6). To obtain a more sensible result a covariate analysis was used with primary as the covariate and fixing the standard deviation. This gave better results though the details of the output are still not ideal but the overall result 'fits' with other results for the species. For sub-adult birds in south-eastern Australia, given the very small dataset (n = 4), the same duration was assumed as for sub-adult birds in north-western Australia and a mean start date calculated back from the four points in the dataset.

Structure of the thesis

The earlier chapters in the thesis focus on the moult strategies of three wader species along the rim of the Indian Ocean with studies from India, Kenya, Australia and South Africa for the Terek Sandpiper. The discussions in each of these chapters focuses mainly on key points arising out of the chapter itself. This avoids having repetitive discussions of interspecies comparisons in each chapter. A multi-species analysis of moult is postponed to Chapter 9. This chapter contains a comparison of the moult strategies of waders around the Indian Ocean rim. Besides the three species considered in this thesis, there are an additional two species for which Underhill-Zucchini moult analyses have been undertaken. The chapter also contains a comparison with moult strategies along the best-known flyway, the East Atlantic Flyway, along the rim of the eastern Atlantic Ocean. The chapter also contains an overall comparison of shorebird moult strategies.

In the species chapters, discussions are deliberately didactic, providing a record of the biological decisions made in relation to the inclusion/exclusion of age groups in analyses, and in the choice of "data type" in the Underhill-Zucchini moult model. The data sets considered in the thesis yielded an interesting variety of complex issues in the application of the model. It is hoped that this decision trail will aid future researchers faced with similar issues in analyses of moult.

Ch.1 Introduction to thesis

Ch.2 Moult of Lesser Sand Plovers – overall moult dates and duration for adult and first year Lesser Sand Plovers; per primary moult differences between locations are described and interpreted.

Ch.3 Moult of Greater Sand Plovers – overall moult dates and duration for adult and first year Greater Sand Plover; per primary moult differences between locations are described and interpreted.

Ch.4 Moult of adult Terek Sandpipers – overall moult dates and duration for adult Terek Sandpipers; description and interpretation of per primary moult differences between locations.

Ch.5 Moult of immature Terek Sandpipers – overall moult dates and duration of first year and sub-adult Terek Sandpipers; per primary moult differences between locations are described and interpreted.

Ch.6 Moult of Terek Sandpipers in South Africa – a description of the moult strategy of Terek Sandpipers in South Africa and a comparison with other populations.

Ch.7 The status and migration of the Lesser Sand Plover and the Greater Sand Plover – a synthesis of what is currently known about the distribution, population status and migration routes and strategy of Lesser Sand Plovers and Greater Sand Plovers.

Ch.8 The status and migration of the Terek Sandpiper – a synthesis of what is currently known about the distribution, population status and migration routes and strategy of Terek Sandpipers.

Ch.9 A comparison of primary moult strategies in migrant waders – a comparison of moult strategies for migrant waders in relation to latitude of moulting grounds and size of bird.

Conclusion and recommendations – this section pulls together, in bullet point format, the main insights that emerged from this project, and summarizes the recommendations for follow-on studies.

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Tables and figures

Table 1. Relative percent feather masses for Greater Sand Plover and Terek Sandpiper primary feathers (C.D.T. Minton unpubl. data).

Primary	Greater Sand Plover	Terek Sandpiper
P1	3.7	4.1
P2	4.4	5.0
P3	5.4	6.1
P4	6.8	7.4
P5	8.5	9.2
P6	10.4	10.7
P7	12.2	12.1
P8	14.3	13.7
P9	16.2	15.2
P10	18.0	16.4

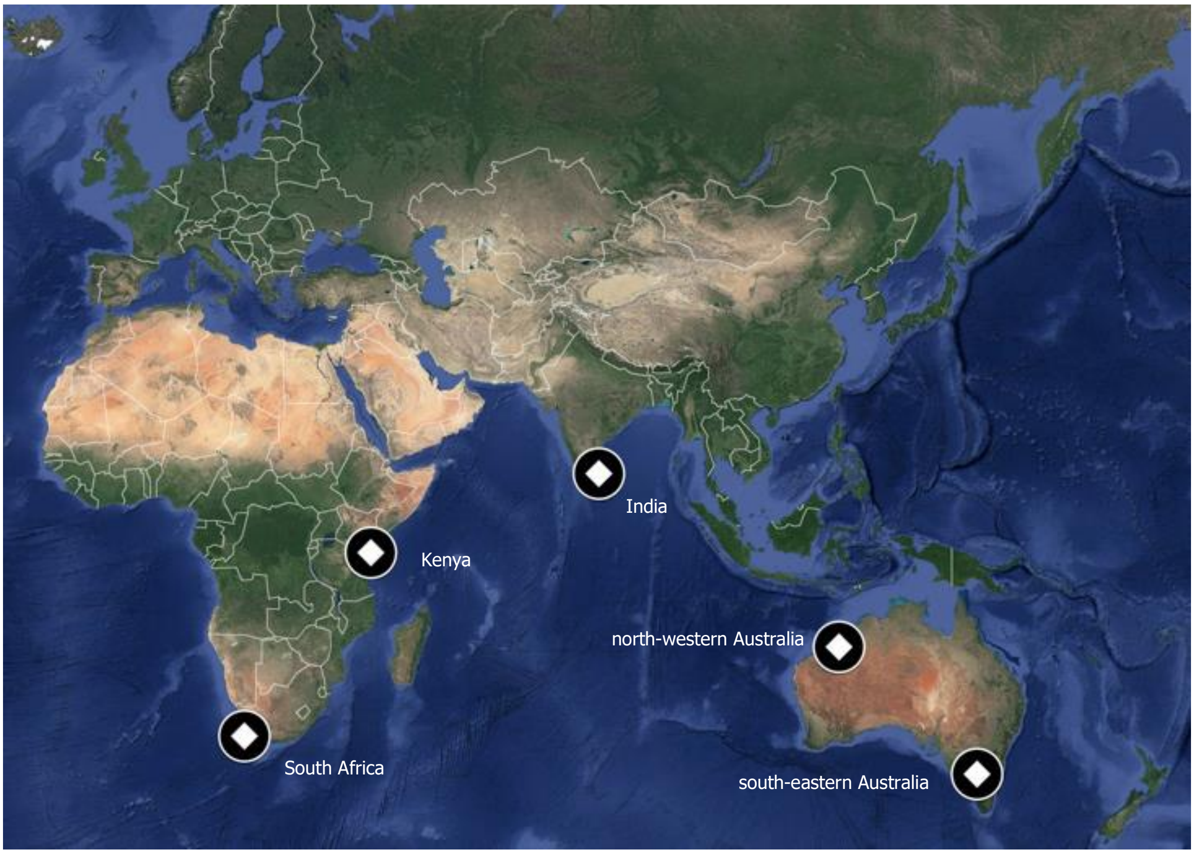

Fig. 1. Location of study sites for this study: Western Cape, South Africa; Kenya coast; south-eastern India; north-western Australia; south-eastern Australia.

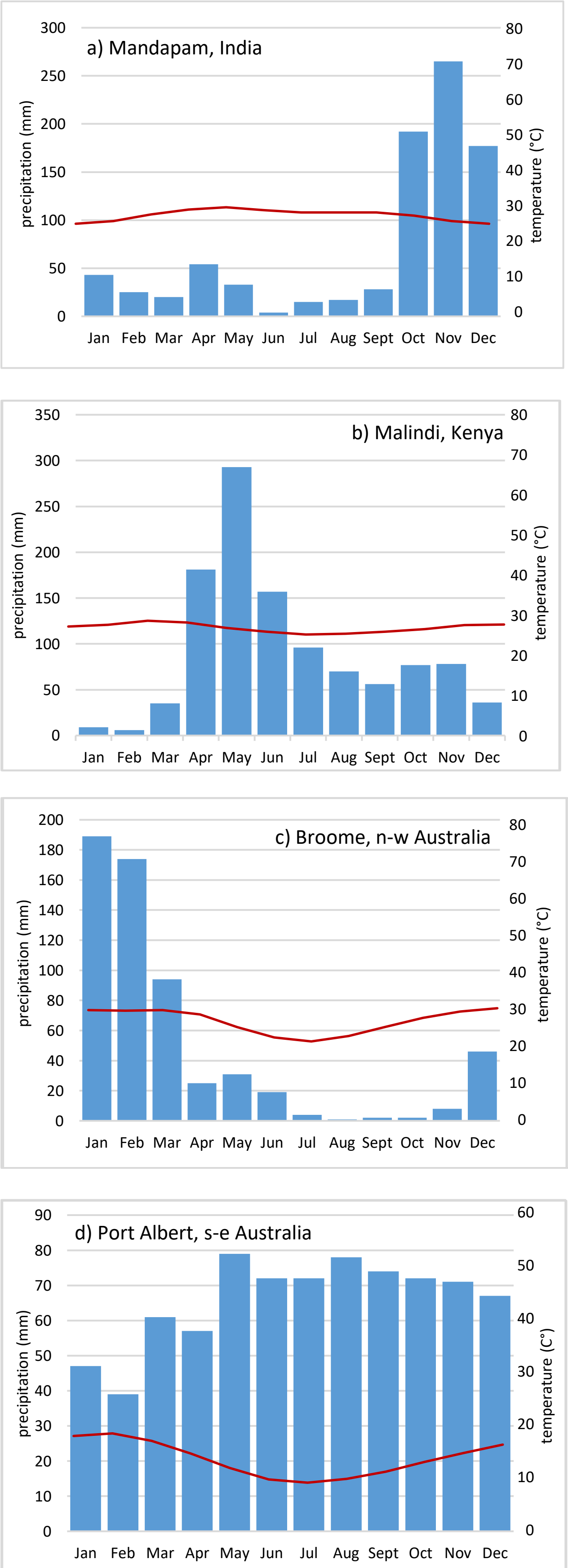

Fig. 2. Rainfall and temperature for a) Mandapam (south-eastern India), Malindi (Kenya coast), Broome (north-western Australia) & Port Albert (Victoria, south-eastern Australia). *Source: http://en.climate-data.org/.*

Chapter 2

Moult of Lesser Sand Plovers in Kenya, India and Australia

Chapter 2. Moult of Lesser Sand Plovers in Kenya, India and Australia

Introduction

The Lesser Sand Plover *Charadrius mongolus* is a poorly known long-distance migrant wader; it breeds in central and eastern Asia and the bulk of the population spends the non-breeding season on the coastline of the Indian Ocean: eastern Africa, south-central and east Asia, and southward to south-eastern Australia (Cramp and Simmons 1983, Hayman et al. 1986, del Hoyo et al. 1996). Five races of *C. mongolus* are recognised: three form the more westerly breeding '*atrifrons* group' which includes *C. m. pamirensis*, *C. m. atrifrons* and *C. m. schaeferi* and the remaining two the easterly-breeding '*mongolus* group' containing *C. m. mongolus* and *C. m. stegmanni* (Fig. 1). From an analysis of museum specimens, *C. m. pamirensis* migrates south-west to spend the non-breeding season in India, the Middle East and south to the East African coastline (Cramp and Simmons 1983, Hayman et al. 1986, Hirschfield et al. 2000). Birds reaching north-western Australia are mostly from the '*mongolus* group' and are considered the larger and paler nominate race (Barter 1991, Barter and Davies 1991, Hirschfield et al. 2000) which breeds east and north of Lake Baikal. Lesser Sand Plovers reaching south-eastern Australia are also thought to belong to the '*mongolus* group' but consist mainly of the *stegmanni* sub-species (Barter and Davies 1991) which breeds in Kamchatka, north-eastern Russia (Fig. 1).

Birds of the far northern populations of the nominate and *stegmanni* sub-species have a substantially longer migration to undertake to reach their non-breeding grounds Parameters of estimated moult per primary and for whole primary tract for adult Greater Sand Plovers in north-western Australia excluding birds with suspended moult (n = 7,346) in Australia (up to c. 13,500 km) than do birds of e.g. the race *atrifrons* some of which only reach southern India (c. 3,000 km) (Fig. 1, Table 7). Differences in distances covered for migration to non-breeding (and moulting) grounds will influence the timing and duration of moult in a species (Serra 2001). Little is known about the moult of the Lesser Sand Plover and the strategies of the different sub-species and populations (Prater et al. 1977). Cramp and Simmons (1983) and Hirschfield et al. (2000) undertook an analysis of museum specimens and Barter (1991) discussed the moult of a small sample from Australia. Nothing has been published relating to the population spending the non-breeding season on the East African coast.

This chapter describes the moult of the various subspecies of Lesser Sand Plover on the coastlines of East Africa, south-eastern India, and north-western and south-eastern Australia. It discusses the subspecies involved in each region and differences in moult timing and strategy between regions.

Methods

Primary moult scores were obtained from Lesser Sand Plovers in Kenya, India and Australia. The Kenyan birds were ringed during regular wader-ringing sessions on site at Mida Creek, Kenya (3°19'S 39°57'E) between 1978 and 2014. Indian data were collected during regular wader ringing carried out at Mandapam (9°17'N, 79°8'E) and at the Great Vedaranyam Swamp (10°18'N, 79°51'E) in south-eastern India between 1985 and 2014. The Australian birds were caught between 1982 and 2012 by the Australasian Wader Study Group in north-western Australia at 12 sites centred on 19°15'S 120°20'E and in south-eastern Australia from eight sites centred on 38°22'S 145°32'E. Adult and immature birds (both first year and sub-adult—those finishing their first year of life and entering the second year) were distinguished as far as possible using (Prater et al. 1977) and previous experience. Further details on location and methodology have been described in Chapter 1.

For the moult analysis using the Underhill-Zucchini moult model an estimate of the relative mass of each individual feather is required (Chapter 1). Underhill and Summers (1993) showed that the relative feather masses of all migrant shorebirds were similar. Differences in the calculation of percent feather mass grown (PFMG), whilst still small, were greatest between different families. Relative primary masses were thus obtained from Greater Sand Plover *Charadrius leschenaultii* feathers in Australia (C.D.T. Minton unpubl. data) following the methodology laid out by (Summers et al. 1983, Underhill and Joubert 1995) and used for the Lesser Sand Plover moult analysis.

To test whether there were regional differences in growth rates, (defined as (relative feather mass) / (moult duration for that feather)), I used India as the baseline, and computed the ratios of feather growth rate for P1 to P8 for Kenya, north-western Australia and south-eastern Australia. For P9 and P10 the sample sizes were small in north-western Australia and south-eastern Australia, and the Standard Errors of growth rates were large. If growth rates were equal for these primaries, the ratios would be equal to one. If there were increases in growth rates relative to India, the growth rates would increase consistently. I tested for this by calculating the correlation coefficient between the relative growth rates and the integers from 1 to 8.

Results

A total of 3,368 Lesser Sand Plovers (LSP) moult scores were used from four non-breeding areas: 1,657 in India, 1,015 in Kenya, 578 in north-western Australia and 119 in south-eastern Australia (see Table 1 for a breakdown by age class).

Adult moult

Kenya

Moult scores for the primary tract of adult Lesser Sand Plovers in Kenya were analysed using the Underhill-Zucchini model with data type 4 (Table 2). The estimated start and end dates for the whole primary tract for adult LSPs in Kenya were 2 October to 15 February, respectively, with an estimated duration of 136 days (Fig. 2b). Estimated standard deviation in start date was 34 days thus 95% of birds were estimated to have started primary moult between 27 July and 8 December. The estimated mean rate of feather growth for the whole primary tract was 0.736% per day (Table 2).

Estimating moult start and duration for each primary individually, 'per primary', P1 was estimated to start moulting on 11 September and P10 to end on 13 February giving a duration of 154 days (Figs. 3b, 4b, Table 4). The estimated duration of moult per primary ranged from 17 days (P2) to 22 days (P10) with an average duration of 20 days (Fig. 6); in contrast, the estimated feather growth rate varied between 0.20% of total primary mass per day for P1 to 0.83% per day for P10, a four-fold increase (Fig. 8b, Table 4). P2 was dropped 11 days after P1 had started and P3 more quickly at eight days later. Thereafter the time between feathers increased to a maximum of 22 days between P8 and P9 (Figs. 6b, 7b). Given the time between feathers dropping and the duration of moult per primary, there was a greater degree of overlap between adjacent growing feathers earlier in the moult period than near the end. On average, there was no overlap between P7 and P8 and a gap of one day between P8 and P9 (Figs. 6b, 9b, Table 4). The largest number of feathers moulting simultaneously was, on average, two (Table 4).

The average estimated date for 50% PFMG in Kenya was 18 November which was 56 days after that for India. With an estimated average distance of 6,400 km from the main presumed breeding grounds of *C. m. pamirensis* to Kenya, the average moult of adult Lesser Sand Plovers here was 16 days per 1,000 km later than for those in south-eastern India (Table 7).

North-western Australia

Eleven adult Lesser Sand Plovers (3%) were found to have suspended primary moult on arrival in north-western Australia. For the whole primary tract of adult Lesser Sand Plovers in north-western Australia, the estimated mean start date was 16 September and duration of moult was 127 days, with an estimated mean end date of 21 January (Fig. 2c, Table 2). With a standard deviation in start date of 27 days, 95% of birds were estimated to start moult between 26 July and 9 November. The estimated mean rate of feather growth for the primary tract as a whole was 0.786% per day.

An analysis of individual primary moult showed that the inside primaries were moulted slowly; the estimated start date of P1 was 18 August with a duration 35 (Figs. 3c, 4c, Table 5). The end date for P10 was estimated as 17 January thus the overall estimated duration for all primaries on a per primary basis was 152 days giving an average growth rate of 0.657% per day (Table 5). The estimated duration of each primary decreased over the moult period from 35 days for P1 to the shortest of 19 days for P7 (Fig. 6c, Table 5). The average duration per primary was 25 days. The estimated average number of days between primaries starting moult began with a gap of 17 days between P1 and P2 and thereafter varied between 11 and 15 days for P2 – P8, increasing slightly to 16 days for P9 before a shorter gap of 9 days to start moulting P10 (Fig. 6c, Table 5). The rate of moult per day started slowly at 0.11% of total primary mass per day for P1 and increased by a factor of 6.6 to peak at 0.71% per day for P9 (Figs. 7c, 8c; Table 5).

With the long duration of moult of each primary there was considerable overlap between adjacent feathers throughout primary moult; the overlap between P1 and P2 was 50%, decreasing to 27% between P7 and P8 and increasing to 60% between P9 and P10 (Fig. 9). On average, there was an overlap of three feathers moulting simultaneously for the inner three primaries, P1–P3, where 10% of the duration of growth for P1 overlapped with P3 (Fig.9c, Table 5). Thereafter, however, there were never more than two feathers moulting simultaneously.

The average estimated date for 50% PFMG in north-western Australia was 18 November which was 35 days after that for India. With an estimated average distance of 8,700 km from the main presumed breeding grounds of *C. m. mongolus* to north-western Australia, the average moult of adult Lesser Sand Plovers here was 6 days per 1,000 km later than for those in south-eastern India (Table 7).

South-eastern Australia

In south-eastern Australia, the estimated mean start date of adult moult for the whole primary tract was 18 November, estimated duration of moult was 105 days and thus the end date was 1 March. Standard deviation in start date was estimated at 21.4 days thus 95% of adult Lesser Sand Plovers in south-eastern Australia were estimated to start moult between 7 October and 29 December (Fig. 2d, Table 6). Estimated mean rate of feather mass grown for the whole primary tract was 0.954% per day.

The per primary analysis of moult for Lesser Sand Plovers in south-eastern Australia gave an estimated start date of 7 September for P1 and an end date for P10 of 22 February (Fig. 3d, Table 6). There were few data for early moulting primaries and thus the standard deviation in start date for P1 was estimated at 45.7 days. Using the per primary analysis, therefore, 95% of birds were estimated to start moult between 7 June and 7 December. Thus, the estimated duration of the primary moult using this approach was 168 days. P1 was estimated to take the longest to moult at 37 days and P7 was the fastest with a duration of 17 days. Average duration across the primaries was 26 days. P9 showed an out of pattern large increase in duration (30 days) which is considered to be a result of poor data coverage rather than an actual duration of this length (Figs. 6d, 7d, Table 6). Growth rates were estimated to start off slowly (0.1% of primary feather mass per day for P1) and increase by a factor of 9.6 to P10 growing in 19 days at a rate of 0.97% per day (Fig. 8d, Table 6). The estimated average feather growth rate for the whole primary tract using the per primary analysis was 0.595% of total primary mass per day.

There was an uneven pattern of overlap in moult between primaries with a range in percentage overlap between 60% for P1 overlapping with P2 and 8% for P6 with P7 (Fig. 9d), however the pattern seen here is likely more due to the uneven spread of data in the dataset than a reflection of a real pattern. Overlap occurred between adjacent feathers right across the primary tract but at no time were more than two feathers moulting simultaneously (Table 6).

The average estimated date for 50% PFMG in south-eastern Australia was 9 January which was 87 days after that for India (Table 7). With an estimated average distance of 13,500 km from the main presumed breeding grounds of *C. m. stegmanni* to south-eastern Australia, the average moult of adult Lesser Sand Plovers here was 8 days per 1,000 km later than for those in south-east India (Table 7).

India

Moult scores for the whole primary tract of adult Lesser Sand Plovers in south-east India were analysed using data-type 2 of the Underhill-Zucchini moult model (Table 2). The estimated start and end dates for the whole primary tract for adult LSPs in India were 17 July to 12 January, respectively, with an estimated duration of 178 days (Fig. 2a). Estimated standard deviation in start date was 54 days thus 95% of birds were estimated to have started primary moult between 2 April and 1 November. The estimated mean rate of feather growth for the whole primary tract was 0.561% per day. The average estimated date for 50% PFMG for adult Lesser Sand Plovers in south-eastern India was 14 October (Table 7).

Estimating moult start and duration for each primary individually, P1 was estimated to start moulting on 10 August and P10 to end on 10 January giving a duration of 153 days (Figs. 3a, 4a, Table 3). The estimated duration of moult per primary ranged from 19 days (P5) to 38 days (P10) (Fig. 6, Table 3). The average duration per primary was 24 days. On average P2 was dropped just under three days after P1 had started. Thereafter the time between feathers moulting increased to a maximum of 27 days between P9 and P10 (Fig. 6, Table 3). Estimated average feather growth rate for the all primaries using the per primary analysis was 0.654% of total primary mass per day. The estimated feather growth rate per individual primary increased by a factor of 3.6 from 0.17% of the total primary mass grown per day (P1) to the 0.61% per day for P8 (Fig. 8a, Table 3).

The relatively long estimated duration of feather growth and short gap between feathers moulting early in the moult period led to a large overlap in feather growth between adjacent inner primaries. At all times during primary moult at least two adjacent feathers were moulting simultaneously (Table 3). Up to 88% of P1 growth overlapped with P2 and on average the four inner primaries were moulting simultaneously for four days (20% of growth period of P1) (Figs. 6a, 7a, 8a, Table 3).

Comparative results between locations

I used the estimated date at which PFMG reaches 50% as the basis for comparison of timing of moult between locations in relation to latitude (Fig. 10, Table 7). The average distance from the breeding grounds for each non-breeding population studied was estimated using what information is available (Table 7). Using this, the mid-moult date for Lesser Sand Plovers at the three southern hemisphere locations (Kenya and the two in Australia) was compared to that of the population in India with relation to the distance travelled from the breeding grounds. Birds in Kenya moulted on average 16 days later than in India. In north-western Australia, they moulted six days later and in south-eastern Australia, eight days later than in India. Thus, on average, for every 1,000 km farther from the breeding grounds, adult Lesser Sand Plovers moulted an additional 10 days after the population in India (Table 7). The general trend was the farther south travelled, the later the moult as shown by the regression line (Fig. 10). Birds in Kenya, however, delayed moult more than might be expected. The mid-moult date in India was 14 October; in Kenya, the mid-moult date was almost two months later on 9 December; in north-western Australia, mid-moult occurred on 18 November, three weeks earlier than Kenya; the southernmost population in south-eastern Australia had a mean mid-moult date of 9 January, nearly three months after the Indian birds and three weeks after the northern Australian population (Fig. 10, Table 7).

Duration of moult for all except the most southern site was estimated at around 153 days (Fig. 11). The south-eastern Australia population was estimated to take 168 days to moult, but given the uncertainty around the actual start date (see above), the actual duration is more likely to be shorter and thus closer to that of the other locations. The same effect is seen in the estimated mean PFMG per day at each location where the three more northern sites were all estimated at a similar overall growth rate of around 0.65% per day while the south-eastern Australian population showed a slower growth rate (Fig. 12), but affected by the particularly slow, drawn-out start resulting from the effect of a poor data set for the inner primaries.

The ratios of growth rates between the other three regions and India were estimated from the growth rates in Table 3 to 6. The correlation between Kenya and India was not significant ($r = -0.23$, $P > 0.05$), but was significant for both north-western and south-eastern Australia ($r = 0.78$ in both cases, $p = 0.012$) indicating growth rates increased in pace at these two localities relative to India.

Sub-adult moult

Kenya

For Lesser Sand Plovers aged as sub-adult in Kenya, 12 had moult scores that were possible to use for analysis (Table 1). The estimated start and end dates for sub-adult Lesser Sand Plovers in Kenya were 9 September and 30 January respectively giving an estimated duration of 143 days (Fig. 13a, Table 8). Given a standard deviation in start date of 24 days, 95% of sub-adult birds were expected to start moult between 24 July and 26 October. Average growth rate of primaries for the whole wing was 0.700% of total PFMG (Table 8).

North-western Australia

51 birds were aged as sub-adult in north-western Australia (Table 1). On average, these were estimated to start moult on 17 July and took 127 days to complete thus finishing on average on 21 November (Fig. 13b, Table 8). Standard deviation in start date was estimated at 31 days thus 95% of sub-adult Lesser Sand Plovers were estimated to start moult between 17 May and 16 September. The average growth rate for all the primaries was 0.787% per day of total feather mass grown (Table 8).

South-eastern Australia

Four sub-adult Lesser Sand Plovers were caught in south-eastern Australia. The small size of the dataset did not allow the use of the Underhill-Zucchini moult model to estimate the moult parameters. Duration of moult was therefore assumed to be the same as in north-western Australia. The mean start date was thus calculated from the datapoints available. Moult was estimated to begin on average on 29 June and assumed to complete 127 days later on 3 November (Fig. 13c, Table 8). The average growth rate was assumed to be the same as in north-western Australia at 0.787% total primary feather mass grown per day (Table 8).

India

There was no evidence for a distinct group of sub-adult birds following a strategy different to the first years and adults. Rather the first year birds had an extended moult (see below) that overlapped with the start of the adult moult which thus could appear as a sub-adult moult.

First Year moult

First year Lesser Sand Plovers at all four locations followed three different moult strategies in varying proportions of the population: 1) retention of all juvenile primaries throughout the first year until moulting in synchrony with adults at the start of their second year; 2) the moulting of a varying number of outer primaries during the second half of their first year, and 3) a ‘normal’ complete ascendant moult preceding the first synchronised adult moult. The most commonly followed strategy was to not moult any primaries in the first year but to retain them through to the adult moult at the start of their second year. Moulting some outer primaries was the least common strategy employed (Fig. 14).

Kenya

The majority (77%) of first year birds in Kenya followed the first moult strategy, that of ‘no moult’. A small percentage (6%) moulted some outer primaries and 17% carried out a normal ascendant moult (Fig. 14b). For the group undergoing normal moult, the lack of data points over 50% PFMG was such that it did not allow for an analysis using the Underhill-Zucchini moult model (Fig. 18a). The first birds to be found in moult were encountered in February and by early May at least one had completed moult of 70% of its relative feather mass. Mid-March was the date by which a substantial fraction of the first year birds were in moult (Fig. 18a) and can be used as a provisional estimate of the commencement of first year moult

Of birds following the second strategy where just some outer primaries are moulted, the most commonly moulted primaries were either three or four feathers (21% for MOP3: ‘Moulted Outer Primaries’, 36% for MOP4). A small proportion moulted only one, two, five or six (7% each) and slightly more seven (14%). No birds were found that moulted more than seven outer primaries (Fig. 15b).

North-western Australia

Only one first year Lesser Sand Plover was caught in north-western Australia between July and January whereas substantial numbers of adults were trapped during this period (Fig. 17). 70% of first year birds in north-western Australia fell into the first moult group which do not moult any primaries in their first year. 4% moulted some outer primaries and 26% carried out a normal ascendant moult (Fig. 14). The absence of first years during the first half of the non-breeding season combined with the lack of moult scores with a PFMG of over 50% (Fig. 14b) prevented an analysis using the Underhill-Zucchini moult model. The first birds found moulting inner primaries occurred in late January and the last with a low PFMG score was the end of April. As a provisional estimate of the commencement of first year moult, mid-March can be used as it was the date by which a substantial fraction of the first year birds were in moult (Fig. 18b). Two birds were caught in June that had completed moult.

Of the 4% of birds following the second strategy of moulting some outer primaries, 43% moulted four feathers and 14% moulted three or five. No birds moulted one, two, six or seven feathers. Note however that the sample size is small (n = 7) (Fig. 15c).

South-eastern Australia

Of the 11 first year birds ringed at this location, equal numbers (45% each) followed the first and third moult strategy. One bird was recorded to be moulting some outer primaries—starting at P6 (Fig. 14d).

India

The results show that the majority (89%) of first year Lesser Sand Plovers in south-eastern India follow the third strategy of undergoing a complete moult (Fig. 14). Only 7% moulted just some outer primaries and 3% retained their juvenile primaries through to the adult moult.

For the majority, the estimated start date for primary moult was 12 April and completion was 22 August with a duration of 133 days. With a standard deviation of start date of 40 days, 95% of first year birds are expected to start moult between 24 January and 29 June (Fig. 16). The average overall growth rate was 0.754% of total feather mass grown per day.

Of birds undergoing a partial moult of some outer primaries only, 43% moulted either four or five feathers (20% four, 23% five). 36% moulted between one and three outer feathers and 20% six to eight (Fig. 15a).

Discussion

The key features of the adult Lesser Sand Plover moult analysis were not only the differences in estimated start date and duration between the different sites but also the striking differences in the estimated start dates and duration of primary moult between an analysis of the primary tract as a whole and that of the per primary analysis (Fig. 4). Taking the whole primary tract, birds in India (9°N) started moult in mid-July followed by birds in north-western Australia (18°S) two months later in mid-September, Kenyan birds (3°S) two weeks after that in early October and lastly the south-eastern Australia population (at 39°S) one and half months later in mid-November (Fig. 5). However, in comparison, an analysis of moult per primary estimated start dates for moult markedly later for the Indian birds (10 August) and earlier for the other locations (Fig. 4, Tables 3-6). The earliest was still India in early August (24 days earlier than the whole tract estimate) followed by north-western Australia in mid-August (29 days earlier) then south-eastern Australia on 7 September (72 days earlier). Kenyan birds showed the smallest difference between results of the two analyses of 21 days earlier on 11 September (Fig. 5).

This strong difference in results between the whole tract and the per primary analysis may be due in part to a lack of data in the early stages of moult (Fig. 2). For the per primary analysis this lack of data will affect both the estimate of start date, 'pushing it forward' to an earlier date, and therefore also the duration, extending it. However, the overall pattern of rapidly moulting inner primaries at the start of moult for birds in India (Fig. 2a) and that of a slow, drawn out moult of these same inner primaries for birds in Australia (Fig. 2c and 2d) emerges as a real pattern of moult and would also affect the start date—putting it forwards in India and drawing it back in the Australian populations.

The per primary analysis showed that the duration of growth for each primary varied from 17 to 37 days (P7 and P1 in south-eastern Australia respectively). Barshep et al. (2011, (Barshep et al. 2013) showed similar results for Curlew Sandpiper *Calidris ferruginea* and noted that the duration of moult for each primary is size-dependent. Thus, variation in mass of different primaries results in different durations of feather growth for each primary. If the underlying assumption of the Underhill-Zucchini moult model is true, that rate of feather material production is constant (Underhill and Zucchini 1988), then the resultant cumulative growth plot from the per primary analysis should be a straight line (Barshep et al. 2011).

The results from analysis of Lesser Sand Plover per primary moult for Kenyan birds (Fig. 4b) showed this to be more-or-less so but not so for Indian and Australian populations (Fig. 4). The rate of feather growth increased strongly from P1 through to P10 at all locations but with a greater difference between inner and outer primaries the farther south the location (Fig. 8). Indian birds showed an increase of average feather growth by a factor of 3.6 between P1 and P10. This was 4.0 in Kenya, 6.6 in north-western Australia and 9.6 in south-eastern Australia (Fig. 7). The most northern population in India showed a more rapid growth of inner primaries, both in growth rate and in shorter interval between feathers moulting (Fig. 3a). The two southern (Australian) populations showed quite a different pattern of a long drawn out start to moult which speeded up with time and each subsequent primary (Fig. 3c, 3d).

Thus, while the analysis of the overall tract would appear to 'look good' (Fig. 2), due to the rapid start of the northern birds and slow start of the southern revealed by per primary analysis, start of moult is actually closer to per primary result with its associated duration. However, as already noted, the lack of data in the early stages of moult does affect the estimation of start date. Thus, the actual start date will lie somewhere in between the estimated date by the full tract analysis and that of the per primary analysis.

Contrasting with these substantial differences in estimated results of start of moult, the mid-moult point where an estimated 50% of feather mass grown is reached is a markedly more reliable point of reference. Even in populations with large differences in estimated start date between the two analyses (e.g. the adult Lesser Sand Plovers in south-eastern Australia, Fig. 5), the two estimates have converged together by 50% PFMG (Fig. 4). Far better for making comparisons of moult strategy between sites and species than start date, therefore, is the use of the estimated 50% PFMG value.

Thus, in this study I have taken the estimated date for the start of moult and duration as that from the per primary analysis with the understanding of it probably being slightly different depending on the volume of data available for the early stages of moult. In the case of Lesser Sand Plovers, this therefore is 10 August in India (duration 153 days), 11 September in Kenya (duration of 154 days), 18 August in north-western Australia (duration of 152 days) and 7 September in south-eastern Australia (duration of 168 days). However, for comparison between sites and species I use the estimated mid-moult date as the best reference point and recommend the same for future studies on moult strategies.

Kenya

Adult Lesser Sand Plovers arrive in Kenya from the end of July to early September (Fogden 1963, Lewis and Pomeroy 1989, Delany et al. 2009). Thus the moult strategy in Kenya is to migrate after breeding and to start primary moult upon arrival in the non-breeding grounds just south of the equator. With a moult duration of 154 days, they have completed on average by mid-February well in advance of needing to fatten up for migration at the end of April / early May (Lewis and Pomeroy 1989, Zimmerman et al. 1996) Chapter 8) to return to their breeding grounds in Kyrgyzstan and Tajikistan (Cramp and Simmons 1983, Hirschfield et al. 2000). Duration of primary growth per primary is more-or-less equal across all primaries while the spacing of feather moult starts in eight days between P2 and P3 after which it *increases* to approximately equal the duration of the last three, outer primaries P8-10 (Fig. 6b). This leads to a large overlap between adjacent moulting feathers in the early stages (52% of P2 overlapping with P3, Table 4) but subsequently little or even no overlap at all between the later, large outer primaries (Fig. 9). This could lead to an apparent 'suspended' moult when examining a bird at this stage and care must be taken in recording such scores so as to not assume a suspended moult when it is actually a slow, protracted moult.

Lesser Sand Plovers in Kenya are of the race *pamirensis* that breed in the Pamir mountains and other mountain ranges of Kyrgyzstan, Tajikistan, Kashmir and northern Tibet, a relatively short distance of c. 6,500 km from the East African non-breeding grounds (Fig. 1). At a flight speed of c. 50 - 70 km/hr (Zwarts et al. 1990, Minton et al. 2013) this would take four to six days of flying. With even two stops en route to re-fuel this would still allow them to complete breeding and reach the non-breeding grounds in a relatively short time. There is therefore no urgency for them to start moult prior to arriving in Africa and they can thus delay until reaching the East African coastline. Moult is steady and growth rates per primary are comparatively high (for P1 being 1.8 that of birds in north-western Australia and 2.5 those in south-eastern Australia) (Fig. 7). The rate increases in proportion to the size of the feathers with maximum growth occurring in January and February. These are the hottest months and follow the short rains when benthic productivity is likely to be high to provide a rich and abundant food source (Mwaluma et al. 2003) to allow birds to complete moult by mid-February. Completing moult by then gives a good margin of time before fattening up for the return migration at the end of April and early May (Delany et al. 2009), Chapter 8).

First year birds in Kenya shared a similar strategy to those in north-western Australia where the majority of birds do not moult in the first year and wait to synchronise with the post-nuptial moult of adults returning from the breeding grounds (Fig. 14). With a sample size of just 11 birds in south-eastern Australia, the results are not definitive but suggest a pattern that is similar though with equal numbers (45%) undertaking a normal complete moult earlier in the year—which was noted and suggested by (Barter 1991). Twelve birds in Kenya were identified as having potentially undergone a distinct sub-adult moult at the end of the first year and starting three weeks prior to the post-nuptial adult moult (Fig. 13a). Data were sparse to confirm this, but the results suggest a moult starting approximately three weeks earlier than the adults (9 Sept compared to 2 October) and of similar duration (one week longer) thus with many sub-adult individuals overlapping with much of the adult moult. Sub-adult birds simply appeared to take advantage of already being on the non-breeding grounds and start moult two to three weeks earlier than the adults. Balachandran and Hussain (1998) suggest that some sub-adult birds in their second year undergo a second moult in India and indeed some moult scores suggest this though no clear pattern emerges. This has not been noted in Kenya.

Australia

Before considering the start date for primary moult, it is important to note the pattern of primary moult followed by Lesser Sand Plovers in Australia which, for both north-western and south-eastern populations, was that of a slow, drawn-out start which speeded up towards the end (Figs. 3, 4, 8). In north-western Australia, the growth rate for the inner primaries was slow (0.11% and 0.16% of total PFMG for P1 and P2 respectively) and even slower in the south-eastern Australia population (0.08% and 0.14% of total PFMG for P1 and P2 respectively) (Figs. 3, 8; Table 5 and 6). As a result, duration of moult per primary was long (Fig. 6c, 6d) and while it reduced across the wing, even the quickest to moult in north-western Australia, P7 (19 days), was similar to the slowest, P10, in the Kenyan population (22 days; Fig. 6). The long duration in moult per primary meant that there was a large level of overlap between moulting feathers (with an average across the whole wing of 43% overlap of one primary's growth with the adjacent subsequent primary in north-western and 35% in south-eastern Australia, Fig. 9c, d). This was nearly double that of Kenyan birds (26%) which on average showed little or no overlap in later primaries (Fig. 9b). However, despite the long duration of over a month for P1 to moult in both Australian populations compared to 18 days in Kenya and 22 in India, the large gap between adjacent feathers starting to moult means there was only ever a maximum average of two primaries moulting simultaneously in south-eastern Australia and three in north-western Australia—and then only for 10% of the moult of P1 (Tables 5 and 6). With the slow start to moult, the estimated start date was a month earlier for the per primary analysis than the full tract analysis in north-western Australia and two and half months earlier in south-eastern Australia. Estimated duration of moult of the whole primary tract was thus extended taking over five months to complete (152 days) in north-western and five and half (168 days) in south-eastern Australia.

When considering the large differences in results from the two estimations, it must be noted that firstly the evidence of some birds arriving in suspended moult, albeit a small number, would extend the estimated start of moult to an earlier date. Secondly, the data limitations in the early stages of moult led to a large standard deviation of the start date for the first primary—and particularly so for the data from south-eastern Australia (Tables 5 and 6). This therefore allows for a variation of around 100 days either way from the estimated date in mid-August (north-western Australia) and early September (south-eastern Australia). It is therefore likely that while the pattern of a longer, drawn-out start to primary moult will be the real pattern of moult, the actual date for the average start of moult lies between that of the per primary and the full tract estimation (18 August and 16 September for north-western Australia, 7 September and 18 November for south-eastern Australia). For the latter, given the particularly few data points for unmoulted and actively moulting birds for P1, P2 and P3 (Table 6), the actual start date is most likely to be closer to that estimated by the full tract analysis (18 November) than the per primary analysis, i.e. towards the end of October. For both analyses, the estimated mid-moult date was effectively the same and is best used for comparison between populations.

Lesser Sand Plovers spending the boreal winter in north-western Australia are mainly of the nominate race *mongolus* from south-eastern Siberia (Barter 1991, Hirschfield et al. 2000). Adults arrive from the breeding grounds in late August and September (Marchant and Higgins 1993). Those birds spending the non-breeding season in south-eastern Australia are considered to be the race *C. m. stegmanni* mixed with individuals of *C. m. mongolus* (Barter 1991, Hirschfield et al. 2000). When taking into consideration the probable migration route followed as indicated by recoveries (Minton et al. 2011), they have extremely long distances of up to 14,500 km to cover from their far northern breeding grounds on the Chukotka Peninsula to the non-breeding grounds in Victoria, south-eastern Australia (Marchant and Higgins 1993, del Hoyo et al. 1996, Hirschfield et al. 2000) (Fig. 1). Detailed arrival dates along the eastern and southern coastline of Australia for Lesser Sand Plovers are not readily available (Marchant and Higgins 1993) but it would appear that the earliest birds can arrive at the end of August with main arrivals in September and into October. Some birds can arrive as late as December (Marchant and Higgins 1993). Taking into consideration the arrival dates of Lesser Sand Plovers in Australia, the implication of the early start date of moult is that while the majority of the population would first arrive at the non-breeding grounds and then start primary moult almost immediately, a proportion of both northern and southern populations would appear to start moulting *before* arrival on the non-breeding grounds (Figs. 3, 4).

On the whole, migrant birds will avoid overlapping moult with actual migration (Zenatello et al. 2002) as the energetic costs of either activity precludes the other if the bird is to survive. However different species and populations within species of some long-distance migrant birds have been shown to employ different moult strategies in order to fit in with the restrictions of their life cycle. Key restrictions include distance from breeding grounds and thus arrival date on non-breeding moulting grounds (Barter et al. 1988, Underhill 2003), time available for moult (Hall and Fransson 2000) and conditions on the breeding and non-breeding grounds (Barta et al. 2008, Barshep et al. 2013). A few species are known to start moult whilst still breeding (e.g. Eurasian Golden Plover *Pluvialis apricaria* (Jukema and Wiersma 2014). Similarly, active primary moult while actually migrating is rare but has been documented with Lapwing *Vanellus vanellus*, Dunlin *Calidris alpina*, Ruff *Calidris pugnax*, Ringed Plover *Charadrius hiaticula*, Greenshank *Tringa nebularia* (Holmgren et al. 1993), Redshank *Tringa totanus* (Pienkowski et al. 1976) and Green Sandpiper *Tringa ochropus* (Cramp and Simmons 1983). It is not unreasonable, therefore, to presume that at least a small proportion of adult Lesser Sand Plovers spending the non-breeding season in Australia drop one or two of the small, inner primaries prior to arrival and moult them slowly whilst completing the migration.

For adult Lesser Sand Plovers reaching north-western Australia, time available to moult is unlikely to be a limiting factor for moult which would cause them to undergo the additional stress of starting moult while completing migration as the return migration does not occur until April. The early but slow start of moult may rather relate to the feeding conditions they encounter upon arrival on the non-breeding grounds. August and September are the driest months of the year with almost nil average precipitation and relatively low temperatures (Chapter 1, Fig. 2), conditions which are poor for benthic fauna and insect productivity (Mwaluma et al. 2003), the main food source for sand plovers (del Hoyo et al. 1996, Snow and Perrins 1998). Thus, food availability for fuelling feather growth is reduced and conditions are poor for moult. In order to maintain the production of a high quality feather, growth rates are slowed down to compensate for lack of nutrients. Average rainfall picks up at the end of the year (Chapter 1, Fig. 2) providing better feeding conditions and thus allowing higher feather growth rates (Fig. 7, Fig. 8). Moulting a few inner primaries on or near the breeding grounds and suspending until arrival on the non-breeding grounds appears to have been an additional strategy that was followed by only a few birds (3%) in north-western Australia.

For Lesser Sand Plovers reaching south-eastern Australia, time available to moult may be more of an issue than in the north-west. These populations must travel an additional c. 5,000 km or 20° farther south before arriving on the non-breeding grounds and, given the need to fatten up for this extra leg, it is logical that they arrive later than those in north-western Australia. Upon arrival in the south-east, foraging conditions are cool (averaging c. 12°C; Chapter 1, Fig. 2d) which, similar to very dry conditions, are sub-optimal for productivity levels of the benthic fauna on which the birds rely for food to fuel feather growth (Mwaluma et al. 2003, Mwaluma and Paula 2004). The poorer feeding conditions together with reduced time available for moult are likely reasons for the early and slow moult of the inner primaries. As temperatures increase in January and February, productivity improves and thus allows the birds to forage more effectively and grow new primaries at the faster rate of increase (Fig. 8) needed to complete by late February (Fig. 2d, Fig. 3d). This leads to a drawn out overall moult duration of nearly six months (168 days), on average two weeks longer than for any other location considered.

India

Lesser Sand Plovers spending the non-breeding season in south-eastern India are mostly of the race *C. m. atrifrons* which breeds in the Himalayas with just a few *C. m. pamirensis* (Balachandran and Hussain 1998, Hirschfield et al. 2000). Adults arrive in August (Cramp and Simmons 1983, Balachandran and Hussain 1998) and immediately start moulting on average several inner primaries simultaneously (Figs. 3a, 6a, 7a). (Balachandran and Hussain 1998) described two groups of adults—those which start moult soon after arriving and a second group which apparently arrive in moult. Balachandran and Hussain pointed out that this latter group are in fact 'second year' birds, i.e. those entering their second year (termed here as 'sub-adult'). When the moult of the birds aged as sub-adult was compared with first year and adult birds, it clearly formed an extension of the drawn-out first year moult and was not, therefore related to the adult moult nor a distinct sub-adult moult as found in other populations. Lesser Sand Plovers breed first at two years old with first year birds mostly staying on or near the non-breeding grounds during the first breeding season with a few possibly migrating to the breeding grounds but not breeding (Cramp and Simmons 1983, Hayman et al. 1986, del Hoyo et al. 1996). Balachandran and Hussein (1998) stated that 'hundreds of first-year birds summer' in south-eastern India. This being so, it is likely that first year birds make short movements north to alternative sites and then return for the longer non-breeding season to their original non-breeding grounds. In Kenya, re-sightings of colour-flagged sand plovers have shown local movements northwards from the non-breeding grounds; this observation suggests that this strategy does exist (pers. obs). The second group of 'adults' referred to by Balachandran and Hussein (1998) that 'arrive in active moult' are thus likely to be non-breeding sub-adults returning from short distance movements along the Indian coast during the breeding season which are completing their full first year moult.

The strategy of adult Lesser Sand Plovers moulting in south-eastern India is consistent with that of birds that are trying to moult as fast as possible. The distance from the breeding grounds is c. 2,500 – 3,500 km. Thus, at flight speeds of 70 km/hr, it is possible for birds to reach the non-breeding grounds in a single flight of two to three days and to start moult after arrival. On arrival in south-eastern India, climatic conditions are hot with a little precipitation (Xue and Yanai 2005, Climate-Data.org 2015), providing excellent conditions for productivity for the benthic fauna that the sand plovers feed on in the inter-tidal zone (Mwaluma et al. 2003, Mwaluma and Paula 2004). As sand plovers are predators that hunt their prey visually from the ground surface (Hockey et al. 1999), in drier conditions with little surface flooding, prey items ought to be more visible and thus easily accessible to the birds. This therefore provides a good food resource to enable rapid moult and feather growth. However, time is limited for the plovers to moult as the monsoon rains arrive in south-eastern India from October to December (Chapter 1, Fig. 2a). While maximum densities of benthic fauna occur prior to the heavy monsoon rain, once the flooding starts densities drop to 50% (Harkantra and Parulekar 1981, Varshney et al. 1981, Owen and Forbes 1997) and thus foraging conditions are substantially poorer making feather synthesis more difficult.

In response to this, adult Lesser Sand Plovers moult as fast as possible. However, there is a limit to how fast feather material can be synthesised. Therefore, to increase the speed of moult, the only option is to drop more feathers simultaneously (Dawson 2004, Rohwer and Rohwer 2013). If a bird is to choose which feathers to drop simultaneously, it makes most sense to do so with the small inner primaries because these play a less critical role in flight. A larger gap in the inner wing impacts active flight less than if it is farther out towards the wing tips (Chai 1997). Thus, in south-eastern India, Lesser Sand Plovers drop several inner primaries in rapid succession (Table 3, Fig. 3). As a result, within five to six weeks of starting moult, on average almost 50% of total feather mass was grown (Fig. 4a); thereafter, unlike at more southern locations, the growth rate per primary only increased slightly (Fig. 8a) while the gap between moulting new feathers increased markedly. Furthermore, with only slightly increased growth rate for the substantially larger outer primaries, the duration of moult for the last two feathers reached almost double that of P5. By the time these outer primaries are moulting (November – December, Fig. 3a), the monsoon has hit in full strength leading to high levels of flooding. Under such conditions the density of benthic fauna which sand plovers feed on is reduced to up to 50% (Hylleberg and Nateewathana 1991). Furthermore, Lesser Sand Plovers hunt their prey on the ground surface by sight (Hockey et al, 1999) and prefer foraging on damp or in only slightly wet mud or sand, not actual open water over mud or very wet mud (Hockey et al. 2005). Thus, it is likely that at times of high flooding and rainfall, the ability to see and capture prey items is likely reduced where there is more surface water to hide evidence of prey. Prey availability is therefore reduced making it harder for birds to obtain the necessary nutrients for significant feather growth leading to the relatively slower growth of the large, outer primaries (Fig. 8). Ultimately this leads to a lower factor of increase (3.6) between relatively rapidly moulted inner primaries and more slowly moulted outer primaries than for the other more southerly populations studied (Fig. 8).

This moult strategy in India was in strong contrast to Lesser Sand Plovers in Kenya and Australia where, particularly for the latter populations, the inner primaries were dropped and grown more slowly and the outer feathers moulted significantly faster than in India (Fig. 8). Furthermore, duration either remained constant (Kenya) or clearly reduced across primaries (Australia) (Fig. 6a). Lesser Sand Plovers in south-eastern India, therefore, appear to get through as much primary moult as possible before the onset of the monsoon rains in October. Thereafter moult progress is slowed down by the twin strategies of spreading the moult of each subsequent feather, and reducing the amount of overlap between the moult of adjacent primaries. This reduces the overall rate of increase in feather material growth. Adults complete primary moult on average in early to mid-January; this allows time for fattening up for the migration north to the breeding grounds in March/April (Balachandran and Hussain 1998).

Comparison between sites

Duration of moult and average feather growth rate for adult Lesser Sand Plovers are basically the same between sites. The birds in south-eastern Australia are likely to have a shorter actual duration than estimated by the model and thus faster average growth rate given the effect of the small sample size for the inner primaries (see above for discussion of this). Using the mid-moult date for better comparison than start date, the general pattern for moult between populations of Lesser Sand Plover along a gradient from north to south is one of a greater delay the farther south the birds have to migrate (Fig. 10). However, the population in Kenya stands out from the others in being 21 days later than the north-western Australia population (Fig. 10). Barshep et al. (2013) demonstrated that rainfall on the moulting grounds affected the start of moult. Precipitation and ambient temperature affects productivity of benthic fauna, the main food source for shorebirds (Piersma 1987, Sardá and Martin 1993, Mwaluma and Paula 2004). On the coast of Kenya benthic productivity is greatest in January through to April (Mwaluma et al. 2003, Mwaluma and Paula 2004, Osore et al. 2004). While it may be best to moult when food resources are at a maximum, it is not feasible for Lesser Sand Plovers to wait until January to start moulting given that they need to fatten ready for migration in April / May. However, the highest growth rates for primary replacement occur with the largest, outer primaries (Figs. 3, 8, Table 4) that are also key feathers for lift in birds (Chai 1997). There would clearly be substantial benefits in timing the moult of these large feathers with higher food availability. Thus, delaying overall moult by a few weeks would achieve this and allow adult Lesser Sand Plovers to optimise on productivity levels of benthic fauna to fuel feather growth.

Sub-adult and first year moult

Different moult strategies have been noted for 'sub-adult' or 'second year' birds, also referred to as 'post-juvenal' moult in north America (Owen Jr and Krohn 1973) as distinct from the moult undertaken earlier by first year birds and later by adult birds (Prater et al. 1977, Prater 1981, Remisiewicz et al. 2010a). The sub-adult moult is a strategy that is well-known to occur in waders though it is an infrequently described phenomenon more often found in larger wader species (Dare and Mercer 1974, Pearson 1981, Prater 1981, Remisiewicz et al. 2010a). In the Lesser Sand Plover populations studied here, the three southern hemisphere populations exhibited a sub-adult moult albeit with a small sample of birds (Kenya, n = 6; north-western Australia, n = 50; south-eastern Australia, n = 4) though the lack of data from Kenya and any at all from India is probably due in part to a lack of identifying the sub-adult pattern in the field and is an area where further work is required.

When determining how many birds fall into each of the three first year moult strategies of 1) no moult in first year; 2) partial moult of a varying number of outer primaries and 3) a 'normal' complete ascendant moult (Fig. 14), it is necessary to assess the condition of wear of the old, retained feathers. If this is not considered with the bird in hand, then it is impossible to later classify many birds. In particular, the first category of the Indian data (where 3% were estimated to remain unmoulted until the first adult moult) is likely to be underestimated due to a lack of detail on feather condition of old feathers in moult scores of sub-adult birds in September – November. A bird entering its second year and undergoing its first adult moult having not moulted anything in its first year would show heavily worn unmoulted feathers, these being juvenile feathers grown well over a year earlier—much more so than for a bird in its third or more year whose old feathers would be less than a year old and better quality (Ginn and Melville 1983). However, if old feathers are simply recorded as 'old' with no reference to 'very worn' or 'slightly worn', then it is impossible to determine whether the bird was in its second or third (plus) year. Lack of such details can only mean a reduced estimate of both birds not moulting at all in their first year and sub-adults as these birds would simply be aged 'adult'. It is a recommendation from this study that condition of old feathers be recorded to assist in determining important detail for the age of the bird in the hand.

First year moult

The primary moult strategy for first year Lesser Sand Plovers appears to be divided between those that moult farther north (the Indian population) that underwent a complete moult and those to the south (Kenya and Australia) which predominantly moulted no primaries (Fig. 14). In each location only a minority undertook the moult of some outer primaries, a strategy which is a known to be a key strategy for first years of other migrant wader species e.g. Curlew Sandpiper, Wood Sandpiper, Common Sandpiper (Pearson 1974, Remisiewicz et al. 2010b, Barshep 2011). (Barter 1991) suggested first year Lesser Sand Plovers probably moult some if not all primaries commencing with the innermost, however our data, while also scarce, indicates that a good portion of birds do not moult and that a minority may moult a few outer primaries (Fig. 14).

Evidence among the first year birds in south-eastern India suggests that those that undertake a full moult between early April and August probably start their full adult moult soon after completing the first year moult. An example is the first year Lesser Sand Plover Ring no. 124118, first caught on 10 April with a PFMG of 0.27 suggesting it would complete by the end of June (Fig. 16). It was retrapped six months later in mid-October with a PFMG of 0.31 which would place it as having started the adult moult approximately around mid-August. It is not clear quite why the majority of first year birds in south-eastern India would undertake the quite considerably energy expensive strategy of undergoing a complete moult of primaries twice in their first two years. Most likely is that foraging conditions are optimal during the northern Spring thus allowing them to replace the poorer condition juvenile feathers (Ginn and Melville 1983) with better quality adult-type feathers.

Minor moult strategies

In each location, a minority of first-year birds undertook a moult of three to five outer primaries (Figs. 14, 15). A partial moult of this sort is a common strategy in first year birds for a number of medium-sized to large waders spending the non-breeding season particularly in the southern hemisphere (Barshep in prep., Pearson 1974, Prater et al. 1977, Prater 1981, Remisiewicz et al. 2010b). For the Lesser Sand Plover, this is clearly not a key moult strategy. For the few that do undergo this strategy, birds in India and Kenya were more spread in the number of outer primaries moulted though approximately half moulted three (group MOP3) to five (group MOP5) feathers (Fig. 15). In north-western Australia only seven birds (4% of all first year moult scores) were recorded with the 'MOP' moult strategy of which nearly one third moulted eight feathers and the rest fell again into groups MOP3 to MOP5.

It should be noted, however, that when analysing which of the three moult strategies birds fell into, many moult scores had to be discarded. This was so because many birds were caught as sub-adults that had started their first normal adult moult from P1 and progressed far enough so as to have re-moulted any feathers previously replaced as part of an earlier first year moult. As such, it made it impossible to tell whether the replaced outer feathers in the first year had started at P1 as part of a complete first year moult or at a more distal inner primary as part of a MOP-type moult.

Summary

The primary moult of adult Lesser Sand Plovers had a similar duration between all the non-breeding populations studied (152 – 154 days) with the population in south-eastern Australia showing a two-week longer duration (168 days) though it is expected that with more data on the inner primaries this would reduce to close to the other populations. This is longer than even that of Grey Plovers *Pluvialis squatarola* in southern Africa (131 days) and south-eastern Australia (128 days) (Minton and Serra 2001, Serra et al. 2001, Underhill 2003) which are markedly larger having a wing length 1.5 times that of Lesser Sand Plovers and thus might be expected to have a longer duration. This might be explained by Grey Plovers breeding substantially farther north than Lesser Sand Plovers (Hayman et al. 1986, Piersma and Bonan 2016) and thus having less time available for moult (Dietz et al. 2015).

Distance from breeding grounds and conditions affecting availability of food on the non-breeding grounds appeared to affect the timing, speed and pattern of moult of individual primaries. Indian birds started the earliest, having a short distance to travel from breeding grounds and moulted rapidly to complete growth of half of the feather mass before the heavy monsoon rains started in October when food becomes more scarce. The Kenyan population are not so distant from breeding grounds and have a more stable climate and food source so that moult rate was more constant throughout the process but delay moult to presumably optimise on better foraging conditions in the new year. The Australian populations have considerably farther to travel from breeding grounds and thus less time available to moult on the non-breeding grounds. They furthermore have poorer foraging conditions upon arrival, and thus moulted immediately upon arrival. A few birds apparently arrived having moulted a few inner primaries, presumably at a staging site along the migration route, and suspended moult to complete upon arrival.

A small percentage of young Lesser Sand Plovers underwent a partial moult of some outer primaries at all locations. Young birds in India mostly undergo a complete moult (Prater et al. 1977) with no birds undergoing an intermediate sub-adult moult between a first year and adult post-nuptial moult. Kenyan and Australian first year birds tended not to moult at all before the adult moult but there were a small percentage that underwent a sub-adult moult that on average was estimated to start three weeks earlier than adult moult in Kenya, six weeks in north-western Australia and 10 weeks in south-eastern Australia.

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Tables and figures

Adult moult

Table 1. Numbers of moult scores used in analyses according to age structure for Lesser Sand Plovers in south-eastern India, Kenya and Australia.

Dominant race	Locality	Adult	Sub-adult	1st Year	Total
C.m. atrifrons	*India*	1,253	-	404	**1,657**
C.m. pamirensis	*Kenya*	753	12	250	**1,015**
C.m. mongolus	*NW Australia*	362	50	166	**578**
C.m. stegmanni	*SE Australia*	108	4	11	**119**

Table 2. Parameters of moult for adult Lesser Sand Plovers taking the whole primary tract together.

									n		
	Start Date	**SE**	**Duration**	**SE**	**End date**	**Start SD**	**SE**	**Growth rate**	**un-moulted**	**active moult**	**new**
India	17 Jul	4.0	178.4	4.9	12 Jan	54.3	9.8	0.561%	49	618	585
Kenya	2 Oct	4.1	135.9	5.4	15 Feb	33.8	6.5	0.736%	56	448	249
NWA	16 Sep	3.0	127.3	5.8	21 Jan	27.1	6.5	0.786%	22	129	211
SEA	18 Nov	5.9	104.8	9.4	1 Mar	21.4	6.5	0.954%	1	87	20

Table 3. Parameters of estimated moult per primary and for whole primary tract for adult Lesser Sand Plovers in India (n = 1,253). The average growth rate per primary = 0.654% per day; average growth rate for all primaries using total moult duration calculated from per primary results = 0.561% per day. '% adj pp overlap' is the number of days of overlap between one primary with the next adjacent one expressed as a percentage of that feather's estimated duration. 2nd pp overlap is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously.

	Duration	SE	Start day	SE	Start SD	SE	Growth rate	Start date	End date	Days apart	% adj pp overlap	Days overlap	2nd pp overlap	3rd pp overlap	Un-moulted	Active moult	New
P1	22.0	2.8	41.7	4.1	32.7	9.5	0.17%	**10 Aug**	2 Sep		88%	19.3	57%	20%	51	62	1,140
P2	22.2	2.7	44.4	3.8	32.4	9.2	0.20%	13 Aug	4 Sep	2.7	70%	15.5	33%	-20%	57	64	1,132
P3	19.8	2.5	51.1	3.3	31.1	8.7	0.27%	20 Aug	8 Sep	7	59%	11.6	-1%	-48%	71	64	1,118
P4	20.7	2.3	59.3	3.0	32.2	8.5	0.33%	28 Aug	17 Sep	8	43%	9.0	-2%	-69%	99	70	1,084
P5	19.3	1.9	71.0	2.4	29.1	7.4	0.44%	9 Sep	28 Sep	12	51%	9.8	-21%	-115%	133	78	1,042
P6	23.5	2.2	80.5	2.3	32.2	7.7	0.44%	18 Sep	12 Oct	10	41%	9.7	-36%	-109%	174	98	981
P7	24.9	2.1	94.3	2.0	30.5	6.9	0.49%	2 Oct	27 Oct	14	27%	6.7	-42%	-151%	233	115	905
P8	23.3	2.1	112.5	2.2	36.4	7.9	0.61%	20 Oct	12 Nov	18	26%	6.1	-91%		316	106	831
P9	30.8	2.4	129.7	2.6	49.2	9.9	0.53%	6 Nov	7 Dec	17	11%	3.2			396	125	732
P10	37.6	2.8	156.9	3.0	64.0	12.7	0.48%	3 Dec	10 Jan	27					509	155	589
	Overall per PP duration: 152.8 days						**Start date: 10 August**			**End date: 10 January**			**Av. growth rate: 0.654%**				
P1-10	178.4	4.9	17.9	4.0	54.3	9.8	0.561%	17 Jul	12 Jan					n = 1,253	51	618	584

Table 4. Parameters of estimated moult per primary and for whole primary tract for adult Lesser Sand Plovers in Kenya (n = 743). The average growth rate per primary = 0.648% per day; average growth rate for all primaries using total moult duration calculated from per primary results = 0.736% per day. '% adj pp overlap' is the number of days of overlap between one primary with the next adjacent one expressed as a percentage of that feather's estimated duration.

	Duration	SE	Start day	SE	Start SD	SE	Growth rate	Start date	End date	Days apart	% adj pp overlap	Un-moulted	Active moult	New
P1	18.2	3.2	74.0	5.7	43.0	13.3	0.20%	**11 Sep**	30 Sep		43%	52	31	660
P2	**16.9**	2.8	84.4	4.7	39.7	11.9	0.26%	22 Sep	9 Oct	11	52%	61	36	646
P3	20.0	2.8	92.5	4.0	37.6	10.7	0.27%	30 Sep	20 Oct	8	44%	75	48	620
P4	18.8	2.5	103.8	3.3	36.5	10.0	0.36%	11 Oct	30 Oct	11	42%	98	52	593
P5	20.2	2.4	114.7	2.9	34.8	9.3	0.42%	22 Oct	11 Nov	11	30%	129	62	552
P6	20.1	2.2	128.9	2.4	31.9	8.3	0.52%	5 Nov	26 Nov	14	21%	166	73	504
P7	20.8	2.2	144.8	2.2	32.3	8.2	0.59%	21 Nov	12 Dec	16	0%	222	80	441
P8	21.1	2.3	165.7	2.2	33.1	7.9	0.68%	12 Dec	2 Jan	21	-4%	301	75	367
P9	19.8	2.3	187.7	2.4	34.6	7.9	0.82%	3 Jan	23 Jan	22	5%	376	57	310
P10	**21.8**	2.5	206.5	2.6	38.2	8.6	0.83%	22 Jan	13 Feb	19		430	62	251
	Overall per PP duration: 154.3 days						**Start date: 11 Sept**		**End date: 13 Feb**		**Av. growth rate: 0.648%**			
P1-10	136	5.4	94	4.1	33.7	6.5	0.736%	2 Oct	15 Feb		n = 743	52	442	249

Table 5. Parameters of estimated moult per primary and for whole primary tract for adult Lesser Sand Plovers in north-western Australia (n = 362). The average growth rate per primary = 0.657% per day; average growth rate for all primaries using total moult duration calculated from per primary results = 0.786% per day.

	Duration	SE	Start Day	SE	Start SD	SE	Growth rate	Start Date	End date	Days apart	% adj pp overlap	2nd pp overlap	Un-moulted	Active moult	New
P1	34.6	8.4	49.5	11.8	51.9	22.6	0.11%	**18 Aug**	22 Sep		50%	10%	23	27	312
P2	26.8	6.3	66.9	8.2	44.7	18.9	0.16%	4 Sep	1 Oct	17.4	49%	-5.6%	31	26	305
P3	23.4	5.2	80.7	5.9	41.1	16.6	0.23%	18 Sep	12 Oct	13.8	38%	-10%	43	26	293
P4	23.7	4.8	95.2	4.5	37.7	14.5	0.29%	3 Oct	26 Oct	14.5	53%	-2%	60	28	274
P5	22.0	4.3	106.4	3.6	32.0	12.1	0.39%	14 Oct	5 Nov	11.2	41%	-12%	73	29	260
P6	19.5	4.1	119.3	3.7	31.0	11.7	0.53%	27 Oct	15 Nov	12.9	40%	-30%	93	23	246
P7	18.8	4.2	131.0	3.7	25.7	10.0	0.65%	8 Nov	26 Nov	11.7	27%	-58%	111	19	232
P8	23.9	5.4	144.7	4.5	26.7	10.0	0.60%	21 Nov	15 Dec	13.7	33%	-5%	126	16	220
P9	22.7	6.3	160.7	5.2	26.6	9.0	0.71%	7 Dec	30 Dec	16	60%		140	7	215
P10	32.1	7.6	169.7	5.5	24.8	7.8	0.56%	16 Dec	17 Jan	9			145	7	210
	Overall per PP duration: 152 days							**Start Date: 18 August**	**End date: 17 January**			**Av. growth rate: 0.657%**			
P1-10	127.3	5.8	78.7	3.0	27.1	6.5	0.786%	16 Sep	21 Jan			n = 362	22	129	211

Table 6. Parameters of estimated moult per primary and for whole primary tract for adult Lesser Sand Plovers in south-eastern Australia (n = 108). The average growth rate per primary = 0.595% per day; average growth rate for all primaries using total moult duration calculated from per primary results = 0.954% per day.

	Duration	SE	Start Day	SE	Start SD	SE	Growth rate	Start Date	End date	Days apart	% adj pp overlap	2nd pp overlap	Un-moulted	Active moult	New
P1	37.0	14.6	69.8	20.9	45.7	18.7	0.10%	**7 Sep**	14 Oct		60%	-9%	1	6	101
P2	28.4	11.4	84.6	17.7	45.7	18.7	0.16%	22 Sep	21 Oct	15	10%	-64%	3	6	99
P3	27.8	8.7	110.3	13.0	35.0	16.1	0.20%	18 Oct	15 Nov	26	25%	-26%	5	10	93
P4	28.0	7.3	131.2	9.3	33.5	14.3	0.24%	8 Nov	6 Dec	21	50%	-11%	12	14	82
P5	29.0	6.1	145.2	6.5	27.7	10.9	0.29%	22 Nov	21 Dec	14	41%	-21%	15	21	72
P6	19.5	4.8	162.3	5.2	27.9	11.4	0.53%	9 Dec	28 Dec	17	8%	-53%	26	16	66
P7	17.1	4.2	180.3	3.5	18.6	8.2	0.71%	27 Dec	13 Jan	18	31%	-51%	38	21	49
P8	21.6	4.7	192.1	2.9	17.8	7.6	0.66%	8 Jan	29 Jan	12	35%	-25%	53	24	31
P9	29.8	5.6	206.2	3.8	21.3	7.8	0.54%	22 Jan	21 Feb	14	57%		68	16	24
P10	18.6	5.3	219.1	4.4	14.7	6.0	0.97%	4 Feb	22 Feb	13			81	6	21
	Overall per PP duration: 168 days							**Start date: 7 September**	**End date: 22 February**			**Av. growth rate: 0.595%**			
P1-10	104.8	9.4	141.1	5.9	21.4	6.5	0.954%	18 Nov	1 Mar			n = 108	1	87	20

Table 7. Estimated date for average 50% feather mass grown for adult Lesser Sand Plovers in south-eastern India, Kenya, north-western Australia and south-eastern Australia and estimated number of days that moult is delayed after moult in India per 1,000 km farther from breeding grounds

	Date of 50% PFMG	Days later than India	Estimated av. km from breeding grounds	No. of days later /1000 km farther
India	14 Oct	0	3,000	0
Kenya	9 Dec	56	6,400	16
north-western Australia	18 Nov	35	8,700	6
south-eastern Australia	9 Jan	87	13,500	8

Average days later than India /1000 km farther from breeding grounds: 10

Table 8. Parameters of moult for sub-adult Lesser Sand Plovers resulting from the Underhill-Zucchini moult model for India, Kenya, north-western Australia (NWA) and south-eastern Australia (SEA).

	Start Date	SE	Duration	SE	End date	Start SD	SE	Mid-moult date	Growth rate	Un-moulted	Active moult	New
India	–	–	–	–	–	–	–	–	–	0	0	0
Kenya	9 Sept	9.8	143	75.0	30 Jan	24.1	18.3	27 Oct	0.700%	4	8	0
NWA	17 July	11.2	127	27.1	21 Nov	31	15.4	23 Jan	0.787%	2	48	1
SEA	29 June	–	127	–	3 Nov	–	–	5 Jan	0.787%	0	2	2

Fig. 1. Global breeding and non-breeding distribution (in part hypothetical) of Lesser Sand Plover *Charadrius mongolus*. Breeding distributions for each race are labelled. Non-breeding distributions by race from west to east are: *pamirensis* = gold*; pamirensis* mixed with *atrifrons = brown; atrifrons/schaeferi* = dark orange; *schaeferi* = yellow; *atrifrons/schaeferi* = purple; *mongolus* = light blue; *mongolus/stegmanni* = dark blue; *stegmanni* = maroon. Based on Hirschfield et al. (2000) and Google Maps.

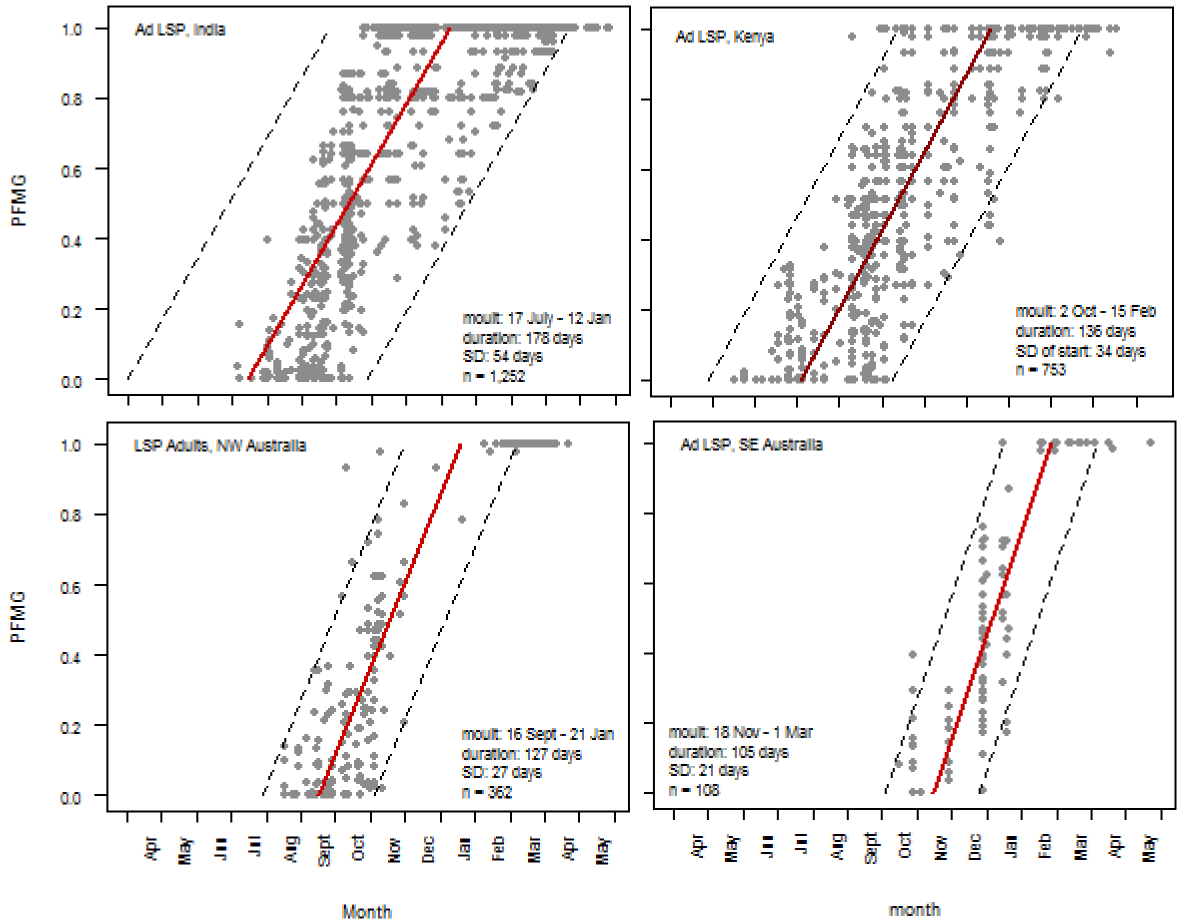


Fig. 2. Primary moult of adult Lesser Sand Plovers in a) India b) Kenya c) north-western Australia and d) south-eastern Australia. Percent Feather Mass Grown (PFMG) is plotted against date using the Underhill-Zucchini moult model. The solid line shows the estimated progression of primary moult for the average bird. Black dashed lines indicate the limits for 95% of the population and thus the parallelogram between them should contain approximately 95% of all birds in active moult.

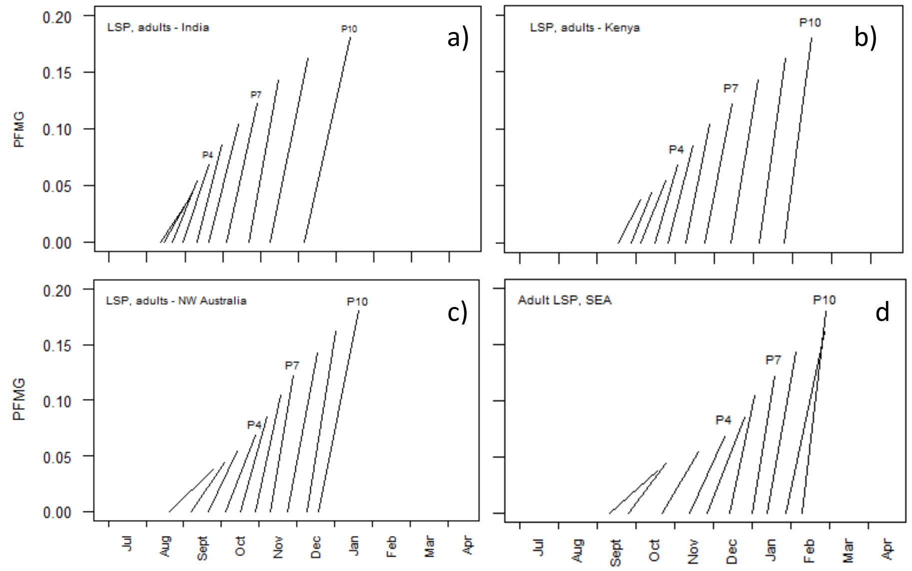


Fig. 3. Progression of moult per primary of adult Lesser Sand Plovers in a) India, b) Kenya, c) north-western Australia and d) south-eastern Australia. Each line represents one primary. The gradient of the line represents the growth rate for that feather

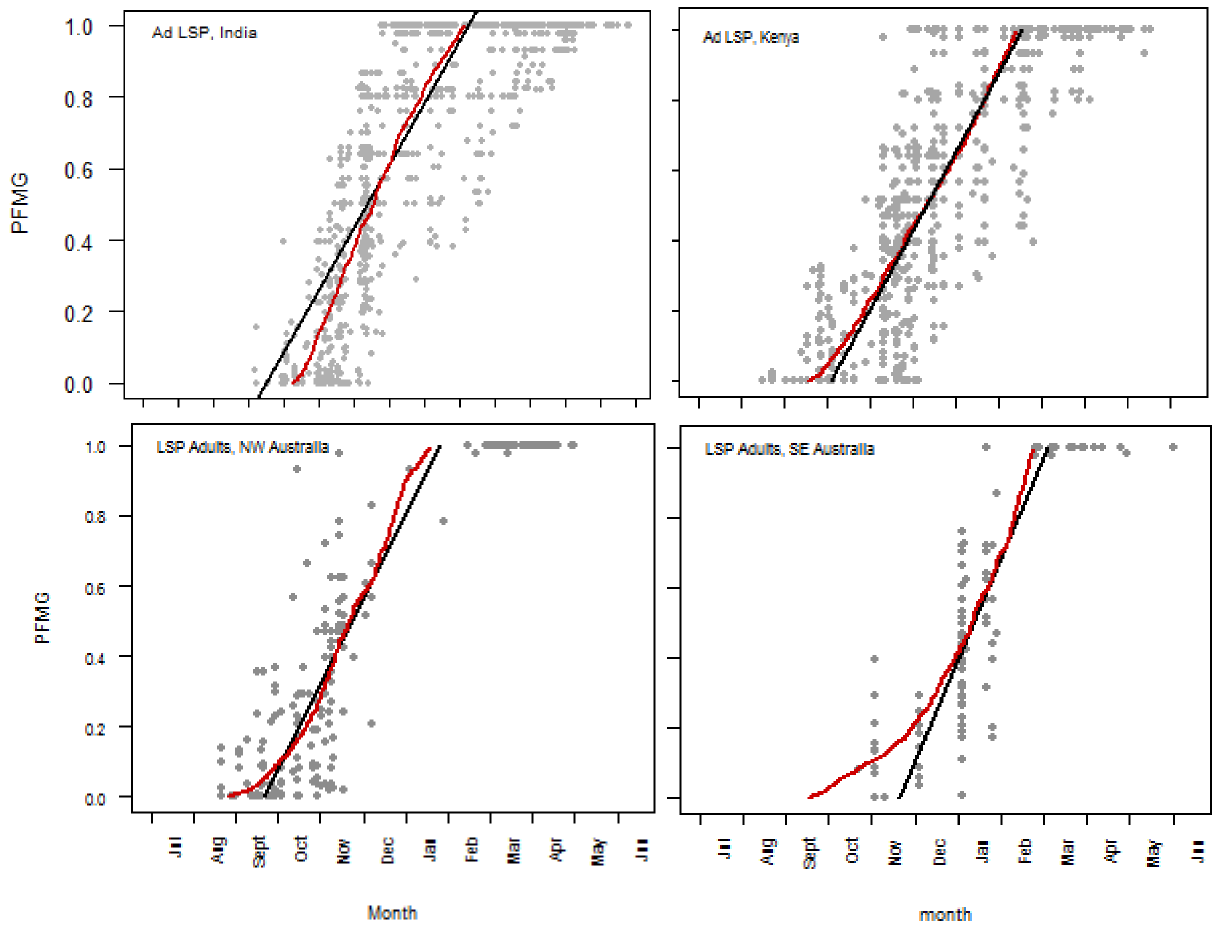


Fig. 4. Cumulative PFMG per primary calculated using each moult score taken (red line) plotted on increase in PFMG for whole primary tract for Lesser Sand Plover in: a) India, b) Kenya, c) north-western Australia and d) south-eastern Australia. For a) to c) the type 2 data analysis of the Underhill-Zucchini moult model was used and for d) the type 4 data analysis.

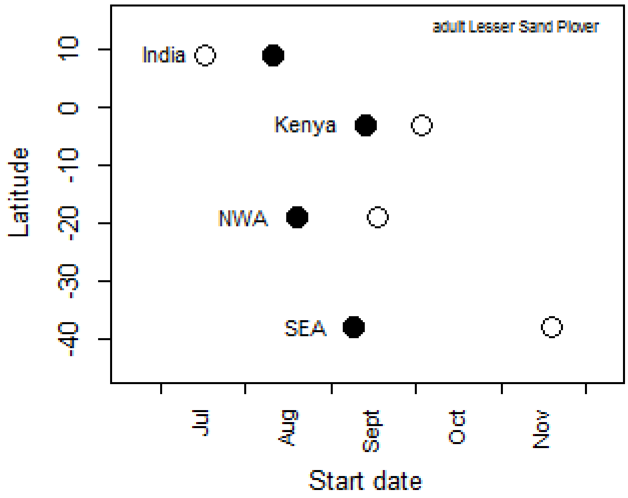


Fig. 5. Start date relative to latitude for adult Lesser Sand Plovers in India, Kenya, north-western Australia and south-eastern Australia. Solid symbols are for the full tract analysis, open symbols are per primary analysis.

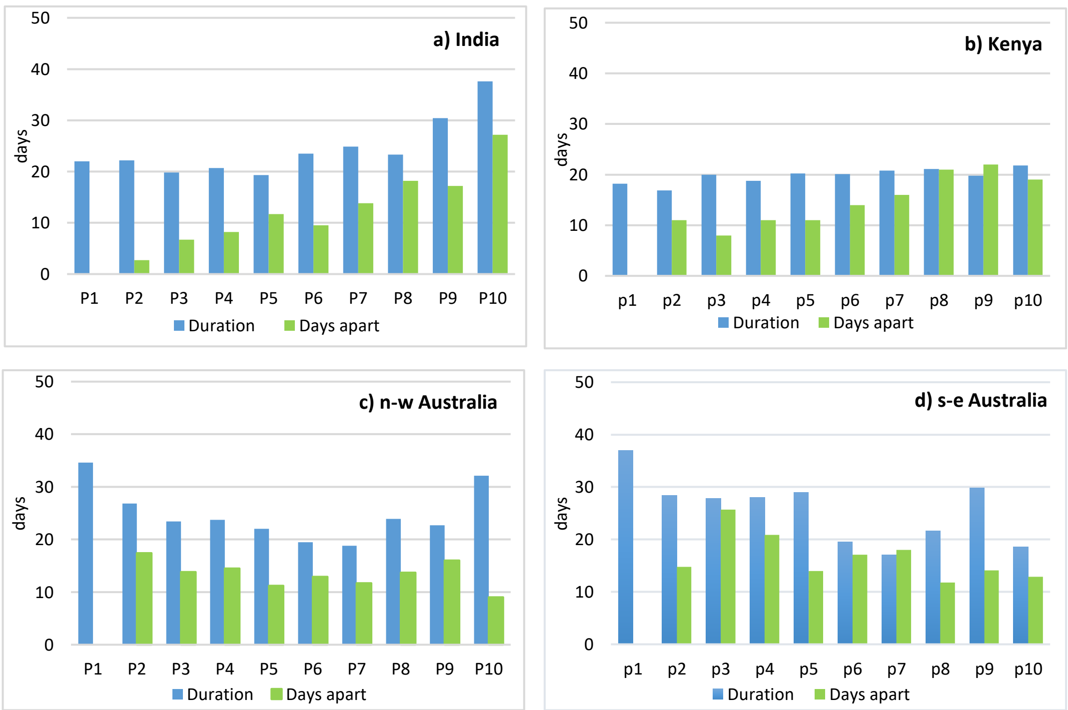


Fig. 6. Estimated duration of individual primary moult (blue bars) and number of days between adjacent feathers starting moult (green bars) for adult Lesser Sand Plovers in: a) India, b) Kenya, c) north-western Australia and d) south-eastern Australia

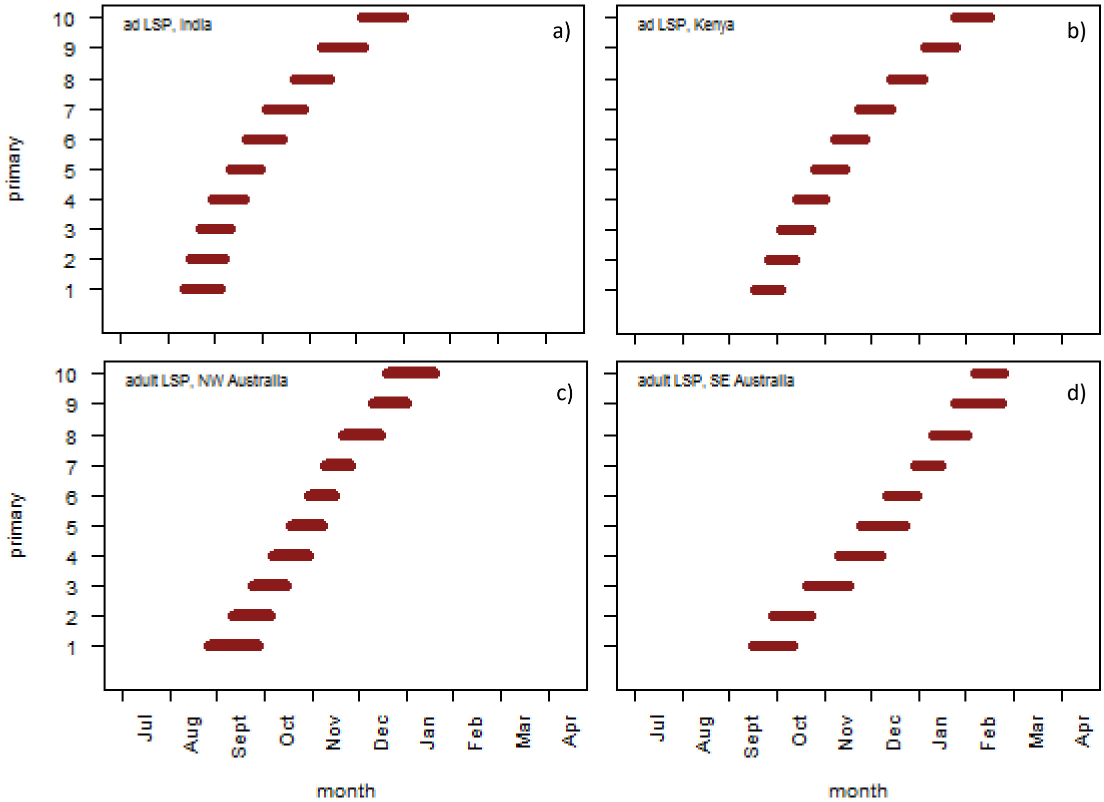


Fig. 7. Estimated growth periods for individual primaries for adult Lesser Sand Plovers in: a) India, b) Kenya, c) north-western Australia and d) south-eastern Australia. Estimates were obtained using the Underhill-Zucchini moult model (Underhill and Zucchini 1988) which was applied to each primary separately.

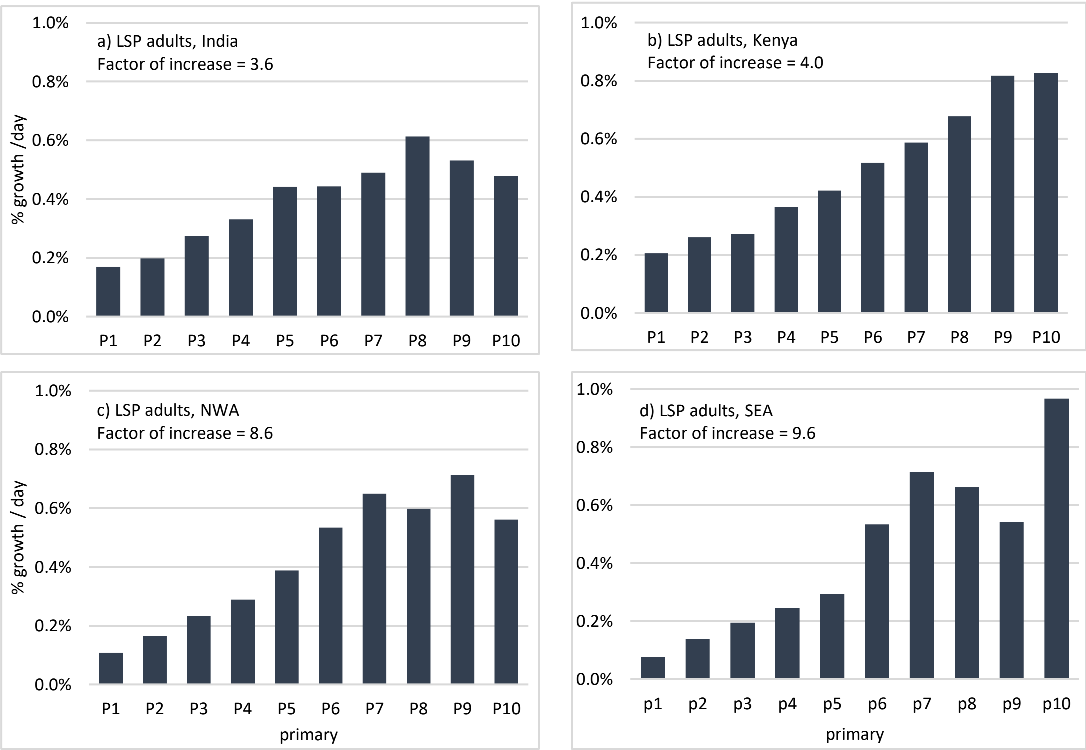


Fig. 8. Growth rate per primary expressed as percent feather mass grown per day for adult Lesser Sand Plovers in: a) India b) Kenya, c) north-western Australia and d) south-eastern Australia

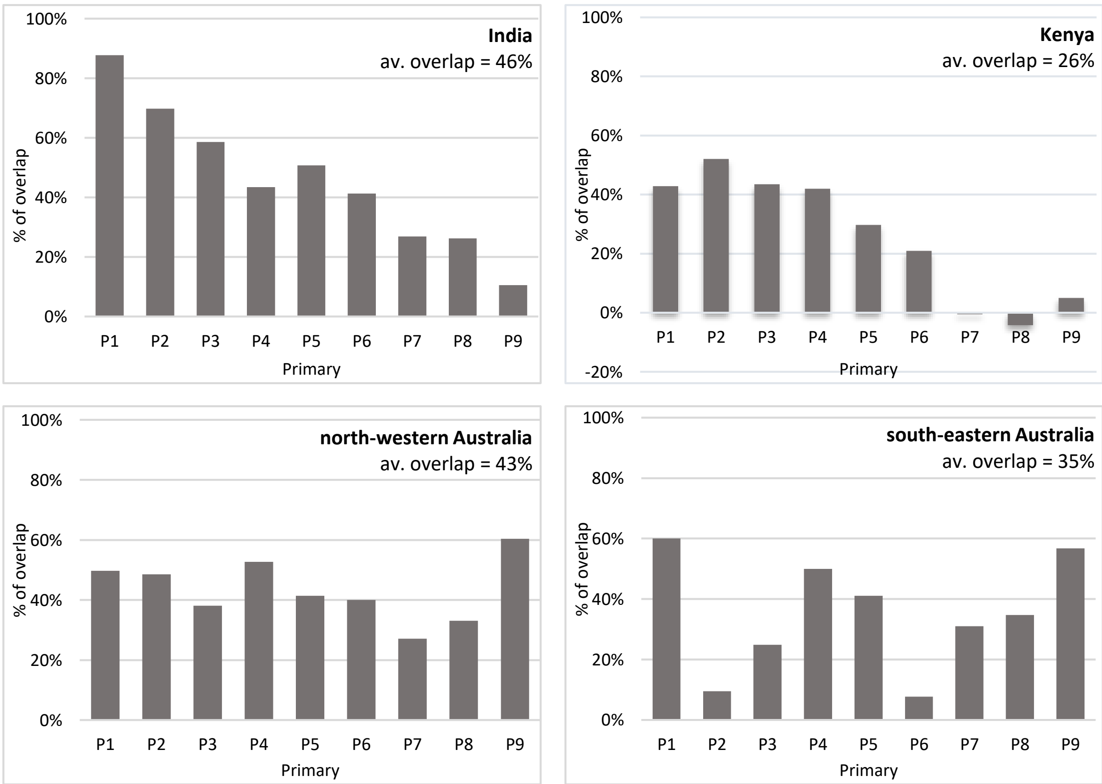


Fig. 9. Percent of time each given primary overlaps with the adjacent primary for adult Lesser Sand Plovers in a) India, b) Kenya, c) north-western Australia and d) south-eastern Australia. Thus for Indian birds, 88% of the duration of moult for P1 overlaps with P2 etc. A negative value indicates there is a gap between the moult of the two adjacent primaries;

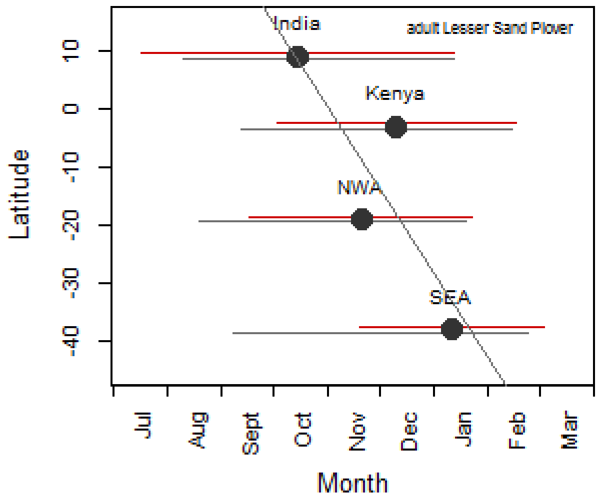


Fig. 10. Average estimated date of 50% PFMG against latitude for adult Lesser Sand Plovers. The horizontal lines indicate the estimated duration of moult for each location *(red = full tract analysis; grey = per primary analysis)*. The diagonal line is the regression line. (In this, and in similar plots in this chapter, and in Chapters 3, 4 and 6, the regression line is plotted only as a visual guide. Statistical tests on regression lines with so few points are not appropriate).

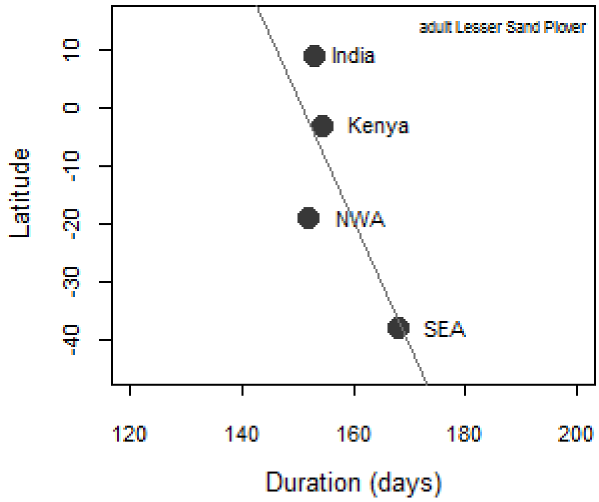


Fig.11. Average estimated duration of moult against latitude for adult Lesser Sand Plovers between four different sites from per primary analysis. The diagonal line is the regression line.

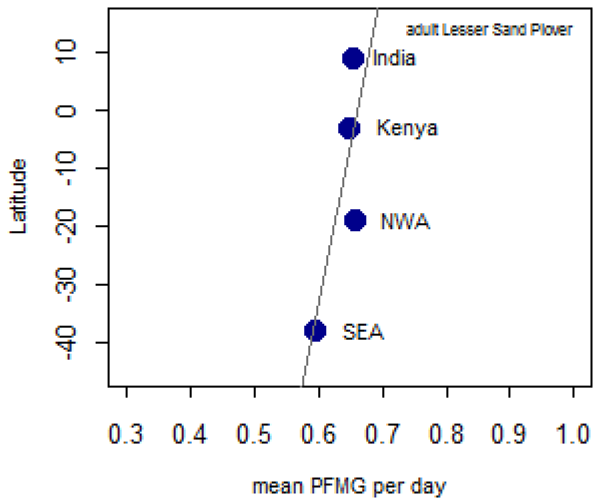


Fig. 12. Estimated mean percent feather mass grown per day for adult Lesser Sand Plovers against latitude for the four sampling locations: India, Kenya, north-western and south-eastern Australia. The diagonal line is the regression line.

Sub-adult moult

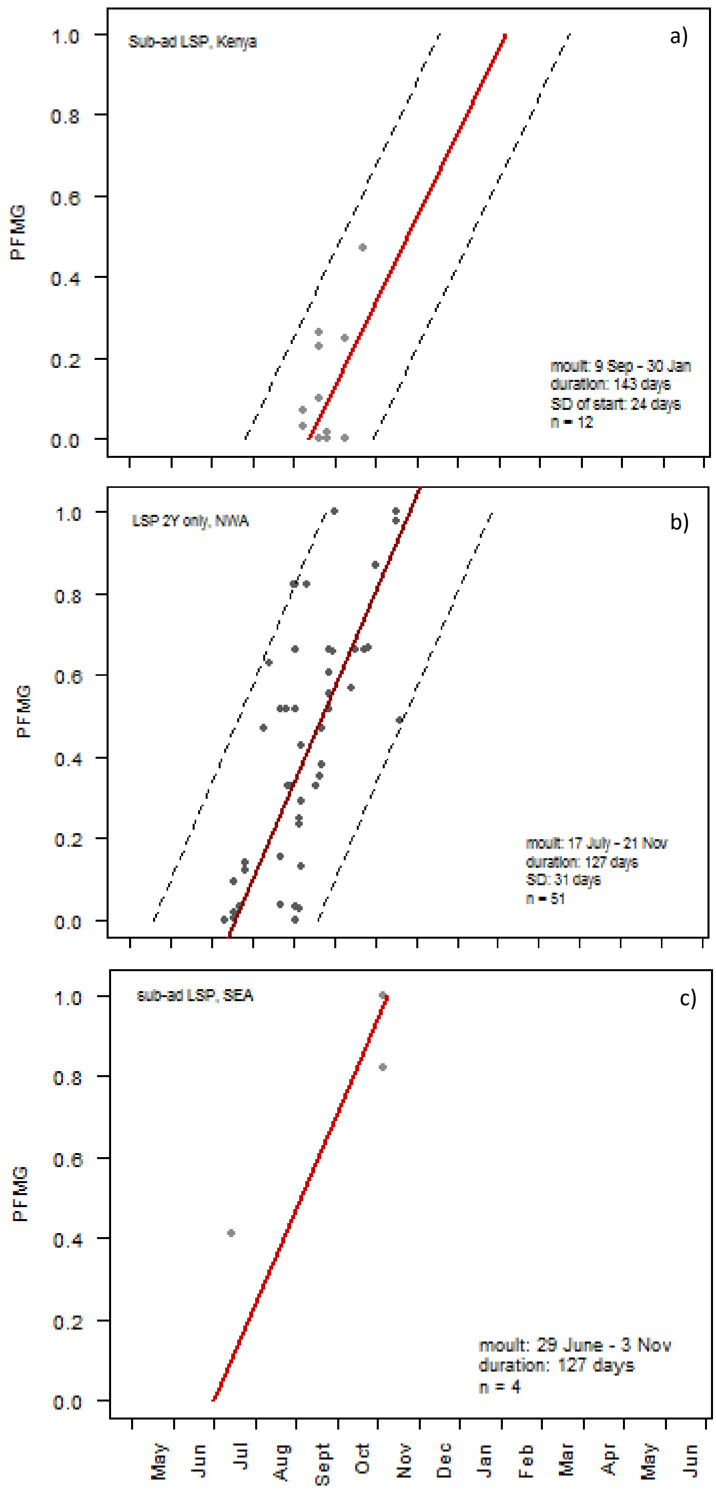


Fig. 13. Progression of primary moult for sub-adult Lesser Sand Plovers in a) Kenya, b) north-western Australia and d) south-eastern Australia. Percent Feather Mass Grown (PFMG) is plotted against date using the Underhill-Zucchini moult model. The solid red line shows the estimated progression of primary moult for the average bird. Black dashed lines indicate the limits for 95% of the population and thus the parallelogram between them should contain approximately 95% of all birds in active moult. For c) south-eastern Australia, data were not sufficient to run the moult model. Estimates were based on an assumption that duration of moult is similar to that of birds in north-western Australia (see text).

First year moult

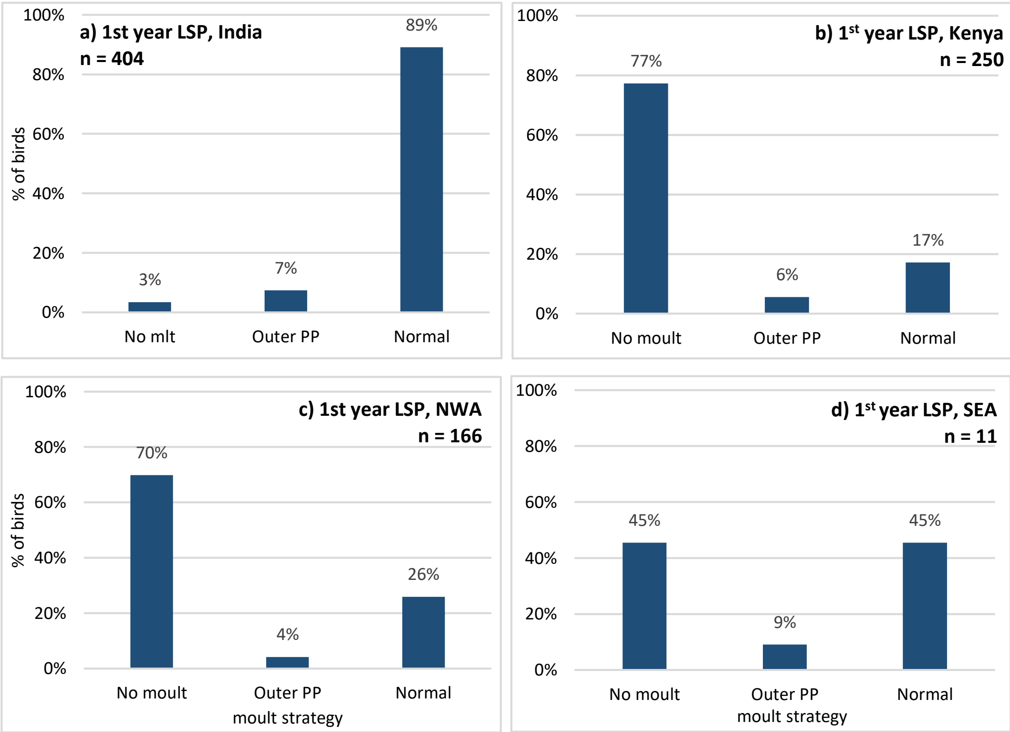
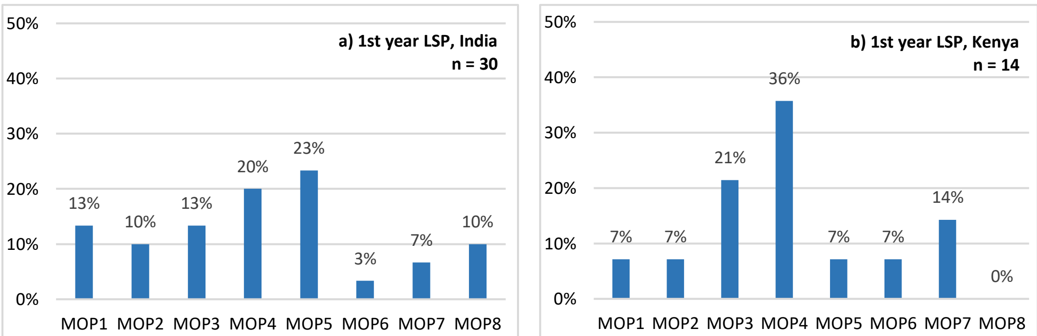


Fig. 14. Proportions of first year Lesser Sand Plovers in each of three moult strategies: no moult, Moult of Outer Primaries (MOP) or normal complete moult for a) India b) Kenya, c) north-western Australia and d) south-eastern Australia.



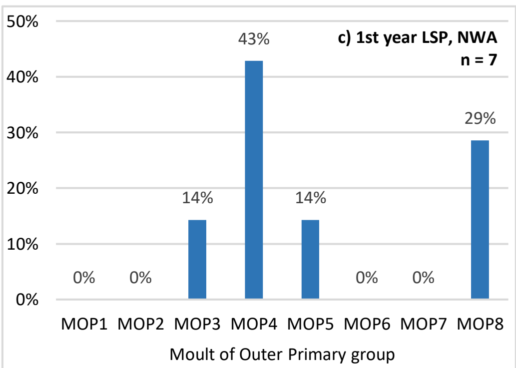


Fig. 15. Proportions of first year Lesser Sand Plovers moulting differing numbers of outer primaries a) India b) Kenya, c) north-western Australia. In south-eastern Australia only one bird was found with moulted outer primaries (MOP5: P6-P10).

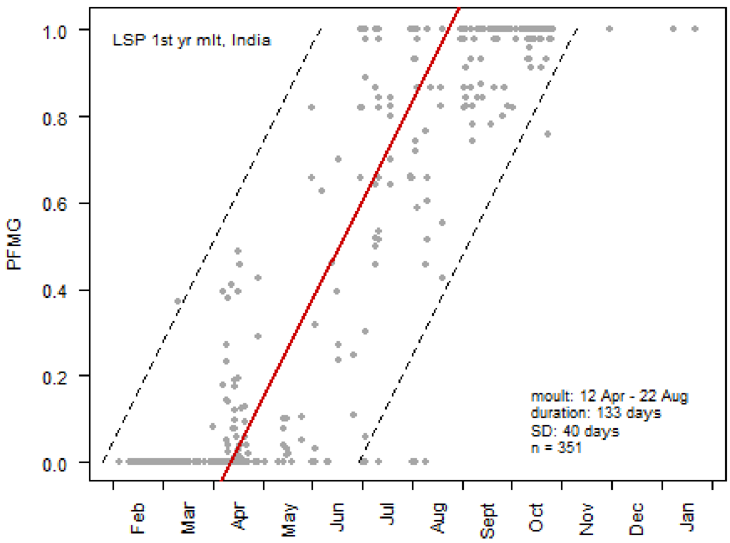


Fig. 16. Progression of primary moult for first year Lesser Sand Plovers in India (n = 351). Primary moult of adult Lesser Sand Plovers in India. Percent Feather Mass Grown (PFMG) is plotted against date using type 4 analysis of Underhill-Zucchini moult model. The solid line shows the estimated progression of primary moult for the average bird. Black dashed lines indicate the limits for 95% of the population.

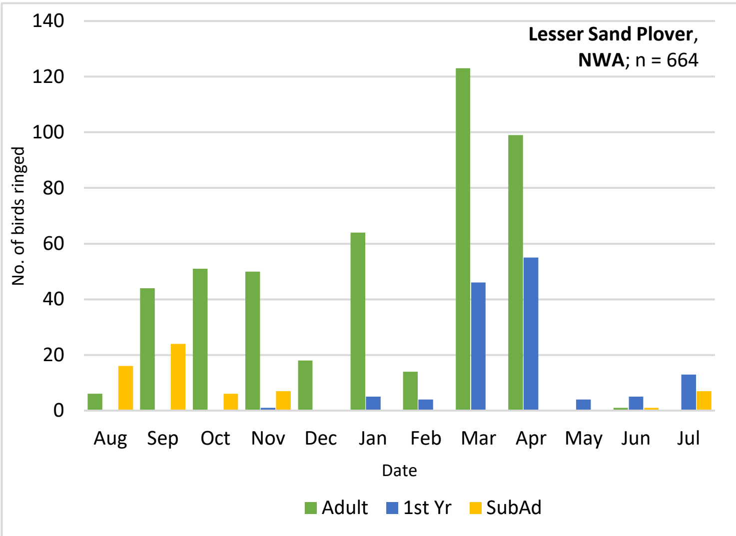


Fig. 17. Numbers by month of first year, sub-adult and adult Lesser Sand Plovers ringed in north-western Australia between 1978 and 2014.

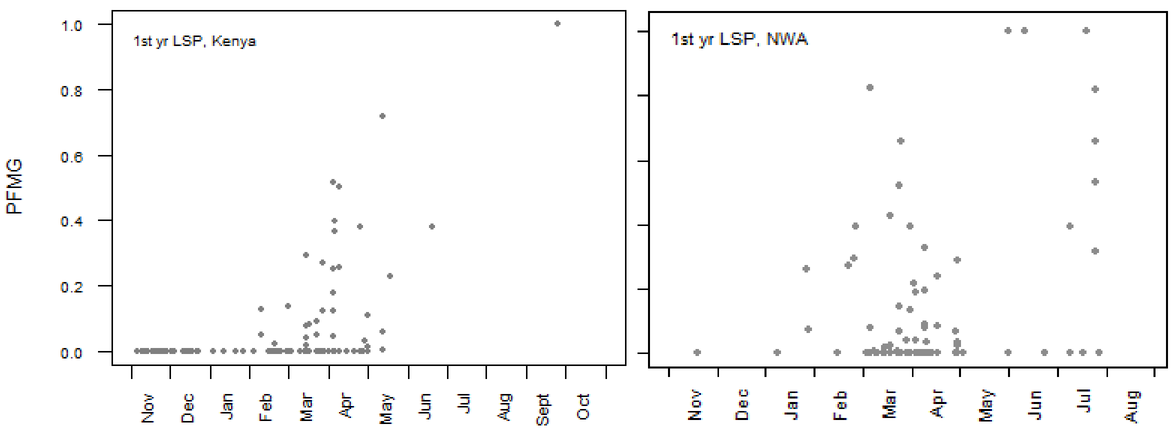


Fig. 18. Spread of percent feather mass grown on date for first year Lesser Sand Plover in Kenya and north-western Australia. The lack of datapoints in the latter half of moult did not allow for convergence of the Underhill-Zucchini moult model. Moult in Kenya started between February and April and in north-western Australia January and April.

Chapter 3

Moult of Greater Sand Plovers in Kenya, India and Australia

Chapter 3. Moult of Greater Sand Plovers in Kenya, India and Australia

Introduction

The Greater Sand Plover *Charadrius leschenaultii* is a species of medium to long-distance migrant wader which breeds in central and eastern Asia and spends the non-breeding season on the coasts of eastern Africa, south central Asia and the Far East south to south-eastern Australia (Cramp and Simmons 1983, Hayman et al. 1986, del Hoyo et al. 1996) (Fig.1). Three races of *C. leschenaultii* are currently recognised: *C. l. columbinus*, breeding in western Iran to Syria and central Turkey and spending the non-breeding season in north Africa and around the coasts of the Red Sea and Persian Gulf; *C. l. scythicus* which breeds from western Transcaspia east to central Syr Darya in southern Kazakhstan and that spends the non-breeding season around the Gulf of Oman, on the shores of the southern Red Sea, and the Gulf of Aden where it mixes with *columbinus*; and *C. l. leschenaultii* which travels the farthest from breeding grounds in eastern Kazakhstan, Xinjiang in north-western China east to Mongolia and Tyva Republits in southern Russia to non-breeding grounds along the east coast of Africa in the west and Indonesia south to Australia in the east (Cramp and Simmons 1983, Hayman et al. 1986, Hirschfield et al. 2000, Delany et al. 2009).

Whilst there have been some description of Greater Sand Plover moult and migration strategies that spend the non-breeding season in Australia (Barter and Barter 1988) and India (Balachandran 1998), generally little is yet known about the moult and migration strategies for the species and in particular for the populations that visit the East African coast (Cramp and Simmons 1983, del Hoyo et al. 1996, Hirschfield et al. 2000, Delany et al. 2009). The East African coast and north-western and south-eastern Australia are sites where large numbers of sand plovers spend the non-breeding season (Higgins and Davies 1996, Zimmerman et al. 1996, Delany et al. 2009). South-east India, however, has only a small non-breeding population with the majority of birds occurring on passage to other, as yet unknown, non-breeding grounds (Balachandran 1998).

In this study, primary moult data for both adult and first year Greater Sand Plovers are considered from south-eastern India, Kenya, north-western and south-eastern Australia. The differences in moult strategy between the four populations are highlighted in the light of factors potentially affecting them such as the different breeding grounds and related migration strategies.

Methods

Primary moult scores were obtained from Greater Sand Plovers in Kenya, India and Australia. The Kenyan birds were ringed during regular wader-ringing sessions at Mida Creek, Kenya (3°19'S 39°57'E), between 1978 and 2014. Indian data were collected during regular wader ringing carried out at Mandapam (9°17'N, 79°8'E) and at the Great Vedaranyam Swamp (10°18'N, 79°51'E) in south-eastern India between 1985 and 2014. The Australian birds were caught between 1982 and 2012 by the Australasian Wader Study Group in north-western Australia at 12 sites centred on 19°15'S 120°20'E and in south-eastern Australia at eight sites centred on 38°22'S 145°32'E. Adult and immature birds (both first year and sub-adult—those finishing their first year of life and entering the second year) were distinguished as far as possible using (Prater et al. 1977) and previous experience. Further details on location and methodology have been described in Chapter 1.

Moult scores were taken following the standard method by (Ashmole 1962) and (Ginn and Melville 1983) where an old, unmoulted feather is scored '0', a new fully-grown feather is scored '5' and the stages in between are scored 1–4. Feathers are numbered descendently, namely the inner primary which is often first to moult is P1 and the outer primary, P10 (Ginn and Melville 1983).

Assessment of immature moult strategy can only be done for birds that have passed the time of year where any first year moult would happen. Prior to this it is impossible to predict which strategy the bird will follow. Furthermore, it is also only possible if while in the field particular details are noted about the primaries of the bird in the hand, in particular the condition of the old, unmoulted feathers. A further complication was that many birds were caught after having already embarked on the next phase of moult (adult) thus 'overwriting' the previous (immature) moult pattern. Thus, the extent of how far advanced the adult moult had reached determined whether it was possible to include the immature moult score in the estimate or not. The assumption is that it is a random selection of birds that undertake the earlier moult overwriting the pattern of a first year moult, however, it is quite possible that fitter birds can moult more feathers and may have even undertaken a complete first year moult that is hidden by the subsequent moult. This would give a lower proportion of birds undergoing complete moult or a moult of outer primaries involving a greater number of feathers. Further in-depth data collection would be required during April to July before the adult moult has started to pick up on this pattern. Those which had been overwritten too far were excluded from analyses as 'non-assignable'. For those where old, worn juvenile feathers were still present separating the new outer feathers replaced in the first year moult and the freshly moulted inner primaries of the adult moult, the two patterns were analysed separately. In north-western Australia moult scores and retained feather condition of second years and adults in August to October were recorded with sufficient detail as to make it possible to identify birds which had either replaced feathers as immatures or retained them. For this population, an estimate of proportions of birds following each strategy was estimated from birds caught in August to October.

Birds identified as sub-adult birds from primary wear pattern (mostly between July and October/November) were excluded from the adult analysis. From some re-trapped birds, it is evident that a sub-adult moult did occur. However, two factors precluded the sub-setting and analysis of sub-adults as distinct from other immature birds. Firstly, birds were aged as sub-adults from the arbitrary date of 1 August and secondly the end of the earlier first year moult merged with the start of any later sub-adult moult between first year and adult moult in such a way as to make it impossible to distinctly subset birds undergoing the sub-adult moult. Average start of moult and duration are therefore estimated for all immature birds together.

Because feather mass between primaries is considerably different, we transformed the traditional moult protocols to percentage feather mass grown (PFMG) to create "moult index" that increases approximately linearly in time to enable estimates of start date and duration of primary moult (Summers 1976, Summers et al. 1983, Underhill and Zucchini 1988). The PFMG was calculated following Underhill and Summers (1993). The parameters of moult were estimated using the Underhill-Zucchini moult model and in particular the moult package in R (Underhill and Zucchini 1988, Erni et al. 2013). This requires the relative feather mass for each primary. Relative primary masses were obtained from Greater Sand Plovers in Australia (C.D.T. Minton unpubl. data) following the methodology laid out by Summers et al. (1983) and Underhill and Joubert (1995). Birds considered as having suspended or arrested moult were excluded from the analyses because the model works for only actively moulting birds. A type 4 analysis was used (taking data from actively moulting and completed scores only) for both adults and immature birds at all locations except for south-eastern Australia where type 3 was used (using data from only actively moulting birds). For immature birds type 4 was used as whilst the whole population was present at the start of moult (a prerequisite for using type 2), it was not possible to determine which unmoulted birds were going to moult and thus be included in the moult analysis and which would remain unmoulted through to the first adult moult and should thus be excluded.

Results

A total of 967 Greater Sand Plovers moult scores were recorded on birds caught in Kenya, 10,968 in north-western Australia, 29 in south-eastern Australia and 182 in India. See Table 1 for the breakdown by age.

Kenya

The estimated start date of moult for adult Greater Sand Plovers taking the PFMG of all feathers in the primary feather tract for Kenyan birds was 22 September with a duration of 132 days giving an end date of 30 January (Fig. 2b). The estimated standard deviation of the start date of moult was 31 days thus 95% of birds were estimated to have started primary moult between 23 July and 21 November. The estimated mean rate of growth for the whole tract was a PFMG of 0.760% per day. 85 adults were recorded as having suspended moult. There was no difference in estimated duration or start date when these were included or excluded from the moult analysis.

The onset of moult from a per primary analysis was 1 September for P1 and the end date for P10 was 27 January, giving a duration of 148 days and a mean rate of growth for all primaries of 0.676% per day. Primaries were shed at shorter intervals between the inner primaries with a minimum of eight days (between P1-P2), the interval increasing towards the outer primaries to a maximum of 21 days (between P8 and P9) (Fig. 3, Table 3). Duration of growth per primary was relatively equal for more than half the wing (P1–P6) varying by three days between the longest duration of 21 days (P5) and the shortest of 18 days (P2). P8 had the longest duration of 32 days (Fig. 3). Overlap between feathers ranged between 5.5 days (26% of the feather moult) for P5 and P6 to 10.7 days (55%) for P1 and P2 (Figs. 6 and 8, Table 3). On average there were more three feathers moulting simultaneously for P1–P3 and P3–P5 (Fig. 6, Table 3).

The average estimated date for 50% PFMG in Kenya was 24 November (Fig. 10, Table 7) which was 79 days after that for India. With an estimated average distance of 7,000 km from the main presumed breeding grounds of *C. l. leschenaultii* to Kenya, the average moult of adult Lesser Sand Plovers here was 24 days per 1,000 km later than for those in south-east India (Table 7).

North-western Australia

The first adults were caught in August. Of 363 birds caught in July, none were aged as adults. 378 adults (5% of total) were recorded with suspended moult of which 91% were in August and September. 28% of adults caught in August when birds arrive had suspended moult (Table 6). The majority had moulted one to three inner primaries in August (85%) with 5% having moulted four and 2% five primaries (Fig. 9). In September the majority showing suspended moult had also moulted one to three primaries but there were more showing a more advanced level of moult before suspension (five having moulted five primaries and six moulted six) (Fig. 9).

The estimated start date for adult Greater Sand Plover moult in north-western Australia (north-western Australia) using the whole primary feather tract was 30 August and the estimated duration of primary moult was 134 days giving an estimated end date of 11 January (Fig. 2c). Estimated standard deviation of start date of moult was 19 days, thus 95% of birds in north-western Australia were estimated to have started primary moult between 24 July and 6 October. The estimated mean rate of growth for the whole tract was 0.746% per day.

Analysing moult per primary, P1 was estimated to start moult on average on 19 August and P10 to complete on 11 January with a duration of all primaries therefore of 144 days (Fig. 3c, Table 4). Using this method gave an estimated mean daily rate of growth for all primaries of 0.694%. While the average gap between moulting primaries was 13 days, the first two primaries were estimated to have moulted only three days apart, a gap which rapidly and steadily increased between feathers to a maximum of 22 days between P9 and P10 (Fig. 5c, Fig. 6b). Estimated duration of individual primary moult was long averaging 21 days after which it increased to peak at over a month (33 days) for P9 (Fig. 5c, Table 4). The growth rate for each primary increased steadily from 0.19% feather mass per day (P1) to 0.61% (P10) (Fig. 7c, Table 4).

There was an estimated large overlap in growth between P1 and P2 of two and a half weeks (87% of the time P1 was moulting) and nine days with P3. P2 also had a large overlap with the adjacent P3 (13 days, 61% of its growth period) but thereafter overlap between primaries was estimated as being relatively constant averaging 10 days or 41% of each feather growth (Figs. 6 and 8, Table 4). Overlap of more than two primaries at the same time occurred between the first four primaries with a maximum of three moulting simultaneously with P2 overlapping with P4 for two days (Table 4).

The average estimated date for 50% PFMG in north-western Australia was 4 November (Fig. 10) which was 59 days after that for India. With an estimated average distance of 7,300 km from the main presumed breeding grounds of *C. l. leschenaultii* to north-western Australia, the average moult of adult Greater Sand Plovers here was eight days per 1,000 km later than for those in south-east India (Table 7).

South-eastern Australia

22 records were available for analysis as Greater Sand Plovers are uncommon in south-eastern Australia (Higgins and Davies 1996). Of these 18 were in active moult and four had completed. No birds were caught with old, unmoulted primaries (Table 5). As most birds were in active moult, type 3 analysis (Underhill et al. 1990) was used to estimate start date and duration. The estimated start

and end dates were 21 October and 4 March respectively with an estimated duration of 134 days. Mean proportion of feather mass grown for the whole wing was 0.746% per day. The standard deviation in start date was estimated as 25.2 days, thus 95% of Greater Sand Plovers in south-eastern Australia were estimated to have started primary moult between 2 September and 10 December.

Data were insufficient to carry out a per primary analysis for PP1–6 and only scant for PP7–10 giving large standard errors particularly for P7 and P10 (Table 5). However, the results for these outer four primaries suggest a completion of moult on 8 April and a generally slow, well-spaced moult of the individual primaries with a slight increase in growth rate between them—other than P10 which both slows down and delays to moult. This, however, is likely a result of poor data (Fig. 3d Table 5).

The average estimated date for 50% PFMG in south-eastern Australia was 27 December (Fig. 10) which was 112 days after that for India. With an estimated average distance of 11,000 km from the main presumed breeding grounds of *C. l. leschenaultii* to north-western Australia, the average moult of adult Lesser Sand Plovers here was 10 days per 1,000 km later than for those in south-east India (Table 7).

India

The estimated start date of moult for adult Greater Sand Plovers in south-east India taking the PFMG of the whole tract was 29 July with a duration of 80 days with moult estimated to complete on average by 7 October. The estimated standard deviation in start date was 24 days thus 95% of birds were estimated to have started moult between 12 June and 14 September (Fig. 2a, Table 2). The estimated mean rate of percent feather mass grown per day for the whole tract 1.252%. The average estimated date for 50% PFMG for adult Greater Sand Plovers in south-eastern India was 6 September (Fig. 10, Table 7).

Insufficient data did not allow for an estimate of moult for primaries P1 to P6. Duration of moult for P7 and P8 were 32 and 30 days respectively though with large standard errors (10.3 and 8.8) reducing to 18 and 22 days for P9 and P10 (Fig. 5, Table 2). Primaries were dropped rapidly with an estimated interval of just six days between P9 and P10 (Fig. 5, Table 2). Estimated rate of moult was high for P9 and P10 at 0.91% and 0.83% of feather growth per day. With the short estimated interval between moulting primaries, there was a high level of estimated overlap of c. 60% between adjacent moulting feathers (Fig. 8, Table 2).

First year and sub-adult moult

Kenya

The majority of first year Greater Sand Plovers (estimated at 79%) underwent a normal complete primary moult. A minority (7%) adopted a Moult of Outer Primaries (MOP) strategy where a few outer primaries are moulted (Fig. 11a). Most (81%) moulted three (MOP3) or four (MOP4) feathers with no record of just one primary moulted or more than five (Fig. 12a). An estimated 14% of first years did not moult (Fig. 11a). For those that underwent a complete moult, the spread of data did not allow for an Underhill-Zucchini moult analysis there being too few data points over 50% of feather mass grown. The earliest found in active moult was in December but the majority of birds encountered in the early stages of moult (with 0 – 25% feather mass grown) were in February (23%) (Fig. 13a). This fits for an expected average start date from the scatter of data points (Fig. 15). There were still small numbers in early stages of moult in May and June but no evidence of a distinct sub-adult moult.

North-western Australia

3,251 birds were aged as first year or sub-adult (Table 1). 112 of these caught in August – October had started a normal descendent complete moult that fell well within the moult timing of the adult post-nuptial moult and were omitted from the moult model analysis. 161 showed an arrested moult where some feathers had moulted and then active moult had been halted. These were also omitted from any analyses.

68% of first year Greater Sand Plovers in north-western Australia were estimated to undertake a normal, descendent moult from the inner primary. 23% did not moult at all during their first year and 9% undertook a MOP moult (Fig. 11b). For the majority, the start of moult was estimated to be spread over a long period with an average start date of 2 February (Fig. 14) with the first birds found starting moult in early November (Fig. 13b) but the majority not starting moult until January (when 60% are in moult). Most had completed by the start of May with a few undertaking sub-adult moult raising the proportion of actively moulting birds in May – August (Fig. 13b).

From the analysis of the whole primary tract together, the estimated duration of moult for immature Greater Sand Plovers was 169 days with an average completion date of 22 July. With an estimated standard deviation of start date of 87 days, 95% of birds were therefore estimated to start moult between 15 August and 24 July.

The average rate of feather growth was estimated at 0.590% of total PFMG per day. Birds considered as undertaking a sub-adult moult appeared to start moult from the start of May as evidenced from re-trapped birds demonstrating a normal moult starting earlier than returning adults and after a prior first year moult; e.g. one first year bird (ring no. 05255369) was ringed on 13 June having moulted its outer three primaries (the first year moult strategy of moulting a few outer primaries). It was re-trapped on 8 August with a PFMG of 0.161 that places it ahead of normal adult moult on this date thus suggesting it was undergoing an earlier, distinct sub-adult moult.

87 sub-adults (19% of those aged as such) showed a 'third moult wave' strategy where three ages of primary were present in the wing: the outer primaries had evidence of being either the (very worn) juvenile primaries or having been replaced in a first year moult; a newer set of feathers mid-wing as part of a 'second moult' wave which matched an adult post-nuptial moult; and a third, fresh moult which started well after the second moult. The spread of data was not sufficient to allow analysis with the Underhill-Zucchini moult model but this third wave would appear to have started in mid to late October (Fig. 16). The pattern can only be noticed when three ages of feather are present. Thus, once the second moult 'overwrites' the first year moult then the pattern is hidden and the third wave cannot be identified. As a result, the maximum PFMG noted is a score of 0.80% in January. The 'third moult wave' was confirmed by five birds retrapped in the same season showing a third moult, e.g. ring 05250730 ringed on 16 Aug with a moult score of RRRRRRRR2V (i.e. eight replaced inner primaries and P8 actively moulting in a first year / sub-adult moult, one 'very worn'—and thus juvenile— outer primary) and subsequently retrapped on 12 Nov the same year with a score '6615551RRR' (i.e. the first year moult completed, a subsequent equivalent of a post-nuptial adult moult had started and was actively moulting P6 but a *third* sequence of moult was starting with the inner primaries again).

South-eastern Australia

Of the six immature moult scores available, 100% showed a normal complete moult starting from the inner primary on average on 7 February and ending 84 days later on 2 May (Fig. 14b). Growth rate over the whole primary tract averaged 1.191% of total feather mass per day. A standard deviation of six days gave an estimate of 95% of birds start to moult between the 26 January and 20 February.

Two birds were aged as sub-adults in their second year (caught November and February) and both were undertaking their first adult moult over the feathers replaced during their earlier first year moult. The November bird had arrested its first year moult at P9.

India

Of 54 birds aged as first year, one was noted to have started moulting three outer primaries in April; no others were found moulting in any other month. Four first years in April had unmoulted primaries and it is possible that these would not moult prior to the adult post-breeding moult starting in July

(Fig. 2a). Lack of records of condition of old feathers on moulting adults in August – September meant that it was not possible to confirm whether some of these would have been sub-adults that had remained unmoulted in this way.

Ten birds were aged as sub-adult, all of which were caught in September. Of these, four were in active adult moult but with the 'old', unmoulted feathers appearing relatively 'new', the pattern indicative of a bird that had undertaken a complete immature (either first year or sub-adult) moult. The remaining six birds had all new primaries and had thus completed moult within an immature or sub-adult moult strategy as it would have been too early to have been part of the normal adult moult.

Discussion

The overall moult strategy for Greater Sand Plovers was for adults to undergo a complete moult soon after arrival on the non-breeding grounds (or passage site in the case of India). Most first years also underwent a complete descendent moult from mid-way through the non-breeding season. A small number of immatures carried out a sub-adult moult that overlapped with the post-nuptial adult moult.

As for Lesser Sand Plovers (Chapter 2), where data were sufficient for a per primary analysis of moult as well as the full primary tract, there was a marked difference in start date, particularly for birds in Kenya (1 September for per primary analysis and 22 September for full tract; Figs. 2, 4a, Table 3). As discussed in detail in that Chapter, while part of the reason for this earlier extended date for per primary results may be due in part to a smaller dataset for the inner primaries, the actual pattern of moult, that of a somewhat slower start of moult, is taken as true. This suggests that the overall rate of moult is not uniform as assumed for the Underhill-Zucchini moult model (Underhill and Zucchini 1988), but rather is slower for the inner primaries and then increases for the larger outer primaries, which is indeed the case for Greater Sand Plovers in Kenya and to a lesser degree in north-western Australia (Figs. 3b, 3c, 7b, 7c). This being the case, the date for the commencement and the duration of moult is taken from the per primary analysis where it is available.

Kenya

Adult Greater Sand Plovers arrive in Kenya from early August to September with the first young birds arriving towards the end of September and into October and November (Fogden 1963, Cramp and Simmons 1983, Hayman et al. 1986). The adult moult strategy is to arrive and start moult almost immediately upon arrival and taking an extended five months (148 days) to moult, with completion by the end of January. Conditions are good for the birds on the Kenyan coast with some rain to reduce excessive heat and temperatures averaging just below 30°C (Chapter 1, Fig. 2b) producing reasonable productivity conditions for the benthic fauna they feed on (Mwaluma et al. 2003, Mwaluma and Paula 2004, Osore et al. 2004). The results from the per primary analysis show a relatively slow rate of growth for the inner primaries with duration of growth being quite constant other than an extension for the larger outer three primaries (Figs. 3b, 5b, 6a). This contrasts with the observed pattern in north-western Australia where the start of moult is rapid with inner primaries dropped just three days apart leading to a substantial degree of overlap (87%) between adjacent inner feathers (Fig. 8c). The slow, drawn out moult of inner primaries also differs to other species e.g. Curlew Sandpiper *Calidris ferruginea* where sometimes an average of more than three primaries may be moulting simultaneously (Remisiewicz et al. 2009, Barshep et al. 2013).

The timing of the moult appears well coordinated with local climatic conditions. By completing moult by the end of January, adult Greater Sand Plovers are then able to exploit the period of highest zooplankton productivity in Mida Creek during February and March (Osore et al. 2004) in order to build up fat reserves for their relatively early return migration to northern China and Mongolia in the second half of April.

In contrast to the strategy given by (Prater et al. 1977) of no moult, 79% of first year Greater Sand Plovers on the Kenyan coast underwent a complete moult (Fig. 11a). The start of this appears to be spread over a long period from December to April with peak numbers starting in February (Fig. 12a). A handful appeared to start moult relatively late in May and June and could thus be considered to be undertaking a distinct 'sub-adult moult'. However, numbers engaging with this approach are so low that it seems unlikely to be a significant strategy for the species.

Australia

The population of Greater Sand Plovers spending the non-breeding season in Australia mostly underwent a complete moult that started immediately they arrive. However, there was a marked proportion of birds which had moulted a few inner primaries prior to arrival, suspended moult for the migration, and then continued once they reached the non-breeding grounds. In north-western Australia 28% of returning adults (in August) had followed this suspended moult strategy, moulting mostly one to three inner primaries (Fig. 9) presumably on or near the breeding grounds. This is consistent with Cramp and Simmons (1983) and Barter and Barter (1988) who reported approximately 25% of adults returning to non-breeding grounds in suspended moult and with the most common number replaced being three, a result that is confirmed by this study. Birds observed in December with one to three unmoulted outer primaries are likely to be birds with a drawn out moult of the outer primaries where a bird may have a gap between completing moult of one primary and starting the next. This can appear as suspended moult. It is possible that these birds had arrested moult and would have retained the unmoulted outer feathers until the next adult moult on their return from breeding. However, there is no evidence of this happening and it would be unlikely that a bird would migrate to breeding grounds 10,000 km away and return on old, inefficient outer primaries which are the most important for efficient flight (Dawson et al. 2000, Serra 2001). In south-eastern Australia the sample size was considerably smaller and just two birds were found with suspended moult which suggests that at least some birds there also follow this strategy.

In both north-western, south-eastern Australia and Kenya the estimated duration of complete primary moult for adult Greater Sand Plovers were similar (144, 134 and 148 days respectively) (Fig.2). However, in north-western Australia moult started three weeks earlier (estimated as 19 August) than in Kenya (1 September) and eight weeks earlier than in south-eastern Australia (21 October) (Fig.2). Adult Greater Sand Plovers are the earliest of the waders to arrive in north-western Australia with a few arriving in the last week of July but most arriving in early August (Minton et al. 2013, C.D.T. Minton pers. com.). They therefore begin moult almost immediately after arrival with some having got a head start already by moulting a few inner primaries on or near the breeding grounds which then suspend to be completed once on the non-breeding grounds. On average adults in north-western Australia tended to moult the inner primaries rapidly (Fig. 3) with only a short gap between feathers but relatively lengthy moult duration per feather (Fig. 5, Table 4). This contrasted with Kenyan birds which had greater intervals between moulting the inner feathers. Both populations showed similar durations of growth per primary (Fig. 5, Tables 3 and 4). This led to a high level of overlap between feathers for the north-western Australia birds (Fig. 8). When the birds arrive in north-western Australia, conditions are dry and with temperatures increasing (Chapter 1, Fig. 2c) which are good for benthic fauna productivity (Sardá and Martin 1993, Mwaluma and Paula 2004, Osore et al. 2004) for the birds to feed on. This therefore allows birds to moult more than one feather simultaneously but which may in turn make birds take longer to grow each feather.

Birds reaching north-western Australia are of the nominate race which therefore have a long journey to cover (8,000 – 8,500 km) to get back to the breeding grounds in Mongolia and China (Higgins and Davies 1996, Hirschfield et al. 2000). With the long distance ahead of them for their return journey to breed, birds require additional fat reserves compared to Kenyan birds which probably travel c. 6,500 km. This is reflected in the maximum recorded mass of 112 g (Kenya) compared to 128 g (north-western Australia) (Jackson 2016) and thus Australian birds need relatively longer to fatten up for the journey. Birds mostly depart from north-western Australia in mid-March to early April (Barter and Barter 1988, Minton et al. 2013) and thus by completing moult by mid-January have a good eight weeks to fatten up prior to departure.

In south-eastern Australia birds arrive at least a month later than those reaching north-western Australia and thus moult is delayed starting until mid to late October. With estimated duration of moult taking 134 days, the average completion of moult is the end of February. As birds will leave for breeding grounds in late March and early April, this does not leave long for them to fatten. It is probable that they start to fatten whilst completing moult particularly as they have even further to travel than north-western Australia birds (up to c. 12,000 km), a strategy that is not ideal and normally avoided (Remisiewicz et al. 2009). Further investigation is needed to confirm this.

First year Greater Sand Plovers in north-western Australia share a similar strategy to those in Kenya with the majority undergoing a complete moult from the inner primaries and spread over a similar period from December to April (a small percentage in north-western Australia started moult in November). There was an apparent gap in birds starting moult (with a PFMG < 0.15) during May suggesting a possible distinction between first year complete moult (starting between November and mid-April) and the first birds of a sub-adult moult starting in June (Fig. 14a). A sub-adult moult starting in June or July was sufficiently early to be potentially distinct from the adult post-nuptial moult (starting in early August). However, the sub-adult moult effectively merged with the adult moult in August/September thus blurring the end of the former to the extent that it became impossible to separate them sufficiently to define parameters for the sub-adult moult.

In south-eastern Australia, the immature moult strategy from the limited data available is also one of undertaking a normal moult starting from the inner primaries. Of the three birds that were not in active first year moult, two had completed suggesting the first year moult is commonly a complete moult. However, the sub-adult bird caught in November with an arrested moult pattern for its previous moult shows that not all first years will complete. Instead they may moult most, but not all primaries, retaining one or two juvenile primaries for almost two years before being replaced in the adult complete moult, a strategy which has been noted in some wader species (Prater 1981). There was no evidence that for Greater Sand Plovers in south-eastern Australia there is a distinct sub-adult moult.

India

Relatively few Greater Sand Plovers spend the non-breeding season (November–April) in south-eastern India (Balachandran 1998) indicating that this location is not a major non-breeding ground but rather a key passage site during the southward migration. Analysis of moult in this study also shows that it is an important site for adult Greater Sand Plovers to moult. Adults moult from the end of July to finish in early October (Fig. 2a) and thus, since they arrive in Mandapam in early September, are likely to have started moult on or near the breeding areas as suggested by Cramp and Simmons (1983) and (Balachandran 1998). Moult progresses fast at a rate that is 1.7 times faster than for Greater Sand Plovers in Kenya (Tables 2, 3) such that with an average duration of just 80 days, by early October they have completed moult. Numbers rapidly drop off between October and

November (Balachandran 1998) which coincides with the extremely heavy monsoon rainfall (Chapter 1, Fig. 2a) that floods the wetlands with freshwater, reducing salinity (Hussain 1987) and thus productivity of food items. Furthermore, Greater Sand Plovers are surface feeders finding their prey items by sight, preferring drier sand surfaces than wetter when compared to Lesser Sand Plover (C. Jackson pers. obs.). Observations that Greater Sand Plovers move greater distances to capture prey than Lesser Sand Plover (Hockey 1993) also suggest they feed on crustaceans and arthropods which are more likely to be on a dry surface, where the prey item is more visible, than on a wet one. This being so, foraging becomes difficult under wet, flooded conditions as occurs during the heavy monsoon rains of south-eastern India. This suggests adults use south-eastern India as a place specifically to moult on passage, pushing to complete moult before the monsoon rain arrives and then leaving for better foraging grounds for the rest of the non-breeding season. The nearest potential destination is northern Sumatra, Indonesia, which is less than 2,000 km distant. It is unlikely that there is a trade-off between using resources for feather growth and building up fat reserves to cover this distance.

No first year birds were recorded moulting in south-eastern India other than one individual in April which was starting to moult its outer primaries, a strategy noted by Cramp and Simmons (1983) for non-breeding birds spending the breeding season on or near the breeding grounds. Another four first year birds caught in April were unmoulted, but the lack of data after this and before September make it impossible to know if they remained unmoulted throughout the northern spring and early summer, or underwent a complete moult before September. The 11 sub-adult birds caught in September showed that at least some of the first years undergo a complete moult probably between April and August. There were no Greater Sand Plovers caught between April and September despite ringing activity during the period and unlike Lesser Sand Plovers (306 ringed) and Terek Sandpiper (16) (Chapters 2, 4, 5) suggesting the species moves from south-east India almost entirely during this period other than a handful of non-breeders (Balachandran 1998). As sub-adult birds were found in Mandapam in September it would suggest they are moving southwards with other adults and therefore had spent the breeding season in or near the breeding grounds which is likely where they would also have moulted.

Summary

Other than the south-eastern Indian population which stop to moult for three to four months while on passage, the general moult strategy for adult Greater Sand Plovers is for most birds to undergo a complete moult having arrived on the non-breeding grounds. Some birds undertake a partial moult of mostly three inner primaries on or near the breeding grounds prior to migration, suspend and continue once having arrived on the non-breeding grounds. This is particularly true for those populations which travel farther to their non-breeding grounds (Australia) since they have less time available on the non-breeding grounds into which to fit moult and pre-migratory fattening. For first years, the most common strategy is to undergo a complete, descendent moult from the inner primaries starting mid-way through the non-breeding season. Most of these birds do not migrate back to breeding grounds thus giving plenty of time for them to moult. A small number of immatures undergo a partial moult of just some outer primaries and fewer still do not moult at all during the first year. A small proportion will undergo a distinct sub-adult moult later than the first-year moult and earlier than but overlapping with the post-nuptial adult moult. There appears to be a strong association with local climatic conditions that would affect food availability. This is an area of study that warrants further investigation, particularly to ascertain the level of importance of the site as a food source and the likely impact of other potentially significant and diverse factors such as human disturbance and climate change.

Having a safe and secure location with good foraging conditions in order to moult is critical in the annual life cycle of a migrant wader (Evans et al. 1991). The results from this study show that the wetlands in south-eastern India around Mandapam are clearly a highly important site for Greater Sand Plovers to stop over and moult before migrating further south. The study further highlights the importance of Mida Creek in Kenya and the locations in Australia where birds were caught as crucial sites for birds to moult into fresh plumage prior to a long flight back to the breeding grounds.

A number of birds were identified as sub-adults entering their second year and following an intermediate moult strategy between the first year and adult moult. However, the lack of recording certain key features in the field in particular the condition of old primaries led to the loss of information which would have enabled the identification of sub-adult birds and better assess the moult strategy of first years. It is recommended that in wader moult studies, a note of feather condition for old, unmoulted feathers, is made in order to provide a full understanding of the moult strategy for the species.

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Tables and figures

Adult moult

Table 1. Numbers of moult scores used in analyses according to age structure for Greater Sand Plovers in Kenya and Australia (Note for moult strategy analysis purposes ‘Adult’ includes birds aged as 2nd Year except for those listed for north-western Australia where moult pattern was mixed – see text).

	Adult	Immature	Sub-adult	Total
India	118	54	10	**182**
Kenya	819	148		**967**
n-w *Australia*	7,722	2,788	463	**10,973**
s-e *Australia*	22	8		**30**

Table 2. Parameters of estimated moult per primary and for whole primary tract for adult Greater Sand Plovers in India (n = 118). The average growth rate per primary = 0.604% per day; Average growth rate for all primaries using total moult duration calculated from per primary results = 1.252% per day. '% adj pp overlap' is the number of days of overlap between one primary with the next adjacent one expressed as a percentage of that feather's estimated duration. 2nd pp overlap is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously.

	Duration	SE	Start day	SE	Start SD	SE	Rate of growth	Start date	End date	Days apart	Days overlap	% adj pp overlap	2nd pp overlap	Un-moulted	Active moult	New
P1-P6																
P7	31.8	10.3	49.7	12.7	25.2	13.0	0.38%	18 Aug	19 Sep	-	18.8	59%	-1%	4	10	104
P8	29.8	8.8	62.7	9.9	28.6	13.8	0.48%	31 Aug	30 Sep	13	10.7	36%	15%	7	14	97
P9	17.8	3.0	81.8	2.4	8.5	0.2	0.91%	19 Sep	7 Oct	19	11.7	66%	-	12	14	92
P10	21.7	5.9	87.9	5.5	25.2	10.9	0.83%	25 Sep	17 Oct	6	-	-	-	18	14	86
										End date: 17 October		**Av. growth rate: 0.604%**				
P1-10	**79.9**	15.3	30.0	13.6	24.0	10.1	1.252%	**29 Jul**	**17 Oct**				**n = 118**	**0**	**32**	**86**

Table 3. Parameters of estimated moult per primary and for whole primary tract for adult Greater Sand Plovers in Kenya (n = 819). The average growth rate per primary = 0.604% per day; Average growth rate for all primaries using total moult duration calculated from per primary results = 0.758% per day. '% adj pp overlap' is the number of days of overlap between one primary with the next adjacent one expressed as a percentage of that feather's estimated duration. 2nd pp overlap is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously.

	Duration	SE	Start day	SE	Start SD	SE	Rate of growth	Start date	End date	Days apart	Days overlap	% adj pp overlap	2nd pp overlap	Un-moulted	Active moult	New
P1	19.4	3.5	63.3	6.4	45.2	14.7	0.19%	**1 Sep**	20 Sep		10.7	55%	9%	50	33	736
P2	18.2	3.1	72.0	5.2	41.0	12.8	0.24%	9 Sep	28 Sep	8	9.2	51%	-12%	67	35	717
P3	22.3	3.1	81.0	4.1	37.2	10.8	0.24%	18 Sep	11 Oct	9	11.0	49%	2%	91	50	678
P4	20.9	2.8	92.3	3.5	36.5	10.2	0.33%	30 Sep	21 Oct	12	10.4	50%	-25%	124	51	644
P5	21.2	2.6	102.8	2.9	33.3	9.0	0.40%	10 Oct	31 Oct	10	5.5	26%	-28%	158	60	601
P6	18.8	2.3	118.5	2.5	31.4	8.3	0.55%	26 Oct	14 Nov	16	7.3	39%	-49%	210	58	551
P7	23.7	2.5	130.0	2.4	30.6	7.8	0.51%	7 Nov	30 Nov	12	7.2	30%	-56%	255	77	487
P8	32.1	2.8	146.5	2.4	32.2	7.4	0.45%	23 Nov	25 Dec	16	11.6	36%	-28%	320	96	403
P9	30.0	2.7	167.0	2.4	31.9	7.1	0.54%	14 Dec	13 Jan	21	9.3	31%	-	386	83	350
P10	23.5	2.6	187.7	2.6	34.2	7.6	0.77%	3 Jan	27 Jan	20	-	-	-	451	59	309
		Overall duration: 148 days					**Start date: 1 September**			**End date: 27 January**		**Av. growth rate: 0.676%**				
P1-10	131.5	4.8	82.8	3.5	31.1	5.7	0.760%	**20 Sep**	**31 Jan**				**n = 736**	**48**	**383**	**305**

Table 4. Parameters of estimated moult per primary and for whole primary tract for adult Greater Sand Plovers in north-western Australia excluding birds with suspended moult (n = 7,346). The average growth rate per primary = 0.694% per day; Average growth rate for all primaries using total moult duration calculated from per primary results = 0.746% per day. '% adj pp overlap' is the number of days of overlap between one primary with the next adjacent one expressed as a percentage of that feather's estimated duration. 2nd pp overlap is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously.

	Duration	SE	Start Day	SE	Start SD	SE	Growth rate	Start Date	End date	Days apart	Days overlap	% adj pp overlap	2nd pp overlap	days of 3 pp overlap	Un-mltd	Active moult	New
P1	19.3	0.8	51.0	0.9	18.5	3.3	0.19%	19 Aug	8 Sep	-	16.7	87%	44%	8.5	364	523	6,459
P2	21.0	0.8	53.6	0.8	18.8	3.2	0.21%	22 Aug	12 Sep	2.6	12.8	61%	8%	1.6	428	596	6,322
P3	21.5	0.7	61.8	0.7	18.2	2.8	0.25%	30 Aug	21 Sep	8.2	10.3	48%	-1%	-0.2	636	671	6,039
P4	20.6	0.7	73.0	0.6	17.6	2.6	0.33%	11 Sep	1 Oct	11.2	10.1	49%	-5%	-1.1	974	653	5,719
P5	21.0	0.6	83.5	0.6	17.6	2.5	0.41%	21 Sep	12 Oct	10.5	9.8	47%	-17%	-3.5	1,311	677	5,358
P6	23.3	0.6	94.7	0.5	17.1	2.4	0.45%	2 Oct	25 Oct	11.2	10.0	43%	-33%	-7.7	1,652	850	4,844
P7	26.6	0.7	108.0	0.5	17.2	2.6	0.46%	15 Oct	11 Nov	13.3	8.9	33%	-34%	-9.1	2,107	1,085	4,154
P8	27.5	0.9	125.7	0.5	17.2	2.9	0.52%	2 Nov	30 Nov	17.7	9.5	35%	-45%	-12.5	2,825	915	3,606
P9	32.9	1.2	143.7	0.7	19.6	3.2	0.49%	20 Nov	23 Dec	18.0	10.9	33%	-	-	3,449	537	3,360
P10	29.3	1.4	165.7	1.0	23.9	3.6	0.61%	12 Dec	10 Jan	22.0	-	-	-	-	3,842	276	3,228
	Overall duration: 144 days							**Start date: 19 August**		**End date: 11 January**			**Av. growth rate: 0.694%**				
P1-10	134.0	1.3	61.2	0.7	19.0	2.1	0.746%	**30 Aug**	**11 Jan**					**n = 7,346**	**349**	**3,769**	**3,228**

Table 5. Parameters of estimated moult per primary and for whole primary tract for adult Greater Sand Plovers in south-eastern Australia (n = 22). Data were sufficient for analysis of P7-P10 alone. The average growth rate per primary = 0.356% per day; Average growth rate for all primaries using total moult duration calculated from per primary results = 0.746% per day. '% adj pp overlap' is the number of days of overlap between one primary with the next adjacent one expressed as a percentage of that feather's estimated duration. 2nd pp overlap is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously.

	Duration	SE	Start Day	SE	Start SD	SE	Growth rate	Start Date	End date	days apart	Days overlap	% adj pp overlap	2nd pp overlap	Un-mltd	Active moult	New
P1-P6	-														*Insufficient data*	
P7	50.5	20.6	135.5	22.8	28.4	17.5	0.24%	12 Nov	1 Jan	-	17.6	35%	-3%	1	6	15
P8	31.8	24.5	168.4	27.0	61.5	49.7	0.45%	15 Dec	16 Jan	32.9	12.6	40%	-75%	7	4	11
P9	37.9	27.4	187.6	19.1	60.3	48.3	0.43%	3 Jan	10 Feb	19.2	1.6	4%		9	5	8
P10	58.6	52.3	223.9	27.0	80.7	73.7	0.31%	8 Feb	8 Apr	36.3				13	5	4
										End date: 8 April			**Av. growth rate: 0.356%**			
P1-10	134	47.1	114.0	29.3	25.2	14.2	0.746%	**21 Oct**	**4 Mar**				**n = 22**	**0**	**18**	**4**

Table 6. Numbers of adult Greater Sand Plovers in north-western Australia with suspended moult by the number of primaries suspended and by month. Total number of birds showing suspended moult are expressed as a percentage of the catch for that month.

No. of pp moulted:	1	2	3	4	5	6	7	8	9	Total	Total adults caught	% suspended
Aug	39	61	68	10	4					182	645	28%
Sep	22	45	57	25	5	6				161	1,247	13%
Oct		1	1	1	2	4	1			10	1,095	1%
Nov			1			1	7	3		12	1,312	1%
Dec								1		1	74	1%
Jan										0	255	0%
Feb									1	1	719	0.1%
Mar								1	1	2	1,589	0.1%
Apr							2	1	6	9	807	1%
Total	**61**	**107**	**127**	**36**	**11**	**11**	**10**	**7**	**8**	**378**	**7,743**	**5%**

Table 7. Estimated date for average 50% feather mass grown for adult Greater Sand Plovers in south-eastern India, Kenya, north-western Australia and south-eastern Australia and estimated number of days that moult is delayed after moult in India per 1,000 km farther from breeding grounds.

	Date of 50% PFMG	Days later than India	Estimated av. km from breeding grounds	No. of days later /1000 km farther
India	6 Sept	0	3,700	0
Kenya	14 Nov	69	7,000	21
north-western Australia	4 Nov	59	7,300	8
south-eastern Australia	27 Dec	112	11,000	10

Average days later than India /1000 km farther from breeding grounds: 13

Fig. 1 Breeding and non-breeding distributions of Greater Sand Plover (source: http://maps.iucnredlist.org/).

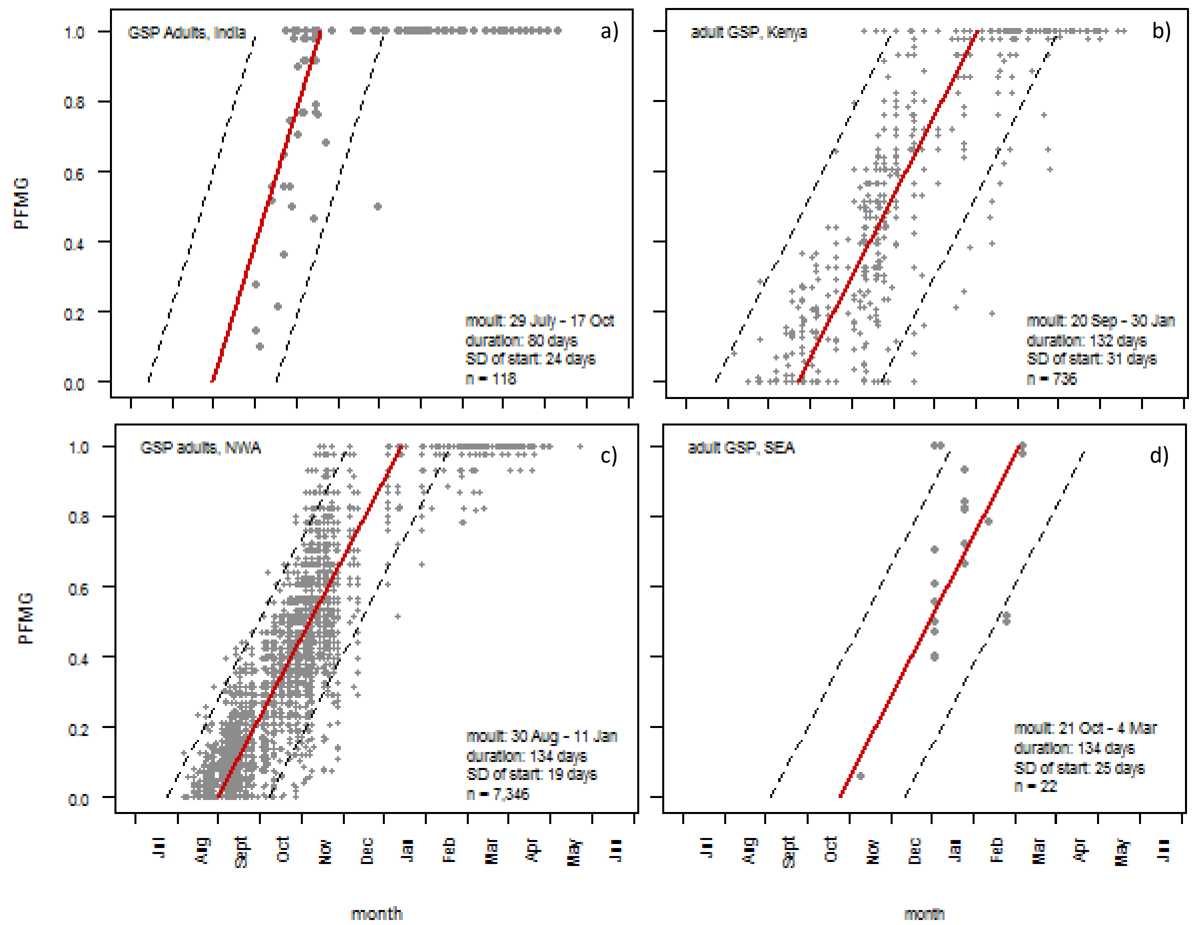


Fig. 2. Primary moult of adult Greater Sand Plovers in a) India b) Kenya c) north-western Australia and d) south-eastern Australia. Percent Feather Mass Grown (PFMG) is plotted against date using type 4 analysis of Underhill-Zucchini moult model. The solid line shows the estimated progression of primary moult for the average bird. Black dashed lines indicate the limits for 95% of the population and thus the parallelogram between them should contain approximately 95% of all birds in active moult.

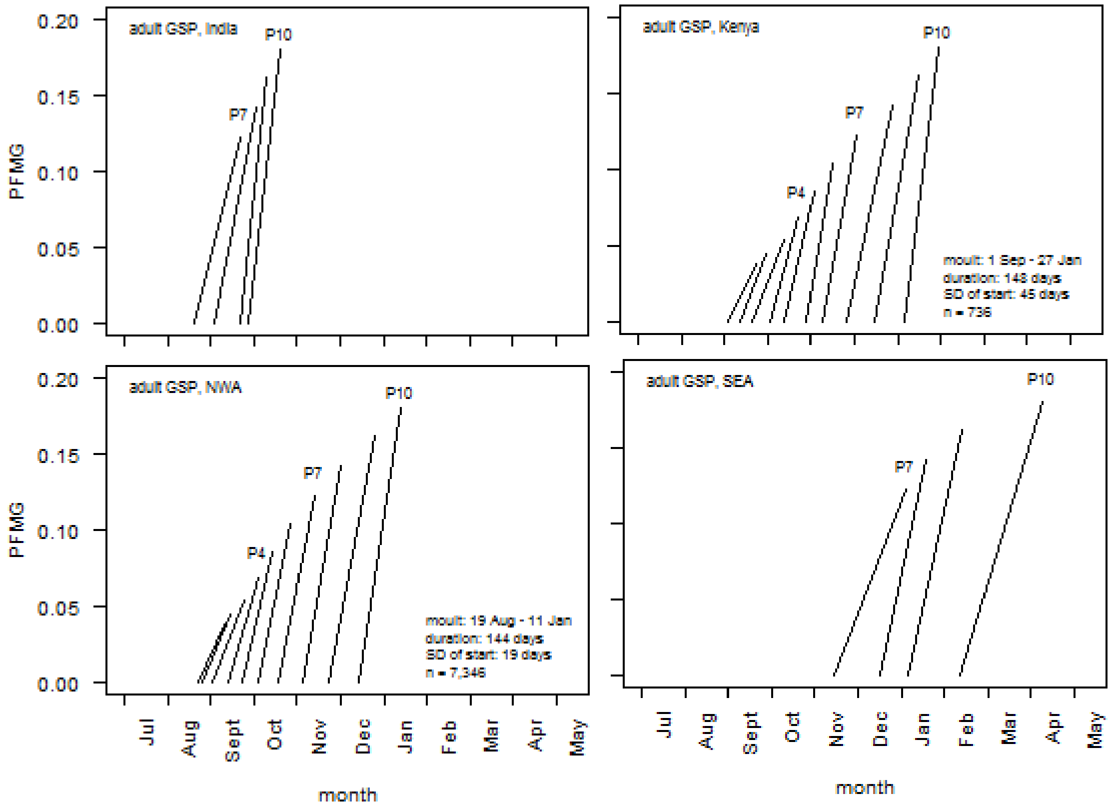


Fig. 3. Moult timing and growth rate per primary for Greater Sand Plover in a) India b) Kenya, c) north-western Australia & d) south-eastern Australia. Each line represents the estimated moult for an individual primary. The slope of the line shows the rate of growth for that feather.

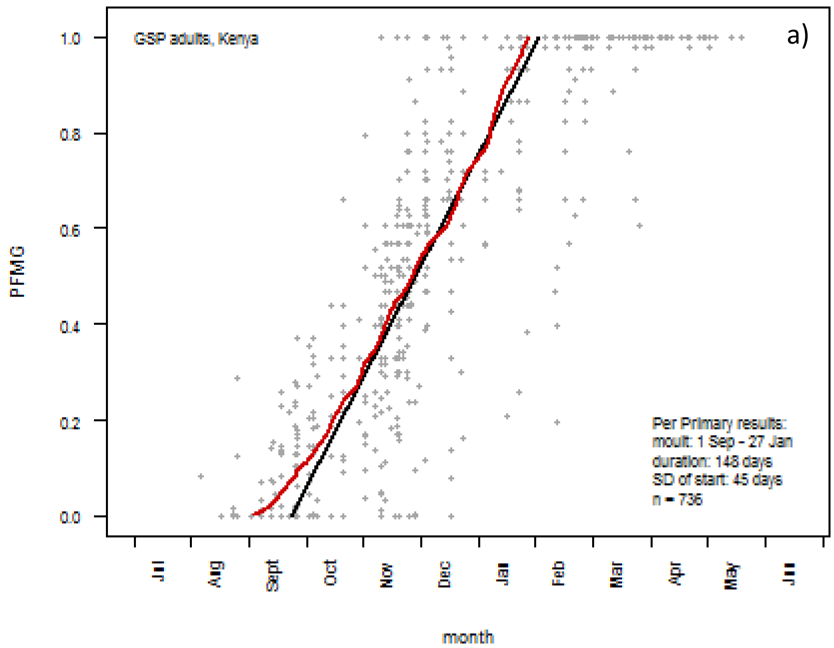


Fig. 4a. cumulative increase of PFMG per primary (red line) plotted over increase of PFMG for whole primary tract (black line – with 5% and 95% limits as dashed lines) for adult Greater Sand Plovers in Kenya b) north-western Australia.

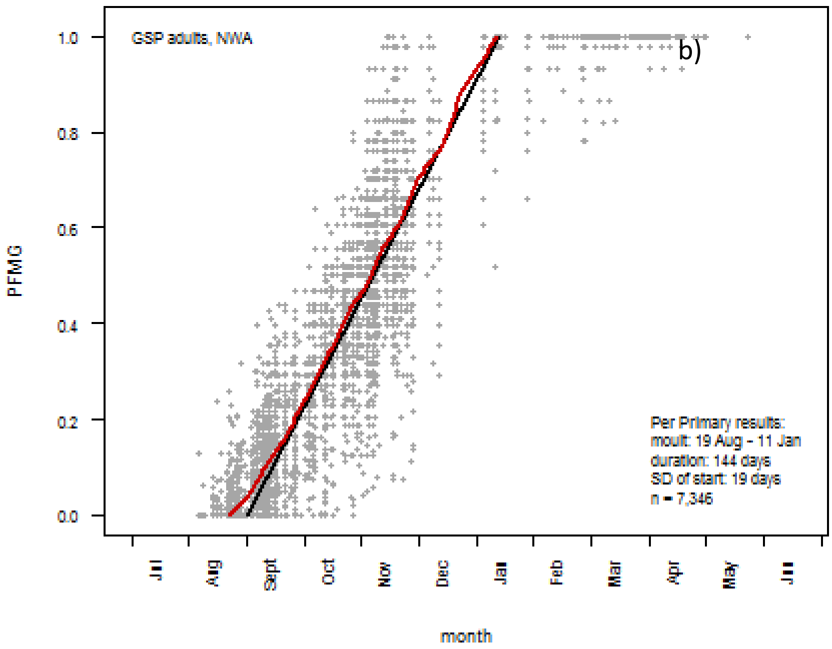
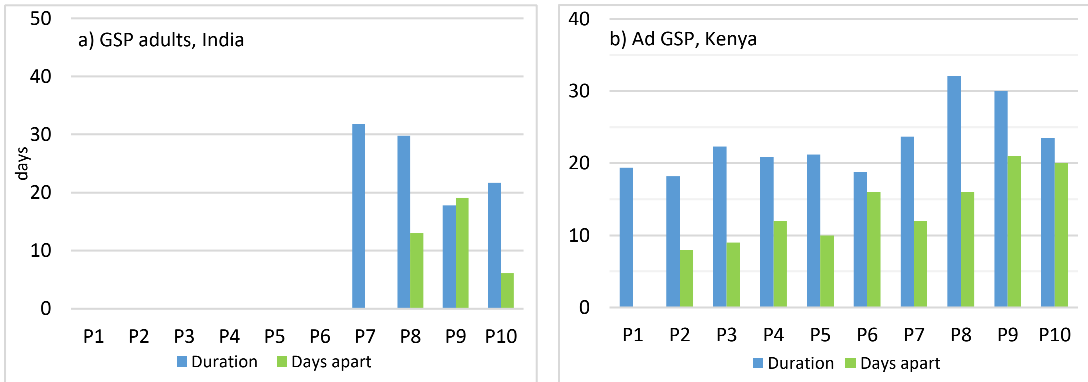


Fig. 4b. cumulative increase of PFMG per primary (red line) plotted over increase of PFMG for whole primary tract (black line – with 5% and 95% limits as dashed lines) for adult Greater Sand Plovers in north-western Australia.



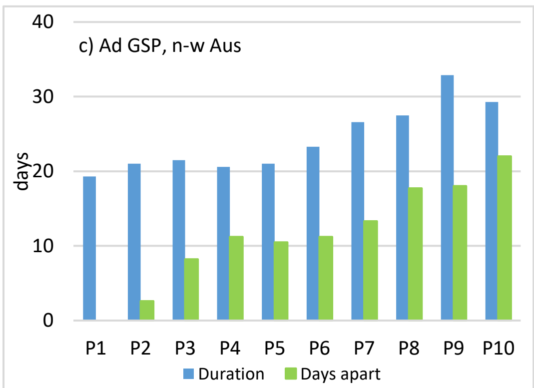


Fig. 5. Duration of moult per primary (blue bars) and interval between moulting primaries (green bars) for adult Greater Sand Plovers in a) India, b) Kenya and c) north-western Australia.

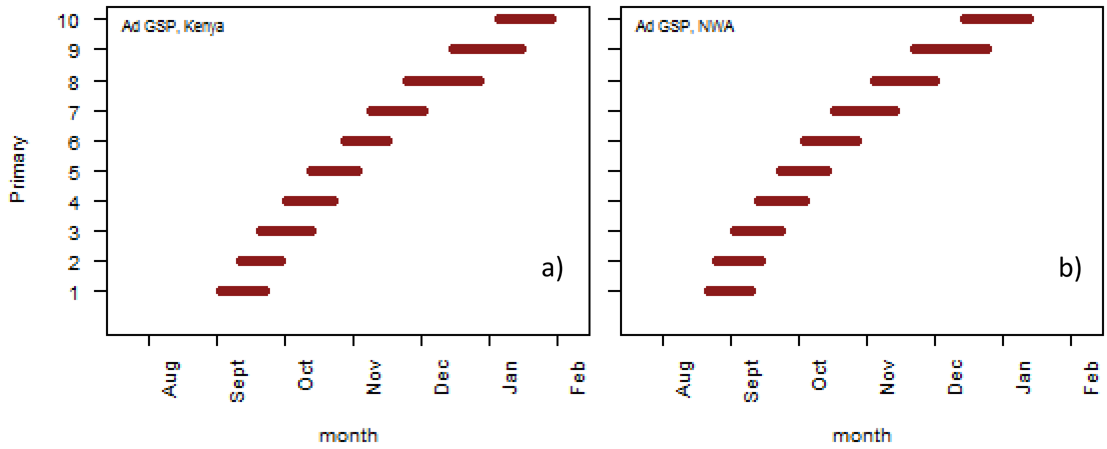


Fig. 6. Timing and duration of per primary moult for adult Greater Sand Plovers in a) Kenya and b) north-western Australia showing overlap of moulting primaries. Each line represents the estimated average duration of moult for each primary.

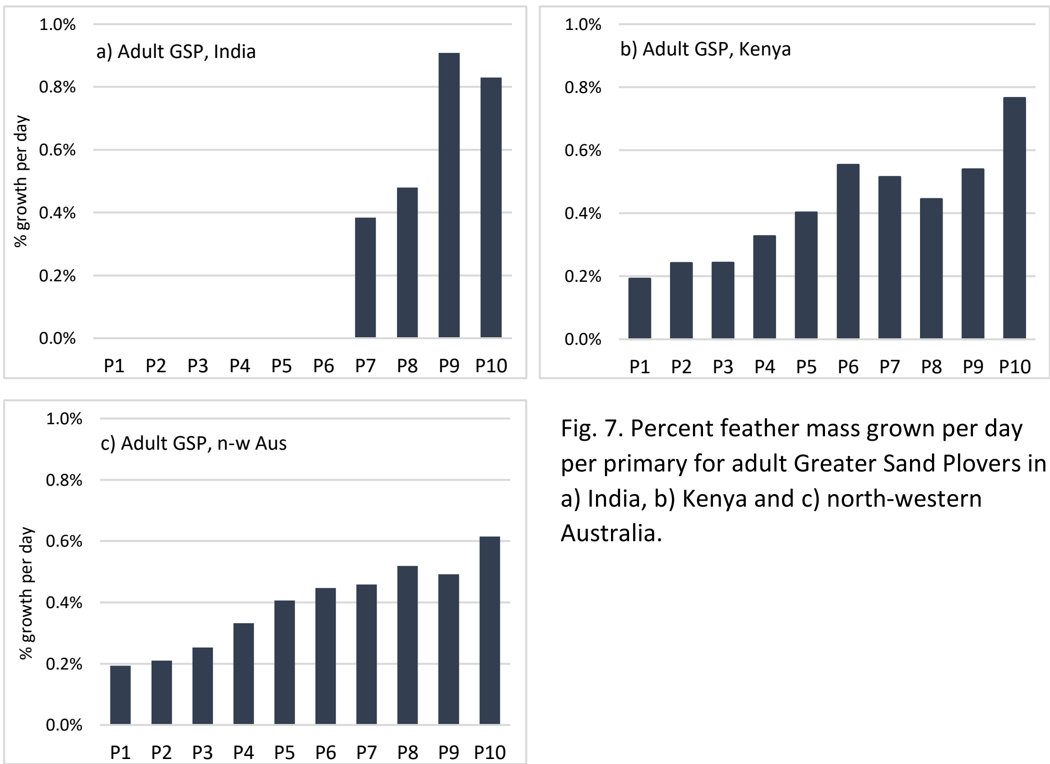


Fig. 7. Percent feather mass grown per day per primary for adult Greater Sand Plovers in a) India, b) Kenya and c) north-western Australia.

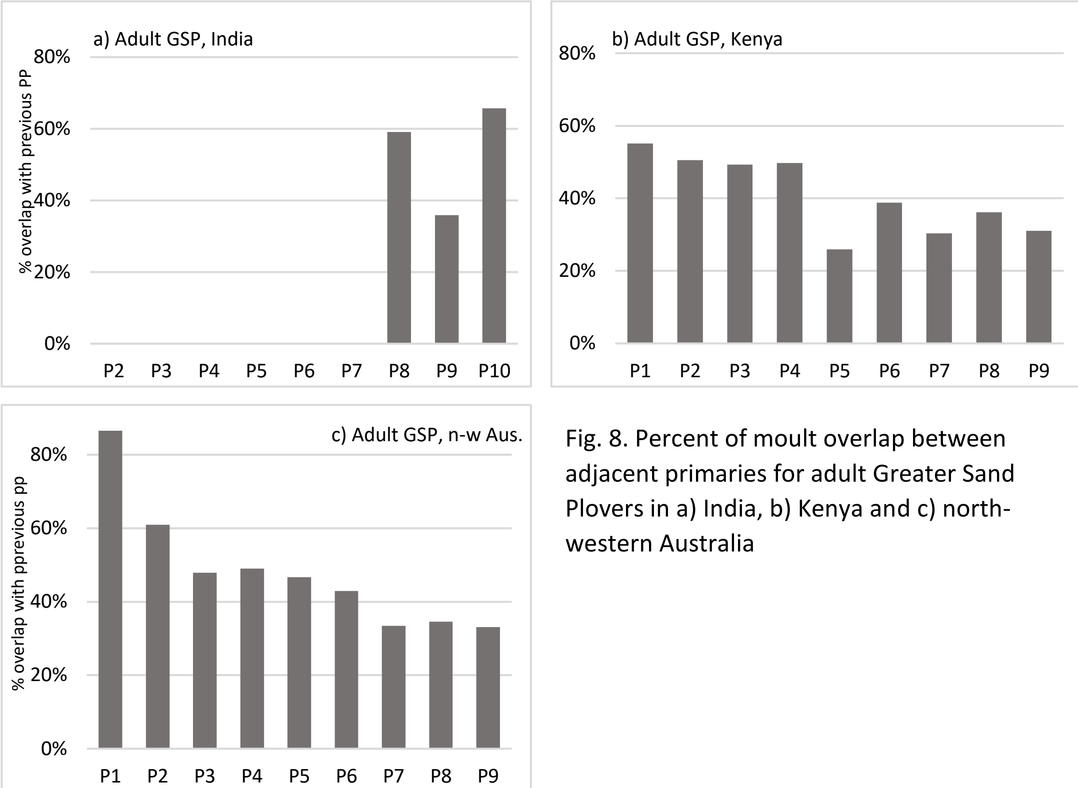


Fig. 8. Percent of moult overlap between adjacent primaries for adult Greater Sand Plovers in a) India, b) Kenya and c) north-western Australia

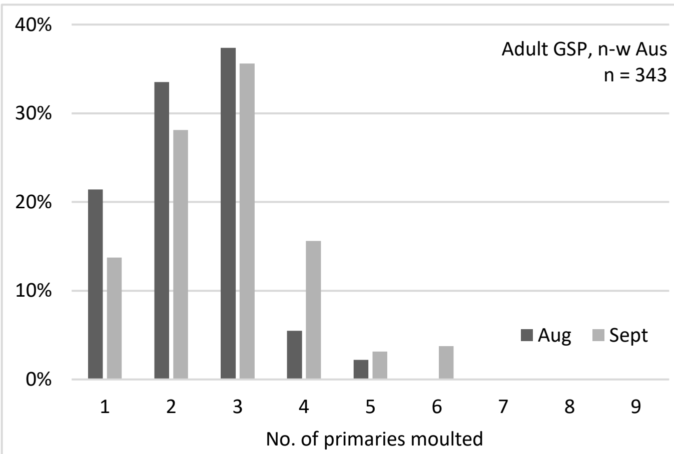


Fig. 9. Frequency of the number of primaries moulted prior to suspension for adult Greater Sand Plovers, north-western Australia in August and September.

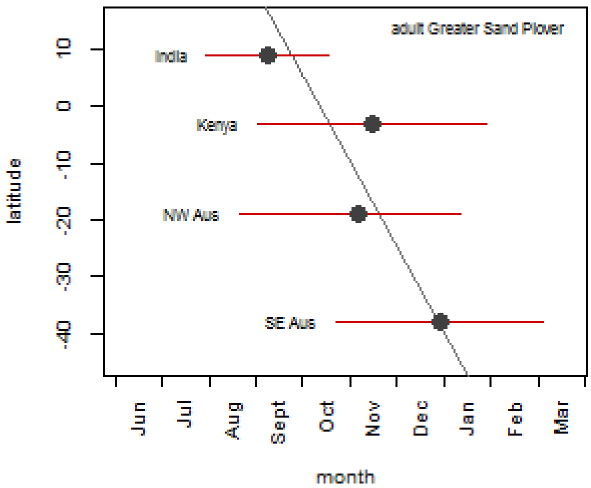


Fig. 10. Average estimated date of 50% PFMG against latitude for adult Greater Sand Plovers. The horizontal lines indicate the estimated average duration of moult for each location. The diagonal line is the regression line and is fitted for visual guidance only.

First year and sub-adult moult

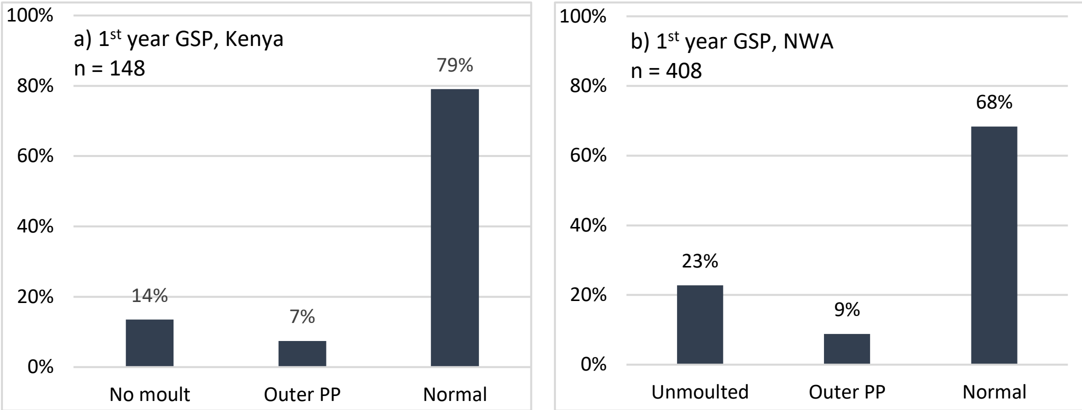


Fig. 11. Percentage of birds following each of the three main immature moult strategies for first year Greater Sand Plovers in a) Kenya and b) north-western Australia.

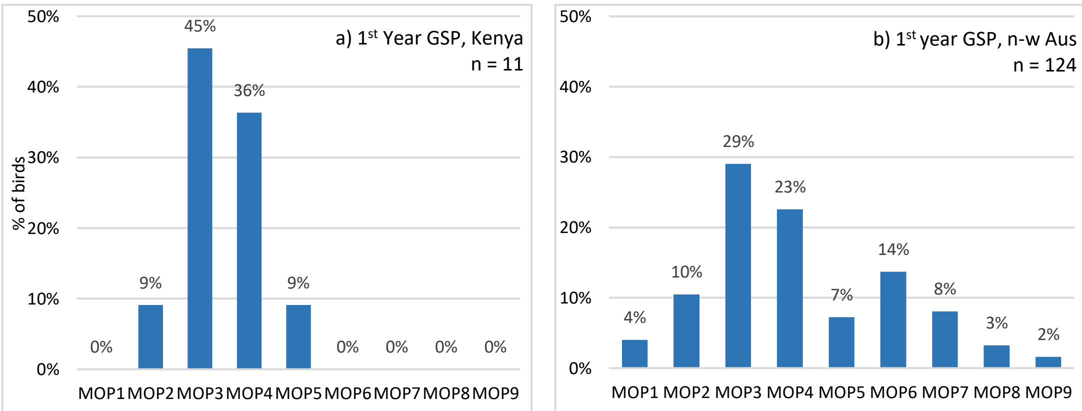


Fig. 12. Proportions of first year Greater Sand Plovers moulting differing numbers of outer primaries a) Kenya, b) north-western Australia. In south-eastern Australia no birds were found moulting outer primaries (n = 8).

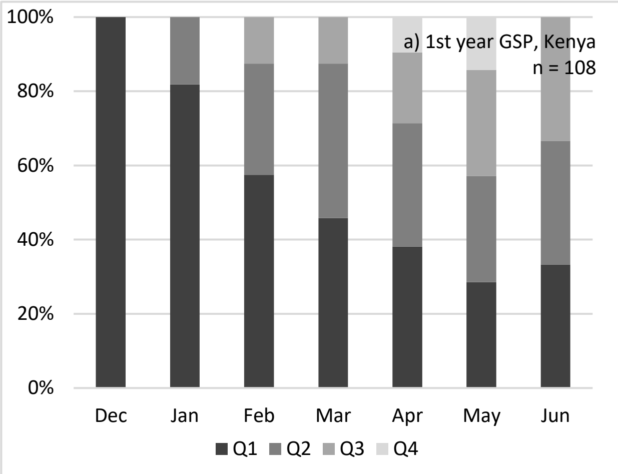
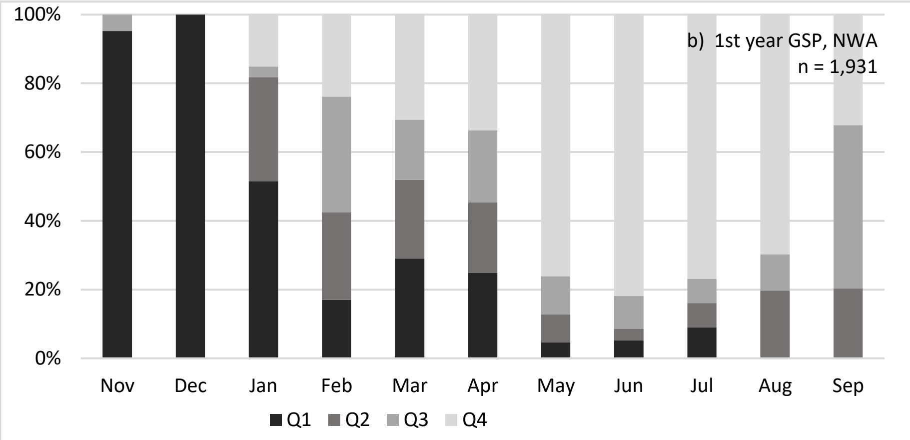


Fig. 13. proportions of first year Greater Sand Plovers at differing stages of moult: Q1 = PFMG of 0-0.25, Q2 = PFMG of 0.26-0.5; Q3 = PFMG of 0.51-0.75; Q4 = PFMG of 0.76-1.0. Proportions are expressed as a percent of total in sample a) in Kenya (n = 108) b) north-western Australia (n = 1,931).



Complete moult in first year birds

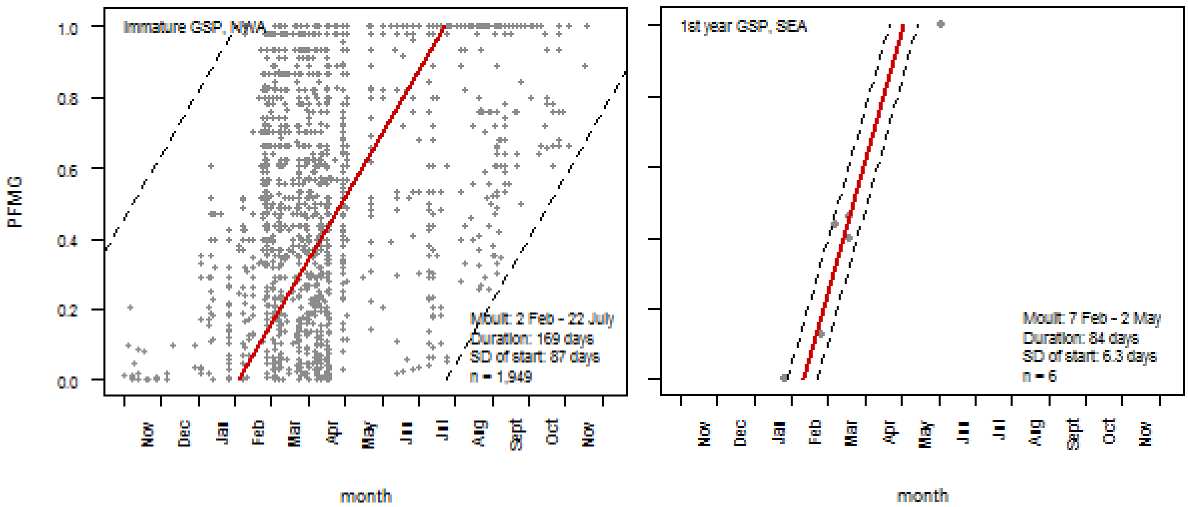


Fig. 14. Primary moult of first year Greater Sand Plovers in a) north-western Australia and b) south-eastern Australia. Percent Feather Mass Grown (PFMG) is plotted against date using type 4 analysis of Underhill-Zucchini moult model. The solid red line shows the estimated progression of primary moult for the average bird. Black dashed lines indicate the limits for 95% of the population and thus the parallelogram between them should contain approximately 95% of all birds in active moult.

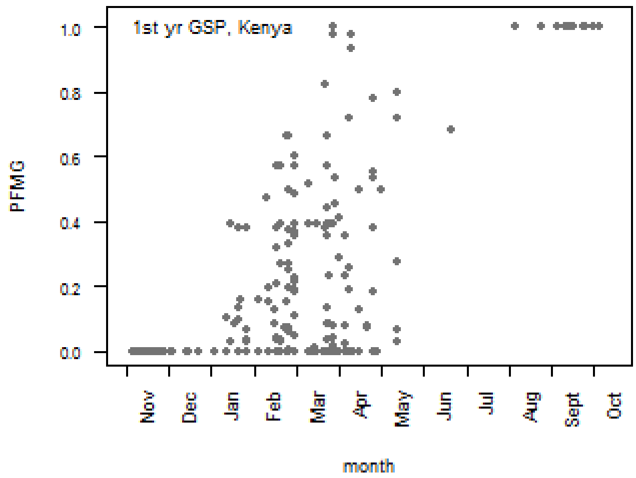


Fig. 15. Spread of moult scores for first year Greater Sand Plovers in Kenya. Spread of data over 50% percent feather mass grown (PFMG) did not allow for an estimate of average moult. However, estimate by eye suggests first year moult may start between January and the end of April with an average date likely to be the end of February.

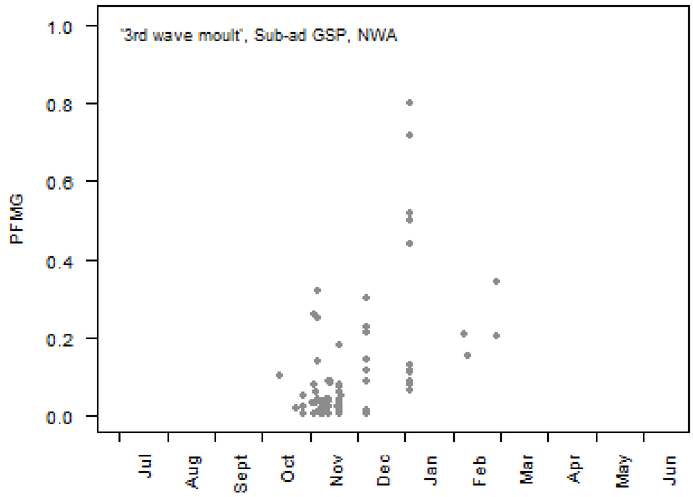


Fig. 16. Spread of moult scores for a ‘third wave’ of moult in sub-adult Greater Sand Plovers, north-western Australia.

Chapter 4

Moult of adult Terek Sandpipers in Kenya, India and Australia

Chapter 4. Moult of adult Terek Sandpipers in Kenya, Australia and India

Introduction

The Terek Sandpiper *Xenus cinereus* is a common Palearctic non-breeding migrant visitor to the East African, Australian, south and south-east Asian coasts between August and late April (Britton et al. 1980, Hayman et al. 1986, Ali and Ripley 1988, Higgins and Davies 1996). Inland it is uncommon with a scattering of African records on the Rift Valley lakes and Lake Victoria and at wetlands across the north of southern Africa (Dowsett 1980, Zimmerman et al. 1996, Hockey et al. 2005) and a handful through central Australia (Atlas of Living Australia 2016). Terek Sandpipers breed across boreal and low Arctic Eurasia; in the west, there is a small outlier western population in Finland (24°30´E) (Ferguson-Lees and Hosking 1959, Cramp and Simmons 1983, Pakanen 2016) and then eastward across Russia to the western end of the Chukotsky Peninsula (180°E) (Lappo et al. 2012). Eastern breeding birds migrate south and east to spend the non-breeding season from south Asia, Indonesia to northern and western Australia with a few reaching south-eastern Australia (Fry 1990, del Hoyo et al. 1996). The western breeding population migrates south-west to spend the boreal winter in the Middle East and along the East African coast as far south as South Africa with a small population extending along the west coast of southern Africa into Namibia (Waltner and Sinclair 1981, Cramp and Simmons 1983, Hirschfeld et al. 1996, Hockey et al. 2005, Delany et al. 2009).

The migration and moult of Terek Sandpipers that reach Australia have been described (Fry 1990, Branson et al. 2010) however little is known about the Indian and East African populations, neither their origins, migration nor moult strategy (Cramp and Simmons 1983, Karlionova et al. 2006, Delany et al. 2009). In this paper I present the timing and duration of moult for adult Terek Sandpipers in Kenya, south-eastern India, north-western and south-eastern Australia.

Methods

Primary moult scores were obtained from Terek Sandpipers in Kenya, India and Australia. In Kenya, birds were ringed during regular wader-ringing sessions on site at Mida Creek (3°19'S 39°57'E) between 1978 and 2014. In India, were collected during wader ringing carried out at Mandapam (9°17'N, 79°8'E) and at the Great Vedaranyam Swamp (10°18'N, 79°51'E) in south-eastern India between 1985 and 2014; in Australia, birds were caught between 1982 and 2012 by the Australasian Wader Study Group in north-western Australia (19°15'S 120°20'E) and Victoria, south-eastern Australia (38°22'S 145°32'E). Further details on location and methodology have been described in Chapter 1.

The age of each bird was determined where possible by plumage characteristics described by Prater et al. (1977) and from personal observation (D.J. Pearson pers. comm. & own observations). Three categories of age were used: 'first year' birds (birds in their first year of life from arrival in juvenile plumage in September-November until 31 July), 'sub-adult' birds (birds in their second year from 1 August to the completion of their first adult primary moult mostly in November/December) and 'adults' (defined as 'more than one year old'). Birds with plumage characteristics which left the age unclear were not aged and omitted from analyses.

Many sub-adult birds were identifiable from August to October by having two or sometimes three generations of primaries: juvenile (grown prior to fledging), first year (a partial moult towards the end of their first year on the non-breeding grounds) and adult (the first moult into fully adult plumage). Where this was observed, the moult score of feathers identified as having moulted as part of the 'adult' moult were included in the adult analyses. Thus a bird may be caught in September with three replaced outer primaries moulted at the end of the first year but having also two actively moulting inner primaries. The score of seven old inners and three new outers was used for analysis for immature moult and that of two active inner primaries and eight old outer was taken for analysis of adult moult.

Moult scores were recorded following the standard method by Ashmole (1962) and Ginn and Melville (1983) and converted to proportion of feather mass grown (PFMG) (Underhill and Summers 1993). For calculating PFMG in Terek Sandpiper moult, relative primary masses were obtained from Terek Sandpipers in Australia (C.D.T. Minton unpubl. data) following the methodology laid out by Summers et al. (1983) and Underhill and Joubert (1995).

Estimates of start date and duration of moult were calculated using the Underhill-Zucchini moult model package in R (Underhill and Zucchini 1988, Erni et al. 2013). Data type 2 analyses (using unmoulted, actively moulting and fully moulted scores) were used where the whole population was understood to be present at the time of sampling; data type 4 (using only actively moulting and fully moulted scores) was used where sampling started before the whole population was present at the study site. A data type 2 analysis was performed on each individual primary, a 'per primary analysis', to obtain the parameters of moult for each primary feather (Serra 2000, Underhill 2003) where the dataset was large enough to enable this (Chapter 1).

The cumulative average growth per day from the per primary analysis was calculated and plotted against the overall primary tract results. The average amount of feather mass grown on each day was calculated for Kenya and north-western Australia where data were sufficient to show detailed daily growth rates (c.f. Chapter 1 for details).

Results

Moult scores from 733 adult Terek Sandpipers caught in Kenya were used for the analysis of adult moult, 5,455 in north-western Australia, 19 in south-eastern Australia and 50 in India. 104 of the Australian birds were considered to have suspended moult (Table 1). The relative masses of the primary feathers taken from both wings of two Terek Sandpipers ranged from 4.13% for the first (inner) primary to 16.42% for the 10th (outermost) (Table 2).

Kenya

The estimated average date for Terek Sandpipers starting to moult primary feathers in Kenya taking the PFMG for all feathers together in the primary tract was 10 August. The estimated duration of moult was 136 days, so that the estimated end date was 24 December. The estimated standard deviation in start date was 31 days thus 95% of birds were considered as having started primary moult between 10 June and 10 October (Fig. 2b). The estimated mean percent of feather mass grown per day for the whole primary tract was 0.735% per day.

In the per primary analysis, P1 was estimated to start on 15 September and P10 to complete on 23 December giving an estimated duration of moult of 99 days (Fig. 3b, Table 3). The estimated growth rate was 1.013% of total primary feather mass per day which is different to the estimate obtained from the analysis of the whole primary tract. The start date is 36 days later in the per primary analysis, duration is 37 days shorter, the end date one day earlier and the rate of growth 37.8% higher. Overlaying the cumulative PFMG per individual primary on the plot for the whole primary tract shows this difference (Fig. 6a, Table 3). The progression of moult estimated by the two methods aligns closely at a PFMG of 0.5 in mid-October.

The inner four primaries moulted in quick succession with an estimated two or three days between feathers starting moult and a short duration of six to eight days per feather (Figs. 3b, 4b, 5b, Table 3). From P5 the duration and interval between feathers steadily increased peaking at 22 and 17 days respectively for P9 and P10 (Fig. 4b, Table 3). The short interval between inner primaries moulting meant a high level of overlap for these feathers particularly P1 and P2; the overlap steadily reduced to almost no overlap between P7 and P8 (Figs. 5b, 9b). The estimated rate of growth per primary was lowest for P1 and P9 at 0.68% PFMG per day and greatest for P5 (1.02%) (Fig. 7b, Table 3); the average rate of growth per primary feather was 0.81% (Table 3).

In Kenya, using the daily total of PFMG calculated per primary (Fig. 8a), Terek Sandpipers showed a high rate of growth peaking between 1.2% and 2.0% per day for primaries P1-P5 with the sharp peaks indicating only relatively small periods of overlap between feathers. 50% PFMG was reached on average by 17 October for Terek Sandpipers in Kenya (Table 7).

North-western Australia

In north-western Australia, 102 adults (2%) were caught in suspended moult with between one and eight inner primaries already replaced. The estimated start date for all primaries combined was 11 September and duration of moult 136 days giving an estimated completion date of 25 January. The estimated standard deviation in start date was 18 days and thus 95% of birds were estimated to have started primary moult between 2 August and 21 October (Fig. 2c). The estimated mean proportion of feather mass grown per day for the whole primary tract for adult NW Australian birds was 0.735%.

Per primary analysis gave an estimated start date for P1 of 22 September and end date for P10 of 29 January and thus a duration of 130 days (Fig. 3c, Fig. 6b, Table 4) and a growth rate of 0.771% of total feather mass per day for the whole wing. The start date was 11 days later in the per primary analysis, duration six days shorter, the end date four days later and the rate of growth 4.9% higher. Overlaying the cumulative PFMG per individual primary on the plot for the whole primary tract shows this difference (Fig. 6c, Table 4). The progression of moult estimated by the two methods aligns closely at a PFMG of 0.23 in mid-October.

P1–P4 were estimated to have a similar moult duration of 15 to 16 days; duration of feather moult then increased from P5 to peak at 34 days for P10 (Fig. 4c). The interval between feathers was estimated to be one day for P1 and P2 increasing to the longest interval between P7 and P8 of 21 days after which the interval decreased to 15 days for P9 and P10 (Fig. 4c, Table 4). The estimated rate of growth per primary was lowest for P1 at 0.28% PFMG per day and greatest for P9 (0.55%) (Fig. 7c, Table 4); the estimated average rate of growth per primary was 0.455% per day.

With the short interval between moulting inner primaries, the estimated overlap between P1 and P2 was 91%. The overlap reduced as the intervals between the start of moult of successive feathers increased, such that P7 and P8 were estimated to overlap by 17%. Overlap increased again after this for the largest, outer primaries to 46% for P9 and P10 (Fig. 8b, Fig. 9c). 50% PFMG was reached on average by 18 November for Terek Sandpipers in north-western Australia which was 73 days later than for birds in south-east India (Table 7).

South-eastern Australia

Terek Sandpiper is not a common species in south-eastern Australia and thus only 19 moult scores were available for adults for this location of which two were discounted being in suspended moult. Therefore, only the full primary tract moult estimate method was possible. The estimated start date of moult was 9 November and duration of 130 days. This gave an end date of 19 March (Fig. 2d, Table 5). The standard deviation parameter was 33 days, so it was estimated that 95% of birds started moult between the 6 September and 12 January. Estimated rate of growth for the whole wing was 0.770% per day. 50% PFMG was reached on average by 13 January for Terek Sandpipers in south-eastern Australia (Fig. 2c, Table 7).

India

The estimated start date for the whole primary tract was 7 July and the estimated duration was 120 days, giving an end date of 6 November (Fig. 2a, Table 6). The estimated standard deviation in start date was 39 days, thus 95% of birds were estimated to have started moult between 20 April and 23 September (Fig. 2a). The estimated mean percent of feather mass grown per day for the whole primary tract together was 0.821%.

Insufficient data were available in early July to enable the start date and duration of the individual inner primaries to be estimated (P1–P3). Results were obtained for P4–P10, though again due to the limited dataset, estimates had large standard errors (Fig. 3a). In Kenya and Australia, the first three primaries dropped rapidly, within a space of four days in Kenya and six days in north-western Australia, and the fourth within seven days of the first for Kenya and 11 days in Australia (Table 3, Table 4). Assuming the same strategy is adopted in India, the start of moult for Terek Sandpipers was estimated as 15 July (11 days prior to P4, Table 6). The estimated duration of moult from the per primary analysis was 121 days and thus a mean rate of feather mass grown per day of 0.829% of the whole tract. The average rate of growth per individual primary was 0.621%. 50% PFMG was reached on average by 6 September for Terek Sandpipers in south-eastern India (Table 7, Fig. 10).

Comparative results between locations

I used the estimated date at which PFMG reaches 50% as the basis for comparison of timing of moult between locations in relation to latitude. The estimated mid-moult date in India was 6 September; in

Kenya, the mid-moult date was almost one and a half months later on 17 October; in north-western Australia, mid-moult occurred on 18 November, a month after Kenya; the southernmost population in south-eastern Australia had a mean mid-moult date of 13 January, four and a half months after the Indian birds and two months after the northern Australian population (Fig. 10, Table 7). Taking the estimated average distance from the breeding grounds for each non-breeding population considered, the average number of days that Terek Sandpipers moulted in the three southern hemisphere locations after the population in India per 1,000 km farther from the breeding grounds was 16 days (Table 7).

While start and mid-moult date differed between locations, the best estimates of the average duration of moult were similar (122–130 days), except in Kenya where the duration was markedly shorter (99 days) (Fig. 11). Similarly, the mean growth rate per primary of percent feather mass grown per day was similar between locations (0.735 – 0.829% per day) but distinctly higher in Kenya (1.013%) (Fig. 12).

Discussion

Apart from a small number of studies (Waltner and Sinclair 1981, Fry 1990, Branson et al. 2010) little is known about the migration phenology, origins, moult and status of Terek Sandpipers in general (Delany et al. 2009). Waltner and Sinclair (1981) described the primary moult strategy for Terek Sandpipers in South Africa briefly, putting more emphasis on the moult of secondaries, coverts and body plumage. The Underhill–Zucchini moult model (Underhill and Zucchini 1988) had not been developed at that time and thus only a general strategy was described of adults starting moult after arriving in late September with last birds completing by the first week of March. It was noted that there appeared to be a rapid start to moult but little other detail was given.

Underhill and Summers (1993) considered that the relative primary masses for migrant wader species were sufficiently similar that averages across all species were adequate for moult analyses using the Underhill-Zucchini moult model (Underhill and Zucchini 1988). Table 2 supports this idea; the relative primary masses for the Terek Sandpiper are closely similar to the mean values presented by Underhill and Summers (1993).

From the analyses of moult scores for Terek Sandpipers undertaken using the Underhill-Zucchini model, there was a marked difference in results for estimated duration and start date between the full tract analysis and the per primary analysis, particularly for Kenya (Fig. 6, Table 3). As already discussed in detail (see Chapter 2), while a lack of data during the early stages of moult will affect the estimation of start date and thus duration, the overall pattern of rapidly moulting inner primaries at the start of moult (Fig. 3) emerges as a real pattern of moult and would also put the start date forwards and shorten the overall duration. This high growth rate in the early stages of moult deviates from the basic assumption of the Underhill-Zucchini moult model of constant growth rate of the primary tract as a whole (Underhill and Zucchini 1988) (Fig. 6) and leads to an overestimation of duration when taking the whole feather tract as a unit. This must be taken into account when estimating start date and duration of moult. Thus, in describing the moult strategy for Terek Sandpipers, I used the estimates of overall start and duration from the per primary analysis except for where data for the earlier moulted inner primaries were not sufficient to calculate moult parameters per primary. In these cases, the overall tract analysis results were used. Fig. 6a shows that the cumulative PFMG per primary for Terek Sandpipers in Kenya gave a substantially earlier estimated start date than the overall tract analysis but then tended towards the overall primary tract PFMG such that from just before or close to 50% growth the two synchronise. This was even more so for the population in north-west Australia; by 50% growth the two estimates were closely synchronised. A better comparison, therefore, for overall moult timing between populations of birds can be made using the 50% PFMG date (Table 7, Fig. 10).

In south-eastern India, Terek Sandpipers are classified as a 'locally common winter visitor' (Grimmett et al. 2011). However, monthly counts over three years showed the first few birds arriving in August with a marked passage of migrants in September of up to over 520 birds. Numbers thereafter drop sharply away to relatively few birds in November and December with totals approximately a factor of nine less than in September (Balachandran 1990). A small peak in January and February up to three times the average number in December may represent a passage of birds as numbers then drop off markedly in March and remain low (10 – 20 birds) until the southward migration in August (Balachandran 1990). The site in south-eastern India therefore appears to be mainly a passage stopover site and a minor non-breeding area. My results suggest that the Terek Sandpipers were using it as their main moulting grounds.

The lack of data early in the season for the inner primaries of Terek Sandpipers in India precludes a per primary analysis for these feathers and thus prevents the estimation of the start of moult. The estimated average start of moult from the full tract analysis (7 July) is certainly too early an estimate because birds are unlikely to have arrived in south-east India by this time and thus likely not to have started moult (Ginn and Melville 1983). There are, however, two possible options for the actual strategy of the early stages of moult: moulting the inner primaries on or near the breeding grounds before migrating (Prater 1981, Ginn and Melville 1983) or dropping the inner primaries almost simultaneously immediately upon arrival in India, as is the case for the populations in Kenya and Australia (Fig. 2) and similarly described for birds in South Africa by Waltner and Sinclair (1981). Further data collection during early July while birds arrive is necessary in order to confirm exactly which strategy is employed. It is unlikely, however, that the former strategy is used given the relative closeness of south-eastern India to the breeding grounds and the lack of available time between completing breeding and arriving in India to be able to stop and moult some inner primaries. Furthermore, no birds were noted as having been in suspended moult during July – September further refuting this option. On the other hand, given the strategy followed by adult Terek Sandpipers in Kenya and Australia, it is not unlikely that the same is followed in south-eastern India, i.e. a rapid start to moult for the smaller inner primaries by dropping several in quick succession followed by a slowing down of the larger outer feathers.

Assuming a similar rate of moult for the inner primaries as in Kenya is probably unreliable given that the Kenyan dataset has major gaps in the early stages of moult (July and early August, Fig. 5, Table 3). The magnitude of the difference between overall tract and per primary analysis methods (Fig. 5a) is thus likely to be exaggerated. The north-western Australia dataset has a better representation of the early moult period and is thus more likely to be realistic. Assuming the Indian Terek Sandpipers follow a similar strategy and applying the (more realistic) interval of 11.7 days between P1 and P4 moulting for north-western Australian birds would give an estimated average start of 15 July which is a more likely start date in Indian birds than 7 July. With an estimated duration of 121 days, birds would complete by early November whereupon many continue further south to the main non-breeding grounds. The heavy monsoon rains start in October and peak in November and as such will flood foraging grounds of Terek Sandpipers. Because they are mostly surface feeders on damp but not flooded surfaces (Cramp and Simmons 1983, del Hoyo et al. 1996, Higgins and Davies 1996), sustained flooding of foraging grounds will affect the foraging efficiency of Terek Sandpipers thus catalysing a move south to drier non-breeding grounds.

The primary moult strategy thus demonstrated by the majority of adult Terek Sandpipers in India, Kenya and Australia is representative of many other migrant wader species where adults reach non-wintering grounds first and then undergo a complete moult while immatures arrive and moult later (Pearson 1974, Spaans 1976, Waltner 1976, Prater 1981, Cramp and Simmons 1983, Fry 1990, Hirschfeld et al. 1996). The inner primaries are moulted relatively quickly while more time and effort are given to the outer, larger primaries. These outer primaries are the most exposed and therefore experience the greatest stress during flight and are always the most worn feathers on the wing. Feathers which are grown more slowly are higher quality and can thus withstand greater amounts of stress and wear (Serra 2001). It therefore stands to reason that these take longer to moult to ensure that they are of sufficient quality to survive the rigours of a year's flight including the return journey to the breeding grounds and back.

A handful of birds in Australia (2% in the north-west, 10% in the south-east) were noted to arrive with a few inner primaries already moulted but then suspended (Table 1) suggesting a few moult some primaries en route at a stop-over site (Cramp and Simmons 1983). Adults arrive in Kenya from late July with most arriving in August and into early September (Fogden 1963, Pearson and Britton 1980, Cramp and Simmons 1983). With no evidence of suspended moult, birds start moult soon after arrival, 15 September, and drop the inner three or four primaries in quick succession before spacing them out for the larger, outer feathers (Fig. 3b). Given the lack of data in July/August, the estimation of P1 starting moult is likely to be even earlier, but additional data collection is needed during this early part of the season to confirm this.

The strategy in north-western Australia is similar to Kenya but, being an additional 2,800 km average distance from the breeding grounds (Table 7), birds do not arrive until the second half of August and through September (Fry 1990, Higgins and Davies 1996, Branson et al. 2010). With an estimated average start date a week later than in Kenya of 22 September north-western Australian Terek Sandpipers start moult soon after arrival. In south-eastern Australia, an additional 2,500 km from the breeding grounds than the north-west, birds arrive in early November (Fry 1990, Higgins and Davies 1996) where they then similarly start moult immediately (9 November) and complete on average by 19 March (Fig. 2d, Table 5). This is the time when they need to start to fatten up for the return migration, so there is no slack time in their annual cycles.

The rate of feather growth estimated for the whole primary tract is effectively the same between sites (Fig. 12) except for the Kenyan population which has a markedly higher growth rate than any other population considered here, about twice that for north-western Australian birds per primary (Figs. 6, 7, 8). Duration of moult is thus short for the Kenyan birds (99 days, Fig. 11, Table 3) with the birds appearing to attempt to complete moult by the end of December. Analysis of moult for other long-distance migrant waders suggests that birds spending the non-breeding season in northern latitudes have a shorter moult than those in southern latitudes such as South Africa and Australia due to the constraints of colder winter conditions in the north and thus reduced food availability (Prater 1981, Serra 1998, 2000, Underhill 2003). In Kenya, the conditions in January to March are the hottest and driest in the year on the Kenyan coast (Chapter 1, Fig. 2b) which, given the push to complete before this, may suggest that food availability is reduced during this period for Terek Sandpipers. Furthermore, detailed counts by pentade (five day periods) at Mida Creek over two years show that numbers of Terek Sandpipers peak at the start of December and thereafter there is a steady decline through December to March (Chapter 8, Fig.1). The implication of this is that Terek Sandpipers appear to start moving away from the non-breeding grounds early, in December / January, and thus would attempt to complete moult by then so as not to overlap moult and any longer distance movements. Further, detailed investigation is required on food types and their abundance in Mida Creek over this period in order to confirm this together with fine resolution counts of Terek Sandpipers farther north along the East African coast during December to April. The duration of moult for the Indian birds is also relatively short at 121 days (both Australian populations are just over a week longer at 130 days). In India, the extreme weather conditions during the heavy monsoon rains coinciding with completion of moult for Terek Sandpipers in November (Fig. 3a, Table 6, Chapter 1 Fig. 2a,) would also suggest a strategy of pushing to complete moult before foraging conditions deteriorate and before the birds move on to their main non-breeding grounds.

For Kenyan birds, the fast growth rate and short duration of moult per primary (Figs. 3b, 4b, 7a) lead to less overlap between moulting feathers than for Australian birds, particularly in the outer primaries (Figs. 8, 9). Adult Terek Sandpipers in north-western Australia grew their feathers at almost half the rate as those in Kenya (Figs. 7, 8) with subsequently greater duration per primary (Fig. 4c) and overlap between adjacent feathers—indicated by the broader peaks in Fig. 8. The Indian and south-east Australian datasets were small (Table 1), the former being mainly a stopover site for clearly a relatively small number of birds and the latter being marginal non-breeding grounds at the far end of the non-breeding season range. Thus, the results from these datasets are not sufficient to give a clear picture of rates of growth and subsequent levels of overlap (Fig. 8).

Summary

The overall strategy for adult Terek Sandpipers appears to be that in south-eastern India theyuse the site as a stop-over to moult before the heavy monsoon rains and then many move farther south for the non-breeding season. In Kenya, birds arrive and start moult almost immediately and moult rapidly in order to complete moult before the hot, dry weather starts in January. In Australia, a fraction (2%) replace a few inner primaries at a stop-over site en route to the non-breeding grounds where they complete moult (possibly close to the breeding grounds). Most, however, start moult soon after arrival and complete in an average of four months and ten days. Moult consistently took place substantially later the farther south the birds had to fly to reach their non-breeding grounds, an estimated 22 days later per 1,000 km farther from the breeding grounds (Table 7). The small south-eastern Australia population, being c. 6,600 km south of the Indian population, thus start an estimated four months, nine days later than the Indian birds in early November (Fig. 10, Table 7).

Adult Terek Sandpipers in Kenya have the highest feather growth rate (an average of 0.81% per day, Table 3) of all populations considered and take the shortest time to moult followed by Indian birds, presumably constrained by climatic factors affecting food availability. The Australian birds appear to be less constrained in this respect and thus have a longer duration of 130 days. South-eastern Australian birds, however, in taking just over four months to moult, complete on average by mid-March and thus do not have a 'break' between moult and needing to fatten up for the return migration in late April/early May.

Further data are required in the initial stages of moult to confirm the details of the early moult pattern in particular for adult Terek Sandpipers in India, Kenya and south-eastern Australia. However, it is clear that the overall strategy for this early stage of moult is dropping the inner three to four primaries rapidly within a few days of each other and then spacing out the larger, outer feathers (Figs. 3, 8).

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Tables and figures

Table 1. Numbers of moult scores used in adult moult analyses for Terek Sandpipers in India, Kenya and Australia.

Adult moult scores:	Normal	Suspended	Total
India	50	0	**50**
Kenya	733	0	**733**
NW Australia	5,353	102	**5,455**
SE Australia	17	2	**19**

Table 2. Primary feather masses of Terek Sandpiper from Australia (g), and the relative masses used in the computation of percentage feather mass grown. The numbers presented are the means of four wings from two birds (C.D.T. Minton unpubl. data).

Primary	Mean mass (g)	Mean relative mass
P1	0.0127	0.0413
P2	0.0155	0.0502
P3	0.0187	0.0606
P4	0.0227	0.0735
P5	0.0285	0.0924
P6	0.0332	0.1075
P7	0.0374	0.1211
P8	0.0423	0.1372
P9	0.0470	0.1522
P10	0.0507	0.1642

Table 3. Parameters of estimated moult per primary and for whole primary tract for adult Terek Sandpipers in Kenya (n = 733). The average growth rate per primary = 0.809%; Av. growth rate for all primaries using total moult duration calculated from per primary results = 1.013%. '% adj pp overlap' is the number of days of overlap between a primary with the next adjacent one expressed as a percentage of that feather's estimated duration. 3rd pp overlap is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously.

	Duration	SE	Start day	SE	Start SD	SE	Growth rate	Start date	End date	Days apart	Days overlap	% adj pp overlap	3rd pp overlap	Un-moulted	Active moult	New
P1	6.1	1.9	78.0	3.9	22.4	7.8	0.68%	**15 Sep**	21 Sep	-	4.9	80%	43%	30	10	693
P2	7.1	2.0	79.2	3.6	21.9	7.4	0.71%	17 Sep	24 Sep	2	4.8	68%	8%	32	12	689
P3	7.1	1.9	81.5	3.3	21.2	7.0	0.85%	19 Sep	26 Sep	2	2.9	41%	-31%	35	13	685
P4	7.7	1.9	85.7	3.0	20.7	6.6	0.95%	22 Sep	30 Sep	3	2.6	34%	-31%	40	15	678
P5	9.1	1.8	90.8	2.6	19.3	5.8	1.02%	28 Sep	7 Oct	6	4.1	45%	-66%	50	21	662
P6	12.4	2.0	95.8	2.5	20.6	5.9	0.87%	3 Oct	16 Oct	5	2.3	19%	-97%	62	33	638
P7	14.5	1.9	105.9	2.2	21.1	5.8	0.83%	13 Oct	28 Oct	10	0.2	1%	-114%	91	51	591
P8	18.6	2.2	120.2	2.3	28.7	7.8	0.74%	28 Oct	15 Nov	15	1.8	10%	-87%	151	68	514
P9	22.3	2.4	137.0	2.3	32.6	8.3	0.68%	14 Nov	6 Dec	17	4.3	19%	-	212	81	440
P10	21.7	2.4	155.0	2.4	35.1	8.4	0.76%	1 Dec	**23 Dec**	17	-	-	-	280	68	385
	Overall duration: 99 days			**Start date: 15 September**				**End date: 23 December**								**n = 733**
P1-10	136.0	6.6	41.6	5.2	31.2	7.0	0.735%	10 Aug	24 Dec					**30**	**319**	**385**

Table 4. Parameters of estimated moult per primary and for whole primary tract for adult Terek Sandpipers in north-western Australia (n = 5,353). The average growth rate per primary = 0.455%; Av. growth rate for all primaries using total moult duration calculated from per primary results = 0.770%. '% adj pp overlap' is the number of days of overlap between a primary with the next adjacent one expressed as a percentage of that feather's estimated duration. 3rd pp overlap is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously.

	Duration	SE	Start Day	SE	Start SD	SE	Growth rate	Start Date	End date	Days apart	Days overlap	% adj pp overlap	3rd pp overlap	4th pp overlap	Un-mltd	Active moult	New
P1	14.5	0.8	84.1	0.8	16.4	3.0	0.28%	**22 Sep**	6 Oct	-	13.2	91%	60%	19%	436	262	4,655
P2	14.7	0.8	85.4	0.8	16.3	2.9	0.34%	23 Sep	7 Oct	1.3	10.2	69%	29%	-16%	459	270	4,624
P3	14.9	0.8	89.9	0.7	16.4	2.9	0.41%	27 Sep	11 Oct	4.5	9.0	60%	15%	-41%	535	283	4,535
P4	16.4	0.8	95.8	0.7	15.3	2.6	0.45%	3 Oct	19 Oct	5.9	9.7	59%	8%	-78%	640	329	4,384
P5	18.0	0.7	102.5	0.7	15.0	2.6	0.51%	10 Oct	28 Oct	6.7	9.6	53%	-25%	–	764	402	4,187
P6	20.2	0.8	110.9	0.6	14.8	2.5	0.53%	18 Oct	7 Nov	8.4	6.1	30%	-74%	–	933	503	3,917
P7	25.4	0.9	125.0	0.6	17.2	3.1	0.48%	2 Nov	27 Nov	14.1	4.3	17%	-57%	–	1,280	566	3,507
P8	26.8	1.2	146.1	0.8	18.3	3.4	0.51%	23 Nov	19 Dec	21.1	8.0	30%	–	–	1,758	356	3,239
P9	27.7	1.5	164.9	1.1	20.3	3.6	0.55%	11 Dec	7 Jan	18.8	12.8	46%	–	–	2,025	202	3,126
P10	34.0	1.6	179.8	1.2	18.9	3.3	0.48%	26 Dec	**29 Jan**	14.9	–	–	–	–	2,157	218	2,978
	Overall duration: 130 days			**Start date: 22 September**				**End date: 29 January**									**n = 5,353**
P1-10	135.8	1.5	73.6	0.9	18.4	2.4	0.735%	11 Sep	25 Jan						436*	1,939	2,978

**Unmoulted primaries excluded from Type 4 analysis*

Table 5. Parameters of estimated moult for whole primary tract for adult Terek Sandpipers in south-eastern Australia. Data were insufficient to do a per primary analysis.

	Duration	SE	Start Day	SE	Start SD	SE	Growth rate	Start Date	End date	Un-mltd	Active moult	New
P1-10	129.8	41.5	132.4	20.8	32.7	18.9	0.770%	9 Nov	19 Mar	2	13	2

Table 6. Parameters of estimated moult per primary and for whole primary tract for adult Terek Sandpipers in India (n = 50). The average growth rate per primary: 0.621%; Av. growth rate for all primaries using total moult duration calculated from per primary results: 0.829%. '% adj pp overlap' is the number of days of overlap between a primary with the next adjacent one expressed as a percentage of that feather's estimated duration.

	Duration	SE	Start Day	SE	Start SD	SE	Growth rate	Start Date	End date	Days apart	Days overlap	% adj pp overlap	Un-moulted	Active moult	New
P1			15.8*					**15 Jul**					5	0	45
P2													5	0	45
P3													5	0	45
P4	13.8	9.8	27.5	18.5	39.0	22.0	0.49%	27 Jul	10 Aug		10.1	73%	5	2	43
P5	19.7	10.7	31.2	16.2	35.6	19.9	0.43%	31 Jul	19 Aug	4	-1.6	-8%	5	3	42
P6	9.5	6.7	52.5	12.0	27.3	15.9	1.10%	21 Aug	30 Aug	21	7.3	77%	7	2	41
P7	21.5	9.4	54.7	11.7	29.1	15.6	0.57%	23 Aug	14 Sep	2	7.8	36%	8	5	37
P8	17.7	7.8	68.4	9.2	28.8	15.5	0.81%	6 Sep	24 Sep	14	8.3	47%	11	5	34
P9	44.4	13.6	77.8	9.6	33.1	17.5	0.36%	15 Sep	30 Oct	9	25.2	57%	15	13	22
P10	39.4	13.5	97.0	8.9	35.9	19.7	0.46%	4 Oct	13 Nov	19			19	10	21
	Overall duration: 121 days				**Start date: 15 July**			**End date: 13 November**				**Av. growth rate: 0.604%**			**n = 50**
P1-10	120.2	23.5	8.5	17.4	39.3	18.4	0.821%	8 Jul	5 Nov				5	24	21

**derived start day*

Table 7. Estimated date for average 50% feather mass grown for adult Terek Sandpipers in south-east India, Kenya, north-west Australia and south-east Australia and estimated number of days that moult is delayed per 1,000 km farther from breeding grounds.

	Date of 50% PFMG	Days later	Estimated av. km from breeding grounds	No. of days later /1000 km farther
India	6 Sept	0	5,800	0
Kenya	17 Oct	41	7,100	32
north-western Australia	18 Nov	73	9,900	7
south-eastern Australia	13 Jan	129	12,400	10

Average days later than India /1000 km farther from breeding grounds: 16

Fig. 1. Breeding and non-breeding distribution map of Terek Sandpiper (from http://maps.iucnredlist.org/).

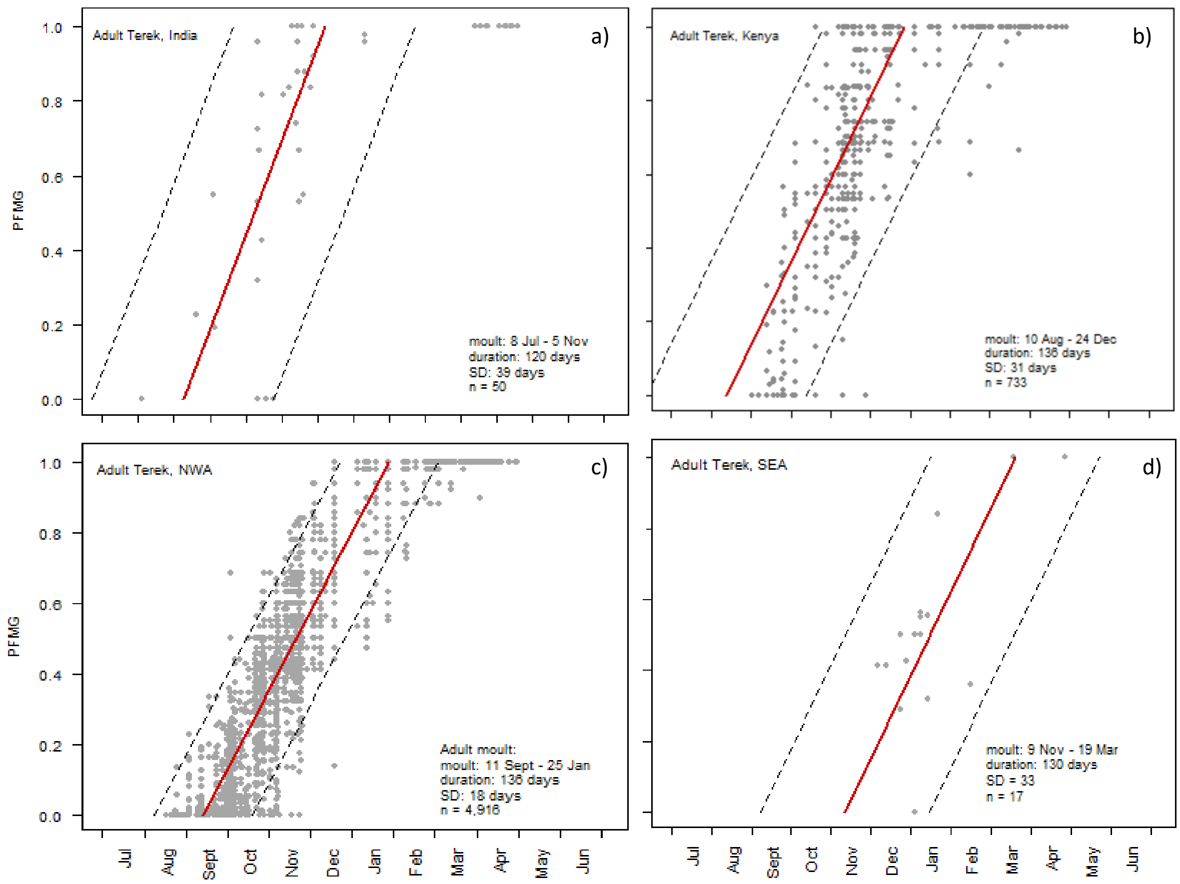
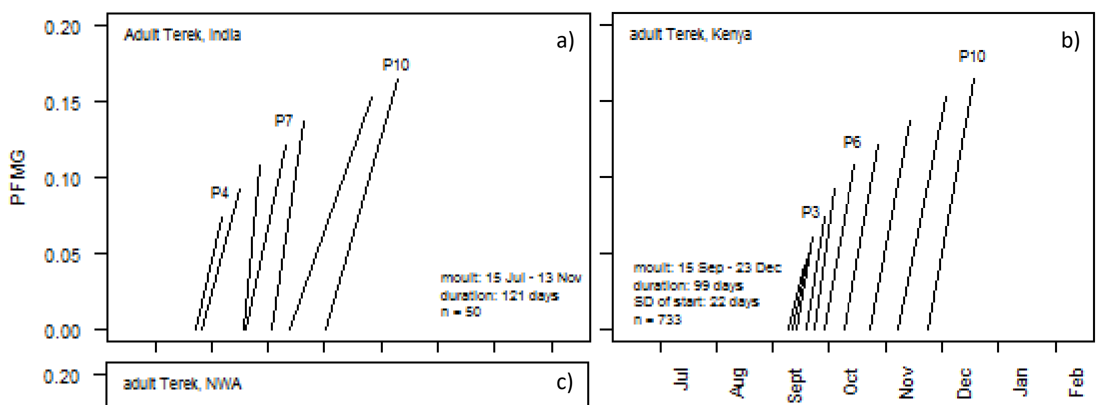


Fig. 2. Moult of adult Terek Sandpipers in a) India, b) Kenya, c) north-western Australia and d) south-eastern Australia. Percent Feather Mass Grown (PFMG) is plotted against date using the Underhill-Zucchini moult model. The solid line shows the estimated progression of primary moult for the average bird. Black dashed lines indicate the limits for 95% of the population and thus the parallelogram between them should contain approximately 95% of all birds in active moult.



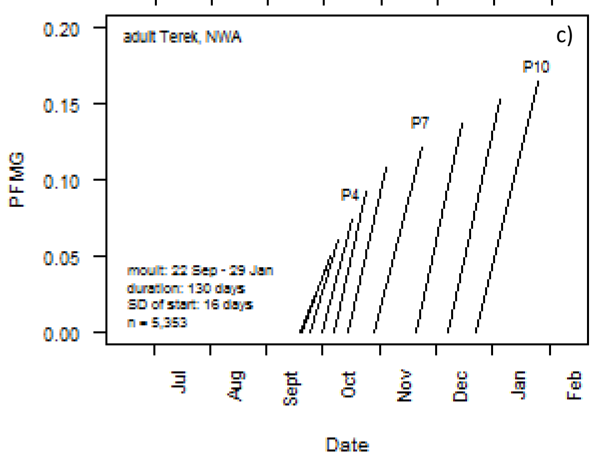
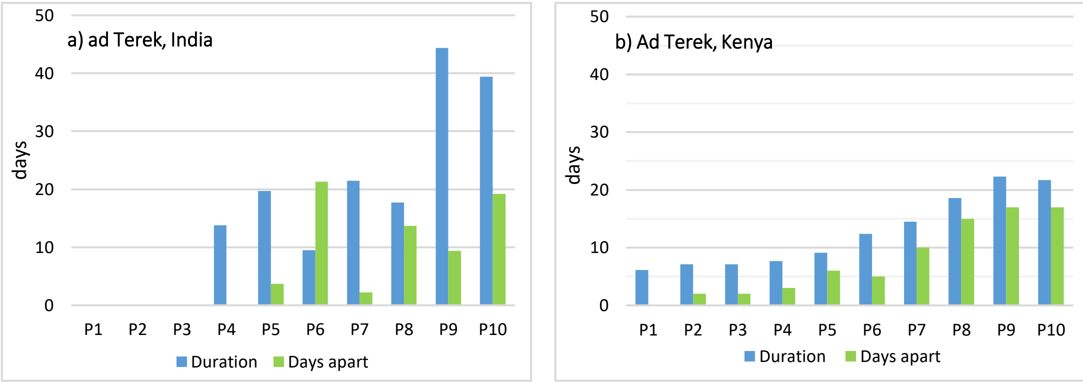


Fig. 3. Moult per primary for adult Terek Sandpipers in a) India, b) Kenya and c) north-western Australia. Each line represents one primary; the gradient of a line is equivalent to the rate of growth for that feather in PFMG per day. For birds in India data were insufficient for P1-P3 to give a result. See text for estimation of start date.



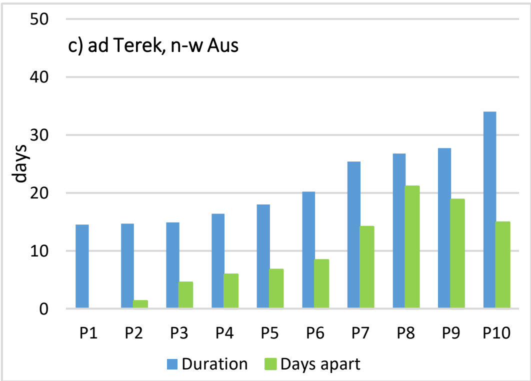
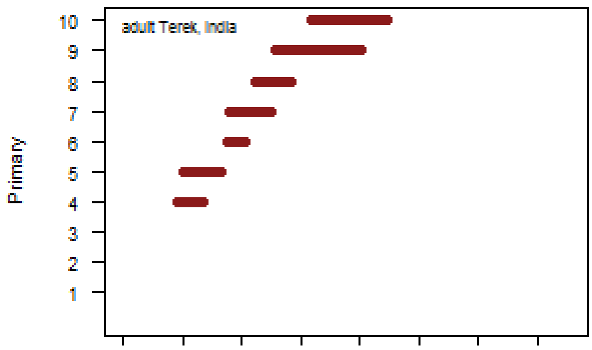
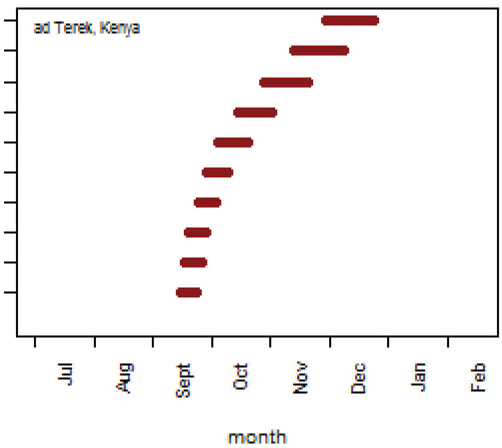


Fig. 4. Estimated average duration of individual primary moult (blue bars) and interval in days between moulting primaries (green bars) for adult Terek Sandpipers in a) India, b) Kenya & c) north-western Australia.





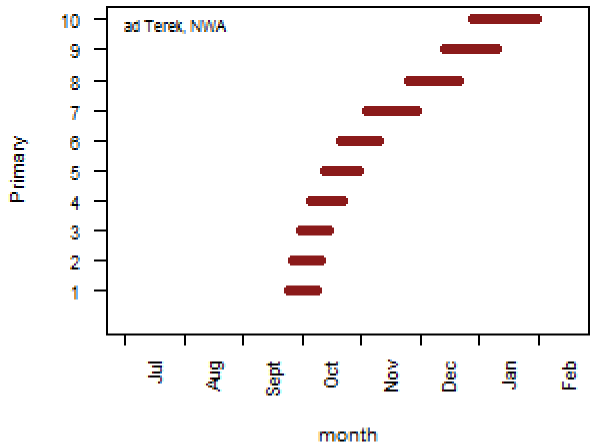


Fig. 5. Estimated duration and overlap of individual primary moult of adult Terek Sandpipers in a) India, b) Kenya & c) north-western Australia. Calculated using type 2 analysis of the Underhill-Zucchini moult model. Each line represents one primary.

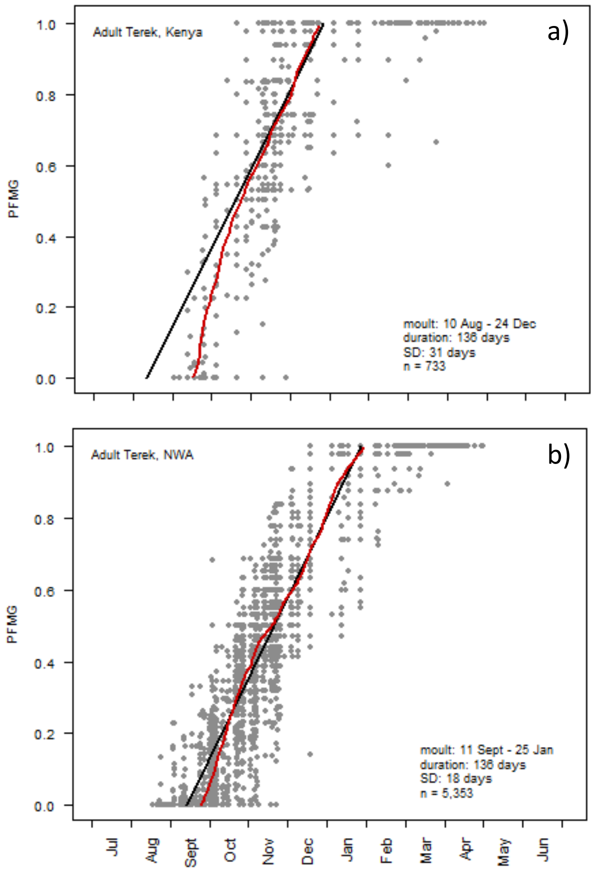
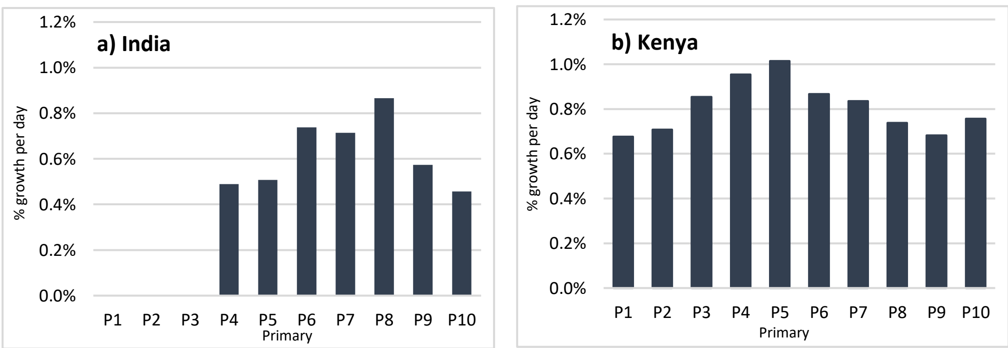


Fig. 6. Primary moult of adult Terek Sandpipers in a) Kenya and b) north-western Australia. Using the Underhill-Zucchini moult model, cumulative Percent Feather Mass Grown (PFMG) per primary (red line) is plotted over whole primary feather tract analysis (black line).



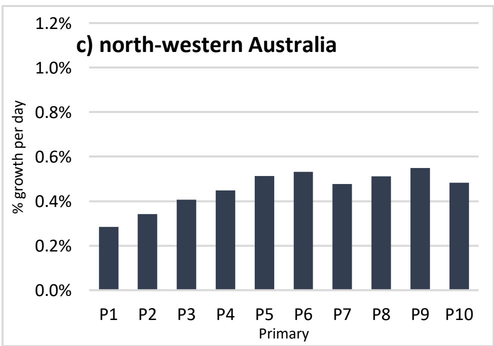


Fig. 7. Estimated rate of daily feather growth per primary for adult Terek Sandpipers in a) India, b) Kenya and c) north-western Australia.

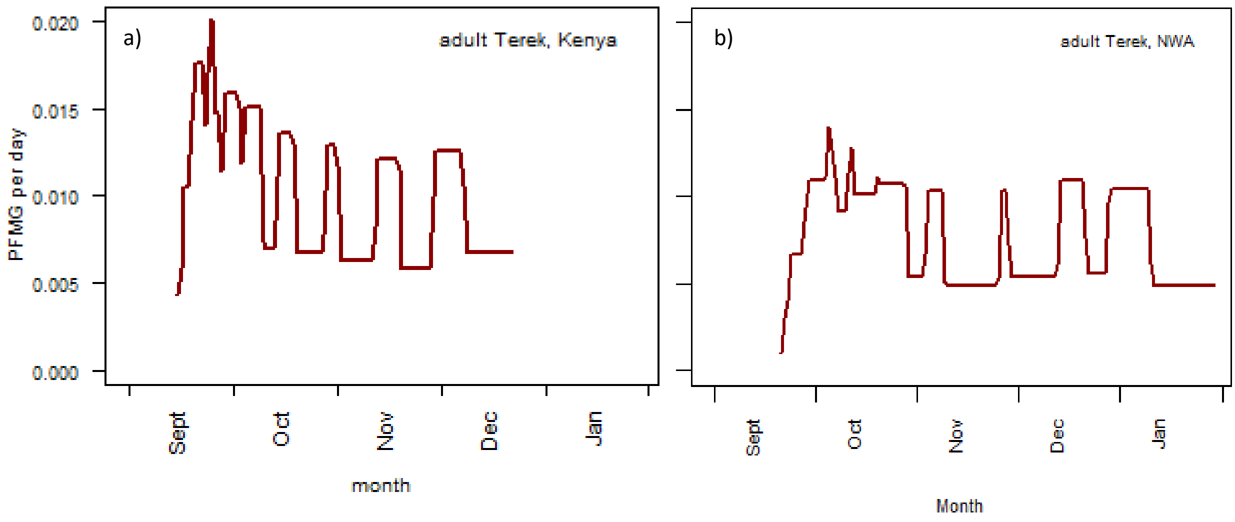


Fig. 8. Estimated rate of percent feather mass grown per day for adult Terek Sandpipers in a) Kenya and b) north-western Australia. This represents the daily total of average PFMG calculated per primary per day. The peaks represent more than one primary growing simultaneously.

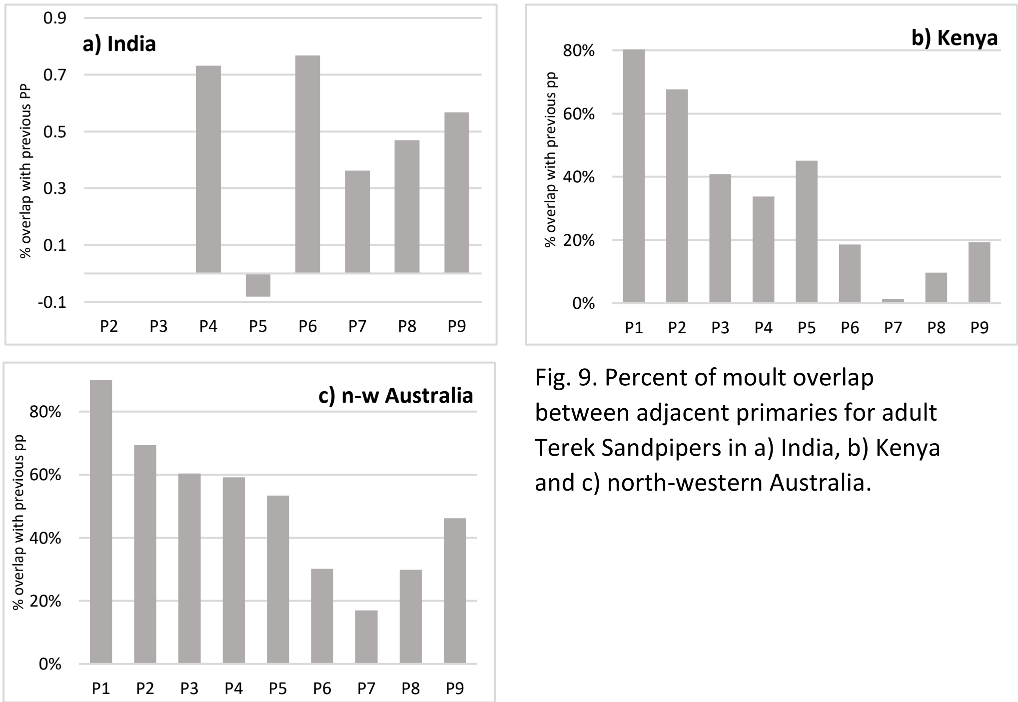


Fig. 9. Percent of moult overlap between adjacent primaries for adult Terek Sandpipers in a) India, b) Kenya and c) north-western Australia.

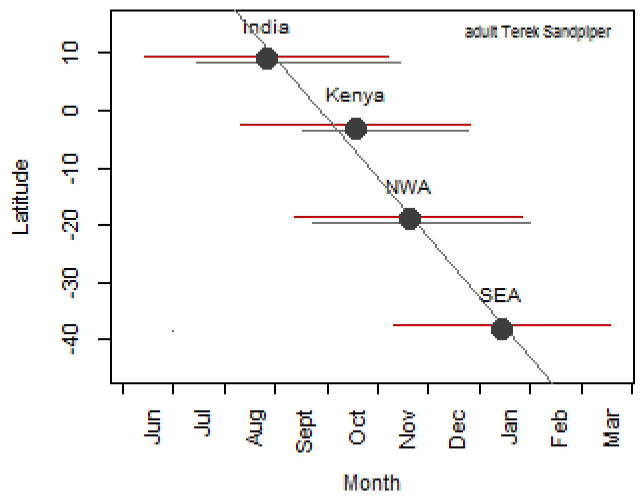
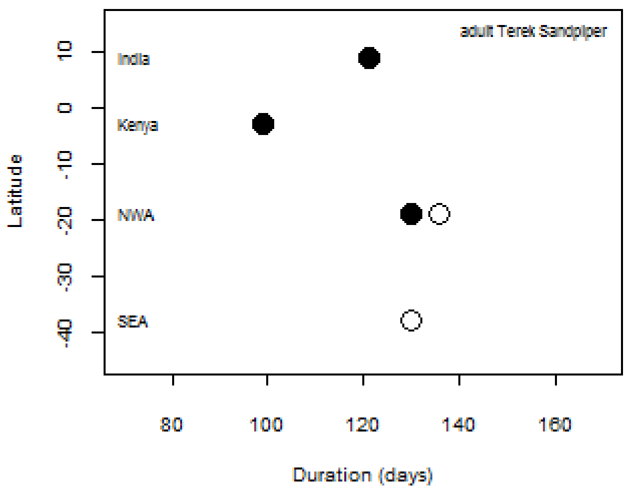


Fig.10. Average estimated date of 50% PFMG against latitude for adult Terek Sandpipers. The horizontal lines indicate the estimated duration of moult for each location *(red = full tract analysis; grey = per primary analysis)*. The diagonal line is the regression line.

Fig.11. Average estimated duration of moult against latitude for adult Terek Sandpipers between four different sites *(open circles = full primary tract analysis, solid circles = per primary analysis)*



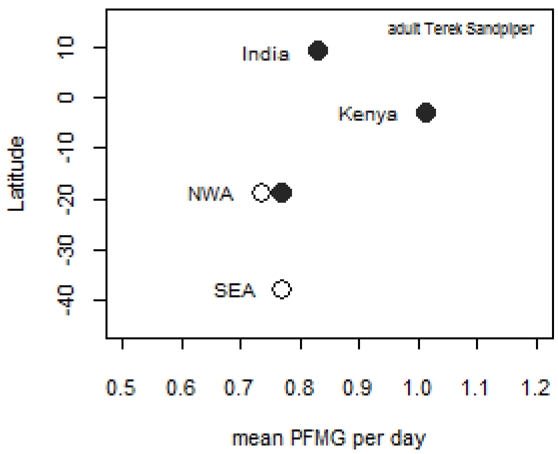


Fig. 12. Mean percent feather mass grown per day for adult Terek Sandpipers against latitude for the four sampling locations: India, Kenya, north-western and south-eastern Australia *(open circles = full primary tract analysis; solid circles = per primary analysis).*

Chapter 5

Moult of immature Terek Sandpipers in Kenya, India and Australia

Chapter 5 Moult of immature Terek Sandpipers in Kenya, India and Australia

Introduction

Moult is one of three key activities in the annual life cycle of any migratory bird together with breeding and migration (Ginn and Melville 1983, Zenatello et al. 2002, Newton 2009). However, for a number of species which do not breed aged one year, breeding is not something that an immature bird needs to fit into the first one-and-a-half annual cycles. In long-distance migrant waders, the immatures of many species remain on or near their non-breeding grounds instead of migrating to the breeding grounds with the adults (Pearson 1974, Elliott et al. 1976, Prater et al. 1977, Remisiewicz 2011). First year birds and those entering their second year in these species are therefore not limited by the time constraints faced by adults which have to complete moult in time to fatten up and migrate back to the breeding grounds. Furthermore, while the structure and condition of juvenile plumage (grown before fledging) are weaker and of lower quality than the plumage of an adult (Dwight 1900, Prater et al. 1977, Ginn and Melville 1983), it has only had to transport the bird on one migration, from breeding to non-breeding grounds. Adult primaries, on the other hand, by the time the bird returns to its non-breeding grounds, have been used to make the migration in both directions. Therefore, adults urgently need to replace their feathers upon arrival at the non-breeding grounds, attested by the often heavily worn primaries of adults in August/September); in contrast juveniles arrive at the non-breeding grounds with relatively unworn feathers which can last many more months of wear before needing replacement (Pearson 1974, Tree 1974, Prater et al. 1977).

The moult strategies of immature birds differ from those of adults (Elliott et al. 1976, Prater et al. 1977, Prater 1981, Svensson 1992, Remisiewicz et al. 2010a) with a wide variety of strategies employed. Of those that do migrate to the breeding grounds at the end of their first year, some do not moult at all, such as for the majority of first year Marsh Sandpipers *Tringa stagnatilis* in East Africa, and thus migrate north on the same juvenile primaries they travelled south with (Pearson 1974, Prater et al. 1977). Others moult all of their primaries prior to return migration e.g. Little Stint *Calidris minuta* and Ringed Plover *Charadrius hiaticula* in East Africa (Stresemann and Stresemann 1966, Dean 1977, Pearson 1984). Others undergo only a partial moult involving some of the outer primaries as in Wood Sandpiper *Tringa glareola* and Ruff *Philomachus pugnax* (Schmitt and Whitehouse 1976, Pearson 1981, Remisiewicz et al. 2010b) prior to returning north. For those that do not migrate, a common strategy e.g. in Curlew Sandpiper *Calidris ferruginea* et and Grey Plover *Pluvialis squatarola* (Elliott et al. 1976, Paton and Wykes 1982, Serra et al. 1999) is to replace varying numbers of outer primaries and then to undergo a complete normal moult from May or June as 'second year' or 'sub-adults' to complete in advance of returned adults (Serra et al. 1999). There are species which, within the same non-breeding population, exhibit more than one of these strategies to a greater or lesser degree e.g. Semi-palmated Sandpiper *Calidris pusilla* and Ruff (Prater et al. 1977, Pearson 1981).

The Terek Sandpiper *Xenus cinereus* is a long-distance migrant wader which breeds across the Western Palearctic between c. 70°N and 50°N and from Finland in the west to Kamchatka in the east (Cramp and Simmons 1983, Van Gils et al. 2016). The entire population migrates south to spend the boreal winter near or south of the equator, along coastlines of East Africa, the Middle East, central and eastern Asia south to south-eastern Australia (del Hoyo et al. 1996, Delany et al. 2009). Adults return to breed the following boreal spring but most first year birds remain on or near the non-breeding grounds for another year and only return to breed at two years of age (Waltner and Sinclair 1981, Cramp and Simmons 1983, Hayman et al. 1986). Little has been published on the moult strategies of Terek Sandpipers and in particular on that of immatures. Furthermore, only a small number of regional comparisons of moult strategies of immature long-distance migrants have been undertaken (Remisiewicz et al. 2010b, Summers et al. 2010). In this chapter, the moult strategies of immature Terek Sandpipers (birds aged up to 20–22 months old) are described for three widely separated localities and compared between four non-breeding localities spread between 9°N and 38°S. Distinct patterns are noted and possible reasons for these suggested.

Methods

Terek Sandpipers were caught, ringed and primary moult scores obtained in Kenya, India and Australia. In Kenya birds were ringed during regular wader-ringing sessions at Mida Creek (3°19'S

39°57′E) between 1978 and 2014. In India, data were collected during wader ringing carried out at Mandapam (9°17′N, 79°8′E) and at the Great Vedaranyam Swamp (10°18′N, 79°51′E) in south-eastern India between 1985 and 2014. In Australia, data were collected during wader ringing activities between 1982 and 2012 by the Australian Wader Study Group in north-western Australia (19°15′S 120°20′E) and south-eastern Australia (38°22′S 145°32′E). First year (0–12 months), sub-adult (those finishing their first year of life and entering the second year) and adult birds were distinguished as far as possible using Prater et al. (1977) and previous experience. Further details on location and methodology were described in Chapter 1.

First year birds were assessed according to the extent of moult undertaken: no moult, partial Moult of Outer Primaries (MOP), and complete moult. Birds following the MOP strategy were further divided into groups according to the number of primaries moulted. Thus a bird that moulted one outermost primary was placed in group MOP1, birds moulting two outer primaries, in MOP2 etc.

Birds found in moult had moult scores recorded following the standard method devised by Ashmole (1962) and Ginn and Melville (1983) where an old, unmoulted feather is scored '0', a new fully-grown feather is scored '5' and the stages in between are scored 1 – 4. Feathers are numbered descendently, so that the inner primary, usually first to moult, is P1 and the outer primary, P10 (Ginn and Melville 1983).

Sub-adult birds frequently showed two cycles of moult: the first year moult that was either complete or nearing completion, and freshly-moulting inner primaries as part of the sub-adult or first adult moult cycle. For these birds, where the moult pattern allowed clear distinguishing (typically first year moult being several months earlier than sub-adult or adult moult), the first year moult was used in the first year moult analysis and the fresh, moult score in the sub-adult moult analysis. Where it was not clear, the moult score was discarded on the assumption that such a moult strategy could be equally undertaken by any bird. It is impossible to test for this with the given dataset, but in reality there might be a bias here in that a certain ‘quality’ of bird could moult sooner and thus show a clear strategy, and thus be the subset sampled, while others of perhaps a ‘poorer quality’ would not and thus be omitted.

Moult scores were converted to proportion of feather mass grown (PFMG) as described in Chapter 1. For calculating PFMG in Terek Sandpiper moult, relative primary masses were obtained from Terek Sandpipers in Australia (C. D. T. Minton unpubl. data) following the methodology laid out by Summers et al. (1983) and Underhill and Joubert (1995).

Estimates of start date and duration of moult were calculated using the Underhill-Zucchini moult model using Type 2 data (Underhill and Zucchini 1988) where data were sufficient to run the model. The analysis was performed using the R moult package (Erni et al. 2013). For first year results, the analysis for Type 2 data was used and for sub-adults in north-western Australia the analysis for Type 4 data. For sub-adults in Kenya, since birds which had completed moult were not distinguished from adults, the data best fit Type 5 for analysis.

Results

First year birds

Three broad primary moult strategies were employed by first year Terek Sandpipers across the four populations studied: no replacement of juvenile primary feathers before starting the first adult moult aged c. 14 months; moulting a varying number of outer primaries (MOP) aged between four and seven months; and a complete, normal descendent moult starting aged about five months.

Kenya

382 birds were caught aged as first year of which 76 had moult scores that could be used to determine the moult strategy followed (Table 1, Fig. 1b). 306 (80%) were unmoulted birds caught between September and March for which it was impossible to tell what strategy they would follow and were thus omitted from analyses. No birds were found to undergo a complete moult of primaries. Most (78%) moulted 2–7 outer primaries (MOP2–MOP7). 22% did not moult at all (Fig. 1b). Those moulting some outer primaries were divided into MOP groups (Table 2). The majority (42%) moulted three primaries (MOP3). 75% moulted PP3-5 (MOP3–MOP5). The largest number of outer primaries moulted was seven (2%: MOP7) (Fig. 1b).

Moult was first observed during January; in this month, 18% of the sample of first-year birds were actively moulting outer primaries and 82% had not yet started moult, termed “unmoulted”, (n = 17) (Fig. 7a). In February this changes to 26% and 74% respectively (n = 34) and in March 72% of Kenyan immatures are moulting of which 22% have completed moult and 50% are in active moult, leaving 28% unmoulted (n = 32). The rate of birds starting moult slowed in April with 23% unmoulted (n = 26) and in May only three first year birds were caught of which none were unmoulted (Fig. 7a). Thus the period of primary moult for first year birds in Kenya covers January to May and probably into June, but lack of data from June do not allow confirmation of this.

North-western Australia

Moult scores were obtained from 931 first year Terek Sandpipers in north-western Australia for determining moult strategy. Three moult strategies were identified: 358 (38%) underwent a normal complete moult between November and March; 547 (59%) moulted varying numbers of outer primaries between October and May, and 26 (3%) did not moult any primaries (Fig. 1c). A further 84 (8% of total caught) first year birds were caught that were unmoulted and caught too early in the season to know which strategy they would follow. These were omitted from any analysis.

For those that underwent a complete moult, the estimated average start date was 5 December, the average duration of moult was 109 days and thus the estimated end date was 25 March (Fig. 2c). Standard deviation in start date was 23 days on average thus giving an estimate of 95% of birds starting primary moult between 22 October and 21 January. Growth rate across the whole primary tract was 0.922%.

The estimated starting date for P1 when analysed alone was 4 December, similar to that for the whole primary tract together; the end of moult for P10 was 24 March (Fig. 3 and Table 3). A marked gap in the data during December and early January (Fig. 2) which is the early period of moult for first year birds, meant that the spread of data for the inner primaries was poor resulting in duration estimates for P1–P4 with large standard errors, and therefore not reliable (Table 3). No data of active moult for P5 was available and thus estimation of moult parameters was not possible (Fig. 3, Table 3). For the outer primaries, P8 to P10, duration of moult averaged c. 25 days and moult intervals were 5 to 13 days (Figs 4 and 5, Table 3). This meant a high level of overlap between these feathers during moult (Fig. 6). Due to sampling variability, growth rate seems to have been biased high for P4 and P6; P8–P10 had a relatively constant rate of growth of 0.6% PFMG per day (Fig. 6).

For the 931 birds that underwent a partial Moult of Outer Primaries (MOP), the first birds encountered moulting were in October (in this study, just one from six caught that month was in active moult: the outer two primaries on 24 October). In November 10% (n = 72) were actively moulting, the proportion increased in December to 31% (n = 16) and to 78% in January (n = 18). The first birds to complete the moult of the outer primaries were recorded in February (11%, n = 28) and in April 76% had completed (n = 97). By May the majority of them (97%, n = 90) had completed such that by June there were no actively moulting birds (Fig. 7b). Thus the period of moult was at least eight months (October, when aged about four months, to May, aged about 10 months) though duration for individual birds varied depending on whether only two or up to eight primaries are replaced.

The most commonly moulted number of primaries was five (MOP5: 28% of all MOP birds) with a further 44% moulting either four primaries (MOP4: 23%) or six (MOP6: 21%) (Table 2). Thus a total of 72% of birds moulted four, five or six outer primaries (Fig. 2c, Table 2). The same proportion of birds (11%) moulted the outer seven primaries (MOP7) as moulted only the outer three (MOP3). The maximum number moulted was eight (MOP8: 2%). No birds moulted nine outer primaries.

Birds moulting more outer primaries started moult earlier than those moulting less. Thus MOP7 was estimated on average to start moult on 3 December and have a duration of 122 days to end on 3 April (Fig. 8, Table 4). MOP5 was estimated to start 17 days later on 20 December and complete on 29 March (with a duration of 99 days). MOP4 was estimated to start three weeks later on 10 January and complete on 4 April. Results for MOP3 were illogical and unlikely to be correct given the low number of actively moulting birds in this group (Fig. 8, Table 4). Data for MOP1 and MOP2, MOP6 and MOP8 were insufficient to allow for an estimation of duration and start date. No birds showed MOP9. The estimated average end date for moult for MOP4, MOP5 and MOP7 all fell within a period of six days (Fig. 8, Table 4). There was a significant difference between the mean wing-length of birds that underwent a complete moult (mean = 131.8 mm, n = 358) and for those that underwent a 'MOP' moult (mean = 133.0 mm, n = 319; t = –3.29, df = 491.3, $p < 0.05$).

75 first year birds (8%) showed moult of both some inner and some outer primaries between January and June. The majority (67%) had moulted just one inner primary and more or less equal numbers had moulted between four and seven outer primaries (Table 5). Three had moulted eight outer feathers. 28% had moulted two inners and one bird in April had moulted three. Of 75 birds, 87% had suspended inner primary moult and the remaining 13% were in active moult.

South-eastern Australia

Eight birds caught in south-eastern Australia were aged as first years. A single bird was caught at the end of August and aged as a sub-adult having replaced all but the outer (very worn) primary and had suspended or arrested moult at that point. This moult would have taken place during its first year and is thus best considered as a first year moult (Table 1). One first year in July had all old, unmoulted primaries, four, including the 'sub-adult' bird, had followed a normal descendent moult starting from the inner primaries. No birds exhibited moult of just some outer primaries (Fig. 1d).

The estimated start of moult was 26 January and the end as 13 May with a duration of 107 days. The average growth rate was thus 0.9337% of feather mass grown per day. With a standard deviation of 11 days, 95% of first year Terek Sandpipers in south-eastern Australia were expected to start moult between 4 January and 16 February (Fig. 2b).

India

Moult scores were recorded from 26 first year Terek Sandpipers. Only 12 could be used for analysis of which 50% moulted between one and three outer primaries, 42% did not moult during the non-breeding season and 8% underwent a complete moult (Fig. 1a). The remaining 14 birds were omitted from the analysis because they were caught early in the season, showing no moult (termed "unmoulted"), so it was not possible to know which strategy they would follow.

Comparison between locations

There was a general trend north to south of an increasing proportion of the population undergoing a complete moult and a decrease in the number of birds not undergoing any moult (Fig. 9). Overall the most commonly followed strategy was the Moulting of Outer Primaries (MOP) except for the most southerly location, south-eastern Australia, where there was no evidence for this, though it should be noted that the sample size was small (n = 8).

Sub-adult birds

Sub-adult birds, entering their second year of life aged about 12 months were most easily distinguished between July and October (13–17 months). A small number could be aged in November (18 months) but only a handful retained signs of being sub-adult into December (19 months). Most showed primary feathers with two or three ages: slightly worn primaries replaced during their first year; freshly moulted primaries, usually with an active moult centre; and old and worn original primaries. Some in July to early September had completed moult and had unworn primaries but were distinguished from first years with similarly unworn feathers by the lack of other juvenile characteristics such as retained juvenile inner median coverts. Fewer still remained completely unmoulted, some even until October, retaining all ten very worn juvenile primaries. In all four locations, the general primary moult strategy for sub-adults was to moult at the same time as the adult post-nuptial moult.

Kenya

40 birds caught in Kenya were aged as sub-adult and underwent a complete moult with scores that could be used for analysis. The estimated start of moult was 15 August with a duration of 119 days giving an estimated end date of 12 December with a standard deviation of 35 days (Fig. 11, Table 7). This estimate was five days later in starting than for adults and 17 days shorter (Fig. 18). The average estimated rate of growth was 0.840% of feather mass per day.

North-western Australia

A total of 680 birds were identified with sub-adult moult in NWA (Table 1). 176 birds (26%) had retained some original juvenile feathers grown before fledging that remained identifiable. No sub-adult birds were found to be actively moulting both the immature and first adult cycles of moult, all had completed the immature moult which they had started and were only in active 'adult' moult.

20 birds (3%) were recorded as having a third cycle of primary moult; this had been started in November or December, after or towards the end of the first adult moult. 16 of these showed two active centres of moult and three ages of feather with the third, new moult 'over-writing' the moult that matched the adult post-nuptial moult. Four birds had just two ages of feather where the second generation had either completed or was moulting the last, outer primaries. Moult scores for the third cycle of moult were low ranging from 200000000 (PFMG 0.0052) (where the feathers recorded as 0 were not in fact "old" but had recently been replaced during the second moult cycle) to 5530000000 (PFMG 0.1294) with two slightly more advanced at 5555100000 (PFMG 0.2372) and 5555510000 (PFMG 0.3314).

66 (10%) sub-adults were recorded showing apparent suspended moult with the majority (62%) suspending after six or seven primaries had been moulted. These were omitted from the Underhill-Zucchini moult analysis.

483 sub-adult birds had moult scores that could be analysed for the parameters of moult. The estimated average start of moult for the whole primary tract was 22 August and the duration was 170 days giving an estimated completion date of 8 February (Fig. 11, Table 5). The standard deviation of start day was 26 days, so that 95% of birds were estimated to have started moult between 1 July and 12 October. Average growth rate across the whole tract was 0.589% of feather mass grown per day.

Analysis of moult per primary gave an estimated start date of 15 August and a duration of 197 days thus completing moult on average on 27 February (Table 5). This was 27 days longer than the full tract analysis and two months longer than the adult moult. The average growth rate for the whole wing from this analysis was 0.508%. The five inner primaries were dropped at regular intervals of c. 10 days. From P6, the interval increased to 22 days and up to a maximum of 30 days between P8 and P9 (Fig. 14, Table 5).

Estimated duration of moult per primary was 26 days for P1, decreasing to 19 days for P3 before steadily increasing to 42 days for P10 (Fig. 12, 13, 14, Table 5). Given the extended duration of moult, growth rates were low with an average rate per primary of 0.37% PFMG per day and a minimum of 0.16% for P1 and maximum of 0.46% for P7 and P9 (Fig. 15, Table 5). The result of long durations of moult per primary and short intervals between dropping of feathers for the inner primaries gave a large degree of overlap between adjacent moulting primaries (P1 to P5 averaged 52% overlap; Fig. 16). However, the greatly extended interval between dropping of feathers for the outer primaries meant that on average there was a gap between P7 completing moult and P8 starting (Fig. 16, Table 5).

The progression of cumulative moult scores per primary closely matched that of the estimate for the overall primary tract though deviated from a PFMG score of 0.6 (Fig. 17). This coincided with the marked gap in data collection from mid-December to mid-January (e.g. Fig. 11a) as well as a lack of being able to distinguish sub-adult birds from adults from December onwards. The deviation thus observed and the markedly extended moult duration estimate from the per primary analysis is therefore likely to be more a result of this lack of data than a representation of the true picture.

South-eastern Australia

One bird was aged as sub-adult in south-eastern Australia (Table 1). However, it was caught at the end of August having replaced all but the outer (very worn) primary in a moult that is best considered a first year moult. Thus no birds were found showing a sub-adult moult.

India

Four birds caught in August and September were aged as sub-adult (Table 1) all of which showed both a first year moult pattern (moulted outer primaries) and freshly moulting inner primaries which overlapped entirely with and matched the post-nuptial moult cycle of adults (Fig. 10). For one bird, the adult moult cycle had 'overwritten' the inner primaries of the first year moult rendering it unusable for the first year analysis.

Suspended and arrested moult, and non-standard moult patterns

A total of 156 immature birds were recorded with suspended or arrested moult with 18 in Kenya, 137 in north-western Australia and two in south-eastern Australia (Table 6). Most birds with non-standard moult strategies had followed one of the clear strategies but then also moulted some additional feathers (Table 6). Of birds in north-western Australia, 49% involved birds that had replaced outer primaries as part of the Moult of Outer Primaries ('MOP') strategy and then started to replace inner primaries and had stopped moult but still retained at least one old juvenile primary in the middle (thus confirming the outer replaced primaries were part of a MOP moult). 39% had moulted outer primaries and then had undergone a normal, descendent moult from the inner primaries and stopped but having already dropped all old juvenile primaries. As a result, it was not possible to determine if the earlier replaced outer primaries had started moulting at P1 in a complete moult or an outer primary as a MOP moult. Given the 49% that had definitely undergone a MOP moult, it is highly likely that these others had also only moulted some outer primaries rather than having undergone a complete moult which was now being repeated.

Discussion

While there were a certain number of 'odd' primary moult patterns encountered in immature Terek Sandpipers as found by Waltner and Sinclair (1981) for the same species and (Summers et al. 2010) in Red Knot *Calidris canutus*, these were in the minority (8% of immatures examined). Overall a number of distinct patterns emerged. There were both distinct strategies for first year birds and also subtly different moult strategies between sub-adults and adults.

First year moult strategies

The same three broad strategies were found for first year Terek Sandpipers as occur in many species of migrant wader (Prater et al. 1977, Prater 1981, Ginn and Melville 1983). However, the proportion of birds which followed each strategy in the population changed according to latitude for the four locations studied (Fig. 1):

A. Juvenile primaries retained until sub-adult or first adult moult

In the northern population in India, a larger percentage of birds followed the retain primaries strategy when compared to the populations farther south (Fig. 1). South-east India is relatively close to the breeding grounds (c. 5,000 km) and therefore the primaries of birds making their first migration this distance would be less worn than those travelling the 8,500 km (north-western Australia) or 12,000 km (to south-eastern Australia). As a result, there would presumably be less need for birds to expend energy replacing the feathers in advance of the first adult moult in July (Fig. 1 Chapter 4). Only a small minority of birds in the other populations south of the equator followed this strategy.

B. Partial moult of varying number of outer primaries ('Moult of Outer Primaries' – MOP)

Partial moult of outer primaries is a well-documented strategy in first year migrant waders that spend the non-breeding season in the southern hemisphere (Pearson 1974, 1981, Tree 1974, Spaans 1976, Remisiewicz et al. 2014). It has been suggested that birds undergoing a partial moult will moult the outer primaries rather than the inner since these are the most important for flight (Videler 2005). Thus this strategy is surmised to occur in populations of waders that need to fly longer distances to reach farther south and is in fact absent from populations in northern temperate regions (Barshep in prep., Spaans 1976, Remisiewicz et al. 2014). In Terek Sandpipers, populations nearer the equator (India, Kenya, north-western Australia) followed this strategy to a greater degree than those farther south (39°S in south-eastern Australia) where no birds were found undergoing a partial moult and most did a complete moult. For those that do undergo a partial moult, the more northern populations (India and Kenya) more commonly moulted fewer primaries (three) than birds farther south in north-west Australia (which most commonly moulted five) (Fig. 2). This is a trend that has also been found with Greenshank where birds in southern Africa moulted more outer primaries than those in Kenya (Remisiewicz 2011, Remisiewicz et al. 2014). In contrast to Greenshank, however, Terek Sandpipers in South Africa had the same pattern of partial moult as the Kenyan population with MOP3 being the most commonly moulted (33% of partial moulters) (Waltner and Sinclair 1981) (Fig. 2, Chapter 6). The Australian population was found to start moult as early as October and by January almost 80% of birds were in active moult (Fig. 7). In contrast in Kenya, first years undertaking the partial 'MOP' moult started in January and, by May, more than 30% were still moulting whereas in north-western Australia most had completed by then (Fig. 7). It is not clear why the Australian birds started so much earlier and completed earlier than the Kenyan birds; the climate is benign in north-western Australia and while May/June is the start of the austral winter conditions, mean temperatures remain above 20°C and benthic fauna productivity should not be limited (Mwaluma et al. 2003) and thus birds should not struggle to forage. Furthermore, the sub-adult moult does not start on average until mid-August with the most advanced birds starting in early July. Thus any birds that have undergone a partial ‘MOP’ moult effectively have a ‘holiday’ from the stress of moult during May, June and probably much of July.

The progression of moult per MOP group in north-western Australia (Fig. 8) matches the pattern of moult found by (Remisiewicz et al. 2010b) for Wood Sandpipers in southern Africa. The MOP groups which moulted more primaries started moult earlier on average than those moulting fewer feathers; all MOP groups completed moult near the beginning of April (Fig. 9). (Remisiewicz et al. 2010b) proposed that Wood Sandpipers synchronise the completion of moult between MOP groups so that they would be ready for departure to the breeding grounds. However, for Terek Sandpipers in north-western Australia, the majority of first years do not migrate but stay on the non-breeding grounds (Minton 2004). It is a challenge to provide a hypothesis to explain why birds which are not constrained either by a departure date for migration or by any obvious climatic factor time their moult so precisely and synchronously. This is an area for further investigation.

Why do first-year Terek Sandpipers moult any primary feathers at all during their first year? They do not need high quality feathers because they are not about to fly the long distance back to the breeding grounds. However, they do still need to fly between foraging and roosting sites and to avoid predators. Having better quality outer primaries would provide survival advantages over those that retain worn feathers (Chai 1997). This would be particularly true for populations farther south where the longer distance travelled to reach their destinations would have a greater effect of wear on the feather tips than those in Kenya or India.

C. Normal, descendent moult starting from inner primaries

This strategy is the most energy-consuming of the three but ensures that the whole wing is of maximum quality. Smaller bodied long-distance migrant waders which breed in their first year such as Little Stint are known to undergo a complete moult as first years (Pearson 1984). Having fresh, new flight feathers is clearly advantageous for the return migration to the arctic breeding grounds.

Terek Sandpipers are at the limit of their non-breeding range in south-eastern Australia and the sample sizes were consequently small, but evidence suggested that the majority of birds follow this strategy in this location. Three of the eight birds caught were caught in the austral winter (two in May, one in July) but most of the Terek Sandpipers leave the far south of Australia during the winter where average temperatures are c. 10°C (Chapter 1, Fig.2d) probably to move farther north to the east coast towards Brisbane where conditions may be more conducive (Marchant and Higgins 1993, BirdLife Australia 2016). This is a distance of c. 1,500 km and thus there would certainly be an advantage to having good quality feathers to fly this distance. The estimated start and duration of moult was such that on average birds completed by 13 May (Fig. 2b), at the right time to be able to move north along the coast for the winter. Larger samples are needed from south-eastern Australia;

a colour-ringing study of first year birds ringed here and searched for during the austral winter would help confirm the actual movement patterns and uncover the reasons for this moult strategy.

First year Terek Sandpipers in north-western Australia displayed a bimodal pattern of moult; 59% underwent a partial moult of outer primaries (MOP2 to MOP8, with mode at MOP5) and 38% underwent a complete moult (Fig. 1c). It is tempting to suggest that this population consists of a mixture of birds from two geographically distinct breeding grounds with two different immature moult strategies. This is supported by the fact that the difference in mean wing-lengths between the two groups is statistically significant, even though it is, at 1.0 mm, relatively small. This pattern should be investigated. Stable isotope and trace element studies of the feathers of first-year birds ought to be able to confirm whether the two groups are indeed from different sectors of the breeding grounds of the Terek Sandpiper (Atkinson et al. 2005, Wakelin et al. 2011). 91% of the first-year birds migrating to Kenya showed a partial moult (Fig, 1b), and the studies of stable isotopes and trace elements might reveal that the provenance of these birds might be the close to that of the partial moulters to north-western Australia.

Sub-adult moult

It is widely recognised that in those species for which first year birds remain on the non-breeding grounds, there is usually a normal descendent moult started in advance of the returning adults (Prater 1981, Serra et al. 1999, O'Hara et al. 2002, Summers et al. 2010, Barshep 2011, Remisiewicz 2011). This moult resembles the post-nuptial moult of the adults and largely matches it such that Serra et al. (1999) termed it an 'anticipated' post-nuptial moult rather than a postponement of the first year post-juvenile moult.

Terek Sandpipers in all four populations studied largely conformed to this pattern. In India, first year birds which had undertaken a partial moult of outer primaries started the sub-adult moult that overlapped entirely with the post-nuptial moult of returning adults (Fig. 10). The north-west Australian population followed the expected typical strategy of starting moult (22 August) on average before the returning adults (22 September) and taking a long drawn out time of 170 days to moult (Table 5, Table 7, Figs 11, 18b) to complete around the same time as the adults (a week later on average). This extended moult of sub-adults is also found in Grey Plovers *Pluvialis squatarola* in South Africa where duration is on average 194 days (Serra et al. 1999).

In south-eastern Australia, the moult score of the one sub-adult caught in late August (5555555550 – where the outer primary was very worn) did not match the adult post-nuptial moult which did not start until early November. Too few birds were caught to allow for a proper understanding of whether some sub-adults have an anticipated post-nuptial moult. Given that at least one bird was caught with no first year moult, it is likely that such birds would indeed follow a more typical sub-adult strategy.

In Kenya, while the results suggested that sub-adult moult was atypical in starting after the returning adults (15 August compared to 10 August) (Fig. 18, Table 7) and being faster (119 days compared to 136 days), the difference of 19 days was not significant (SE of difference = 32 days, $p > 0.05$) and, given the small sample size and poor distribution of data (Table 7), it is not possible to say if there is any difference in duration between adult and sub-adult moult or not.

Suspended or arrested moult. The relatively small proportion of birds that displayed suspended or arrested moult (9% of immatures) suggested that this is not a major component of the moult strategies employed by young Terek Sandpipers at the four locations. In north-western Australia, suspended or arrested moult probably occurs mainly within the group of birds which undergo a 'MOP' moult (Table 7).

Third moult cycle. It is unclear why the 'third cycle' of moult is undertaken in a small number of birds (20, 3% of sub-adults) in north-western Australia. It only is found in sub-adults and appears to involve mostly just a few inner primaries and then stop. Once it has suspended, the third cycle of feathers appear similar in age and condition to the previous generation of sub-adult or first adult moult. Thus once the third cycle has suspended, it is very unlikely the pattern would be distinguished in the field and hence none are reported after January. A possible reason for this third cycle is that a few birds have the time and energy to be able to moult a few inner primaries in order to improve the overall quality of their flight feathers and thus their flying capacity (C.D.T. Minton pers. comm.) in advance of migrating back north to breed. Sub-adults will not have undergone any southward migration as the adults will have done. They will therefore not have expended energy on migrating and may thus be in a relatively better condition to do an additional partial moult than the adults. Such multiple cycles of moult are well-known as an adult strategy in a number of tern species (Van der Winden 2003, Fullagar et al. 2013), but appears not to have been reported in wader species. However, in Terek Sandpipers it has not been found in adults but in a small percentage (3%) of sub-adults. There is room for further investigation into this phenomenon to better understand and explain it.

Summary

Young Terek Sandpipers followed a variety of moult strategies that appeared to depend on both how far south they had migrated and possibly their breeding origin. The more northern populations in the non-breeding areas typically moulted fewer primaries than birds flying farther south; the latter more frequently underwent a complete moult that took 109 days to complete starting from between the end of October to the end of January. Birds that underwent a partial moult of some outer primaries started to moult on average earlier when more feathers were moulted. These birds tended to belong to the more southern populations (October in north-western Australia where moulting the outer five primaries is the commonest strategy), and later when fewer primaries were moulted (January for the Kenyan birds which mostly moulted the three outer primaries). Indications were that whichever number of outer primaries were moulted, the start was timed such that all birds finished their partial moult around the same time (for example, the end of March in north-western Australia).

Of particular interest were the north-western Australian first year Terek Sandpipers where the population is divided almost in half between birds that undergo a complete moult and those that only do a partial moult. A significant difference between mean wing-lengths of these two groups suggests that further detailed, study of the provenance of these birds would be of real interest to understand fully what is going on here.

At the end of their first year, most Terek Sandpipers remain on the non-breeding grounds and do not migrate back north. As a result, the first complete moult for many of them (those that have not followed the complete moult for the first year) tends to start slightly earlier than the post-nuptial moult of returning adults but for the majority there is very little difference in start date. North-western Australian sub-adults, however, appeared to have a long drawn out moult of almost six months duration, despite having more time available being that much closer to the breeding grounds and therefore a shorter distance to travel, took a shorter time than even the adults to complete moult.

Overall first year Terek Sandpipers follow diverse moult strategies some of which appear to reveal differences in populations that might be related to breeding areas. Further, more detailed investigation is warranted to better understand the patterns within these populations.

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Tables and figures

Table 1. Numbers of moult scores available for analyses and timing according to age structure for immature Terek Sandpipers in India, Kenya and Australia.

	First year	Sub-adult	Total
India	12	4	16
Kenya	76	40	411
n-w Australia	931	680	1,611
s-e Australia	9	0	9

Table 2. Numbers and proportion of first year Terek Sandpipers in each group Moulting Outer Primaries. 'MOP0' is the group that moulted <u>no</u> outer primaries; MOP1 – those that moulted <u>one</u>; MOP2 – those that moulted <u>two</u> *etc*. The maximum possible new PFMG for each group is given.

	Kenya			north-western Australia			PFMG at completion of moult
Group	n	% of n	% of MOP birds	n	% of n	% of MOP birds	
No moult	6	9%	-	26	3%	-	0.0
MOP1	0	0%	0%	1	0.1%	0.2%	0.1800
MOP2	6	9%	10%	8	1%	1%	0.3417
MOP3	27	42%	47%	61	7%	11%	0.4846
MOP4	11	17%	19%	128	14%	23%	0.6066
MOP5	10	16%	17%	153	16%	28%	0.7107
MOP6	3	5%	5%	114	12%	21%	0.7959
MOP7	1	2%	2%	61	7%	11%	0.8643
MOP8	0	0%	0%	21	2%	4%	0.9186
MOP9	0	0%	0%	0	0%	0%	0.9627
Complete	0	0%	-	358	38%	-	1.0
Total:	64			931			

Table 3. Parameters of estimated moult for first year Terek Sandpipers in north-western Australia (n = 350). Estimates are given for per primary analysis and also the whole primary tract (“P1-P10”). ‘% adj pp overlap’ is the number of days of overlap between a primary with the next adjacent one expressed as a percentage of that feather’s estimated duration. 2^{nd} pp overlap is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously. Estimates for P5 and associated calculations could not be given due to insufficient data.

	Start Date	SE	Duration	SE	End date	Start SD	SE	Growth rate	Days apart	Days overlap	% adj pp overlap	2^{nd} pp overlap	Un-mltd	Active moult	New
P1	4 Dec	3.4	39.7	5.3	12 Jan	27.7	8.3	0.10%		24	59%	36%	89	32	229
P2	20 Dec	4.0	24.9	5.1	13 Jan	27.5	8.4	0.20%	16.2	16	63%	21%	107	15	228
P3	30 Dec	4.4	15.9	5.0	14 Jan	25.2	8.0	0.38%	9.3	6	35%	-	115	7	228
P4	9 Jan	4.9	6.3	4.1	15 Jan	22.4	7.7	1.17%	10.3	-	-	-27%	120	2	228
P5	-	-	-	-	-	-	-	-	-	-	-	-	122	0	228
P6	17 Jan	5.2	8.1	3.4	25 Jan	20.3	4.6	1.33%	8.0	0	5%	-53%	122	3	225
P7	25 Jan	5.1	12.7	4.2	6 Feb	13.0	6.0	0.95%	7.7	8	63%	-39%	122	7	221
P8	30 Jan	4.9	24.8	4.9	23 Feb	17.9	7.0	0.55%	4.7	12	48%	-	128	21	201
P9	12 Feb	4.1	24.6	4.3	7 Mar	21.9	7.7	0.62%	13.0	13	52%	-	136	28	186
P10	23 Feb	3.7	28.5	4.0	22 Mar	23.1	7.3	0.58%	11.9	-	-	-	151	36	163
	Overall duration: 110 days					**Start date: 4 December**			**End date 22 March**			**Av. growth rate: 0.912%**			
P1-10	**5 Dec**	**2.6**	**108.4**	**3.9**	**24 Mar**	**23.1**	**5.7**					**Av. growth rate: 0.923%**	**89**	**98**	**163**

Table 4. Coefficients of moult for the MOP groups (Moult of some Outer Primaries) for first year Terek Sandpipers in north-western Australia. The spread of datapoints for MOP6 was insufficient to allow convergence in the moult model in order to produce sensible results. These have been ignored in the interpretation of the results.

Group	Start Date	SE	Duration	SE	End date	Start SD	SE	Growth rate	Un-mltd	Active moult	New
MOP3	9 Jan	70.2	119.7	115	9 May	45.8	43.6	0.835%	0	9	52
MOP4	10 Jan	11.3	83.9	12.7	4 Apr	22.6	8.4	1.192%	0	31	96
MOP5	20 Dec	9.9	99.2	11.7	29 Mar	20.6	6.9	1.009%	0	36	117
MOP6	*22 Apr*	*35.1*	*442.2*	*38.6*	*9 Jul*	*74.2*	*24.0*		0	31	82
MOP7	3 Dec	14.0	121.6	16.9	3 Apr	21.0	8.2	0.822%	0	22	38

Table 5. Parameters of estimated moult for sub-adult Terek Sandpipers in north-western Australia (n = 609). Estimates are given for per primary analysis and also the whole primary tract ("P1-P10"). Estimates for P5 and associated calculations could not be given due to insufficient data. '% adj pp overlap' is the number of days of overlap between a primary with the next adjacent one expressed as a percentage of that feather's estimated duration. '2nd pp overlap' is the percent of overlap with the next but one primary. Where this is a positive number there are three feathers moulting simultaneously. Estimates for P5 and associated calculations could not be given due to insufficient data.

	Start Date	**SE**	**Duration**	**SE**	**End date**	**Start SD**	**SE**	**Growth rate**	**Days apart**	**Days overlap**	**% adj pp overlap**	**2nd pp overlap**	**Un-mltd**	**Active moult**	**New**
P1	15 Aug	2.9	25.7	2.6	9 Sep	35.2	9.6	0.16%	-	16.1	63%	22%	126	109	374
P2	25 Aug	2.1	21.8	2.1	15 Sep	29.8	7.6	0.23%	9.6	11.4	52%	6%	155	107	347
P3	4 Sep	1.8	18.8	1.8	22 Sep	26.6	6.5	0.32%	10.4	8.8	47%	-7%	202	98	309
P4	14 Sep	1.7	19.8	1.8	3 Oct	26.0	6.2	0.37%	10.0	9.6	48%	-11%	254	100	255
P5	24 Sep	1.7	22.5	2.0	16 Oct	26.0	6.2	0.41%	10.2	10.8	48%	-42%	304	107	198
P6	6 Oct	1.7	24.6	2.1	30 Oct	25.3	6.1	0.44%	21.9	4.4	18%	-91%	367	107	135
P7	26 Oct	1.9	26.4	2.5	21 Nov	22.1	5.8	0.46%	20.2	-0.3	-1%	-116%	457	81	71
P8	22 Nov	2.8	32.9	4.0	24 Dec	25.7	7.4	0.42%	26.7	2.7	8%	-	529	49	31
P9	22 Dec	4.9	32.9	5.7	23 Jan	31.5	10.0	0.46%	30.2	6.5	20%	-	570	24	15
P10	17 Jan	7.8	41.7	8.5	27 Feb	36.2	13.0	0.39%	26.4	-	-	-	589	15	5
	Overall duration: 197 days				**Start date: 15 August**			**End date: 27 February**			**Av. growth rate: 0.508%**			**n = 609**	
P1-10	**22 Aug**	**3.0**	**169.9**	**6.6**	**8 Feb**	**26.3**	**5.5**				**Av. growth rate: 0. 589%**		**126**	**478**	**5**

Table 6. Categories of suspended or arrested moult encountered in 156 immature birds and the number of birds in each category for Kenya (n = 18), north-western Australia (NWA) (n = 137) and south-eastern Australia (SEA) (n = 2). No immature birds with suspended moult were recorded in India. 'MOP' stands for the 'Moult of Outer Primaries' strategy followed by some first year birds. Where there are no central primaries described, there were only two generations of feather present.

Inner primaries	**Central primaries**	**Outer primaries**	**Months**	**Kenya** n = 18	**NWA** n = 137	**SEA** n = 2
Juvenile, old	Replaced as part of MOP, suspended	Juvenile	Mar, Jul		2	
1st year normal moult, suspended	-	Juvenile	Nov, Feb		2	1
Replaced as part of sub-ad moult, suspended	Juvenile, old	Replaced as part of MOP – *completed*	Apr-July		62	
Replaced as part of sub-ad moult, suspended	Juvenile	Replaced as part of MOP – *active*	Apr		5	
Replaced as part of sub-ad or first adult moult*, suspended	-	Replaced as either MOP or a complete 1st Yr moult – impossible to tell	Aug-Dec	18	53	
Replaced as part of sub-ad or first adult moult, suspended	-	Juvenile, very worn	Sept-Oct		5	1
Replaced – but impossible to tell if sub-ad or adult moult, suspended	-	Recorded simply as 'old' – can't tell if old juvenile or replaced	Aug-Sept		4	
Active adult moult	Replaced in sub-ad moult, arrested	Juvenile, very worn	Oct-Nov		3	
Proportion of all immatures involved (1st year & sub-adult):				4%	9%	25%

** earlier birds likely to be part of a sub-adult moult, later birds more likely to be an adult moult*

Table 7. Parameters of primary moult for adult and sub-adult Terek Sandpipers in Kenya and north-western Australia (NWA) estimated using the whole primary tract with the Underhill and Zucchini method (1988).

		Start Date	**SE**	**Duration**	**SE**	**End date**	**Start SD**	**SE**	**Growth rate**	**Un-mltd**	**Active moult**	**New**
Kenya	Sub-adult	15 Aug	12.1	118.8	31.3	12 Dec	35.2	18.1	0.842%	8	32	0
	Adult	10 Aug	5.2	136.0	6.6	24 Dec	31.2	7.0	0.735%	30	319	385
NWA	1st Year	5 Dec	2.6	108.5	3.9	25 Mar	23.2	5.7	0.922%	89	98	163
	Sub-adult	22 Aug	2.9	169.1	6.6	8 Feb	26.0	5.5	0.589%	126*	478	5
	Adult	11 Sept	0.9	135.8	1.5	25 Jan	18.4	2.4	0.736%	436*	1,939	2,978

** unmoulted scores are excluded from Type 4 analyses*

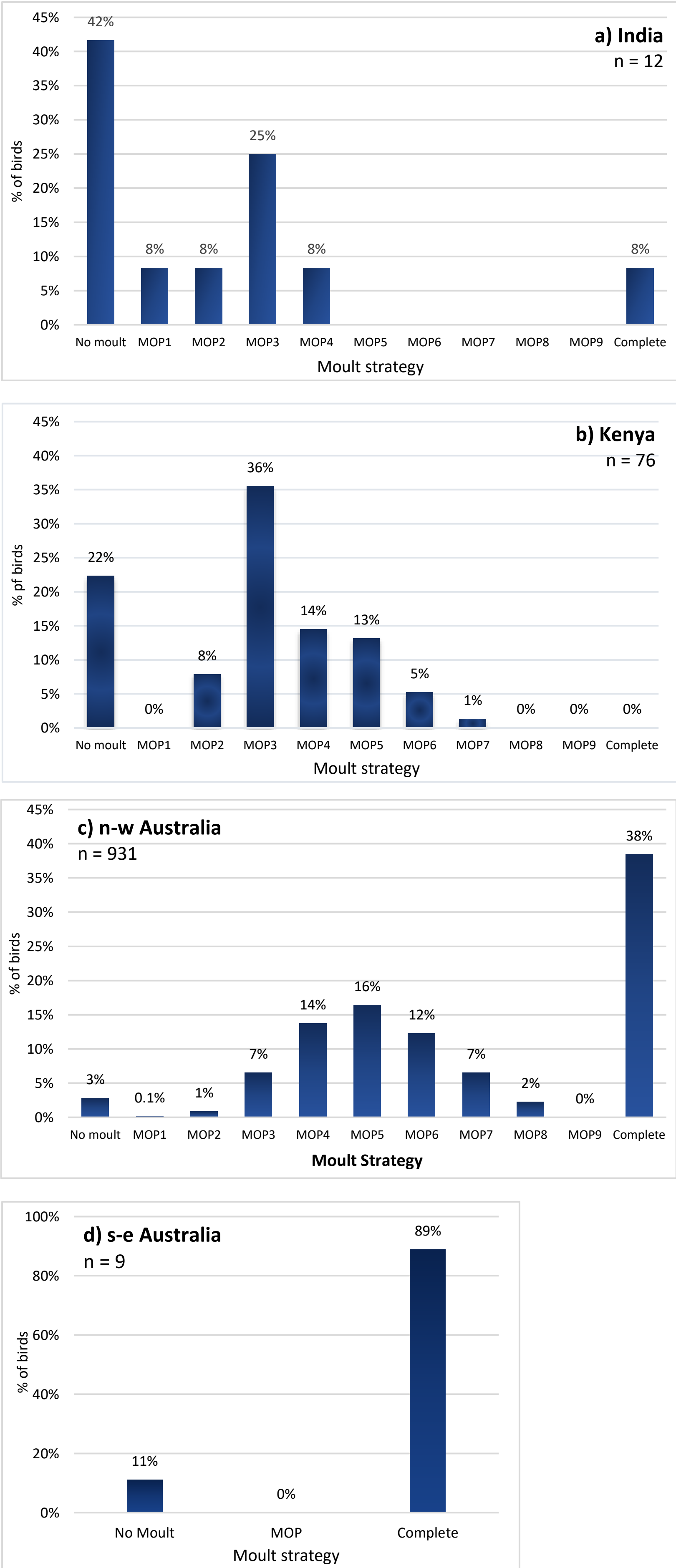

Fig. 1. Proportions of first year Terek Sandpipers following each of detailed moult strategy: no moult, moult of outer primaries (MOP groups 1-9) and complete moult in a) India b) Kenya, c) north-western Australia and d) south-eastern Australia.

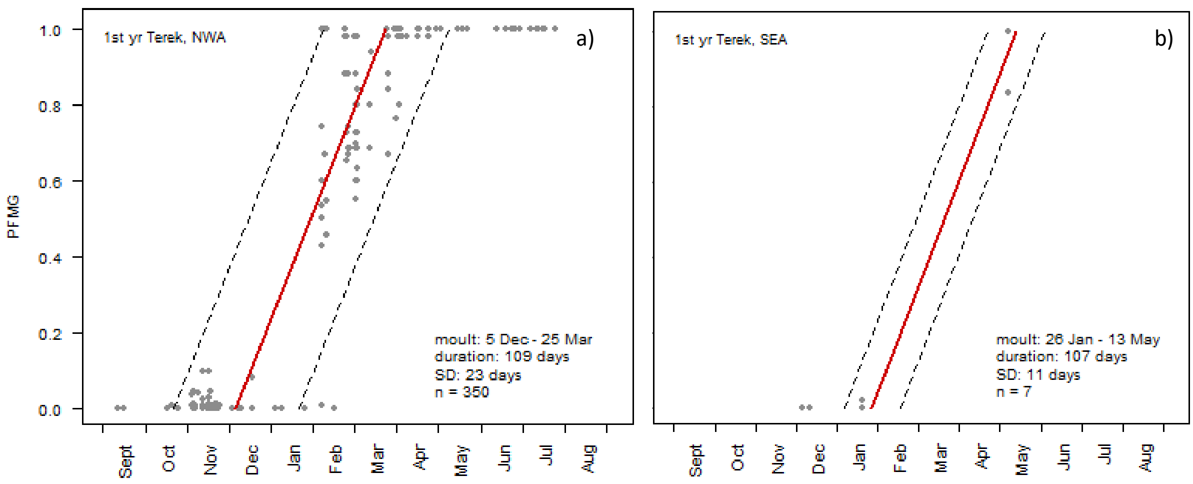

Fig. 2. Primary moult of first year Terek Sandpipers in a) north-western Australia (NWA) and b) south-eastern Australia (SEA). Percent Feather Mass Grown (PFMG) is plotted against date using the Underhill-Zucchini moult model. The solid line shows the estimated progression of primary moult for the average bird. Black dashed lines indicate the limits for 95% of the population and thus the parallelogram between them should contain approximately 95% of all birds in active moult.

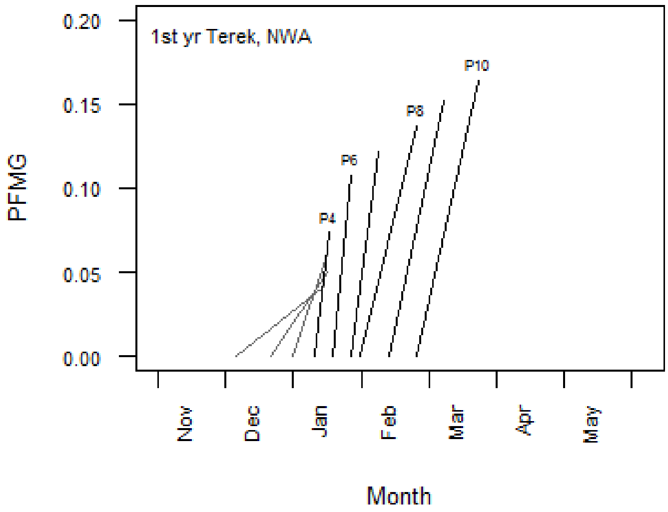

Fig. 3. Per primary moult of P7-P10 for first year Terek Sandpipers undergoing a complete moult, north-western Australia. The P6 estimate was obtained from a covariate analysis of P4-P10. Data was insufficient to give a sensible plot for P1-P3 which are therefore plotted in grey. P5 lacked sufficient data to plot at all.

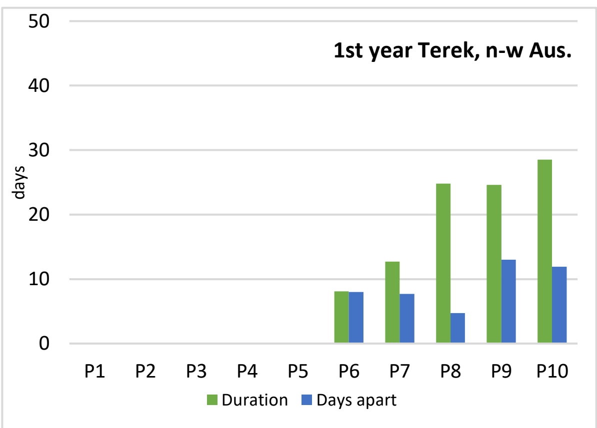

Fig. 4. Moult duration (green bars) of each primary and the number of days between each feather moulting (blue bars) for first year Terek Sandpipers, north-western Australia. Data was insufficient to give values for P1-P5.

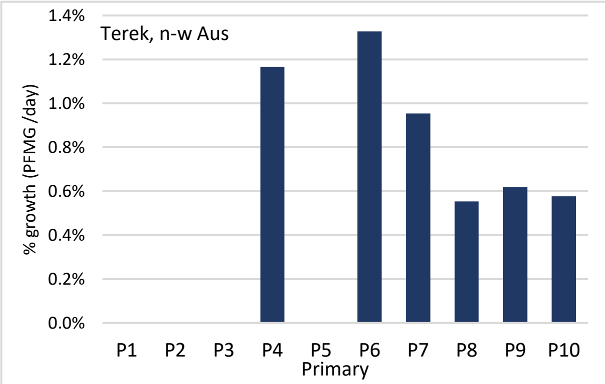

Fig. 5. Rate of growth per primary as the proportion of feather mass grown per day for first year Terek Sandpipers, north-western Australia.

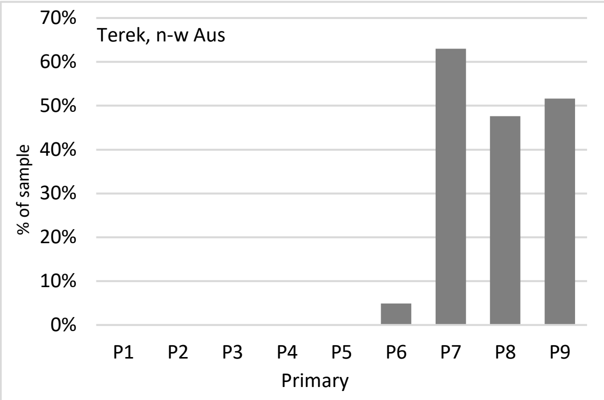

Fig. 6. Percent overlap of moult by each primary with the subsequent adjacent primary for first year Terek Sandpipers, north-western Australia.

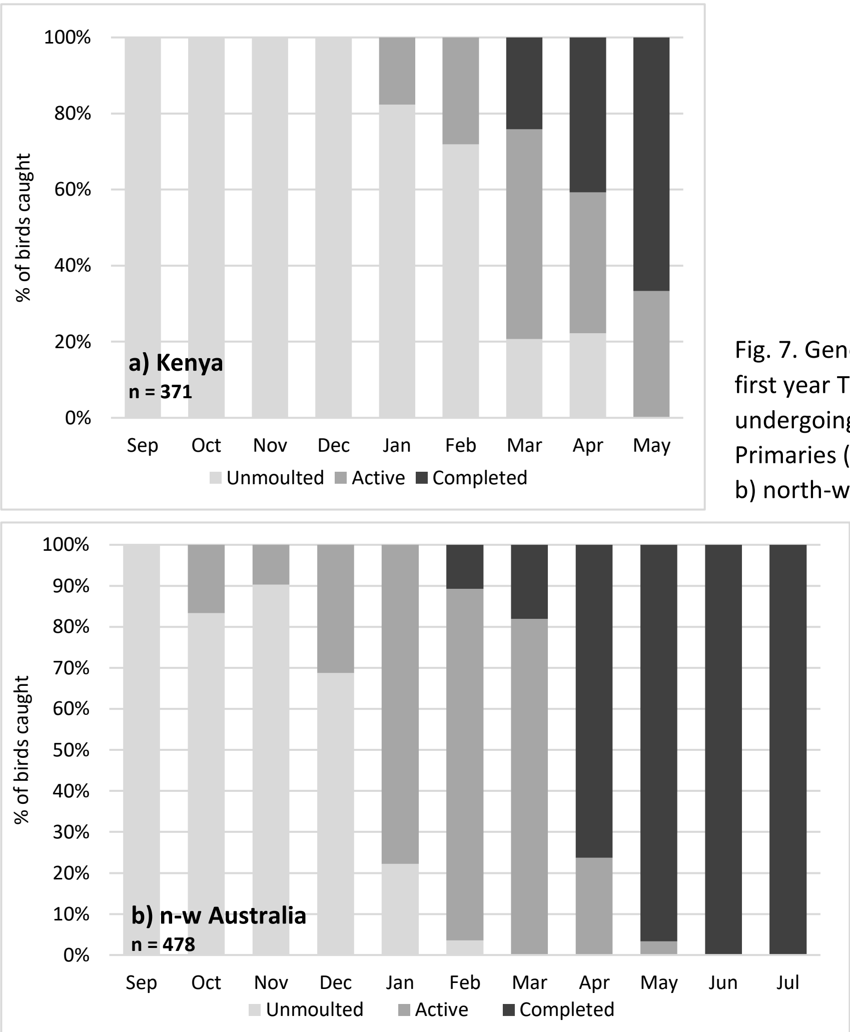

Fig. 7. General timing of moult for first year Terek Sandpipers undergoing Moult of Outer Primaries (MOP) for a) Kenya and b) north-western Australia.

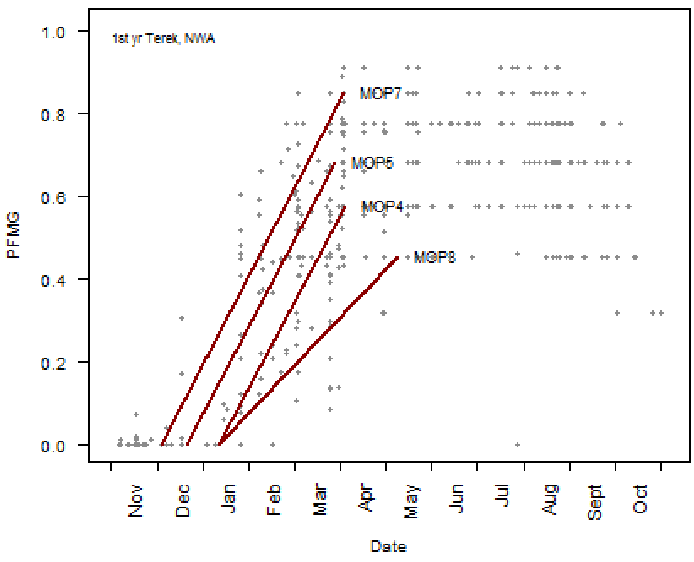

Fig. 8. moult of MOP (Moult of Outer Primaries) groups MOP3-MOP5 and MOP7 for first year Terek Sandpipers in north-western Australia.

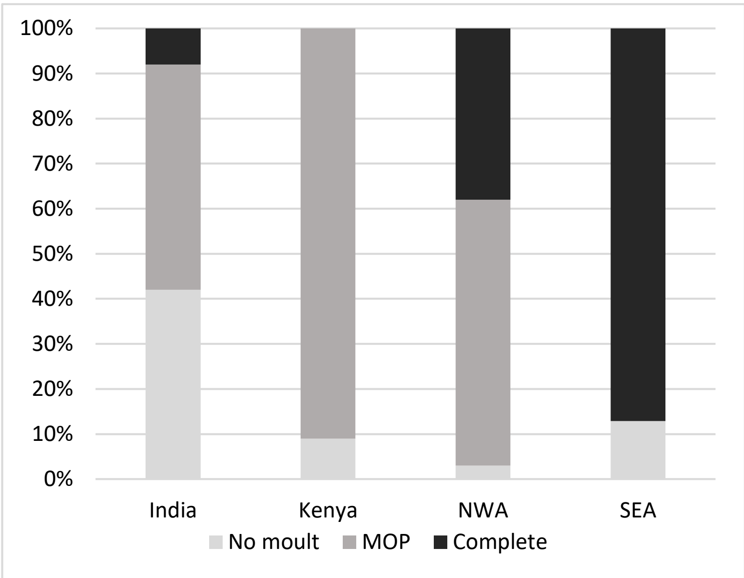

Fig. 9. Proportions of first year Terek Sandpipers in India, Kenya, north-western Australia (NWA) and south-eastern Australia (SEA) following each of the three broad primary moult strategies identified: no moult, moult of outer primaries (MOP) and complete moult..

Sub-adult moult

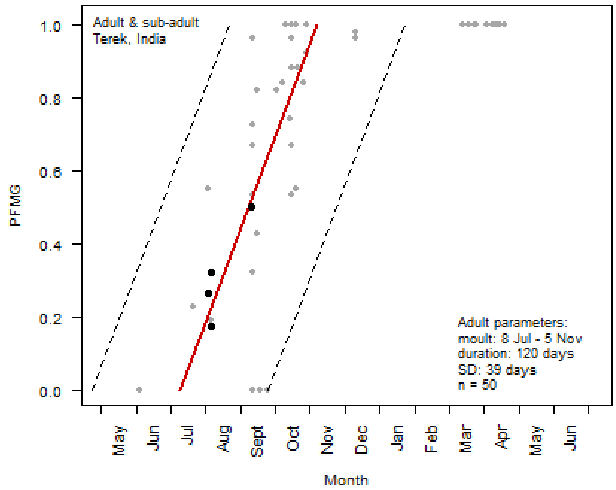

Fig. 10. Dates and moult scores for sub-adult Terek Sandpipers (large black dots) in India with relation to adult scores (grey dots). The red line shows the estimated average progression of adult moult. Dotted lines indicate the 95% confidence limits for the progression of moult.

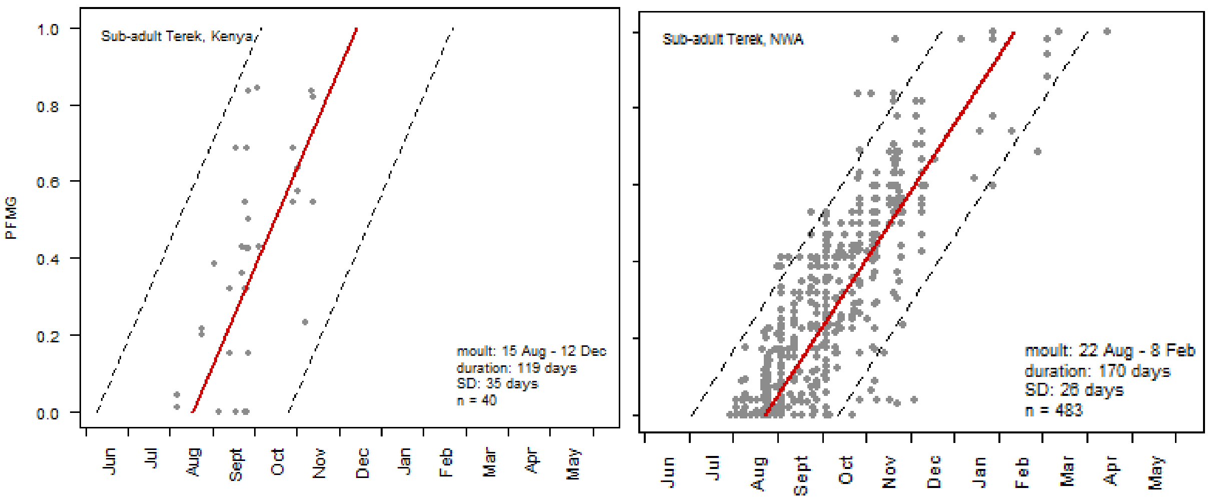

Fig. 11. Primary moult of sub-adult Terek Sandpiper in a) Kenya and b) north-western Australia. Percent Feather Mass Grown (PFMG) is plotted against date using the Underhill-Zucchini moult model. The solid line shows the estimated progression of primary moult for the average bird. Black dashed lines indicate the limits for 95% of the population and thus the parallelogram between them should contain approximately 95% of all birds in active moult

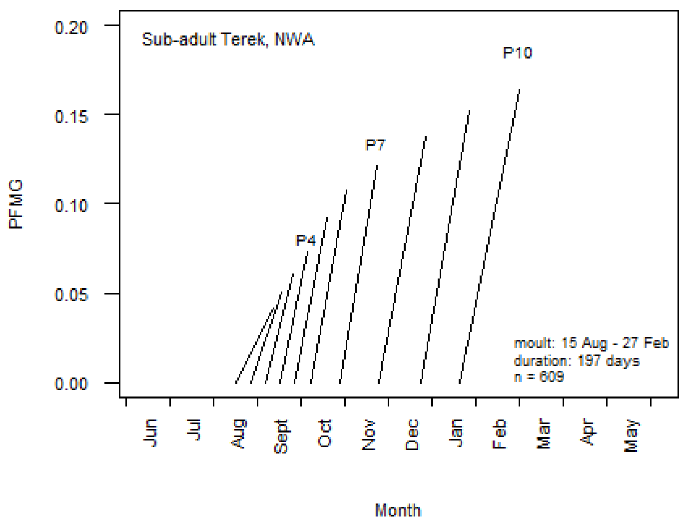

Fig. 12. Estimated moult per primary for sub-adult Terek Sandpipers, north-western Australia. Each line represents one primary; the gradient of a line is equivalent to the rate of growth for that feather in PFMG per day.

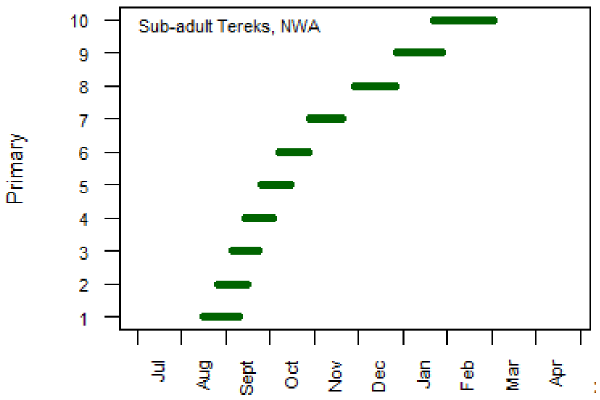

Fig. 13. Duration and overlap of individual primaries for sub-adult Terek Sandpipers, north-western Australia.

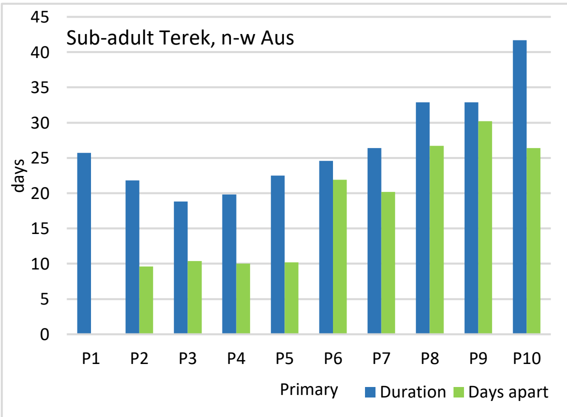

Fig. 14. Moult duration (blue bars) of each primary and the number of days between each feather moulting (green bars) for sub-adult Terek Sandpipers, north-western Australia.

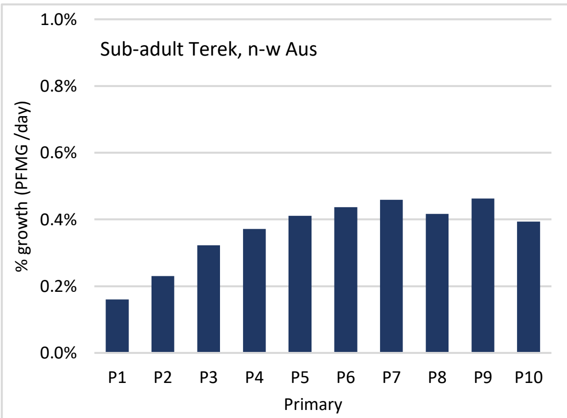

Fig. 15. Rate of growth per primary as the proportion of feather mass grown per day for sub-adult Terek Sandpipers, north-western Australia.

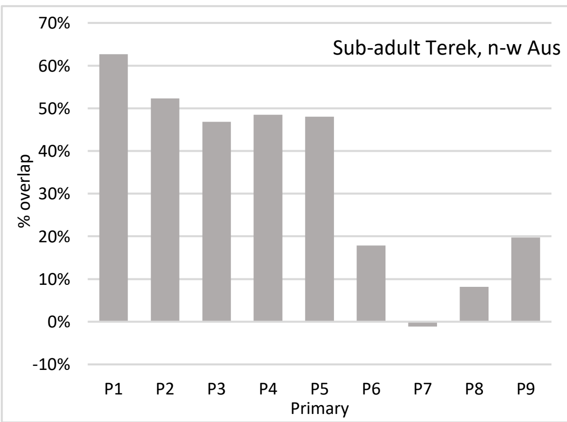

Fig. 16. Percent overlap of moult by each primary with the subsequent adjacent primary for sub-adult Terek Sandpipers, north-western Australia.

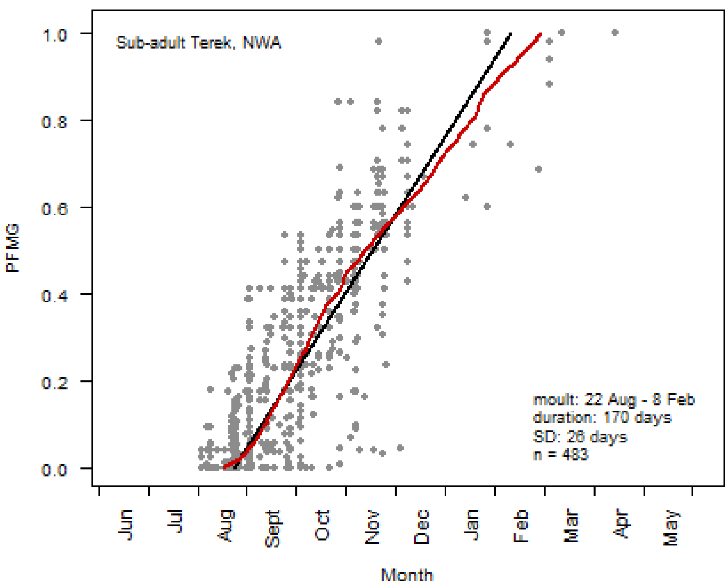

Fig. 17. Cumulative plot of moult per primary (red line) on overall estimated plot of moult for whole primary tract (black line) for Sub-adult Terek Sandpipers in north-western Australia.

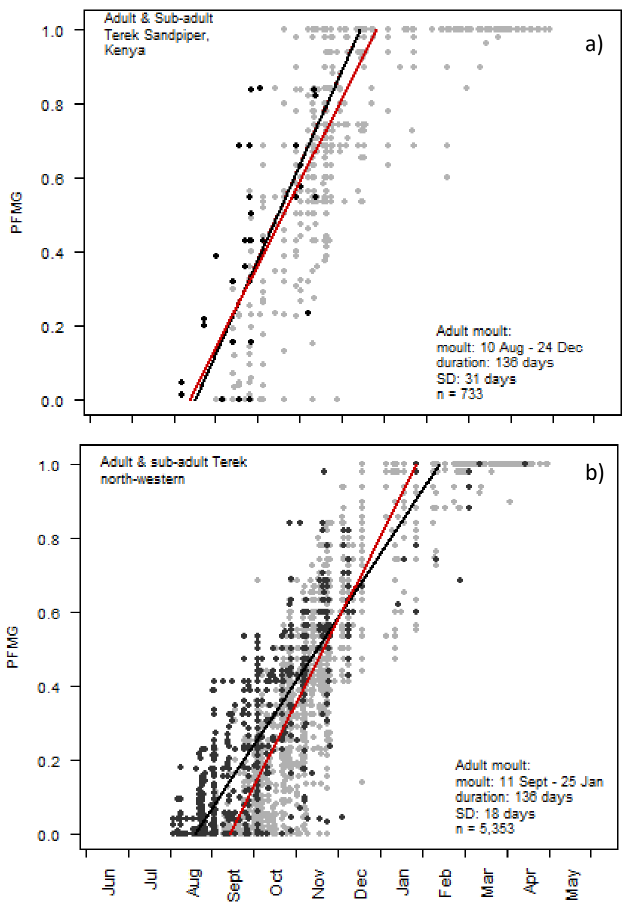

Fig. 18. Progression of adult and sub-adult Terek Sandpiper moult plotted together for a) Kenya and b) north-western Australia. The grey points & red line represent the adult moult; the black points & black line represent sub-adult moult.

Chapter 6

Moult of Terek Sandpipers in South Africa

Chapter 6. Moult of Terek Sandpipers in South Africa

Introduction

Of a global population exceeding 100,000 Terek Sandpipers Xenus cinereus, probably less than 1,000 reach South Africa (Waltner and Sinclair 1981, Underhill 1997, Delany and Scott 2002, Animal Demography Unit 2016). Thus, while not a particularly substantial proportion of the population, the location of the non-breeding grounds at the southern tip of Africa affords an interesting insight into the moult strategy of the species with relation to distance from breeding grounds and in comparison with other non-breeding populations of Terek Sandpipers. Waltner and Sinclair (1981) carried out a thorough synopsis of Terek Sandpiper distribution, biometrics and moult in southern Africa but this was carried out prior to the development of the Underhill-Zucchini moult model (Underhill and Zucchini 1988) which has provided a better window into understanding moult strategies in birds.

In this chapter, the original data used by Waltner and Sinclair (1981) are taken and analysed using the Underhill-Zucchini moult model (Underhill and Zucchini 1988) and the results compared with the original results. These are then discussed in the light of moult strategies shown by non-breeding populations of Terek Sandpipers in Kenya, Australia and south-eastern India.

Methods

Primary moult scores were obtained from Terek Sandpipers in south-west South Africa from birds ringed mostly at Langebaan in the Western Cape (33°05'S 18°17'E) with a small number (eight) at the mouth of the Olifantsrivier (31°42'S 18°12'E) between 1971 and 1979. Further details on location and methodology are described by Waltner and Sinclair (1981).

Moult scores were taken following the standard method by Ashmole (1962) and Ginn and Melville (1983) where an old, unmoulted feather is scored '0', a new fully-grown feather is scored '5' and the stages in between are scored 1–4. Feathers are numbered descendently, namely the inner primary that is often first to moult is P1 and the outer primary, P10 (Ginn and Melville 1983). Moult scores were converted to Percent Feather Mass Grown (PFMG) (Underhill and Summers 1993) for use in the Underhill-Zucchini moult model (Underhill and Zucchini 1988). The moult model was run in R using the moult package developed for this analysis (Erni et al. 2013).

Results

Adults

Moult scores from 52 adult and 34 first year Terek Sandpipers were obtained for moult analysis. Data were insufficient to allow the estimation of moult per individual primary and thus results are only taken from the full tract analysis. The primary moult of adult Terek Sandpipers in South Africa was estimated to start on 6 October and last for an average of 134 days. Birds were thus estimated to complete on average on 17 February (Fig. 1). With a standard deviation of 48 days, 95% of adults were estimated to start moult between 5 July and 7 January.

The average daily rate of feather growth for the whole wing was 0.746% per day. The date at which 50% PFMG was reached, i.e. the 'mid-moult' date, was estimated to be 12 December on average.

First years

One first year Terek Sandpiper was starting to moult one inner primary at the end of December with a score of 1 or PFMG of 0.005%, assumed to be the start of a complete moult. Three birds, fledged the previous northern summer, and hence close to one year old, were caught in May, June and August, and had completely renewed their primaries (PFMG = 1.0). 9% of the 34 first years underwent a complete moult. All other birds undertook a partial 'Moult of Outer Primaries' (MOP) moult of varying numbers of outer primaries. 16% of these had also moulted between one and three inner primaries. The majority (32%) replaced the three outer primaries (MOP3) (Fig. 2). The next most followed strategy was MOP4 (21%) and then MOP5 (15%). 80% of birds moulted between three and six outer primaries (Fig. 2).

Discussion

The moult of Terek Sandpipers in southern Africa was described by Waltner and Sinclair (1981) but this was prior to the development of the Underhill-Zucchini moult model analysis (Underhill and

Zucchini 1988). The estimate for the duration of primary moult in this study using the moult model at four and a half months was substantially shorter than the estimated five to six months by Waltner and Sinclair (1981), though they noted that starting dates were widely spread and thus it was difficult to estimate a start date.

The estimated mid-moult date fitted the expected pattern when compared to other locations; it was later than more northerly populations and earlier than the most southern population in south-eastern Australia (Fig. 3). Birds that need to fly farther south to non-breeding grounds delay moult due to the additional distance flown and tend to start moult immediately on or soon after arrival (Pearson 1974, Prater 1981, Summers et al. 2010, Remisiewicz 2011). On arrival in South Africa, conditions are good and birds can take the optimum amount of time (around 135 days) to moult in order to grow good quality feathers and complete in time (end of February) to fatten for the return journey to breeding grounds (Serra 2001).

First year birds appear to follow a similar pattern to those in Kenya in that the majority undergo a partial moult of some outer primaries. As in Kenya, the outer three primaries were the set most commonly moulted (c.f. Fig. 1b in Chapter 5). However, in contrast to Kenya where a small proportion of birds did not moult at all and none underwent a complete moult, in South Africa the opposite was true. This pattern was also present in the Australian populations (Figs. 1c and 1d, Chapter 5). While Terek Sandpipers in Australia may involve two different populations of breeding birds which follow a different moult strategy in their first year (Chapter 5), there is a suggestion that birds which travel farther south have a greater tendency to replace all their primaries in the first year (Remisiewicz 2011). Relatively little work has been done on the moult patterns of first year migrant waders (Remisiewicz et al. 2010), but in young Greenshank *Tringa nebularia*, the farther south birds migrate in Africa, the larger the proportion of birds that moult primaries and the more primaries are involved (Remisiewicz et al. 2014). In first year Terek Sandpipers in Kenya, 75% moulted between three and six outer primaries compared to 62% in South Africa. However, 7% moulted six to eight outer primaries in Kenya compared to 21% in South Africa (Fig. 2, Fig. 2b in Chapter 5). This, together with c. 10% of the population in South Africa undergoing a complete moult, further suggests that birds that migrate farther south moult more primaries. Juvenile feathers are poorer in quality and thus durability (Ginn and Melville 1983, Jenni and Winkler 2011). For birds that need to fly farther and thus endure greater wear and abrasion, it therefore pays to put additional energy into replacing more of primaries.

Summary

As in Kenya and Australia, adult Terek Sandpipers migrating to South Africa for the non-breeding season moult their primaries upon arrival at their non-breeding grounds. Moult is delayed later than for populations farther north such as Kenya and take an optimum estimated duration of 135 days. Most First year birds undergo a partial moult of some outer primaries but on average more feathers than in first year birds farther north in Kenya. A small proportion (10%) carry out a complete primary moult.

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Tables and figures

Table 1. Parameters of moult for per primary and full tract analysis of adult Terek Sandpipers in South Africa (n = 50). The average growth rate per primary = 0.702% per day; average growth rate for all primaries using total moult duration calculated from per primary results = 0.748% per day. '% adj pp overlap' is the number of days of overlap between a primary with the next adjacent one expressed as a percentage of that feather's estimated duration.

	Duration	SE	Start Day	SE	Start SD	SE	Growth rate	Start Date	End date	Days apart	Days overlap	% adj pp overlap	Un-moulted	Active moult	New
P1	29.8	17.8	96.6	33.8	60.3	36.6	0.14%	4 Oct	3 Nov				3	3	46
P2													3	2	47
P3													3	2	47
P4	16.8	11.9	120.2	24.0	48.8	29.1	0.44%	28 Oct	13 Nov				4	2	46
P5													6	1	45
P6													7	0	45
P7													7	4	41
P8	29.2	11.4	159.6	13.8	43.3	21.1	0.47%	6 Dec	4 Jan	-	5.8	20%	9	6	37
P9	25.2	9.8	183.0	11.4	44.0	20.8	0.60%	29 Dec	24 Jan	23	11.9	47%	14	6	32
P10	42.7	12.0	196.3	10.9	45.9	20.3	0.38%	12 Jan	24 Feb	14			17	11	24
	Overall duration: 142 days			**Start date: 4 October**			**End date: 24 February**			**Av. growth rate: 0.702%**					**n = 50**
P1-10	133.7	21.7	98.5	18.9	47.5	19.7	0.748%	6 Oct	17 Feb				5	24	21

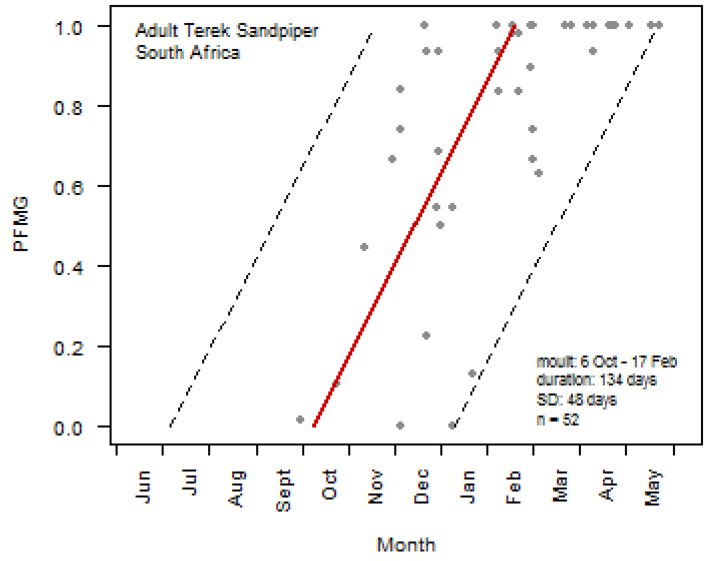

Fig. 1. Progression of estimated moult of primaries for adult Terek Sandpipers in South Africa. The red line shows the estimated average moult progression. Dashed lines show the limits for 95% of the population with a standard deviation of 48 days. 50% PFMG was reached on average by 12 December.

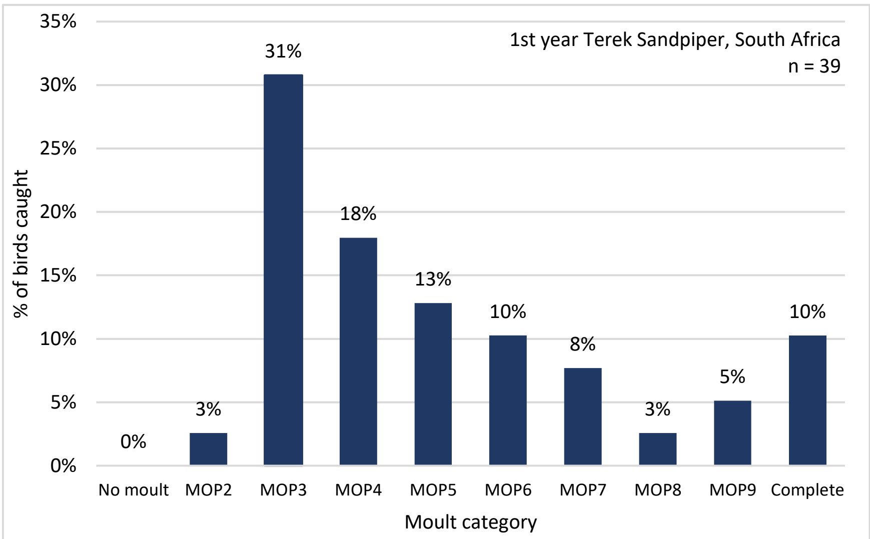

Fig. 2. Moult categories in first year Terek Sandpipers in South Africa. MOP = partial 'Moult of Outer Primaries'.

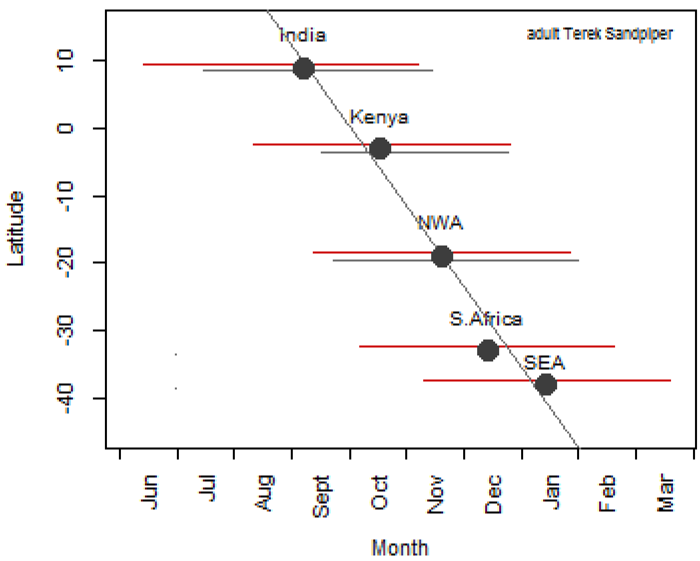

Fig. 3. Mid-moult date and moult duration for adult Terek Sandpipers in South Africa compared to India, Kenya, north-western and south-eastern Australia (data for non-S. African locations taken from Chapter 4).

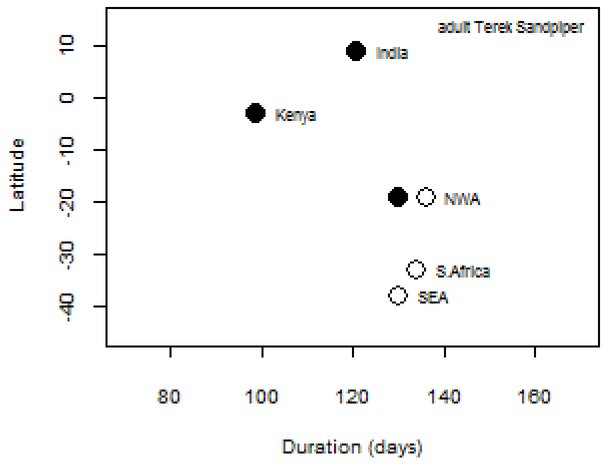

Fig.4. Average estimated duration of moult against latitude for adult Terek Sandpipers for five sampling locations: India, Kenya, north-western Australia, South Africa and south-eastern Australia *(open circles = full primary tract analysis; solid circles = per primary analysis).* Data for non-S. African sites taken from Chapter 4.

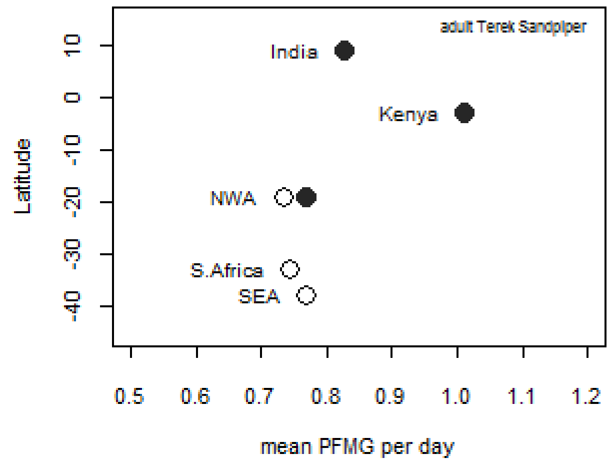

Fig. 5. Mean percent feather mass grown per day for adult Terek Sandpipers against latitude for five sampling locations: India, Kenya, north-western Australia, South Africa and south-eastern Australia *(open circles = full primary tract analysis; solid circles = per primary analysis).* Data for non-S. African sites taken from Chapter 4.

Chapter 7

Status and migration of the Lesser Sand Plover and the Greater Sand Plover

Chapter 7. Status and migration of the Lesser Sand Plover and the Greater Sand Plover

Introduction

A large volume of research publications has focused on a number of long-distance migrant wader species to understand their population status, distribution and life cycle. The majority of this research has been undertaken on species which occur in large numbers in Europe, North America, South Africa and Australia e.g. Grey Plover *Pluvialis squatarola*, Red Knot *Calidris canutus*, Curlew Sandpiper *C. ferruginea*, Dunlin *C. alpina*, Little Stint *C. minuta*, Western Sandpiper *C. mauri*, Ruff *Philomachus pugnax*, Bar-tailed Godwit *Limosa lapponica* and Ruddy Turnstone *Arenaria interpres* (Senner and Martinez 1982, Cramp and Simmons 1983, Hayman et al. 1986, Pearson 1987, Summers et al. 1987, del Hoyo et al. 1996, Battley 1997, Serra et al. 1998, 1999, Minton et al. 2006). These are the continents and countries where the majority of researchers are based. In contrast, relatively little has been published on Lesser Sand Plovers *Charadrius mongolus* and Greater Sand Plovers *C. leschenaultii* despite being quite widely distributed as breeding birds across central and eastern Asia and being a common species in their non-breeding grounds along the shores of the Indian Ocean, in Africa, south and South East Asia, and Australasia (Cramp and Simmons 1983, del Hoyo et al. 1996, Delany et al. 2009). Sporadic reports have been published on wader surveys in the Middle East and on the eastern African coastline that include counts of both sand plover species (Bryant 1980, Baker 1996, Klaassen and de Fouw 2008, Borghesio and Gagliardi 2011) but Delany et al. (2009) highlight the substantial gaps in our knowledge of populations and their movements.

This chapter presents an overview of the status, distribution and migration of the closely related Lesser Sand Plover *Charadrius mongolus* and Greater Sand Plover *C. leschenaultii*. It seeks to draw together scattered data and information relating to population estimates and movements in an attempt to review these and provide a more realistic estimates of the status of both species. Using these it is possible to set better thresholds for identifying key sites for directing conservation efforts for these species (Delany et al. 2009, Wetlands International 2016).

Material and Methods

A thorough search of the published literature was carried out for information on Greater and Lesser Sand Plover population estimates, distribution and migration routes. This included peer reviewed papers together with some unpublished reports and an analysis of bird atlas data where available with a focus on populations within the Indian Ocean basin. This was supplemented by additional unpublished observations made on the Kenyan coast, as described below.

In addition to trapping and ringing birds (c.f. Chapter 1 for details), regular surveys were done of foraging waders at Mida Creek, Kenya (3°19'S 39°57'E). Birds were counted along a transect measuring 800 × 100 m in size (8 ha) once in every five-day period (pentade) for two years (June 2012 to May 2014) over a tide that was as close to a neap high tide as possible and during the morning when tourist numbers (and thus disturbance) were least. The transect started where the sand flats meet the mangroves and ran out to the deep water channel in the middle of the creek thus covering a sample of all the 'microhabitats' exploited by the different species of wader from the drier shoreline along the trees to the wetter muddy sand area close to the deep water channel. The survey was conducted over the low tide by the same observer on foot using binoculars and a telescope. The 800 m long transect was counted by following the eastern edge of the transect and stopping to count all birds up to a maximum distance of 150–200 m from the observer. All waterbirds present were identified to species and the numbers of each species counted and recorded. Numbers were converted into birds/ha. Data were plotted against date for the two years and a linear regression line fitted. The Underhill locally weighted smoothing function was applied to optimise the data output with a window of 20 days (Summers et al. 1985, 1992, Mullers et al. 2009).

Results and Discussion

Lesser Sand Plover *Charadrius mongolus*, Pallas, 1776

Distribution and populations

The Lesser Sand Plover is a poorly known long-distance migrant wader. It breeds in central and north-eastern Asia from the Pamir Mountains in Kyrgyzstan and Tajikistan in central Asia east in a broken distribution to the Chukotsky Peninsula in the north-east with breeding also recorded in Alaska (Cramp and Simmons 1983, Hirschfield et al. 2000, Delany et al. 2009).

Five races of *C. mongolus* are recognised: three form the more westerly breeding '*atrifrons* group' which includes *C. m. pamirensis* Richmond, 1896, *C. m. atrifrons* Wagler, 1829 and *C. m. schaeferi* de Schauensee, 1938 and the remaining two the easterly-breeding '*mongolus* group' containing *C. m. mongolus* Pallas, 1776 and *C. m. stegmanni* Portenko, 1939 (Cramp and Simmons 1983, Hirschfield et al. 2000). All five races are migratory, flying south from the breeding grounds to spend the boreal winter along the coastlines of East Africa, south and east Asia and Australia (Nielsen 1971, del Hoyo et al. 1996, Hirschfield et al. 2000) (Fig. 1). Due to the difficulty in separating the different races of Lesser Sand Plover when in non-breeding plumage, it has been difficult to identify exactly where each of them migrate to in the non-breeding season. From a careful analysis of museum specimens, however*, pamirensis* migrates south-west to spend the non-breeding season in India, the Middle East and south to the East African coastline (Cramp and Simmons 1983, Hayman et al. 1986, Hirschfield et al. 2000). Birds reaching north-western Australia are mostly from the '*mongolus* group' and are considered to belong to the larger and paler nominate race (Barter 1991, Barter and Davies 1991, Hirschfield et al. 2000) which breeds east and north of Lake Baikal. Lesser Sand Plovers reaching south-eastern Australia are also thought to belong to the '*mongolus* group' but consist mainly of the *stegmanni* sub-species (Barter and Davies 1991) which breeds in Kamchatka, north eastern Russia.

The breeding grounds of the Lesser Sand Plover are rarely visited by ornithologists. Consequently, there are no estimates of population sizes. Likewise surveys on most of the non-breeding grounds are few and far apart. However, I have attempted to make estimates for each race from the available data.

***C. m. pamirensis* Richmond, 1896**, is slightly larger than *atrifrons*. It breeds in montane valleys, elevated tundra and mountain steppe in an arc from Tien Shan in Xinjiang, north-western China west to the Pamir Mountains in Kyrgyzstan and Tajikistan and south-east to western Kun Lun in southern Xinjiang. The current "official" Wetlands International estimate of the global population of this subspecies, on which the 1% criterion of 1,250 birds for Ramsar wetland status is based, is 100,000–150,000 birds (Hirschfield et al. 2000, Delany et al. 2009, Wetlands International 2016).

The majority of *pamirensis* appear to spend the non-breeding season on the Indian coastline (estimated at 100,000) with c. 50,000 in the Middle East and along the East African coastline (Cramp and Simmons 1983, Hirschfield et al. 2000, Delany et al. 2009). Counts of up to 1,470 Lesser Sand Plovers have been made at Khor Dubai in January and similarly high numbers in the northern Spring at the end of April which, when extrapolated, gave estimates of almost 20,000 birds present during the Spring (Keijl et al. 1998). Similar large numbers were estimated for 200 km^2 of intertidal flats along the Saudi Arabian coastline in January/February where over 3,000 Lesser Sand Plovers were counted giving an estimate of 28,000 birds (Zwarts et al. 1991). The north-eastern shores of the Arabian Gulf on the Iranian coastline have an estimated 2,500–5,000 birds (Scott 2010). Along the eastern coastline of the Middle East, 8,800 were counted for the whole coast of Oman excluding Barr al Hikman where 9,000 were counted the same year (2008) (Green and Harrison 2008, Klaassen and de Fouw 2008). Added up, this suggests a total in the Middle East of 70,000–80,000 birds. However, in 2013, 72,378 Lesser Sand Plovers were counted at Barr al Hikman by de Fouw et al (Wetlands International 2014) and in January 2016 even more, 123,000 birds (de Fouw in press). The explanation for this large increase in numbers in recent years is not understood. Such a large and rapid increase cannot possibly be the result of greatly improved breeding success. More likely it is a shift of a population from somewhere else where perhaps the non-breeding grounds have been destroyed, e.g. by development as has been a threat all around the Gulf of Arabia (Aspinall and Hellyer 2006). It would be necessary to survey other key sites around the Gulf to ascertain whether birds have indeed moved to Barr al Hikman from elsewhere in the Middle East—or have come from farther afield such as the Indian or Pakistan coastline. Thus, assuming this is a shift of birds rather than a previously undetected population, the total figure for this area lies in the region of 70,000–80,000.

Along the East African coast, little is known about Somalia (T. Dodman pers. comm.) but evidence points towards there being little area of suitable habitat (muddy sand flats), and the Lesser Sand Plover population is unlikely to exceed 5,000–10,000 birds. In Kenya up to 1,400 have been counted across several wetlands on one weekend survey in the Watamu/Malindi area of the north coast with a single maximum count at Mida of 1,264 in 2010 (pers. obs.); a count of 2,340 was recorded at the Tana River Delta basin in 1993 (Bennun and Njoroge 1999) but subsequent counts at this location have not exceeded 160 (pers. obs.). On the Kenyan coast south of Mombasa, (Pearson 1984) counted 700–800 and estimated a total of 1,000–3,000 birds from Malindi south to the Tanzanian border. These surveys are not necessarily representative of the Kenyan population; however, given what is known, it is likely to be in the region of 6,000-8,000 birds. The maximum count at Mida Creek of 1,264 therefore made up c. 15–20% of the Kenyan population. In its non-breeding range, Lesser Sand Plovers are strictly coastal and tend to prefer tidal mud and sandflats, hence Mida Creek is an optimum location for it (see site description, Chapter 1).

In Tanzania no counts have been made that surpass the 1% criteria for the biogeographical regional population (1,250) with a maximum of 722 counted on the Rufiji River Mouth (Nasirwa et al. 2001). While recognising that there is a bias in the number of observers in the north, the majority of Tanzanian records come from the northern section of the Tanzanian coastline but with the comment 'large flocks are sometimes seen during return passage' (Baker and Baker 2016). This is in contrast to Harvey (1974) who recorded larger flocks of up to 200 in the southward migration with 'little evidence of a return passage' and only small flocks during the main boreal winter period. Lesser Sand Plovers have been recorded regularly as far south as Durban and counts of almost 500 have been made in southern Mozambique (Dodman et al. 1999, Parker 1999), but concentrations of this size appear to be the exception and not the rule with Greater Sand Plover being markedly more common in general (Parker and de Boer 2000, Oschadleus and Lotz 2004, Wilson 2009). Borghesio and Gagliardi (2011) recorded relatively large numbers of Lesser Sand Plover in Quirimbas National Park, Mozambique, compared to Greater Sand Plover. However, they noted the difficulty of differentiating the two species and investigation with others familiar with the area suggest that in fact Greater Sand Plovers outnumber Lesser Sand Plovers (M. Wilson pers. comm.). This is certainly the pattern with other surveys from Tanzania south. There are, nonetheless, many estuaries along the Tanzanian and Mozambique coastline which have never been surveyed and thus the possibility of undiscovered concentrations of birds cannot be ruled out. Current knowledge, however, indicates that this species is relatively uncommon along the Indian Ocean coastline south of Kenya. An estimate for the Tanzanian and Mozambique coastline, therefore, lies in the region of 5,000–10,000 birds.

Its status in the Malagasy region is unclear due to uncertainty regarding correct separation with Greater Sand Plover *Charadrius leschenaultii*. However small numbers are known to reach Seychelles (Cramp and Simmons 1983) and it would appear that the species is widespread along coasts throughout the region (Safford and Hawkins 2013) though unlikely to be numerous. A first estimate would put the total number at 1,500-2,000 birds.

Altogether, therefore, with the 100,000 estimated for India and Pakistan, up to 80,000 for the Middle East and probably in the region of 25,000 for the East African coast, a global estimate for the population of the race *pamirensis* would be 200,000 birds. This is at least 50,000 more than was taken as the estimate by Delany et al. (2009).

C. m. atrifrons **Wagler, 1829,** is a small, dark, short-billed subspecies that breeds south and east of *pamirensis* in the Himalayas and southern Tibetan plateau with a global population estimated at 100,000 (Hirschfield et al. 2000, Department of the Environment 2016) or 120,000–150,000 (Wetlands International 2016). It spends the non-breeding season from Sindh in Pakistan east along the Indian coastline, around the Bay of Bengal, and south and east to Sumatra (Cramp and Simmons 1983, Balachandran and Hussain 1998, Hirschfield et al. 2000, Department of the Environment 2016) where it is probably the commonest wader along the Indian coastline (Ali and Ripley 1988). An estimated 40,000 birds of this race occur in the East-Asia Australasian Flyway focused around the Bay of Bengal, Malaysia, Thailand, and western Indonesia (Bamford et al. 2008).

C. m. schaeferi, mongolus and ***stegmanni*** population estimates. The total population for Lesser Sand Plover including all subspecies for the East Asian–Australasian Flyway was estimated to be a minimum of 130,000 birds (Bamford and Watkins 2005). However figures provided by Wetlands International (2016) suggest a much smaller population of 68,000 birds. With many threats to staging and non-breeding grounds along this flyway, this probably indicates a real decline in overall numbers. Due to the difficulty in distinguishing between subspecies in the field in non-breeding plumage, however, the following are estimates.

C. m. schaeferi **de Schauensee, 1938,** is a larger, paler, long-billed subspecies that comprises the eastern part of the '*atrifrons* group' of *C. mongolus*. It breeds from southern Mongolia through Qinghai to eastern Tibet and the other adjacent provinces of China, and spends the non-breeding season from coastal Thailand to the Greater Sunda Islands with concentrations such as 5.8% of the biogeographical population estimated to spend the non-breeding season in Malaysia (Wei et al. 2006). There is a suggestion that some might regularly visit northern Australia as well. The global population is estimated at 25,000-100,000 (Lane 1986, Hirschfield et al. 2000, Bamford et al. 2008, Wetlands International 2016, Wiersma et al. 2016b).

C. m. mongolus **Pallas, 1776,** is a paler race that breeds from Lake Baikal in inland eastern Siberia and northern Mongolia, through the Russian Far East to the Verkhoyansk mountain range. It spends the boreal winter from Taiwan to Australia and together with *stegmanni* forms the non-breeding population of Lesser Sand Plovers found in Australia (Cramp and Simmons 1983, Lane 1986, Department of the Environment 2016). The global population has been estimated at 25,500 (Wetlands International 2016) and 40,000 (Bamford et al. 2008). Frequently *mongolus* population estimates are combined with *stegmanni* to be 25,000-100,000 since estimates have only been made on the non-breeding grounds where in non-breeding plumage, the two races are inseparable in the field. 20,000 were estimated (Watkins and Royal Australasian Ornithologists' Union 1993) to spend the boreal winter in Australia of which 84% are considered to occur in Queensland in the north-east

(Minton 2006). The rest are expected to spread out between China, Philippines, Indonesia and Papua New Guinea (Bamford et al. 2008).

***C. m. stegmanni* Portenko, 1939,** is a darker, short-legged race that breeds in north-eastern Russia, especially around Kamchatka, on the northern Kuril and Commander Islands and on the Chukotski Peninsula. It spends the boreal winter from southern Ryukyu Island and Taiwan south to Australia where it mixes with the nominate race. This is likely to be the race that migrates to south-eastern Australia, although the non-breeding population there is small; the population in Victoria was estimated to be 100 birds by Barter and Riegen (2004). It has subsequently declined and is considered to be 10 birds in 2016 (C.D.T. Minton pers. comm.). The population size for this subspecies is unknown but is considered together with *mongolus* to number in the region of 25,000-100,000 birds (Cramp and Simmons 1983, Hirschfield et al. 2000, Bamford et al. 2008, Department of the Environment 2016, Wiersma et al. 2016b). Wetlands International (2016) suggested a population of 13,000, based on expert opinion.

Migration strategy

All populations and races of Lesser Sand Plover are fully migratory; none remain on the breeding grounds during the boreal winter. The *mongolus* group of Lesser Sand Plover follow the East Asian-Australasian Flyway to the Far East and Australasia as does the race *schaeferi* of the *atrifrons* group. *C. m. atrifrons* follows the Central Asia Flyway together with the bulk (estimated at c. 60%) of the *pamirensis* population (Delany et al. 2009) which are likely to come from a particular part of the breeding area though this has yet to be ascertained. The remainder of the *pamirensis* population follow the West Asia-East Africa Flyway to spend the boreal winter in the Middle East and Africa. Most of these remain in the northern hemisphere with only a small proportion crossing the equator, probably at most 15,000.

As with many migrant waders, the adults depart first leaving the newly fledged juveniles behind on the breeding grounds to follow a few weeks later; the adults similarly arrive on the non-breeding grounds earlier than the juveniles (Fogden 1963, Pearson and Britton 1980, Cramp and Simmons 1983, Marchant and Higgins 1993, Department of the Environment 2016). Adults tend to depart from their Asian breeding grounds from early August (*pamirensis* and *atrifrons*) to the end of September (*stegmanni*) (Pearson and Britton 1980, Cramp and Simmons 1983, Summers et al. 1987, Harrington et al. 1991). Departure timing for *mongolus* is unknown but it is probably similar to that of *stegmanni* (Marchant and Higgins 1993). From the breeding grounds in central Asia, it appears that birds fly non-stop overland to reach coastal stop-over sites as there are few inland records that would suggest stopping at wetlands en route. Once on the coast they tend to follow the coastline (Cramp and Simmons 1983, Marchant and Higgins 1993, Department of the Environment 2016).

Arrival on non-breeding grounds starts in late July (south-eastern India), early to mid-August (Middle East), late August / early September (Kenya), August to October (north-western Australia) and late August / September to November (south-eastern Australia) (Pearson and Britton 1980, Cramp and Simmons 1983, Marchant and Higgins 1993, Balachandran and Hussain 1998, Department of the Environment 2016). There is good evidence of strong site fidelity for Lesser Sand Plovers on their non-breeding grounds where ringed birds have been retrapped in several subsequent years (Balachandran and Hussain 1998).

There is little published information on dates and routes for the return migration to the breeding grounds. In general, Lesser Sand Plovers appear to migrate later than other species with departures from non-breeding grounds mainly from mid to late April and early May (Pearson and Britton 1980). However, from northern Australia there appears to not be the later departure but also an earlier wave at the end of March (Marchant and Higgins 1993). In populations of *stegmanni*, birds reach their breeding grounds at the end of May and early June (del Hoyo et al. 1996).

Arrival and departure at non-breeding grounds

India. Adult Lesser Sand Plovers arrive in south-eastern India in August with first years arriving a month or so later (Cramp and Simmons 1983, Balachandran and Hussain 1998). Counts carried out over three years in the Gulf of Mannar, south-eastern India, showed markedly large numbers of birds in September/October (up to 13,000) and again in January/March (more than 10,000) with relatively few (maximum less than 4,000) in November/December (Balachandran and Hussain 1998) suggesting the location is used as a stop-over site for moult during southward migration and for fattening during both south- and northbound migration than as a continuous non-breeding area for the whole season. Where the birds move on to from the south-east of India is uncertain. Both *atrifrons* and *pamirensis* occur in south-eastern India but, of the two, only *atrifrons* occurs farther south in Sumatra and Indonesia (Hirschfield et al. 2000). It is possible that birds cross the Indian Ocean to reach there, a distance of c. 1,800 km which well within the capability of a long-distance waders to fly without stopping (Minton et al. 2011). There is a lack of ring recoveries from south-eastern India to date to help understand patterns; this represents an opportunity for further research.

Australia/South-east Asia. Most birds of the nominate and *stegmanni* races pass south through Japan, the Yellow Sea, south-east Asia and reach Australia between July and September. Arrival in northern Australia begins from late August through to October (Cramp and Simmons 1983, Marchant and Higgins 1993, Department of the Environment 2016). The northern and north-eastern coastlines form an important staging area for migrants heading farther south. Birds stop here for a week to ten days as suggested by evidence in the south-eastern corner of the Gulf of Carpentaria from observations of colour-flagged waders, albeit of other species such as Red Knot *Calidris canutus* (Roger Jaensch pers. comm.). After a stop off to fatten up, birds continue to south-eastern Australia with the earliest arriving at the end of August with main arrival in September and latest through to November and even December (Marchant and Higgins 1993), C.D.T. Minton pers. comm.). Large numbers (c. 10,000 or 6% of the estimated flyway population) of mostly *mongolus* stopover on foraging grounds in South Korea on southward migration (Moores 2006, Rogers et al. 2006) from where it is likely they fly non-stop to their non-breeding grounds.

Northward migration from the southernmost non-breeding grounds is thought to start as early as February; however, the main departure, particularly from the northern part of the non-breeding grounds, occurs in April and continues into May with an earlier 'wave' of departure in March (Marchant and Higgins 1993, Department of the Environment 2016). Northward migration passes through Wallacea in February and April-June where the species is mainly found on passage (White 1975). On the Bohai Sea (mouth of the Huang He river) and the Yellow Sea numbers appear to peak towards the end of April and early May (Zhu et al. 2000, Barter and Riegen 2004) and birds are seen on the Korean peninsula in April and May where large numbers occur presumably fattening for the last leg of their migration to the northern breeding grounds (Moores 2006, Department of the Environment 2016).

As expected, adult birds precede first years in their migration timing, usually by several weeks. But in north-western Australia ringing showed that adults arrive in September, and that first-years must delay somewhere en route because the first juvenile birds arrive in January and the majority delay arrival until March and April. The evidence for this is that during 35 years of ringing, 679 Lesser Sand Plovers were ringed of which 136 were first years. Of these, only one first year Lesser Sand Plover was caught between August and January compared to 170 adults. Seven were caught in January, four in February, 47 in March and 55 in April (Fig. 2). Further research is needed to understand why the first years delay their arrival so substantially. Segregation by age occurs in other wader species, but is rarely as large as this. For example, juvenile Red Knots *Calidris canutus rogersi* reach the non-breeding grounds in New Zealand at the beginning of their second year (Minton 2003). The reasons for the delay are unknown and where they stop between leaving the breeding grounds in July and arriving in north-western Australia in March is also unknown.

One possibility is that foraging conditions in north-western Australia are suboptimal during these months for Lesser Sand Plovers to be able to support the larger population of both adults and young. Between July and November conditions are dry in north-western Australia with average monthly precipitation ranging from 1 – 8 mm (Chapter 1, Fig. 2c). The main rainfall occurs in January and February which may only then stimulate good production of the invertebrates the sand plovers feed on. Considering therefore, the enormous distances to be covered (these are mainly *mongolus* birds that breed up to 9,000 – 10,000 km away) and the possible lack of good feeding in north-western Australia, in the light of competition for resources by experienced adults, young birds may delay their arrival by stopping for longer at some stop-over sites along the migration route and only time their arrival when foraging conditions have improved. Ideally young birds would be ringed at breeding or stop-over sites and recovered between August and December—or better still to have satellite transmitters placed on juveniles on the breeding grounds to learn their migration route and timing. Otherwise trapping and ageing birds at stop-over sites to the north during August to December would also give an indication of the first year migration strategy. Many of the first year birds remain on the non-breeding grounds over their first boreal summer and are aged as sub-adults come August (Fig. 2).

The Middle East. In contrast to the eastern populations, most surveys and fieldwork in this area have been undertaken during the boreal winter (Eriksen 1996), with some surveys during the northward migration and only a few during the southward migration, and then mostly towards the end, in September/October. Thus knowledge of arrival dates in the region is weak (Keijl et al. 1998, Klaassen and de Fouw 2008). Cramp and Simmons (1983) considered Lesser Sand Plovers to arrive in "southern Arabia" from early to mid-August which corresponds with arrival dates in East Africa (Fogden 1963). Large numbers spend the non-breeding season in the region (see above) and birds appear to be late in departing for breeding grounds compared to other species such as the similar Greater Sand Plover (Keijl et al. 1998).

Cramp and Simmons (1983) gave the departure from non-breeding grounds as 'the first half of April' with breeding grounds of *pamirensis* reoccupied mid-April to early May. However most evidence from work carried out over the past 40 years suggests Lesser Sand Plovers migrate notably later than other species with a migration peak through United Arab Emirates in late April/early May (Keijl et al. 1998). This relatively late departure date (with birds still present on 18 May) from the Arabian Gulf is logical in the light of the species' breeding grounds at high altitude where the phenology of temperatures and snow cover are comparable to the high arctic; the late timing of the thaw results in conditions becoming favourable for breeding at a later date than would be anticipated for the latitude.

East Africa. At the Mida Creek study area, small numbers of Lesser Sand Plovers between April and the end of June consisted of non-breeding sub-adult birds, remaining behind when the adults returned to the breeding grounds (Fig. 3). A clear increase in numbers from mid-July marked the main arrival of adult Lesser Sand Plovers, and continued through to the end of August. A small reduction in numbers at the end of September suggested that some birds were in passage and moved farther south. From early October numbers increased sharply with the arrival of first year birds, an arrival which continued through to peak in the second half of November with a density of c. 6 birds/ha (Fig. 3). The proportion of juveniles in the samples trapped while ringing over 27 years supports this with an increase in percentage of juveniles present from 0% in August, 10% and 16% in September and October respectively to 27% in November after which the percentage is stable until adults start to depart in April (Fig. 4). The departure for the return migration was relatively late. Numbers decreased by c. 15% during December to February but most birds remained until the first half of March at which point there was a rapid departure, the majority of adults having departed by the first week of May (Fig. 3). There was an early influx of birds in July and August. A likely interpretation of this is that it consisted of adults which had failed to breed and left breeding grounds early. The main arrival of adults is in September, and juveniles arriving only in November through to December.

The counts at Mida Creek confirmed Lesser Sand Plovers as present throughout the year in Kenya including during the breeding season in June and July. These non-breeding birds are generally first years that remain on non-breeding grounds during their first boreal summer and only return to breed at two years of age (Pearson and Britton 1980, Cramp and Simmons 1983, Marchant and Higgins 1993, del Hoyo et al. 1996).

The pattern of arrival and departure at Mida confirms previous observations. The main adult arrival period is in September and there is a late departure for breeding grounds (Fogden 1963, Pearson and Britton 1980). There have been two recoveries of ringed birds from Mida Creek that further support these observations, one on the Pakistani coastline on 3 September 1985 (ringed 12 December 1982) confirming the late southward migration to Kenya and similarly for the return an adult found on the coast at Modhava, western India on 22 May 2016 that was ringed on 20 January 2013 (Jackson 2016), (Table 5).

The decrease in numbers during November (Fig. 3) may reflect a departure of birds on passage moving farther south, however retrap histories of birds ringed in August–October suggested that at least a certain proportion of birds that arrive in this period remain throughout the non-breeding season (Table 3). Furthermore, a gap in the data collection during this period is likely to have had an effect on the results shown. Further fieldwork is needed to obtain a better dataset to reveal the full patterns of Lesser Sand Plover arrivals and departures on Mida Creek, for all age categories. This fieldwork would involve both regular ringing and regular surveys.

South of Kenya, information on arrival and departure dates is scanty. In Dar es Salaam, Tanzania, Harvey (1974) noted the main arrival of Lesser Sand Plovers was mid-September with a peak in October. Thereafter numbers dropped and there is no sign of a return migration with birds just dwindling in number as adults leave for breeding grounds. Baker and Baker (2016), however, noted that large flocks of birds are occasionally recorded on return passage.

There are a small number of inland records of Lesser Sand Plover in Africa (Dowsett 1980). It is a vagrant to the interior of Africa, and it is almost exclusively a coastal species during the non-breeding season, confined mostly to the shorelines of the Indian Ocean between the tropics (Hayman et al. 1986, del Hoyo et al. 1996).

Greater Sand Plover *Charadrius leschenaultii*, Lesson, 1826

Distribution and populations

The Greater Sand Plover overlaps with Lesser Sand Plover both in its breeding range and on the non-breeding grounds (Cramp and Simmons 1983, del Hoyo et al. 1996, Hirschfield et al. 2000). It generally breeds in inland desert or semi-desert areas from Turkey and the Middle East east through Transcaspia, southern Kazhakstan, northern China and across much of Mongolia to southern Siberia (Cramp and Simmons 1983, Delany et al. 2009, Wiersma et al. 2016a). While there is overlap in overall range with Lesser Sand Plover, it is segregated by altitude; Greater Sand Plover generally breeds in low alititude areas in contrast to the mountain steppe and tundra preferred by the Lesser Sand Plover. However, Greater Sand Plover has been recorded breeding up to 3,000 m (Wiersma et al. 2016a). Three subspecies are recognised across the breeding range. *C. l. columbinus* is the most westerly race, *C. l. scythicus* is found in western central Asia, and *C. l. leschenaultii* occurring furthest east and extending slightly farther north than *scythicus* (Fig. 5). Except for a small population of *columbinus* all three are entirely migratory spending the non-breeding season along the coastlines of the south-east Mediterranean, Middle East, East and southern Africa, Malagasy, India and commonly throughout South East Asia and Australasia (Cramp and Simmons 1983, Hayman et al. 1986, del Hoyo et al. 1996).

The Greater Sand Plover can be a common bird particularly on the non-breeding grounds in Australia and East Africa (Pearson 1984, Minton et al. 2013a). An intense programme of ringing and deployment of leg-flags and geolocators in Australia and elsewhere in the East-Asia–Australasia Flyway has led to a reasonable understanding of migration routes and given good indications of breeding areas (Minton et al. 2011). Such level of information is still lacking for the populations that reach the Middle East and Africa. Detailed analysis of museum specimens revealed general distributions of the races in the non-breeding grounds and in particular showed that the Greater Sand Plovers reaching East Africa are in fact the nominate race and not *scythicus* as was previously assumed (Hirschfield et al. 2000). However the migration routes and in particular the relationship between breeding and non-breeding grounds for many of the populations and in particular those migrating south-west to Africa remain almost unknown (Hirschfield et al. 2000, Delany et al. 2009, Wiersma et al. 2016a).

***C. l. columbinus* Wagler, 1829**—the smallest, weakest-billed and most westerly race breeding from Turkey, Syria, Jordan and south and east into Iran. Birds breeding in Azerbaijan and elsewhere in Transcaucasia are often considered to be this race (del Hoyo et al. 1996, Wiersma et al. 2016a) but detailed study of museum skins has suggested birds from here are in fact *scythicus* (Hirschfield et al. 2000, Delany et al. 2009). This is the least numerous of the races with a total estimate of <10,000 birds but in fact probably far few than this (Delany et al. 2009). Wetlands International has thus reviewed the estimate to a maximum of 5,000 (Wetlands International 2016). It migrates a short distance to spend the boreal winter along the coastline of the south-eastern Mediterranean Sea, the Red Sea and northern Persian Gulf (Hirschfield et al. 2000, Delany et al. 2009). There is one recovery of a ringed bird of this race which confirms the Red Sea non-breeding grounds; it was ringed 7 September 1981 near Suakin on the Red Sea coast of Sudan and killed on its nest in Syria on 3 April 1982 (Nikolaus and Backhurst 1982).

***C. l. scythicus* Carlos, Roselaar & Voisin, 2012**—previously known as the subspecies *crassirostris* (Carlos et al. 2012, Wiersma et al. 2016a), this race breeds across Transcaspia, south to Pakistan and east to southern Kazakhstan and possibly Tajikistan. It is normally in warm or hot, arid or semi-arid climates, nesting in open, generally level, uncultivated and treeless sites and often near water (Cramp and Simmons 1983, Hirschfield et al. 2000). Its non-breeding range overlaps strongly with that of *columbinus* as well as the northern non-breeding range of *leschenaultii* around the shores of the Red Sea, Persian Gulf, along the eastern seaboard of Arabia and the northern coastline of Somalia (Hirschfield et al. 2000, Delany et al. 2009). There is much uncertainty regarding the population size for this race because its range has been poorly covered by surveys of waterbirds. Earlier estimates for this race (Perennou et al. 1994) are now known to have included the nominate race which was not thought to visit Africa until Hirschfield et al. (2000) undertook a detailed study of museum skins. Delany et al. (2009) thus adopted the broad estimate proposed by Stroud et al. (2004) of 25,000–100,000.

A summary of published numbers of Greater Sand Plovers counted or estimated around the Middle East gives 5,000–10,000 birds along the Iranian coastline in the 1970s (Scott 2010) and 8,000 estimated along the Saudi Arabian gulf coastline ((Zwarts et al. 1991). Along the coast of the United Arab Emirates, a key feeding area for waders in the Arabian Gulf (Summers et al. 1987, Evans 1994), Greater Sand Plovers were described as ‘common’ in contrast to ‘very common’ for Lesser Sand Plover of which c. 1,200 birds were counted (Keijl et al. 1998). In January 2008, c. 5,000 were estimated to be present at Barr al Hikman (Klaassen and de Fouw 2008); simultaneous surveys along the remainder of the Omani coastline totalled 644 birds (Green and Harrison 2008). Altogether, therefore c. 26,000 birds are estimated for the Arabian Gulf and the eastern seaboard of the Arabian Peninsula. The Red Sea shores are possibly significant for the species with 10,000–25,000 estimated for the Sudanese shoreline (Summers et al. 1987), but these estimates need confirmation through further fieldwork. The total number of waders thought to use the Arabian Gulf is in the region of four million (Zwarts et al. 1991) and there are undoubtedly concentrations of Greater Sand Plovers which have not been found. Altogether, it would seem likely that a more realistic total population spending the boreal winter in the region 50,000–65,000 birds. This would include a large proportion of the race *columbinus*. Thus a more likely estimate for the race *scythicus* is in the range 45,000–60,000 birds.

***C. l. leschenaultii* Lesson, 1826** – is the eastern race with the largest breeding distribution stretching from Tajikistan, southern Kazakhstan east through the semi-arid steppes to arid north-western China and including almost the whole of Mongolia north into southern Siberia. Until Hirschfield et al. (2000) published a detailed analysis of museum skins, it was thought that all nominate birds migrated south-east to south east Asia and Australasia. It is now realised that a large number migrate south-west to the East African coast, and presumably it is the most westerly-breeding birds that do this (Hirschfield et al. 2000, Delany et al. 2009). An estimated 100,000 migrate south-east along the East Asian/Australasian Flyway to spend the non-breeding season along the shores of South-East Asia and Australia (del Hoyo et al. 1996, Hirschfield et al. 2000, Department of the Environment 2016). Of these, 75,000 are considered to reach Australia of which the majority (65,000) remain in the north-west with a small number reaching the south-eastern coast (Marchant and Higgins 1993, Minton and Chandler 1996, Minton et al. 2013a, Department of the Environment 2016, Wiersma et al. 2016a).

Those that migrate south-west spend the non-breeding season from southern Somalia south to South Africa and around the coast of Madagascar and associated islands (Summers et al. 1987, del Hoyo et al. 1996, Tree 1997, Hirschfield et al. 2000, Delany et al. 2009, Safford and Hawkins 2013, Wiersma et al. 2016a).

Summarising published counts and estimates, Pearson (1984) counted just over 2,600 birds at roost sites along most of the coast of Kenya south of Mombasa and estimated 6,000–12,000 for the coastline from the Sabaki River Mouth (c. 120 km north of Mombasa) to the Tanzanian border. Surveys of the same stretch of coastline south of Mombasa but including Vanga in 1995 counted 700 Greater Sand Plovers (Nasirwa et al. 1995). The same year counts along the coast from Sabaki north to near the Somali border produced 1,300 birds (Nasirwa unpubl. data). Seys et al. (1995) only counted c. 300 birds on the larger tidal inlets and creeks on the Kenyan coast. Annual January counts from Mida Creek to the Kensalt saltworks at Gongoni 40 km north of Malindi from 1999–2016 and on 50% of the Tana River Delta (2007–2016) gave a maximum of 1,550 birds in 2013 for all sites (pers. obs.). Monthly counts have been done at Mida Creek and Sabaki between 2010 and 2015; the highest single count was 1,300 at Mida Creek in November 2009. There are wetland areas north of Sabaki which have not yet been surveyed for waders; these might hold additional concentrations of birds. Assembling these data suggests that the total population for Kenya is less than Pearson's estimate of 12,000 (Pearson 1984). An estimate of 5,000–6,000 birds is more realistic for the Kenyan coastline.

Noted as 'very common' along the northern Tanzanian coast (Harvey 1974), the Greater Sand Plover appears to be more numerous in Tanzania than in Kenya. Five sites along the Tanzanian coastline have held more than 1,000 Greater Sand Plovers 1995; 4,201 were recorded during the extensive 1995 waterbird count prompting an estimate of 15,000 in total for Tanzania though with a caveat that the actual number may be substantially lower than this (Baker 1996, Baker and Baker 2016). Dodman (2002) suggested that there are likely to be 10,000 in Tanzania which is the estimate used by Delany et al. (2009) and is probably a more realistic figure. South of Tanzania numbers are small. Published figures for Mozambique have maximum numbers of 446 for Quirimbas National Park (Borghesio and Gagliardi 2011) and 200 for Inhaca, Maputo (Nilsson and Shubin 1998, Oschadleus and Lotz 2004) with other counts not exceeding 40 (G. Allport pers. comm.). However, ad hoc surveys of waders in Quirimbas National Park backed by ringing results suggested larger numbers of Greater Sand Plover in this area (Wilson 2009). Borghesio and Gagliardi (2011) suggested that their estimates from Quirimbas National Park were likely to be less than they ought to have been, due to the difficulty of distinguishing this species from the Lesser Sand Plover, a bias which has been confirmed by M. Wilson (pers. comm.). Furthermore, many suitable sites along the coast of Mozambique have not been surveyed and may reveal hitherto unknown concentrations of Greater Sand Plovers. A realistic estimate for population of Greater Sand Plovers spending the non-breeding season in Mozambique thus lies in the range 5,000–10,000 birds.

In South Africa the Greater Sand Plover is an uncommon species with maximum numbers found on the east coast (65 at Richard's Bay, KwaZulu-Natal) (Animal Demography Unit 2016a, 2016b). Tree (1997) estimated no more than 200 birds for South Africa; but numbers appear to have increased. For example, at the Zwartkops River Estuary, Eastern Cape, between 1992 and 1999 the maximum recorded was one bird; in 2000, 11 were recorded and the subsequent average has been 23 birds with a maximum of 47 in January 2005 (Animal Demography Unit 2016a). In contrast, there has been a decrease at the far south-western end of the range in the Western Cape. A more current total for South Africa would therefore lie in the region of 400–500 birds.

Delany et al. (2009) summarised population estimates for *C. l. leschenaultii* as being 10,000 in Somali and Kenya, 10,000 in Tanzania and about 10,000 for all other areas with an overall estimate of 25,000–50,000 birds. The discussion above narrows the estimate of the population range of the Greater Sand Plover to be in the interval 25,000–35,000.

Migration strategy

Almost all Greater Sand Plovers are migratory, the exception being a small population in southern Turkmenistan which are reported to be resident (Cramp and Simmons 1983). After breeding, adults form pre-migratory flocks that disperse locally, a movement which gradually turns into migration (Snow and Perrins 1998). Adults thus leave northern breeding grounds in late July and early August. With only a few inland records e.g. the south-east Caspian Sea coast in Iran (Delany et al. 2009), most are considered to migrate in a broad front making long flights without stopping to reach key stop-over sites on their non-breeding grounds (del Hoyo et al. 1996, Snow and Perrins 1998, Delany et al. 2009). Juveniles delay their migration arriving on non-breeding grounds two weeks to a month after the adults, as is common in a number of migrant birds (Pearson and Britton 1980, Cramp and Simmons 1983, Wiersma et al. 2016a). On the non-breeding grounds retrapping of ringed birds has shown a strong level of site fidelity for Greater Sand Plovers between years (Barter and Barter 1988, Balachandran 1998, Wiersma et al. 2016a). This same site fidelity has also been noted for Lesser Sand Plovers.

The race *columbinus* moves a short distance (700–1,200 km) south to the south-eastern shores of the Mediterranean Sea and Red Sea leaving their breeding grounds apparently earlier than other races in early July (Wiersma et al. 2016a). Some birds of this race move through the northern end of the Arabian Gulf in August–September en route to their non-breeding grounds but do not stopover. The race *scythicus* spends the boreal winter almost exclusively on the shores of the Persian Gulf, the northern and western shores of the Arabian Sea, the Red Sea and the Gulf of Aden with peak movements through the southern end of the Caspian Sea in the second half of August (Cramp and Simmons 1983, Hirschfield et al. 2000).

The first migrant Greater Sand Plovers appear in Pakistan and northern India in early August, some possibly being *scythicus* en route to Arabia but most probably being nominate birds from the western end of their breeding grounds in Kyrgyzstan and north-western China. It seems likely that birds breeding in the central area of the *leschenaultii* breeding range in central north China and the eastern part of Mongolia follow the Central Asia Flyway south to the eastern Indian coastline and the shores of the Bay of Bengal and from there south to Malaysia and Indonesia where they mix with more easterly breeding birds. Eastern nominate birds breeding in the eastern half of Mongolia and central China follow the East Asia/Australasia Flyway crossing over eastern and south-eastern China including Hong Kong, Vietnam, Philippines and Borneo from late July, through August and into early September (Cramp and Simmons 1983, Marchant and Higgins 1993, Minton et al. 2013b, Department of the Environment 2016). Data from geolocators attached to Greater Sand Plovers in north-western Australia revealed that on the southward migration from central Mongolia, birds will fly over 3,500 km to Taiwan or the southern Chinese coastline in a single flight. Others travel a more easterly route through the Philippines but of those that were tracked on the southward migration, all had only three or four 'legs' in the migration with either two or three stops between the breeding grounds and north-western Australia (Minton et al. 2013b). More studies, using both rings and geolocators are needed to unravel the patterns of migration of this race.

Greater Sand Plovers reach **south-eastern India** in early September in numbers of 'low hundreds' where ringing studies and counts have shown that most birds use the site as a staging location to complete moult before leaving for as yet unknown non-breeding grounds farther south (Balachandran 1998). Birds moult rapidly to complete by early October and then leave with the onset of the heavy monsoon rains. A small population of c. 30–60 birds remain during the boreal winter. There is a small peak of birds (c. 60–110 birds) in February taken to be passage birds passing through on the return northward migration at a time which matches for a peak in early March through Bangladesh 1,800 km to the north (Balachandran 1998, Islam 2006).

The main arrival in **Australia** is considered to be late July where it is one of the first migrant waders to arrive in the north-west (C.D.T. Minton pers. comm.) but in some years birds appear to delay arrival until August and even early September (Minton et al. 2013b). The lack of records from inland Australia suggests the small number which move south follow the coastline rather than fly overland (Department of the Environment 2016). The first juveniles arrive in north-western Australia at the end of August with a greater influx in September (Minton 1982, Department of the Environment 2016).

Movement north starts earlier than in Lesser Sand Plovers, beginning as early as February for adults in Australia and south-east Asia (Cramp and Simmons 1983, del Hoyo et al. 1996, Wiersma et al. 2016a). Southern Australian coasts are usually vacated by March with influxes of birds farther north e.g. Queensland recorded in late March (Department of the Environment 2016). Departure from the key Australian non-breeding grounds in the north-west occurs mainly in the first two weeks of April and earlier, by the end of March, from Queensland such that by mid-April c. 80% have left (Barter and Barter 1988, Marchant and Higgins 1993, Minton et al. 2013b). Adults pass through Indonesia between February and June and through the Malay Peninsula from early March to mid-April. In China passage occurs in April and May and arrival on breeding grounds is not until early or mid-May in the east whilst western races and populations may be back and breeding in mid-March (Cramp and Simmons 1983, Minton et al. 2011, 2013b, Department of the Environment 2016).

Little information has been published on timing or route followed of the southward migration of the races *columbinus*, *scythicus* and the western populations of *leschenaultii* through the Middle East into Africa. The former two races do not have large distances to cover between breeding and non-breeding grounds. It is likely that they fly overland from the breeding grounds to reach the coastline of the Arabian Gulf from where it is probable that those spending the non-breeding season on the Red Sea cross the Arabian Peninsula; if they are in Pakistan or the north-east shores of the Arabian Sea, it is likely that they follow the coastline of Oman south to the Gulf of Aden. Westerly breeding birds of the race *columbinus* seem likely to follow the eastern coastline of the Mediterranean Sea south to their non-breeding grounds.

Arrival in **East Africa** of *leschenaultii* has been suggested as being early compared with other migrant wader species with a build-up during July and August (Fogden 1963, Harvey 1974, Pearson and Britton 1980). The pentade counts over two years at Mida Creek supported this and revealed a clear increase in birds during late July and August suggesting an arrival in late July/early August (Fig. 6). A second wave of arrivals in October and November represents the arrival of the first year birds on the non-breeding grounds; the first juvenile was caught on 4 September with the majority arriving later in the month and almost twice as many arriving in October (73% of juveniles ringed in September were caught in the second half of the month, n = 23) (Fig. 7). These observations match those of (Pearson and Britton 1980) and Harvey (1974) in Kenya and northern Tanzania respectively. Numbers of non-breeding birds peaked between November and mid-January after which there appeared to be a gradual but constant departure through to April (Fig. 6).

The route followed to East Africa from the breeding grounds is thought to first occur as a broad front of birds with no marked concentrations—the only reported concentration being small numbers following the coast of the south-eastern Caspian Sea where Dementiev (Cramp and Simmons 1983) recorded 250–300 birds moving through in a five hour period. The likely hypothesis is that birds stop along the coast of the Persian Gulf, Gulf of Oman and along the coast of Pakistan to that of north-western India in order to refuel to cross the Arabian Peninsula and Arabian Sea in the reverse to what appears to be the route taken in the northward migration (Jackson 2016).

Birds migrate southward along the East African coast in flocks of 20–30 birds (pers. obs.) with passage birds recorded flying south along the coastline in August (Pearson and Britton 1980). On the return migration, a Greater Sand Plover ringed on 8 November 2004 and retrapped and flagged at the same location, Mida Creek, Kenya on 16 September 2013, was photographed on Modhava Beach near Mandvi, Gujarat, India (22°46'N 69°26'E) on 10 April 2015. The same bird, ring number Nairobi

Museum A70821, was photographed at the same location a year later on 29 March 2016 (Table 5). This confirms the use of the north-western Indian coast as a staging site for Greater Sand Plovers migrating north to breeding grounds in China or Mongolia. It is likely that birds follow the East African coastline to the horn of Africa from where they could either fly directly to the Indian coastline, a distance of c. 4,300 km from Kenya, or follow the Yemen and Oman coastlines before flying almost due east to India, a route that would add c. 500 km to the journey. An analysis of the departure mass of birds leaving Mida Creek and the possible distance birds could travel on these fat levels suggests that in fact the latter strategy is followed with a likely stop in Oman at Barr al Hikman, a major foraging site for large numbers of waders (Klaassen and de Fouw 2008, Jackson 2016). Further fieldwork is needed during periods of passage migration at Bar al Hikman to confirm the presence of East African birds on passage.

(Dowsett 1980) suggested that inland records are evidence that some Greater Sand Plovers migrate across inland Africa presumably to reach non-breeding grounds in the south-west. However, despite an increase in observers across Africa, there has been little further evidence to support this theory. In South Africa, the distribution of Greater Sand Plover appears to have shifted since the first Southern African Bird Atlas Project, when it was reported as annual in small numbers at Langebaan in the Western Cape (Tree 1997). Since the South African Bird Atlas Project 2 was started in 2007 there has yet to be a record anywhere on the west coast north of Cape Town (Animal Demography Unit 2016b), yet waterbird survey data farther east from the Eastern Cape and KwaZulu-Natal suggests an increase in numbers. The reason for this possible shift is unknown.

Preferred habitat

On non-breeding grounds Greater Sand Plovers are found mostly on coastal mudflats, sandy beaches, tidal creeks in mangrove forest, fresh or brackish water lakes near the sea. Preferential habitat is mixed mud and sand (Cramp and Simmons 1983, Safford and Hawkins 2013) as found at Mida Creek where large numbers occur (Seys et al. 1995).

Concluding remarks

Lesser Sand Plovers appear very similar to Greater Sand Plovers particularly in non-breeding plumage which has led to confusion in reporting them and therefore challenges in understanding their specific distribution and status (Hirschfield et al. 2000, Borghesio and Gagliardi 2011). The breeding range for Lesser Sand Plovers extends considerably farther north (Fig. 1) than that of Greater Sand Plovers (Fig. 5). This more northerly distribution is echoed in the non-breeding season both in the East Asian–Australasian Flyway where the majority of Greater Sand Plovers reach Australia (Bamford et al. 2008) and for those birds migrating to Africa where Lesser Sand Plovers are more numerous than Greater Sand Plovers in Arabia and are in the minority in Mozambique and farther south (Oschadleus and Lotz 2004, Klaassen and de Fouw 2008). Lesser Sand Plovers, which overlap in general breeding distribution with Greater Sand Plovers, are mostly separated by altitude, breeding at much higher and therefore colder altitudes than Greater Sand Plovers (Delany et al. 2009). The Greater Sand Plovers breeding farther south and at lower altitudes thus experience warmer conditions sooner than Lesser Sand Plovers and as a result have an earlier breeding season. This in turn means Greater Sand Plovers both arrive from and depart for their breeding grounds earlier than their smaller congeners (Delany et al. 2009, Newton 2010).

While much has been learnt about the populations and movements of both species in the East Asian–Australasian Flyway (Bamford et al. 2008, Minton et al. 2011, Choi et al. 2016), large gaps remain in our knowledge and understanding for those populations using the West Asia–East Africa flyway. Results from this study have confirmed the importance of the coastline of Pakistan and north-western India as a staging post for both species on migration and suggested that Bar al Hikman in Oman is likely to be a similarly critical passage site. An acute lack of wader population estimates from much of this flyway means population trends are more or less unknown (Delany et al. 2009, BirdLife International 2012). Recent substantially larger counts of Lesser Sand Plovers in Oman than had ever previously been recorded (J. de Fouw pers. comm.) have highlighted this resulting in questions as to whether these are a result of a shift in a population due to possibly human-related activity or whether counting method and identification skills of observers have simply improved from previous estimates. One hypothesis is that climate change has had a positive impact on the breeding success of Lesser Sand Plovers such that the population has increased dramatically. Further, more detailed research is needed to investigate this. In Kenya estimates of wader numbers were made in the early 1980s (Pearson 1984) and annual counts have been carried out at some sites since 1999. These suggest that numbers of both species in Kenya appear not to have remained relatively stable (pers. obs.). Data from the southern limits of their range in South Africa suggests a similar trend (Animal Demography Unit 2016a).

In contrast, for the East Asian–Australasian Flyway declines of up to 84% in Lesser Sand Plovers in Australia have been recorded (BirdLife Australia 2016) and Greater Sand Plovers have shown a ‘significant decline’ in key sites such as Moreton Bay, Queensland (Wilson et al. 2011). As a result, Lesser Sand Plover has been nominated for listing as regionally Endangered (BirdLife Australia 2016). The declines in the eastern flyway are attributed to destruction of foraging habitat at key stop-over and non-breeding sites for waders (Bamford and Watkins 2005, Rogers et al. 2006).

A concerted and well-coordinated effort is now being made by conservationists in the East Asian-Australasian Flyway to halt the decline in many of the wader species (Gosbell and Clemens 2006, BirdLife Australia 2016). As well as widespread counts of waders, the use of technology such as light level geolocators and satellite transmitters to track birds migration routes in this flyway has made substantial contributions to a better understanding of their movements and needs (Davidson and Gill 2008, Minton et al. 2013b). A similar approach is recommended for addressing the lack of information in the Middle East and Africa.

Greater Sand Plover Ring no. A70821 ringed on Mida Creek, photographed here on Modhava Beach, NW India

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Tables and figures

Table 1. Number of Lesser Sand Plovers retrapped in subsequent seasons after initial capture at Mida Creek, Kenya. '2Y' birds are those ringed as first years and retrapped in their second year—which therefore would not have left Mida Creek between captures.

Seasons after first capture:	0	1	2	3	4	5	6	7	8	9	10	2Y	Total
No. of retraps:	31	39	18	10	5	3	4	10	4	0	1	9	134

Table 2. Number of Greater Sand Plovers retrapped in subsequent seasons after initial capture at Mida Creek, Kenya. '2Y' birds are those ringed as first years and retrapped in their second year—which therefore would not have left Mida Creek between captures.

Seasons after first capture:	0	1	2	3	4	5	6	7	8	9	10	13	15	2Y	Total
No. of retraps:	25	16	17	4	5	4	4	1	3	1	1	2	1	16	100

Table 3. Histories of retrapped Lesser Sand Plovers ringed initially in the period August–October and retrapped later in the non-breeding season at Mida Creek, Kenya indicating at least some birds arriving in this period remain at Mida Creek and do not move on farther south.

		Ringed			Retrapped						
Ring #	Age	Aug	Sept	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Year
A55092	Ad	15				15					+1
A55093	Ad	15			26						0
A25687	Ad	22					2				0
A25688	Ad	22			26						+2
A56958	Ad		11		13						+1
A70765	Ad		25			13					+6
K19236	Ad		25							1	+7
A69263	Ad			3		15			27		0
A69270	Ad			3						26	0
A69284	Ad			3						1	+1
A69297	Ad			3				16			+1
A71632	Ad			27					28		+3
F00294	Ad			31				19			0

Table 4. All known recoveries of ringed Lesser Sand Plovers and Greater Sand Plovers involving eastern Africa to date.

Species	Ring No.	Ringed Date	Age	Location Ringed	Country ringed	Coordinates	Recovery Date	Recovery location	Country	Coordinates	Distance Km	Elapsed time Days	Elapsed time yy.mm.dd
Lesser Sand Plover	A43250	12/12/1982	Ad	Mida Creek	Kenya	03° 22S, 39° 58E	3/9/1985	Shadi Kor, Pasni, Baluchistan	Pakistan	25° 13'N, 63° 30'E	4,065	996	2y 8m 22d
	F00344	20/1/2013	Ad	Mida Creek	Kenya	03° 22S, 39° 58E	22/5/2016	Modhava coast near Mandvi	India	22°46' 50"N 69°26' 35"E	4,318	1,218	3y 4m 1d
Greater Sand Plover	A42779	7/9/1981	Ad	10 km south of Suakin, Red Sea Coast	Sudan	19°01'N, 37°23'E	3/4/1982	Habara Steppe	Syria	35°40'N, 37°45'E	1,850	208	0y 6m 25d
	A70821	8/11/2004	Ad	Mida Creek	Kenya	03° 22'S, 39° 58'E	16/9/2013	Mida Creek	Kenya	03° 22'S, 39° 58'E	0	3,234	8y 10m 10d
	A70821	8/11/2004	Ad	Mida Creek	Kenya	03° 22'S, 39° 58'E	10/4/2015	Modhava coast near Mandvi	India	22°46' 50"N 69°26' 35"E	4,318	3,805	10y 5m 3d
	A70821	8/11/2004	Ad	Mida Creek	Kenya	03° 22'S, 39° 58'E	29/3/2016	Modhava coast near Mandvi	India	22°46' 50"N 69°26' 35"E	4,318	4,159	11y 4m 22d

Lesser Sand Plover tagged 'S6' on Mida Creek photographed here on Mandvi Beach, India, 22 May 2016

Fig. 1. Global breeding and non-breeding distribution (in part hypothetical) of Lesser Sand Plover *Charadrius mongolus*. Breeding distributions for each race are labelled. Non-breeding distributions by race from west to east are: *pamirensis* = light orange*; pamirensis* mixed with *atrifrons = brown; atrifrons/schaeferi* = dark orange; *schaeferi* = yellow; *atrifrons/schaeferi* = purple; *mongolus* = light blue; *mongolus/stegmanni* = dark blue; *stegmanni* = maroon. Based on Hirschfield et al. (2000) and Google Maps.

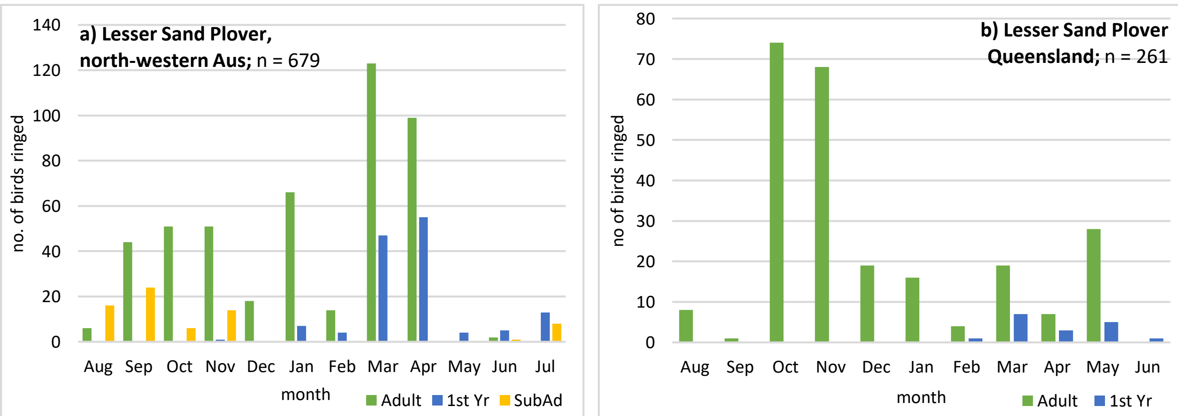

Fig. 2. Numbers by month of adult, sub-adult (where data available) and first year Lesser Sand Plovers ringed in a) north-western Australia between 1978 and 2014 and b) Queensland.

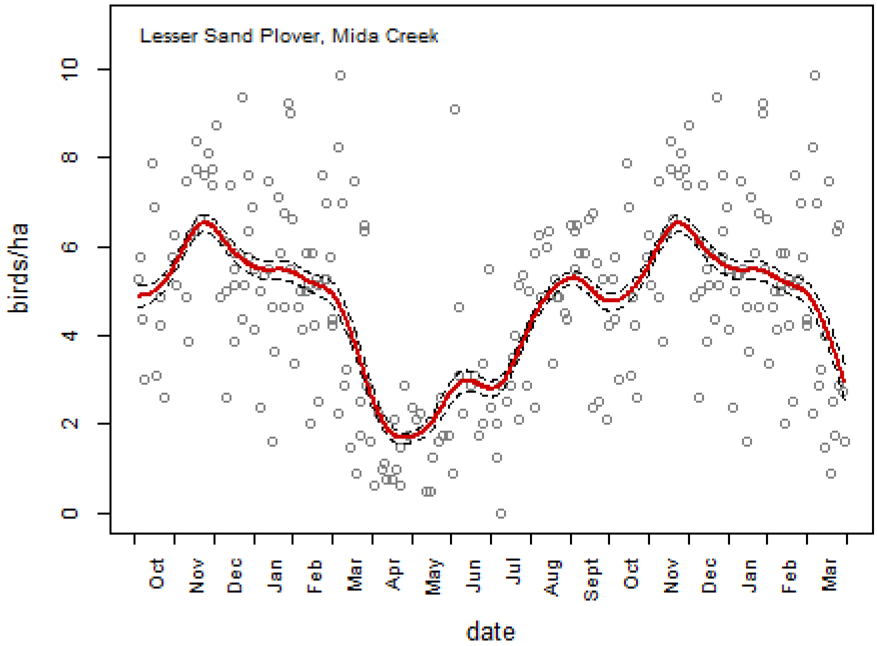

Fig. 3. Abundance of Lesser Sand Plovers (birds /ha) foraging over low tide on Mida Creek on an 800 m x 100 m transect counted once a pentade over two years. The line is fitted using the Underhill locally weighted linear regression smoothing function using a window of 20 days (see text). Given the warping of results at the limits from an edge effect, a buffer of three months data has been appended at the start and end of the year.

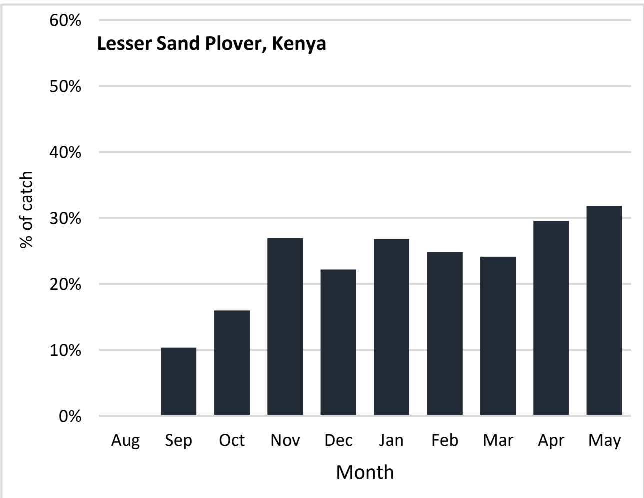

Fig. 4. Percent of catch which was juvenile for Lesser Sand Plovers in Kenya (totalled from all data over 35 years).

Fig. 5. Global breeding and non-breeding distribution (in part hypothetical) of Greater Sand Plover *Charadrius leschenaultii*. Breeding distributions for each race are labelled. Non-breeding distributions by race from west to east are: *columbinus* = green; *columbinus* mixed with *crassirostris* = light blue; *crassirostris* = dark blue; *crassirostris/leschenaultii* = orange; *leschenaultii* = purple; Based on Hirschfield et al. (2000), BirdLife International (2012) and Google Maps.

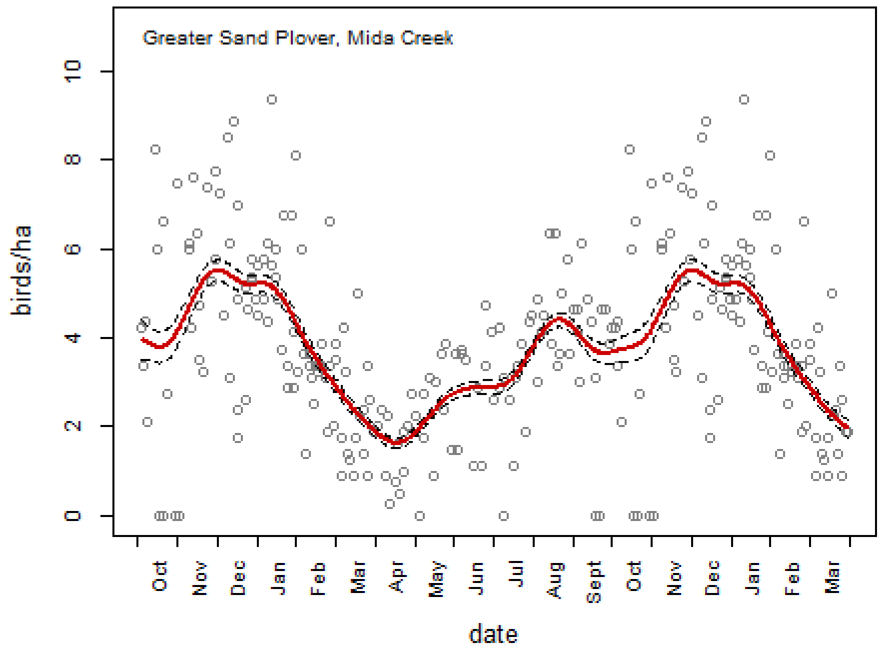

Fig. 6. Abundance of Greater Sand Plovers (birds /ha) foraging over low tide on Mida Creek on an 800 m x 100 m transect counted once a pentade over two years. The line is fitted using the Underhill locally weighted linear regression smoothing function using a window of 20 days (see text). Given the warping of results at the limits from an edge effect, a buffer of three months data has been appended at the start and end of the year.

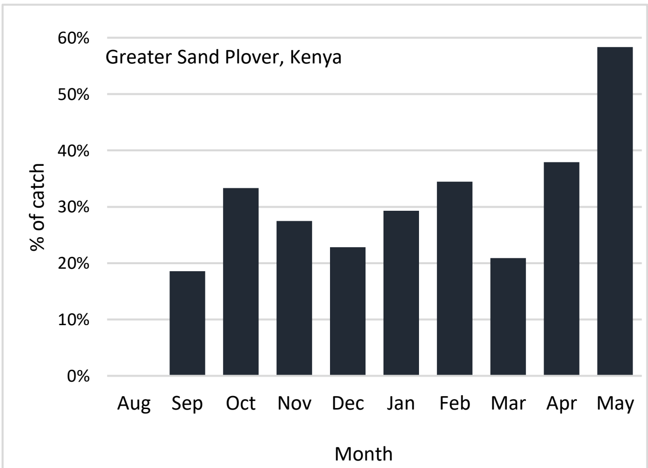

Fig. 7. Percent of catch which was juvenile for Greater Sand Plovers in Kenya (totalled for all data over 35 years).

Chapter 8

The status and migration of the Terek Sandpiper

Chapter 8. The status and migration of the Terek Sandpiper

Introduction

Many species of migrant wader are now well-studied and we have a reasonable to good understanding of at least the main breeding grounds, migration routes and non-breeding grounds used. Species such as Ruddy Turnstone *Arenaria interpres*, Grey Plover *Pluvialis squatarola*, Red Knot *Calidris canutus* and Dunlin *C. alpina* have been studied in this way along more than one flyway and for more than just one population (Branson and Minton 1976, Gromadzka 1989, Summers et al. 1989, Balachandran 1998, Serra et al. 1998, Pearson and Serra 2002).

The Terek Sandpiper *Xenus cinereus* is a common breeding wader across much of the northern Palearctic as well as being commonly encountered along the coastlines of its broad non-breeding range (Cramp and Simmons 1983, Hayman et al. 1986, del Hoyo et al. 1996) (Fig. 1 of Chapter 4). Some focused work has been carried out on one or two small breeding western populations (Karlionova et al. 2006) and the migration route and timing of the Australian non-breeding population is becoming better understood (Branson et al. 2010). However, for much of its breeding range and for the rest of its non-breeding range away from the East Asia/Australasian Flyway little is known regarding its populations, origins and migration strategies (Delany et al. 2009). This is particularly true for those birds visiting the East African coast. This chapter collates and summarises the known information regarding Terek Sandpiper populations and migration with a particular focus on the population found in Kenya.

Methods

In addition to assembling, from the literature, information and data about population sizes and migration patterns of Terek Sandpipers throughout their range, regular counts were done at Mida Creek, Kenya (3°19’S 39°57’E). Birds were counted along a single transect measuring 800 x 100 m in size (8 ha) once in every five-day period (pentade) for two years (June 2012 to May 2014) over a tide that was as close to a neap tide as possible and during the morning when tourist numbers (and thus disturbance) were least. The transect started where the sand flats meet the mangroves and ran out to the deep water channel in the middle of the creek thus covering a sample of all the ‘microhabitats’ exploited by the different species of wader from the drier shoreline along the trees to the wetter muddy sand area close to the deep water channel. The survey was conducted over the low tide by the same observer on foot using binoculars and a telescope. The 800m long transect was counted by following the eastern edge of the transect and stopping to count all birds up to a maximum distance of 150–200 m from the observer. All waterbirds present were identified to species and the number counted and recorded. Numbers were converted into birds/ha. Data were averaged for each week across the two years and plotted against date. A locally weighted linear regression smoothing function was applied to optimise the data output (Summers et al. 1985, 1992, Mullers et al. 2009).

Results and discussion

Taxonomy

Terek Sandpiper *Xenus cinereus* (Güldenstädt, 1775). First described from the Terek River near the Caspian Sea as the Terek Snipe *Scolopax cinerea* (Van Gils et al. 2016) in the woodcock genus, it was later recognised as being unique and placed in its own genus *Xenus* (Kaup 1829). It is now considered to be monotypic (del Hoyo et al. 1996, Delany et al. 2009) though the subspecies *Xenus cinereus javanicus* was described by Horsfield (1821) as being ‘very slightly paler’ than the nominate bird as well as slightly smaller but with an apparently “distinctly smaller, more slender bill”. A second subspecies, *Terekia cinerea australis*, was described by Mathews in 1917 (Longmore 2008), however lack of any good evidence for racial differences has led to both of these being discarded (Marchant and Higgins 1993, Lappo et al. 2012, Van Gils et al. 2016).

Distribution and populations

Terek Sandpipers breed across boreal zone of low-Arctic Eurasia, extending from a small western outlier population in Finland (24°00'E) eastwards across Russia to the base of the Chukotsky Peninsula (179°30'E) (Ferguson-Lees and Hosking 1959, Cramp and Simmons 1983, Delany et al. 2009, Golovatin et al. 2010) (Chapter 4, Fig. 1.) Lappo et al. (2012) considered a core breeding area as to be between 60°E and 90°E in an area west, of the Yenisey River valley, with indications that the valley forms a division between western and eastern populations. Golovatin et al. (2010) however suggest the highest densities of breeding Terek Sandpipers occurs in the northern and north-eastern parts of its breeding range. West of the Yenisey River, the most southerly breeding Terek Sandpipers occur at 50–55°N where the Belarus population has been shown not to be isolated from the western Russian birds as previously considered (Golovatin et al. 2010). To the east of the Yenisey River, breeding does not extend so far south (59-60°N) and in fact the vast area of southern Siberia previously thought to be part of the breeding range has been shown to probably not hold any pairs (Golovatin et al. 2010, Lappo et al. 2012). However recent records show that Terek Sandpipers breed farther north than previously thought with nests as far north as 72°N (Golovatin et al. 2010). The scant data available from the breeding grounds indicate that Terek Sandpipers are most common in the mid- to northern taiga and forest-tundra between 60–68°N where they prefer larger river valleys running through mixed woodland or coniferous forest. In the west these tend to be with mud or clay banks whilst the eastern end of its range the species is found on faster-flowing rivers with sand or gravel substrate (Cramp and Simmons 1983, Rogacheva 1992, del Hoyo et al. 1996, Lappo et al. 2012).

Eastern breeding birds migrate south and south-east to spend the non-breeding season from southern Asia and Indonesia south to northern and western Australia with a “hundred” estimated to reach south-eastern Australia (Cramp and Simmons 1983, Fry 1990, del Hoyo et al. 1996, Atlas of Living Australia 2016). The more westerly breeding population migrates south-west to spend the boreal winter in the Middle East and East African coast as far south as South Africa (Waltner and Sinclair 1981, Cramp and Simmons 1983, Hirschfeld et al. 1996, Delany et al. 2009). The far western-breeding birds in the isolated Finnish population have been shown to have at least some connectivity with eastern Africa with a recovery of Mida Creek-ringed bird breeding in Finland. However, the majority of recoveries from the Finnish population suggest a more south-westerly movement with a possible destination being western Africa, though real evidence of this has yet to be shown.

Population estimates

Due to poor coverage of breeding birds, estimates for the global population range widely from 160,000 birds (Wetlands International 2016) or 187,000 (Department of the Environment 2016, Van Gils et al. 2016) to 1,200,000 individuals (BirdLife International 2016). The breeding population has been estimated across Eurasia to be in the interval 45,000–240,000 birds by BirdLife International (2004) and to be 670,000 birds by Thorup (2006) for the European population. Due to the large variation, Delany et al. (2009) took a broad range estimate of 100,000–1,000,000 pairs for Europe and thus a global population of up to 1,200,000 individuals (BirdLife International 2016).

However, combining all published counts and estimates of non-breeding populations suggests a substantially smaller total than this. For the West Asia/Africa Flyway estimates for the south Iran coast range from 2,000–3,000 (Scott 2010) to 7,900 (Amini and van Roomen 2009) but for the rest of the Middle East relatively few birds are found during the non-breeding season: in United Arab Emirates Terek Sandpipers are considered 'fairly common'—though this was for birds on passage, not wintering (Keijl et al. 1998); in Oman, 1,000 were estimated in January 2008 at Barr al Hikman with a further 13 counted for the entire Oman coastline that same month (Green and Harrison 2008, Klaassen and de Fouw 2008); on the Sudanese Red Sea coast Terek Sandpipers do not stay for the non-breeding season but only occurs on passage (Summers et al. 1987). On the north-western coast of Somalia around the Gulf of Aden, it is considered to 'overwinter singly along the whole coast' (Ash and Miskell 2013) which suggests low densities of birds. From a survey total of 504 in Somalia 84% were in the south of the country and 28% of all birds were recorded in April with 'only a few in December-January'. As flocks are commonly seen actively migrating along the coast it is thus likely that it is predominantly a passage migrant and not a non-breeding visitor (Ash and Miskell 2013). Altogether, therefore, the non-breeding population of Terek Sandpipers in the Middle East is unlikely to exceed 10,000 and at most 15,000.

In Africa south of Somalia counts along the northern coast of Kenya suggest a higher density among the mangrove fringed creeks and channels north of Lamu with single counts of e.g. up to 1,348 in Wange Creek and a total of 3,220 between Tana River and the Somali border (O. Nasirwa unpubl. data). This being an actual count of only a portion of the available habitat, many more birds would have been missed. A reasonable estimate for the northern coastline probably lies in the region of 5,000–6,000 birds. South of the Tana River the largest population is at Mida Creek with 150–300 birds counted most years but with individual counts of 800 to 1,100 birds on occasion (pers. obs.). Pearson (1984) estimated a total population for the southern half of the Kenya coast as 1,000–2,000 Terek Sandpipers. An estimate for the Terek Sandpiper population for whole of Kenya is therefore 6,000–8,000 birds.

Tanzania is considered to be important non-breeding grounds for Terek Sandpipers with an estimated non-breeding population of 10,000–15,000 birds with a concentration along the northern coastline (Baker and Baker 2016). Mozambique has had few surveys of waders and little is known ornithologically about the 1,300 km of coastline from the Tanzanian border south to Beira. Borghesio and Gagliardi (2011) recorded 416 in their December 2009 surveys of Quirimbas National Park however in January 2009, Wilson (2009) found at least two roosts of 5,000–10,000 waders in the same area which consisted of 'mostly Greater Sand Plovers, Curlew Sandpipers and Terek Sandpipers'. Furthermore 107 waders were ringed of which 58 (52%) were Terek Sandpipers suggesting it is relatively common in that area. Sinclair counted 3,200 at Inhaca Island (Waltner and

Sinclair 1981) though other counts since then have been in the region of 300–500 birds (Oschadleus and Lotz 2004) with an overall estimate of 2,000 birds reaching southern Mozambique for the non-breeding season (Delany et al. 2009). All together it is reasonable to estimate a non-breeding population of 10,000–12,000 for Mozambique. Underhill (1997) estimated 1,000 Terek Sandpipers spend the non-breeding season in South Africa, however there have been fewer recorded in South Africa since 2007 (Animal Demography Unit 2016) with indications of a decline with a more likely population now at 500–600 birds.

In south-western and south-central Asia, the impression is of relatively small numbers with the majority of the population for where these birds originate considered to fly south-west to spend the boreal winter in East Africa (Perennou et al. 1994). Of those wintering in south central Asia, greater numbers appear to occur farther east in India and south to Malaysia suggesting lower densities in Pakistan (Cramp and Simmons 1983). Estimates given by Stroud et al. (2004) based on non-breeding season counts in south-western Asia and Africa came to 15,800.

While this is certainly an underestimate, summing the estimates per country listed above gives a range of 25,000–55,000 birds. This is substantially less than the 100,000–1,000,000 estimate used by Delany et al. (2009) and Wetlands International (2016), but fits the previously estimated 44,000 taken by Perennou et al. (1994) and del Hoyo et al. (1996) for the West Asia/East Africa Flyway population and would appear to be a more realistic figure.

For Terek Sandpipers migrating into south east Asia and Australasia, a comprehensive assessment has been made and the population estimated at 60,000 of which 23,000 are estimated to reach Australia with 25,000 in Malaysia and Indonesia combined (Bamford et al. 2008). Given these overall estimates, it would strongly suggest that the actual global population is nearer the lower end of the estimates made on the breeding grounds and a realistic global population figure may be rather 115,000–200,000 birds.

Migration strategy and routes

The entire breeding population of Terek Sandpipers leave their breeding grounds at the end of the boreal summer and migrate south into Africa, southern Asia and Australasia (Vandewalle 1988, del Hoyo et al. 1996, Delany et al. 2009). Those populations that breed in the western part of the Russian breeding range migrate south merging along the coastline of north-western India, Pakistan and the Middle East before moving southwards to spread out along the eastern African coast (Pearson 1984, Summers et al. 1987, Hirschfeld et al. 1996, Hockey et al. 2005, Delany et al. 2009). A small number reach Madagascar and Reunion (Safford and Hawkins 2013). The tiny isolated population in the far west of Finland appears to move both south-east and south-west (Pakanen 2016). The easterly breeding populations migrate south and east into south-eastern Asia and

Australasia with many using the Yellow Sea, the east coast of mainland China and Taiwan as a staging area (Branson et al. 2010). However, the watershed between the westerly and easterly-migrating populations is unclear (Delany et al. 2009).

Most Terek Sandpipers using the East Asia/Australasia Flyway to reach north-western Australia employ a two-stop migration strategy on the southward flight, stopping on the shores of the Yellow Sea and again on the east coast of China or in Taiwan. Evidence from ringing recoveries suggests that the same route is used for both southward and northward migrations and whilst the number of recoveries for the northward leg is limited, there is nothing to say birds do not also employ the same two-stop strategy as the southward leg. Birds spending the non-breeding season in eastern Australia clearly mix with those reaching north-western Australia at many Asian stopover sites though it also appears that a higher number of them take a more easterly route through Japan—these presumably being birds headed for the most eastern breeding grounds in Chukotka, Russia (Branson et al. 2010).

Adults leave the breeding grounds gradually and unnoticeably from the first half of July with females preceding males (Rogacheva 1992, Marchant and Higgins 1993). Juveniles follow the adults a month later in August. Departure of birds from the natal area in Russia can continue up to early September (Rogacheva 1992, Marchant and Higgins 1993). The route from central Siberia is not known and it would appear that a different route is used for the southward and northward migrations, it being a common migrant near Krasnoyarsk in the boreal autumn but absent in the spring (Rogacheva 1992). This could, however be a result of birds overflying in the spring in their push to reach breeding grounds more quickly. Farther east, migration through the Yellow Sea occurs during July and August, through Hong Kong in late July to mid-August (Choi et al. 2016), and along the east coast of China and through Taiwan from mid-August to October. Through central Asia and into India, the first Terek Sandpipers reach south-eastern India in August but with the main arrival in September. Numbers then drop off rapidly through October and by November relatively few are left in India suggesting this is mostly a passage stopover site than a major non-breeding ground (Balachandran 1990).

Arrival and passage through south-eastern Asia and Wallacea, where it is considered mainly transient, starts in mid-August and continues to November with earliest birds reaching Papua New Guinea in mid-September (White 1975, Marchant and Higgins 1993). Terek Sandpipers reach Torres Strait, Cairns, Queensland, and Northern Territory in August and arrive in north-western Australia towards the end of August and in the first week of September. They move down the east coast of Australia reaching New South Wales in October and arrive in Victoria in November (Marchant and Higgins 1993, BirdLife Australia 2016).

The main departure of Terek Sandpipers from Australia is in mid-April though some birds leave substantially earlier as shown by a recovery of a bird ringed in north-western Australia on 1 April in southern China (Branson et al. 2010). Birds spending the non-breeding season in south-eastern Australia appear to delay longer in their departure with some still present in Victoria in early May (Marchant and Higgins 1993). Adults migrate north for Siberian breeding grounds from stopover areas in Korea and northern China around mid-May and arrive in eastern Siberia during late May (Department of the Environment 2016). In northern central Siberia on Lake Keta at 69°N, Terek Sandpipers arrive in the first two weeks of June (Rogacheva 1992).

While the core breeding areas for Terek Sandpipers are more easterly and therefore birds from these populations migrate south into south-eastern Asia and Australasia, a substantial number from the western end of the Russian breeding range migrate into south-central Asia and Africa. These depart overland from early July stopover sites around the Persian Gulf and Middle East. A study on the breeding population in southern Belarus showed adults departing by the end of June and juveniles delaying until 17–20 July (Karlionova et al. 2006). An important route is considered to be between the Volga and Ural Rivers and through Transcaucasia and Ukraine, west of which Terek Sandpipers are rare visitors or vagrant (Cramp and Simmons 1983). Along the west Caspian Sea coast, Terek Sandpipers are common on passage and this coastline is thought to probably be the main stopover site for them in the region before reaching the Arabian Gulf. In contrast, on the east coast of the Caspian Sea, Terek Sandpipers are ‘extremely rare’ (Shubin 1998). A few reports have been published in Russian from this area on migrant numbers (Shubin 1998) but little exists in English. Around the Arabian Peninsula, some locations are known as important passage sites for waders such as Bahrain and other sites along the Iran coastline (Evans 1994), but there is a surprising lack of information regarding sites of importance for migrating waders in this flyway particularly for the southern migration (Summers et al. 1987). Barr al Hikman in Oman is one of the most important known sites (Klaassen and de Fouw 2008) where Terek Sandpipers are ‘very common’ on southward passage in September (Eriksen 1996). Otherwise it would appear that Terek Sandpipers mostly move through Arabia, rather than stay there, to spend the boreal winter south of the equator on islands in the west Indian Ocean and coastline of eastern and southern Africa (Cramp and Simmons 1983).

Small numbers of Terek Sandpipers spend the boreal winter along the north-western coast of Somalia. Higher numbers occur along the southern Somali coast towards Kenya. Large increases in numbers during September and April suggest, however, that the species is more of a passage migrant in Somalia than a non-breeder (Ash and Miskell 2013). Pearson and Britton (1980) gave the main arrival of adult Terek Sandpipers in Kenya as August to early September. Results of low tide counts at Mida Creek in every pentade over two years suggested, however, that the main arrival of adults starts earlier at the end of July through to the end of August (Fig. 1). There was also a small increase in numbers in June (Fig. 1) which are likely to be non-breeding sub-adult birds that wander to other local sites before returning to the main non-breeding grounds (Harvey 1974). This is supported by five of the six Terek Sandpipers caught in August which were aged as sub-adult, the earliest caught in the season; none were caught during June or July at Mida Creek due to poor weather conditions that do not allow for mist-netting during this period. First year birds arrive in October as shown by the second clear increase in numbers at Mida Creek (Fig. 1) and from ringing data (Pearson and Britton 1980). The main arrival in Tanzania, a stretch of the eastern African coastline considered to be of major importance for this species (Baker 1996), is in late September through to early November (Harvey 1974). Arrival farther south in South Africa occurs at the same time of September to November (Hockey et al. 2005) though the small population reaching Namibia arrives later in December and, from a band of sightings across central Namibia, through Zambia, inland Tanzania and Kenya to Ethiopia, are therefore considered to be birds that follow an overland route across the continent from eastern Africa (Dowsett 1980, Hockey et al. 2005). The recovery of a South African ringed Terek Sandpiper on Lake Koka (8°22'N 39°04'E), Ethiopia, on 21 April 1976 (Table 2) further supports this overland migration theory. This is in contrast to what has otherwise been suggested that these birds originate from western Europe (the Finnish population) and migrate down the west coast of Africa (Waltner and Sinclair 1981, Hockey et al. 2005). However, given the increase in observers in East Africa and elsewhere over the past 20 years and yet the few inland records of Terek Sandpipers, it is unlikely to be a major migration route. It is quite possible that small numbers follow both the West African coastline route and others the overland route through eastern Africa.

The main departure from southern Africa to the breeding grounds begins in March though some adults will remain until May (Cramp and Simmons 1983, Harrison et al. 1997, Hockey et al. 2005). Return passage through Dar es Salaam, Tanzania, is given as most apparent in late March and April (Harvey 1974) while Pearson and Britton (1980) suggested that the main adult departure from Kenya occurs in late April. However, the detailed counts at Mida Creek showed that numbers start to decline substantially earlier than this, as early as the beginning of December, and continue to decline steadily through to the start of April with an indication of an increase in departure in early February (Fig. 1). Passage through the Arabian Gulf is thought to occur in early May (median departure date from Khor Dubai, United Arad Emirates, is c. 3 May (Keijl et al. 1998)) though first arrivals in southern Belarus are 10–26 April with a median laying date of first egg of 30 April (Karlionova et al. 2006) suggesting that these birds are unlikely to be those leaving Khor Dubai. There is a wide range of departure date from non-breeding grounds and it is likely that the Belarus population, being farther south than most others and thus able to start breeding earlier than those in the colder north, would be among earlier birds leaving non-breeding grounds. Birds nesting in the northern limits of the breeding range where climatic conditions are not conducive for breeding until quite a lot later would likely delay in leaving non-breeding grounds and staging sites until April and May. More recoveries of birds on the breeding grounds are needed to confirm this. As noted in Kenya, some birds appear to leave much earlier than previously thought (Fig. 1) and, given that Belarus is more or less along the route probably taken by birds that we know from recoveries go to Finland (Pakanen 2016), it is not unreasonable to suggest in the light of any direct recoveries, that southern Belarus birds spend the non-breeding season on the eastern Africa coast. A Terek Sandpiper ringed during the non-breeding season at Langebaan Lagoon, South Africa, and recovered in Komi, Russia (65°02'N 51°58'E) on 15 June is evidence of the breeding grounds for some birds reaching the farthest south in Africa.

The isolated most western breeding population of Terek Sandpipers at the northern end of the Gulf of Bothnia in Finland was thought to migrate across central and eastern Europe, the Mediterranean Sea and Sahara desert in one flight to reach west African non-breeding grounds (del Hoyo et al. 1996, Van Gils et al. 2016). The paucity of records along the north African coastline together with rare though regular records from desert pools in central Chad led to this conclusion (Cramp and Simmons 1983). Recent analyses of ring recoveries from Finnish-ringed birds, however, suggests that in fact Finnish birds do not follow a species-specific migration route but spread out between a western and an eastern route (Pakanen 2016). Strong evidence through multiple sightings of ringed birds along the northern coast of western Europe supports the use of a western route including a resighting in southern France of the same bird in two consecutive years. However, a likely bias is recognised for this route as a result of a higher density of observers; Terek Sandpipers are relatively uncommon and are therefore specifically picked out of a flock of waders. In comparison, there are few observers at sites along the eastern route. Evidence of the eastern route for Finnish birds is provided by a recovery of a Terek Sandpiper ringed in November in Kenya and found breeding in Finland five years later (Pakanen 2016). The non-breeding destination of western-migrating birds is unknown but it is likely that they are thinly spread out around the northern, western and central coast of Africa. The occurrence of four boreal autumn records from Lake Chad (Cramp and Simmons 1983) suggests that some carry out a trans-Sahara flight on southward migration, and probably reach the Nigerian coastline. The numbers of birds involved in this movement to western Africa, however, are small and difficult to detect. Satellite tracking should help reveal the whereabouts of the non-breeding grounds of westerly-migrating Finnish birds.

Many Terek Sandpipers have been retrapped at the same location in subsequent years in both Kenya and Australia and there are few between-site movements recorded in Australia suggesting Terek Sandpipers are highly site-faithful to their non-breeding grounds (Branson et al. 2010) (Table 1). From 2011 to 2015 277 Terek Sandpipers were ringed with white colour-flags at Mida Creek of which to date one has been sighted away from the ringing site, on the Gongoni salt works 44 km to the north of Mida Creek on 27 January 2013. This suggests there is some exchange between feeding sites on the non-breeding grounds. The flag number was not seen so it is not known if it was ringed as a first year and was thus a 'wanderer', or if adults use different sites during the non-breeding season. Further fieldwork is required to conduct thorough searches for colour-flagged birds at other local sites to fully understand what local movements are undertaken.

Conclusion

Population estimates for Terek Sandpipers from the eastern part of the breeding range migrating south and east into south-east Asia and Australasia are considered relatively robust (Bamford et al. 2008, Wetlands International 2016) and the migration route is beginning to be better understood (Branson et al. 2010). In contrast, birds migrating into south-central Asia and Africa are not well-understood and many gaps remain in our knowledge of their populations, migration routes and strategies. Current population estimates for these latter birds of 160,000–1,200,000 birds (BirdLife International 2012) or 100,000–1,150,000 (Wetlands International 2016) are both vague and un-useful. Conservation protocol for recognising any wetland site as important for a species' conservation is that the upper limit of any population estimate is used to calculate the population threshold above which the site is considered important for that species. This means that for Terek Sandpipers in Africa and western Eurasia, the 1% population threshold for a site is set at 10,000 individuals (Delany et al. 2009). No site has been found that comes near to this threshold and it is clear that this should be revised. The thorough search for count data of non-breeding Terek Sandpipers in the Middle East and Africa undertaken for this study suggests the population is in fact at the smaller end of current estimates: 115,000–200,000 birds. This puts the 1% population threshold at 2,000 for which it is more possible to identify sites that would qualify (e.g. 3,200 at Inhaca Island, Mozambique, in November 1976) (Waltner and Sinclair 1981).

The three long-distance recoveries of ringed Terek Sandpipers from the Africa and western Eurasia population give an indication of spatial connectivity within the species. Colour flagging of birds at the study site in Kenya has yet to add any further information to what was already known, however an increase in citizen involvement in watching for and photographing tagged birds is leading to additional contributions to our knowledge of migration routes for birds in this flyway e.g. sand plovers in India (Jackson 2016). Further fieldwork is needed to increase the number of colour-flagged Terek Sandpipers combined with publicity to increase awareness among the increasing number of birders along the flyway to watch out for and report marked birds.

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Appendices & figures

Table 1. Number of Terek Sandpipers retrapped in subsequent seasons after initial capture at Mida Creek, Kenya. '2Y' birds are those ringed as first years and retrapped in their second year—which therefore would not have left Mida Creek between captures.

Seasons after first capture:	**0**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**2Y**	**Total**
No of retraps:	10	15	20	11	6	8	6	5	3	2	2	1	1	1	5	96

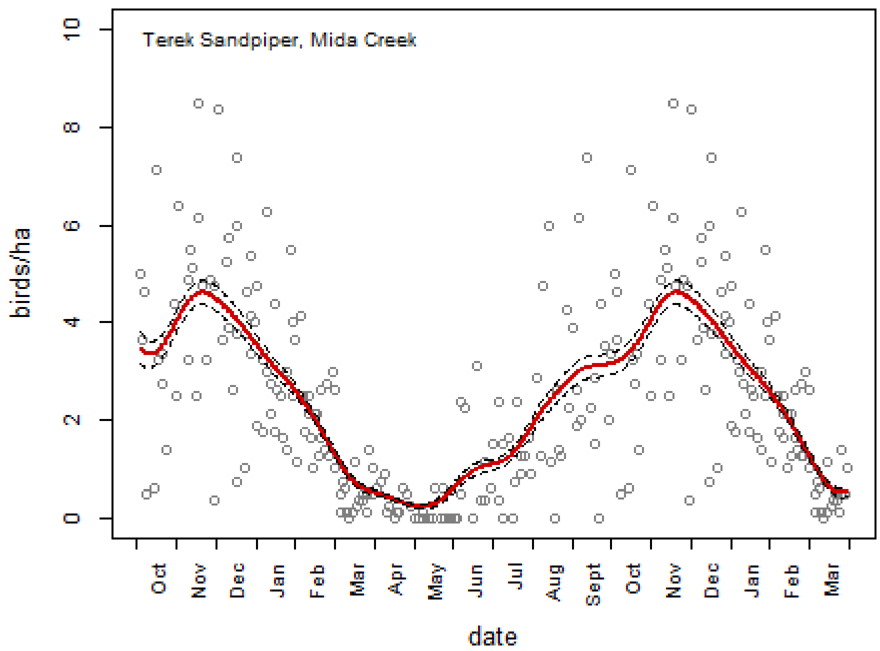

Fig. 1. Abundance of Terek Sandpipers (birds/ha) foraging over low tide on Mida Creek on an 800 m x 100 m transect counted once a pentade (five-day period) over two years. The line is fitted using the Underhill locally weighted linear regression smoothing function using a window of 20 days (see text). Given the warping of results at the limits from an edge effect, a buffer of three months data has been appended at the start and end of the year.

Table 2. Available ringing and recovery information for Terek Sandpipers on the West Asia/East Africa Flyway to 2016. 11 additional recoveries of birds ringed in Finland and recovered or sighted in Europe between 1967 and 2015 are given by Pakanen (2016).

Ring No.	Date	Age	Location Ringed	Country ringed	Coordinates	Date	Recovery location	Country	Coordinates	Distance Km	Elapsed time Days	yy.mm.dd
Moskwa 460860	21/7/1984	Full grown	Lake Sorbulak, Alma-Ata O.	Kazakhstan	43°46’N 76°05’E	1/6/1986	Verkhneketskiy district, Belyy Yar, Tomsk O,	Russia	57°32’N 88°46’E	1,767	680	1y 10m 11d
Moskwa 619009	18/7/1979	Full grown	Lake Sorbulak, Alma-Ata O.	Kazakhstan	43°46’N 76°05’E	21/9/1982	Point Calimere	India	10°18’N 79°51’E	3,712	1,161	3y 2m 5d
248356	25/2/1973	Ad	Langebaan	South Africa	33° 9'S 18° 4'E	21/4/1976	Lake Koka	Ethiopia	8°22'N 39°4'E	5,120	1,151	3y 1m 25d
59302686	11/12/1966	Full grown	Langebaan	South Africa	33° 9'S 18° 4'E	15/6/1967	Zamezhnoe, Komi	Russia	65°2'N 51°58'E	11,299	186	0y 6m 3d
A71968	20/11/2003	1 yr	Mida Creek	Kenya	3°19’S 39°57’E	21/6/2008	Kemi, Lappi	Finland	65°45'N 24°32'E	7,777	1,675	4y 7m 2d
JT11570	18/8/2007	1 yr	Southern Poland	Poland	50°42'N 18°10'E	20/8/2007	North-western Hungary	Hungary	47°40'"N 16°49'E	351	2	0y 0m 2d

Chapter 9

A comparison of primary moult strategies in migrant waders

Chapter 9. A comparison of primary moult strategies in migrant waders

Introduction

Moult is a critical component of a bird's annual cycle and especially so for long-distance migrants (Pearson 1974, Ginn and Melville 1983, Newton 2009). Within the order Charadrii, the waders or shorebirds, there is a large variety of migration strategies (Newton 2010), and the order includes many of the best studied long distance migrants (González et al. 1996, Holmgren et al. 2001, Atkinson et al. 2005). There are large data sets of moult data, for many species, accumulated over the decades, and collected according a protocol that has remained unaltered since it was devised in 1962 (Ashmole 1962). In an era of climate change, moult is therefore particularly interesting, largely because it can be quantified extremely well. There is a standard statistical approach to the analysis of moult data, the Underhill-Zucchini moult model (Underhill and Zucchini 1988, Underhill et al. 1990, Erni et al. 2013). Furthermore, it is difficult to both access the remote breeding locations of long-distance migrant waders to study breeding biology and to accurately and sufficiently monitor migration timing and numbers in order to study long-term changes in timing of these activities. These factors make moult the most amenable to study of the three key components of the annual cycle: breeding, migration and moult.

Remisiewicz (2011) and Dietz et al. (2015) both noted that there were sufficient results of moult estimates for migrant waders using the Underhill-Zucchini moult model (Underhill and Zucchini

1988) to start to undertake analyses of patterns. Remisiewicz (2011) described how wing length, geographical latitude and migration distance all affect moult strategies in waders. Dietz et al. (2015) demonstrate that while body mass does affect duration of moult for migrant waders, it is not a direct correlation as suggested by Rohwer et al. (2009). Rather, there is a play off between latitude of the moulting grounds and body mass with both having a strong impact on duration of moult though not in a simple relationship. While overall Dietz et al. (2015) showed an increase in duration with latitude, when they divided birds into 'northern' and 'southern' moulters they found that while a strong allometric relationship exists for birds moulting in the northern hemisphere, there was no such relationship south of the equator (Dietz et al. 2015). In their study, however, no note of *timing* of moult was considered, only duration. Furthermore, the sample size used was limited, in particular with regard to range of body size.

In this chapter I compare the results of moult analyses of 51 different populations of 21 different wader species, both between and within species and in relation to latitude and body mass. Results of moult analyses using the Underhill-Zucchini moult model (Underhill and Zucchini 1988) from published studies of moult for migrant waders are combined with results from this thesis and some as yet unpublished results (Remisiewicz, Sitters & Minton in. prep., M. Remisiewicz unpubl.).

Methods

Following the precedent set by Remisiewicz (2011) and Dietz et al. (2015), I assembled data on moult parameters estimated using the Underhill-Zucchini moult model (Underhill and Zucchini 1988). The estimated duration and start date of primary moult for migrant wader species Charadriidae were obtained from the two published studies (Remisiewicz 2011, Dietz et al. 2015) together with published results which these two papers had overlooked, unpublished results, and the results from this thesis (Table 1). Mean mass and wing length were taken either from the same published studies where given or from other published data for that species.

Instead of using only the estimated start date or the end date of moult for the multispecies analysis, I chose to use the date on which percentage feather mass grown (PFMG) reached 50%. This mid-date was selected as the measure for describing the timing of moult across species. The experience gained in the moult analyses undertaken for this thesis is that the start date and the end date were the quantities which varied the most with choice of approach to doing the analysis (i.e. the choice between per-feather analysis and a whole tract analysis) and with choice of data type to fit the model to the whole tract. In contrast, the mid-date of moult was relatively insensitive to these choices. This can be seen, for example, in Fig. 4 of Chapter 2, where the start dates and end dates clearly are sensitive to the choice of approach and data type, but all approaches gave similar results for the date at which PFMG reached the 50% level.

Intraspecific comparisons were carried out on moult duration and timing between different populations for five species where four or more populations have been studied to give a spread of results across a minimum range of 50° latitude: Grey Plover *Pluvialis squatarola*, Lesser Sand Plover *Charadrius mongolus*, Greater Sand Plover *C. leschenaultii*, Curlew Sandpiper *Calidris ferruginea* and Terek Sandpiper *Xenus cinereus*. 51 different populations involving 21 species were considered for the wider analysis of the relationship of latitude and body size on moult duration and timing in migrant waders. Quantile regressions were used to explore these relationships (Koenker and Bassett 1978, Cade and Noon 2003). For a biological application of quantile regression, see Lubbe et al. (2014).

Plots with latitude on one axis were laid out so that latitude (even though it was the explanatory variable) was placed on the Y-axis in order to facilitate understanding the concept of what is being shown. This is because it is easiest to conceptualise latitude as running north – south vertically rather than horizontally. The response variable was therefore plotted on the X-axis. The regression models, however, were calculated with the response variable (start date, 50% PFMG date, duration) depending on the explanatory variable (latitude). This non-standard strategy helps in visualising and interpretation of the results.

Results

Intraspecific variation with latitude

Timing of moult

The five species, Grey Plover, Lesser Sand Plover, Greater Sand Plover, Curlew Sandpiper and Terek Sandpiper, all showed a clear delay in the timing of moult, both start date and mid-moult date, with decreasing latitude (Figs. 1 and 2). In Grey Plovers, for every 10° of latitude farther south, moult was delayed on average by 7.24 days (SD = 0.74, $P < 0.001$). In Terek Sandpipers the delay was greater at 24.80 days per 10° (SD = 2.36, $P < 0.001$). In Lesser and Greater Sand Plovers and Curlew Sandpiper, the regressions were not formally significant, but $0.05<P<0.10$ (Table 2). Combining all the data points for the five species, the delay per 10° of latitude farther south is 10.51 days (SD = 1.96, $P < 0.001$). This pooled value should be treated with caution.

Grey Plover had the least variation in estimated start date and mid-date with change in latitude (34 days difference between India (9°N) on 1 September and south-eastern Australia (38°S) on 5 October) and Terek Sandpipers the most (117 days: 15 July in India and 9 November in south-eastern Australia). Most populations fitted the overarching trend of more southerly latitudes delaying later than those to the north, the main exception being populations of the two sand plover species and Curlew Sandpiper in Kenya (3°S). In these three there is a marked delay in moult past what might be expected putting the timing behind that of the more southerly population in north-western Australia (19°S) (Figs. 1 and 2).

Duration of moult

For Grey Plover, Lesser Sand Plover, Curlew Sandpiper and Terek Sandpiper duration generally increased with decreasing latitude (Fig. 3). In Grey Plovers, the far northern populations had a markedly shorter duration of moult than those in the tropics and farther south. These latter populations had a relatively similar duration of moult (121 days to 131 days) (Table 1). Three out of four Lesser Sand Plover populations also had little variation in duration of moult (152 days to 154 days), with only south-eastern Australia being different (168 days). In the latter population, the estimate for the start of moult had large standard deviation (45.7 days) thus it is likely the start was in fact later than estimated and therefore the duration shorter (Ch. 2). In Curlew Sandpiper, duration of moult was eight days different between locations south of the equator. The population in India had a shorter duration of moult at 105 days (Table 1). In Terek Sandpiper the population in Kenya was different to the other populations being shorter (99 days) compared to 121–134 days for the other latitudes. Greater Sand Plover showed the greatest differences in duration between latitudes. The Indian population was the only one to follow the overall trend of shorter duration for more northerly populations and then was shorter (80 days) than any other population examined here. In contrast to this, Greater Sand Plovers in Kenya take a longer time to moult (148 days) with the Australian populations farther south taking shorter to moult (Fig. 3).

Interspecific variation of moult with body size and latitude

We now consider results for the 51 population of 21 species (Table 1, Fig. 4). The quantile regression provides insights into the relationship between duration of moult (the response variable) and latitude (the explanatory variable) (Fig.4). Duration of primary moult is short for waders that moult at high northern latitudes (e.g. 48 and 51 days for Purple Sandpipers *Calidris maritima* in Norway and Iceland respectively; Fig. 4, Table 1). For birds moulting north of the Tropic of Cancer (23°26′ N) the variation in moult duration was relatively constant and small (c. 50–90 days) (Fig. 4). For populations spending the non-breeding season and moulting in the tropics, the variation in duration of moult increased substantially; the shortest values were 70 days for Long-toed Stints *Calidris subminuta* in Thailand and 80 days for Greater Sand Plover in south-east India, and the longest values were 140 days for Little Stint *C. minuta* in Kenya, 153 days for Lesser Sand Plover in south-east India and 148 days for Greater Sand Plovers in Kenya (Fig. 4, Table 1). Variation in the duration of moult was reduced for birds moulting farther south; in Australia and South Africa the extremes were 95 and 150 days. On average, moult duration is markedly longer than in the equivalent northern temperate zone (average for birds south of 18°S was 124 days, and for populations north of 18°N was 73 days) (Fig. 4).

Using the mid-moult or 50% PFMG date as an index of the timing of moult, moult in migrant waders showed a strongly significant trend of later moult with decreasing latitude. On average for every 10° farther south, moult is delayed by 10.21 days (SD = 0.11, $P < 0.001$) (Fig. 5), similar to the pooled value for the five species considered above.

The quantile regressions provide guidance to the relationship between duration of moult and body size (mass) (Fig. 6). The 50% quantile regression suggests that duration of moult generally increases with mass. The 90% quantile regression is horizontal, suggesting an upper limit of about 160 days irrespective of mass. The 10% quantile regression suggests that for birds with a body mass greater than c. 100 g, there is constraint on the shortest possible durations achievable (Fig. 6).

The northernmost wintering waders were Purple Sandpipers, with a body mass of 79–85 g, in Iceland and Norway (Table 1, Fig. 7). Species with heavier and lighter body masses appeared to winter farther south (Fig. 7).

Discussion

The overarching picture with regards to moult in adult migrant waders relative to latitude is that at high northern latitudes moult starts early (Fig. 5) and is kept short (Fig. 4), the most likely explanation being in order to complete prior to the arrival of harsh winter conditions (Underhill 2003, Dietz et al. 2015). At low latitudes, effectively within the tropics, conditions are generally good and while moult is delayed compared to farther north, birds can afford to have a large variation in duration depending on local conditions. Thus Long-toed Stints on freshwater pools in Thailand (13°N) moult rapidly towards the end of the wet season when food is most abundant while Greater Sand Plovers in Kenya (3°S) take their time to moult as conditions are good and constant and the sole constraint is to complete in time to fatten for migration in February/March. As birds migrate still farther south, however, the time available for them to moult is reduced. Moult is timed later than for those populations farther north (Fig. 5) because these populations take the longest time to reach their non-breeding grounds. They then have limited time to moult before they need to start fattening up and have to make an early start to northwards migration to cover the long distance to the breeding grounds. Thus, duration is constrained to be short even for the large birds (Figs. 4 and 6). On the other hand, because they have to cover the largest distances on a set of primary wing feathers, these feathers need to be of high quality to maintain efficiency of flight, which requires slow growth (Dawson et al. 2000, Serra 2001). Thus, the southernmost populations tend to utilize the entire period available to undertake primary moult.

In general, for many families of birds, as species size increases duration of moult also increases (Rohwer et al. 2009). Large birds need longer to breed (and therefore have less time between annual breeding events), take longer to grow their larger feathers than small birds (Rohwer et al. 2009) and have a greater wing load and thus must moult feathers more slowly so as to reduce inefficiencies in flight (Kjellén 1994). Members of several groups of large avian taxa such as the Anseriformes and Gaviidae get around this problem by dropping all flight feathers simultaneously (Kjellén 1994), thus becoming flightless. This strategy allows them to reduce moult duration to that of the longest feather. Large birds that do not follow this strategy have greatly extended primary moult and either may be forced to skip a year of breeding as in Black-footed Albatrosses *Phoebastria nigripes* (Edwards 2008, Rohwer et al. 2011) or be fully obligate biennial breeders as in many other albatross species (Edwards 2008) in order to fit in a complete moult, or take up to four years to complete one cycle of moult e.g. White-tailed Eagle *Haliaetus albicilla* (Edelstam 1984, Newton 2010). Some small species in other groups such as seabirds also have a long, drawn out moult as the result of, again, a long, extended breeding event e.g. British Storm Petrels *Hydrobates pelagicus* which have an adult moult of about seven months (Bolton and Thomas 2001). However, it would appear that in migrant waders there is an upper limit for the duration of moult at c. 160 days irrespective of the size of the bird (Fig. 6). Furthermore, small waders (mass of less than 100 g) are able to vary their duration extensively. As the size of the bird increases above 100 g, however, duration must be extended (Fig. 6). Therefore, given the constraints of harsh winters reducing time available for moult, large waders are forced to migrate south to reach sites where they are able to take longer to moult (Figs 4 & 7). Fig. 7 also suggests that the smallest waders do not winter in the far north, this being because as they are able to store disproportionally less fat than larger birds when needing to survive for longer periods of time without feeding, therefore make it energetically impossible to survive there. The sample of species in Table 1 suggests that the smallest waders winter south of about 30°N.

Primaries that are grown more slowly are of better quality and therefore last longer before becoming worn than rapidly grown feathers (Dawson et al. 2000, Serra 2001, De La Hera et al. 2009). It is therefore an advantage for a migrant bird to be able to take longer to grow its feathers. However, while actively moulting, birds experience other limitations that arise as a result of growing feathers, in particular loss of efficiency of flight (Chai 1997, Swaddle and Witter 1997) which can result in a higher risk of predation due to reduced escape flight performance (Kjellén 1994, Swaddle et al. 1996). Considering the 51 different populations of migrant wader in this study, it would appear that the majority take around 120 days (four months) to moult.

The novel synthesis insights from this chapter are encapsulated in Figs 4 and 6. The relationship between latitude and moult duration (Fig. 4) has constraints, imposed by environmental considerations, at the northern and the southern limits of non-breeding areas. But in the northern tropics and along the equator, moult duration can be (and is) flexible. Fig. 4 would be strengthened by having more data points between 50°N and 10°N, and also south of 35°S, which requires moult studies in southern South America and New Zealand. The relationship between body mass and moult duration (Fig. 6) shows that, although the shortest duration achievable is constrained by body mass, a duration of c. 120 days seems a gold standard. I suggest that, independent of the size of the bird, this duration enables high quality feathers to be grown, as suggested by Serra (2001), while minimising the time in active moult when risk of predation is increased. This is shown by the almost horizontal 50% quantile regression line (Fig. 6), and appears to apply to an observed range from 20 g to 900 g (Table 1). This result would be strengthened by the availability of more data points for birds with heavier body mass, especially body masses more than 500 g.

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Tables and figures

Table 1. Moult parameters, location, latitude, mean wing and mass of migrant wader populations. There are 51 sets of results for 21 species. Moult parameters were all estimated using the Underhill-Zucchini moult model (Underhill and Zucchini 1988).

Species	Location	Lat	Duration	Start Date	End Date	Mid Date	Wing	Mass	Source
Grey Plover	England	52	90	19 Aug	17 Nov	3 Oct	204.2	230	(1)
	Italy	45	93	18 Aug	19 Nov	3 Oct	204.2	230	(2)
	India	9	127	1 Sep	5 Jan	3 Nov	204.2	220	(3)
	n-w Aust.	-19	121	10 Sep	9 Jan	9 Nov	204.2	220	(4)
	Kenya (coast)	-3	130	13 Sep	19 Jan	17 Nov	204.2	220	(5)
	S. Africa	-33	131	30 Sep	8 Feb	4 Dec	204.2	220	(6)
	s-e Aust.	-38	128	5 Oct	9 Feb	8 Dec	204.2	220	(4)
Lesser Sand Plover	India	9	153	10 Aug	10 Jan	14 Oct	130.5	55.4	(27)
	n-w Aust.	-19	152	18 Aug	17 Jan	19 Nov	130.5	55.4	(27)
	Kenya (coast)	-3	154	12 Sep	13 Feb	9 Dec	130.5	55.4	(27)
	s-e Aust.	-38	168	7 Sep	22 Feb	9 Jan	130.5	55.4	(27)
Greater Sand Plover	India	9	80	30 Jul	17 Oct	8 Sep	146.3	81.5	(27)
	n-w Aust.	-19	144	20 Aug	11 Jan	5 Nov	146.3	81.5	(27)
	Kenya (coast)	-3	149	1 Sep	27 Jan	25 Nov	146.3	81.5	(27)
	s-e Aust.	-38	134	22 Oct	5 Mar	28 Dec	146.3	81.5	(27)
Black-tailed Godwit	n-w Aust.	-19	127	4 Sep	9 Jan	6 Nov	202.4	350	(7)
Bar-tailed Godwit	n-w Aust.	-19	124	10 Sep	12 Jan	11 Nov	229.1	400	(7)
	s-e Aust.	-38	105	22 Oct	4 Feb	13 Dec	229.1	400	(7)
Whimbrel	n-w Aust.	-19	124	29 Sep	31 Jan	30 Nov	246	350	(7)
Bristle-thighed Curlew	Hawaii	25	92	2 Sep	3 Dec	18 Oct	245	490	(8, 9)
Eastern Curlew	n-w Aust.	-19	137	5 Sep	20 Jan	12 Nov	314.6	900	(7)
	s-e Aust.	-38	116	20 Sep	14 Jan	17 Nov	314.6	900	(7)
Common Redshank	Scotland	56	79	31 Jul	18 Oct	8 Sep	159.2	152	(10, 11, 12)
Wood Sandpiper	S. Africa / Zim	-19	131	1 Aug	20 Dec	5 Oct	125.5	60.7	(13)
Terek Sandpiper	India	9	121	15 Jul	13 Nov	6 Sep	135.5	73.9	(27)
	Kenya (coast)	-3	99	16 Sep	23 Dec	17 Oct	135.5	73.9	(27)
	n-w Aust.	-19	130	22 Sep	29 Jan	18 Nov	135.5	73.9	(27)
	S. Africa	-33	134	6 Oct	17 Feb	12 Dec	135.5	73.9	(27)
	s-e Aust.	-38	130	9 Nov	19 Mar	13 Jan	135.5	73.9	(27)
Ruddy Turnstone	Scotland	56	94	27 Jul	28 Oct	11 Sep	158.3	105	(16, 19)
	S. Africa	-33	119	10 Oct	5 Feb	8 Dec	158.7	105	(19)
Red Knot spp *canutus*	S. Africa	-33	95	25 Oct	28 Jan	11 Dec	166.7	133	(18, 19)
Red Knot spp *islandica*	Scotland	56	77	20 Jul	5 Oct	27 Aug	170.1	139	(18, 19)
	Netherlands	53	71	6 Aug	16 Oct	10 Sep	170.1	145	(22, 23)
Sanderling	S. Africa	-33	98	9 Nov	15 Feb	28 Dec	126	60	(10, 19, 14)
Western Sandpiper	Mexico	24	62	29 Jul	29 Sep	29 Aug	98.5	24	(10,
Little Stint	n-w S. Africa	-26	123	1 Oct	1 Feb	1 Dec	96.2	23.2	(26)
	Kenya (coast)	-3	140	28 Sep	15 Feb	7 Dec	96.2	23.2	(25)
	Zimbabwe	-17	144	29 Sep	20 Feb	10 Dec	96.2	23.2	(26)
	Kenya (inland)	0	107	25 Oct	9 Feb	17 Dec	96.2	23.2	(25)
	S. Africa E.C.	-33	124	17 Oct	18 Feb	18 Dec	96.2	23.2	(26)
	S. Africa W.C.	-33	102	1 Nov	11 Feb	22 Dec	96.2	23.2	(26)

Long-toed Stint	Thailand	13	70	14 Aug	23 Oct	18 Sep	95	28	(21)
Least Sandpiper	Mexico	24	54	29 Jul	21 Sep	25 Aug	90.9	20	(10,
Curlew Sandpiper	India	9	105	15 Aug	30 Nov	6 Oct	133.5	57	(20)
	Kenya (inland)	0	127	2 Oct	7 Feb	13 Dec	133.5	57	(20)
	n-w Aust.	-19	128	17 Sep	23 Jan	21 Nov	133.4	57	(20)
	S. Africa	-33	129	30 Sep	7 Feb	7 Dec	133.5	57	(20)
	s-e Aust.	-38	121	15 Oct	13 Feb	17 Dec	133.6	57	(20)
Purple Sandpiper	Iceland	65	51	22 Jul	11 Sep	16 Aug	140.4	85	(15, 17)
	England	55	61	21 Jul	20 Sep	20 Aug	134.8	64.6	(15, 17)
	Norway	70	48	15 Sep	2 Nov	9 Oct	133.4	79.2	(15, 17)

Sources of data: *(1) Serra et al. (2006), (2) Serra and Rusticali (1998), (3) Balachandran et al. (2000), (4) Minton and Serra (2001), (5) Pearson and Serra (2002), (6) Serra et al. (2001), (7) M. Remisiewicz, H. Sitters, C.M.D. Minton (unpubl. data), (8) Marks (1993), (9) Higgins and Davies (1996), (10) Prater et al. (1977), (11) Underhill et al. (1990), (12) Mitchell et al. (2000), (13), Remisiewicz et al. (2010), (14) Cramp and Simmons (1983), (15) Summers et al. (1988), (16) Summers et al. (1989), (17) Summers et al. (2004), (18) Summers et al. (2010), (19) Underhill (2003), (20) Barshep (2011), (21) Round et al. (2012), (22) Dietz et al. (2013), (23) Dietz et al. (2015), (24) Galindo-Espinosa et al. (2013), (25) C.H.W. Jackson, D.J. Pearson, M. Remisiewicz (unpubl. data), (26) M. Remisiewicz, A.J. Tree (unpubl. data), (27) this study;*

Key*: S. Africa E.C. – Eastern Cape, South Africa; S. Africa W.C. – Western Cape, South Africa; n-w – north-western, s-e – south-eastern;*

Table 2. Regression coefficients for mid-moult date on latitude for adults of five migrant wader species.

Species	**estimate**	**SD**	**t-value**	**probability**
Grey Plover	-0.724	0.075	-9.686	< 0.001
Lesser Sand Plover	-1.507	0.684	-2.204	0.079
Greater Sand Plover	-1.924	0.883	-2.179	0.081
Curlew Sandpiper	-0.985	0.610	-1.617	0.102
Terek Sandpiper	-2.480	0.237	-10.48	< 0.001

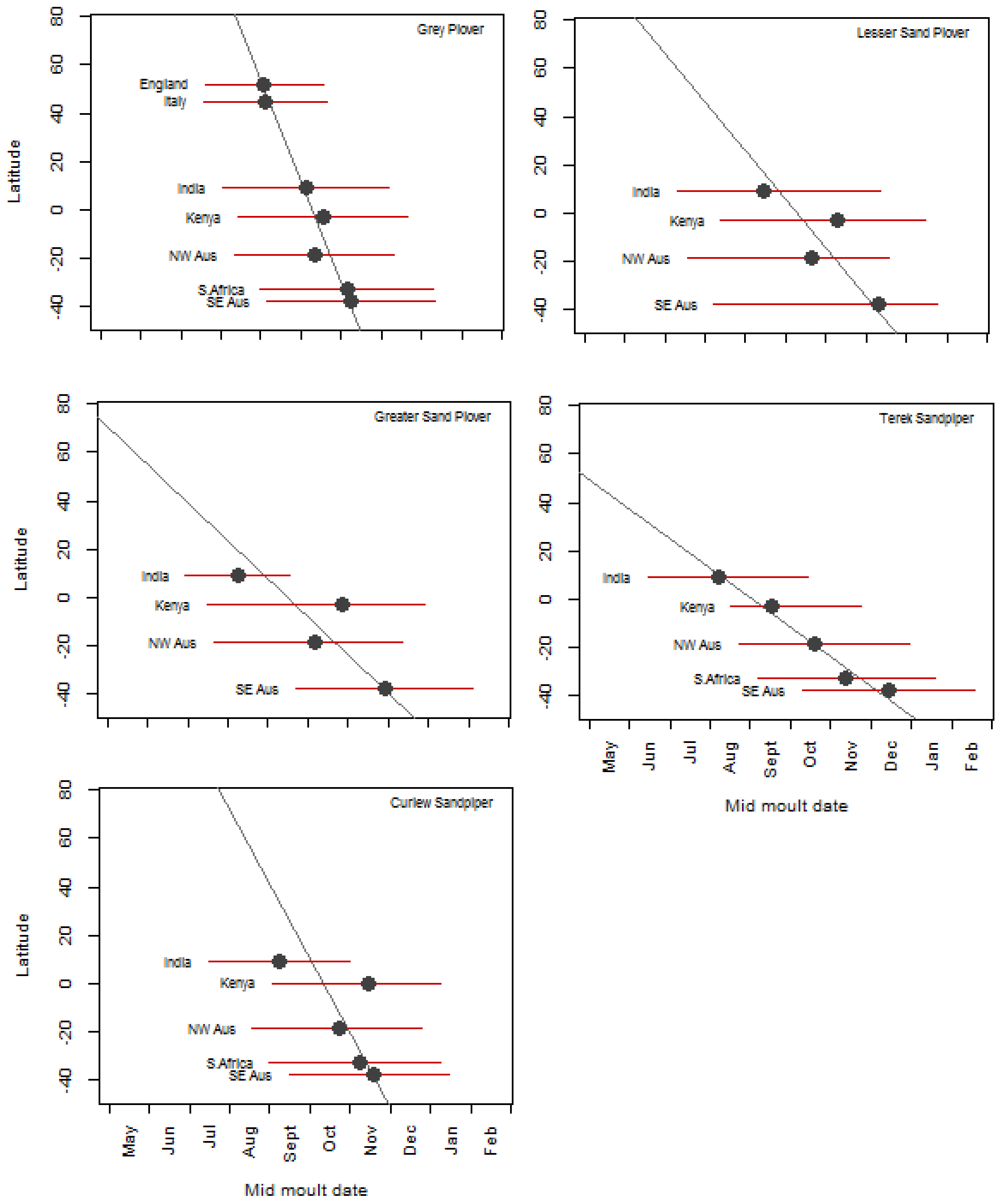

Fig.1. Average estimated date of 50% PFMG against latitude for adults of five wader species: Grey Plover, Lesser and Greater Sand Plovers, Curlew Sandpiper and Terek Sandpiper in India, coastal Kenya, north-western Australia, south-eastern Australia and South Africa. Dates are also given for Grey Plovers in England and Italy. The horizontal lines indicate the duration of moult for each location (*red = full tract analysis*). The linear regression line is shown (the Y-axis contains the explanatory variable, the X-axis the response variable, see Methods).

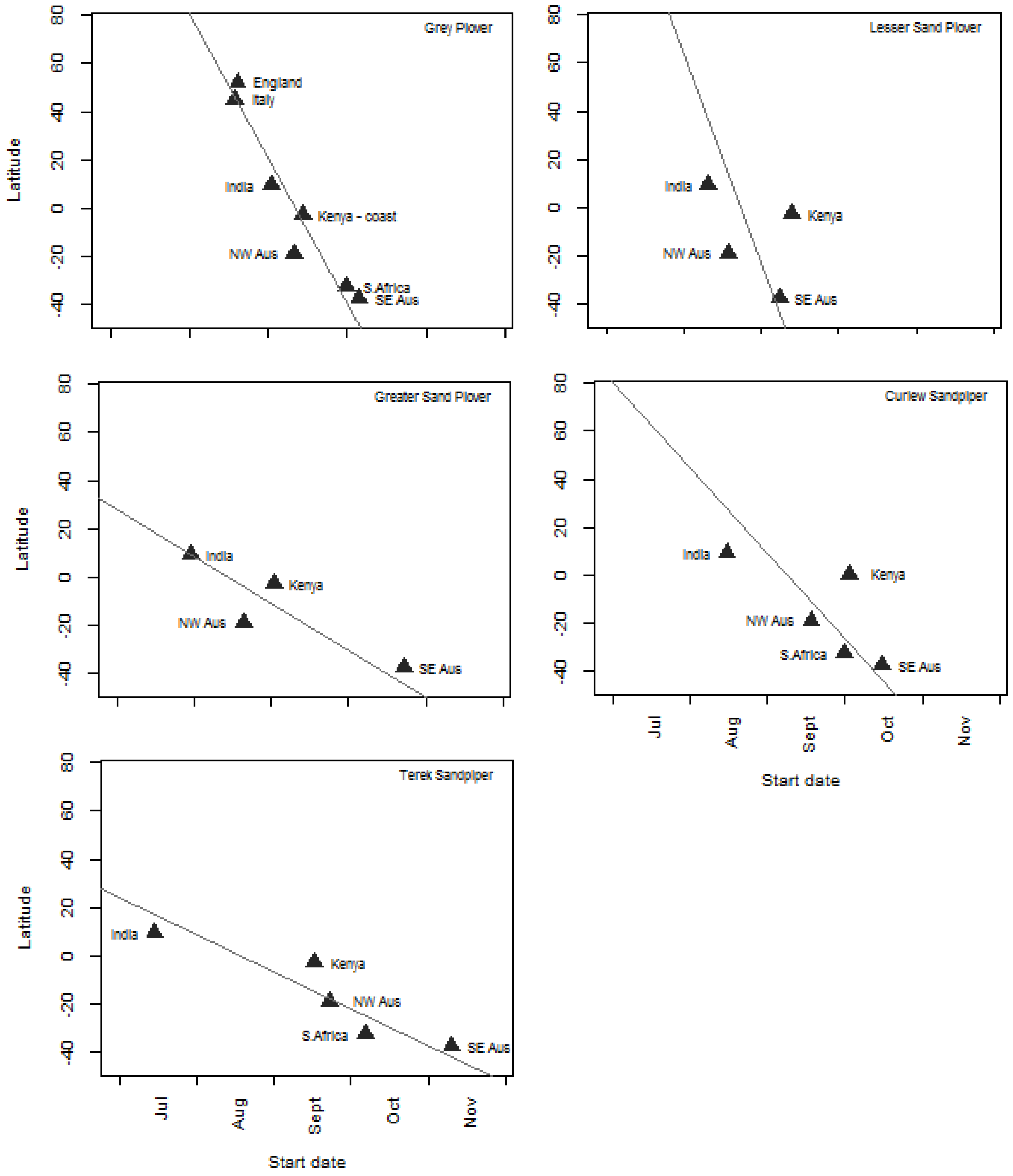

Fig. 2. Estimated average date for the onset of primary moult against latitude for adults of five wader species: Grey Plover, Lesser and Greater Sand Plovers, Curlew Sandpiper and Terek Sandpiper in India, coastal Kenya, north-western Australia, south-eastern Australia and South Africa. Dates are also given for Grey Plovers in England and Italy. The linear regression line is shown (the Y-axis contains the explanatory variable, the X-axis the response variable, see Methods).

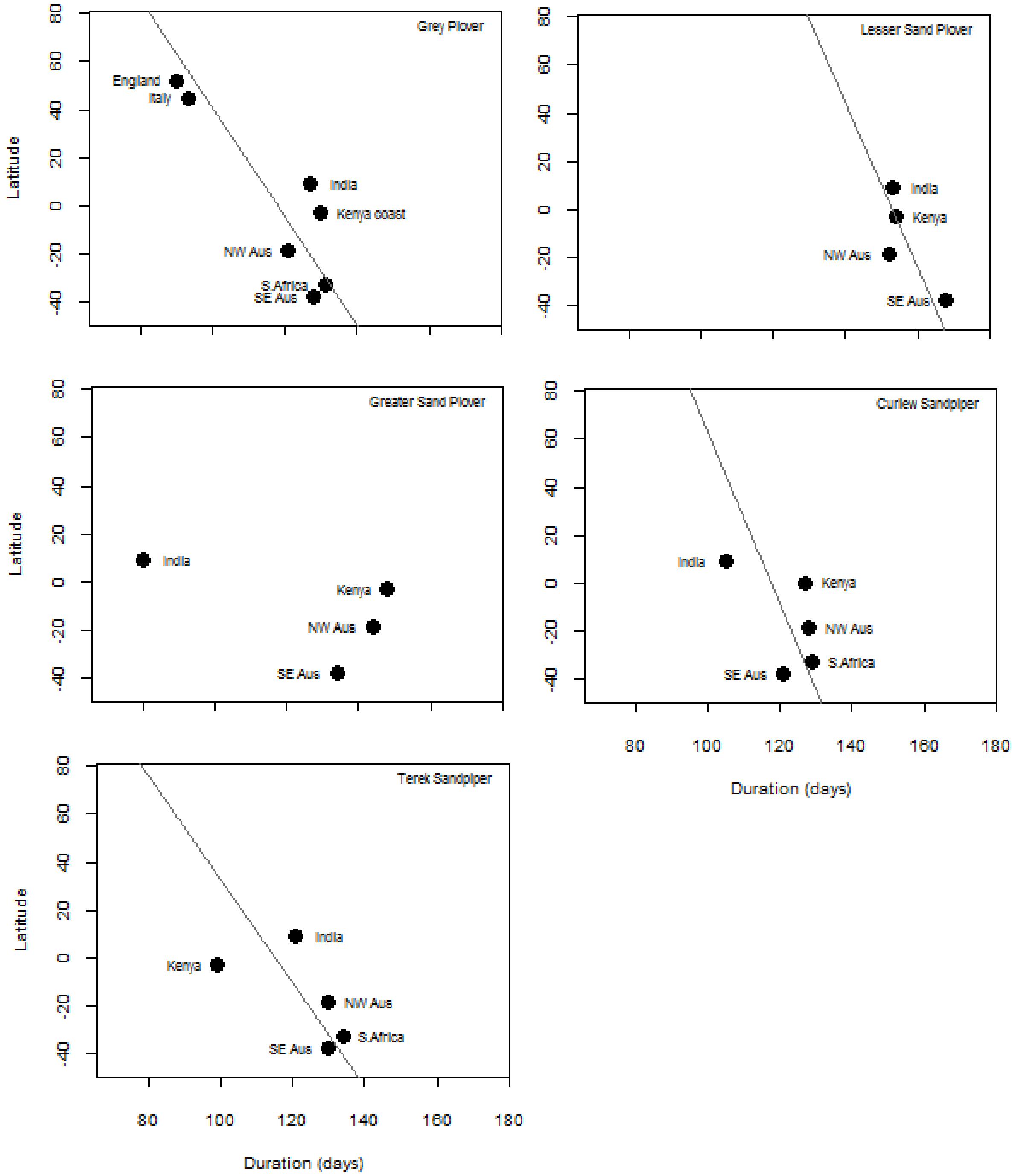

Fig. 3. Average estimated duration of primary moult against latitude for adults of five wader species: Grey Plover, Lesser and Greater Sand Plovers, Curlew Sandpiper and Terek Sandpiper in India, coastal Kenya, north-western Australia, south-eastern Australia and South Africa. Durations are also given for Grey Plovers in England and Italy. The linear regression line is shown (the Y-axis contains the explanatory variable, the X-axis the response variable, see Methods).

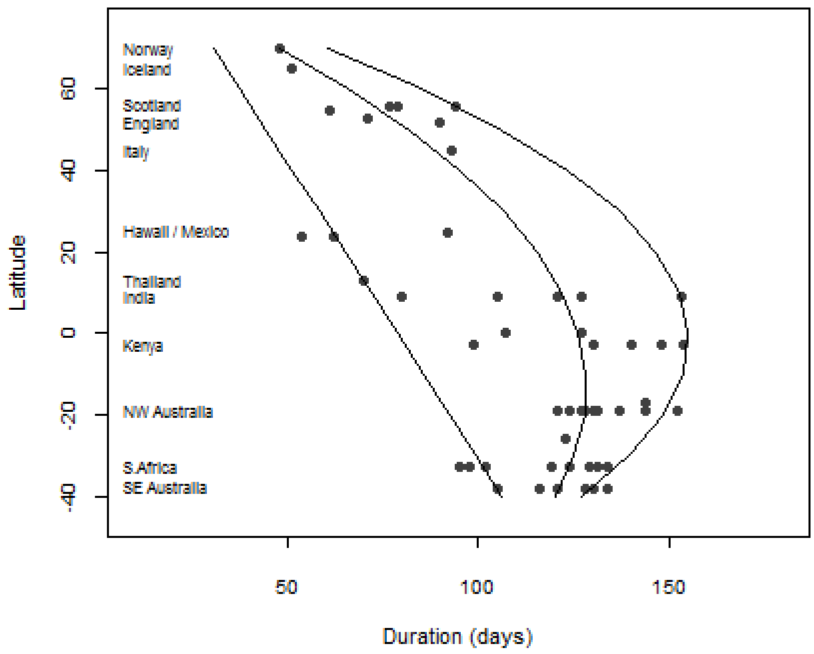

Fig. 4. Estimated average duration of primary moult with latitude for adults of 51 populations of 21 migrant wader species. The three lines are the 10%, 50% and 90% quantile regression lines. The 50% line and the 90% line are quadratics. A quadratic for the 10% line was not supported by the data, and the straight line was significant. (The Y-axis contains the explanatory variable, the X-axis the response variable, see Methods).

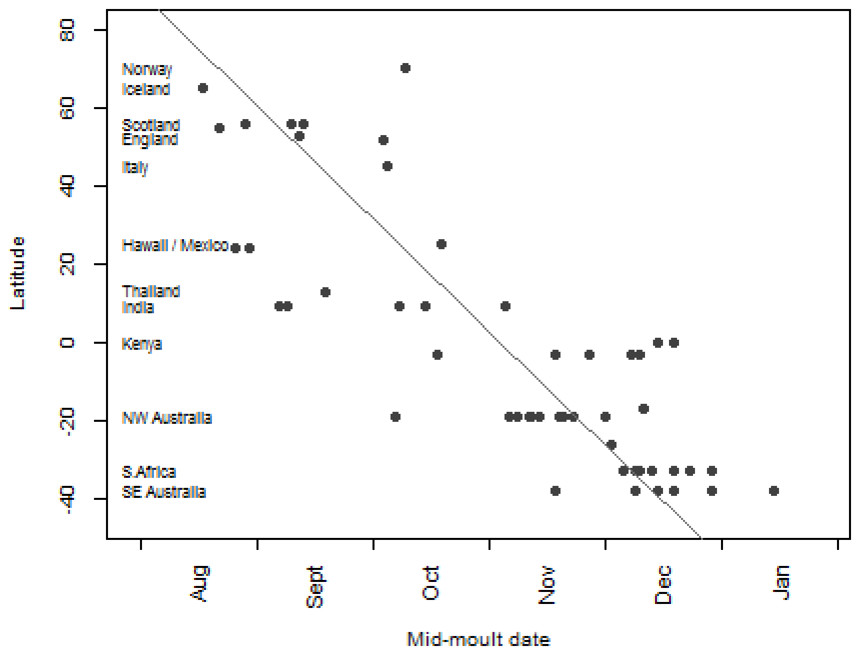

Fig. 5. The estimated mid-moult date plotted on latitude for 51 populations of 21 migrant wader species. The grey line is the fitted regression line (SD = 0.11, P < 0.001). Moult estimates were calculated using the Underhill-Zucchini moult model (Underhill and Zucchini 1988). (The Y-axis contains the explanatory variable, the X-axis the response variable, see Methods).

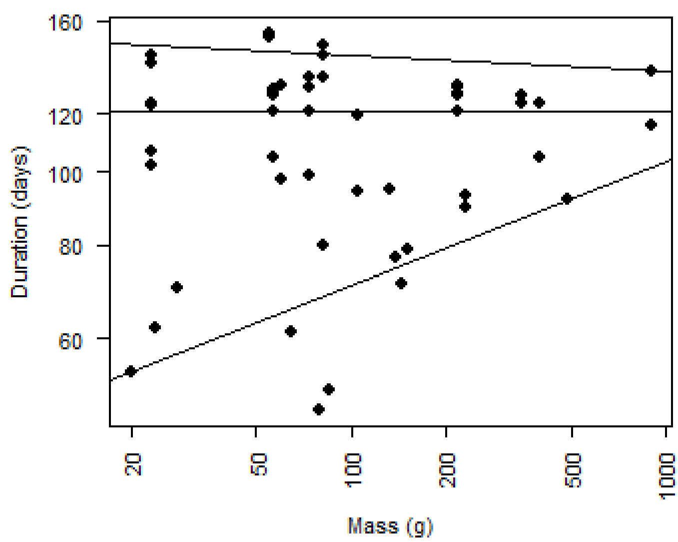

Fig. 6. Estimated average duration of primary moult with mass for adults of 51 populations of 21 migrant wader species. The three lines are the 10%, 50% and 90% quantile regression lines.

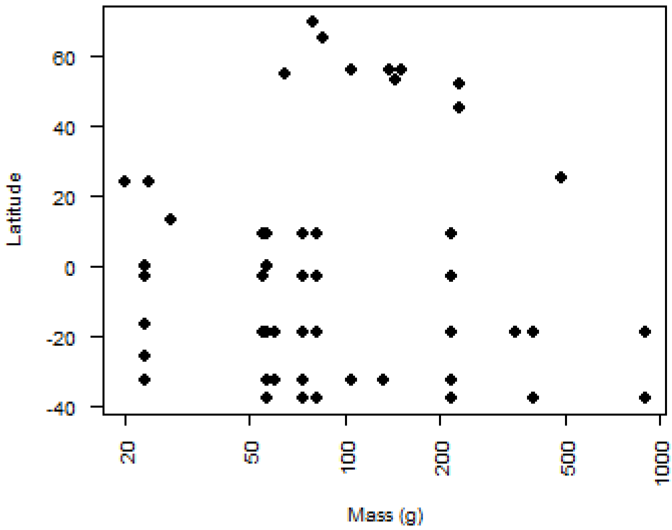

Fig. 7. Body size (mass in grams) plotted on latitude for 51 populations of 21 migrant wader species. (The Y-axis contains the explanatory variable, the X-axis the response variable, see Methods).

Conclusions and recommendations

The major findings from this thesis are:

- The Underhill-Zucchini moult model assumes constant growth of PFMG throughout the moult [primary feathers] so does not take into account scenarios in which the rate of growth varies; the rate of increase of PFMG might either increase or decrease towards the end of moult. The per primary analysis can give a better estimate of start date though this is data hungry, and dependent on having a good representative dataset for each primary, especially for P1, the innermost, and for P10, the outermost. This is frequently a challenge because especially the early stages of moult are often not covered as well by ringers (there are usually fewer birds present and thus catch rate is much lower and less interesting, sometimes climatic conditions less conducive to trapping, e.g. in Kenya)
- For the Underhill-Zucchini model to work, it is important to have moult data from throughout the moult process and not just at one end of it
- Mid-moult date is a better parameter to use than start date for comparing strategies related to the timing of moult between populations and species. The main insight is that with decreasing latitude (southwards), moult is timed later, by roughly 10 days per 10° of latitude. A key factor in driving this is likely to be increasing distance of the moulting grounds from breeding grounds that necessarily delays the start of moult for migrants.
- Comparison of a wide sample of moult strategies for birds of different body mass and latitude revealed a pattern hitherto undescribed of constrained duration of moult at high latitudes (both north and south) but a wide range of duration adopted by birds moulting within the tropics. Small birds, due to less effort required to moult their smaller wings, have

the luxury of choosing to either take a long time to moult or moult fast while large species are forced to travel farther south in search of good enough conditions to allow them longer to moult.

- However, while the shortest duration achievable by a bird is determined by its body size, it appears that a duration of c. 120 days is the “gold standard” period for a wader to moult, independent of its body size, presumably in order to produce high quality feathers.
- Unique among known migration strategies for migrant waders, first year Lesser Sand Plovers of the race *mongolus* and *stegmanni* do not reach the non-breeding grounds in Australia until six or seven months after the adults.
- Moult strategies for first year Terek Sandpipers in north-western Australia suggest there may be two distinct populations involved with the likely explanation that they originate from distinct breeding areas that has led to the evolution of the different strategies.
- The moult and migration strategy of adult Greater Sand Plovers in south-eastern India suggests a strong limitation on moult by local extreme climatic conditions given the feeding ecology of the species. In contrast to other species, Greater Sand Plovers moult rapidly (80 days) and mostly leave the area once the heavy monsoon rains begin in October presumably for more southerly non-breeding grounds. South-eastern India is therefore a stopover site on migration for the key purpose of moulting thus highlighting the importance of these wetlands for the conservation of the species.

Recommendations

- Emphasis is often placed on estimated start date in moult studies. While important for understanding moult periods for a species, this study highlighted the large variation in estimated start date that results from poor data sampling at the start and end of moult (a common phenomenon). The mid-moult date (when 50% Percent Feather Mass Grown is reached) was found to be substantially less variable. Thus for describing and comparing the timing of moult within or between, species it is recommended that mid-moult date be the preferred parameter to use.
- Effort is needed to catch waders in the early part of the moult cycle, in particular for the first adults returning from the breeding grounds to fill substantial gaps in datasets at a key time in understanding moult strategies for any given species.
- Much work has been done on adult moult strategies but studies of immature moult strategies are less frequent due to the challenges of a lack of data, inconsistencies and difficulties in ageing younger birds together with a diverse array of moult patterns present even within a single species. Indeed, the results from these analyses confirm a mostly uniform moult strategy for adult birds, at least within a population, but a diverse array of

strategies for immature birds even at the same location. More fieldwork is needed to provide datasets that can contribute to a better interpretation of these often complex immature strategies.

- There are now sufficient studies of the moult and migration of waders (Charadrii) to start reviewing the evolutionary implications of the diverse strategies represented in this family. An interesting topic could be to investigate whether the variation in moult strategies both for adults and first year birds is driving population differentiation and, plausibly, speciation. For example, first year Terek Sandpipers in north-western Australia where almost half underwent a complete primary moult and half only moulted the outer primaries (Chapter 5, Fig. 1c)
- All three species considered in the thesis exhibited moult of the outermost primary feathers in first year birds to a greater or lesser extent. However, there is not yet enough information on the topic for sufficient species to understand an interpretation of the phenomenon. This is an area for future studies.
- A certain amount of data was inapplicable to first year and sub-adult moult strategy analysis mostly as a result of a lack of proper understanding and care taken in recording moult scores correctly from birds in the hand. Much of this is due to a lack of reference material and proper training and there is thus a need to improve on this among wader ringers.
- Non-breeding sites are essential as safe moulting grounds for long-distance migrants. There is therefore a need to conserve places like Mida Creek in Kenya, to manage it well to reduce disturbance, and to maintain a good food source for waders.
- More studies on primary moult are needed for waders spending the non-breeding season between 50°N and 10°N (e.g. in southern Europe, the Mediterranean basin and north Africa) and also south of 35°S (in southern South America and New Zealand), in order to fill gaps to confirm results of this analysis.
- Furthermore, additional studies on waders with a heavy body mass of more than 500 g are needed in order to strengthen and confirm the results of comparing body mass with moult strategy.
- Satellite tracking of Greater Sand Plovers from south-eastern India to confirm where they move on to. Alternatively, finer temporal resolution and a wider spread of wader counts in South East Asia would likely reveal changes in numbers of birds to indicate an arrival of Greater Sand Plovers in late October/November reflecting the departure from India at the onset of the monsoon.
- Satellite tracking of first year Lesser Sand Plovers migrating to Australia is required in order to tease open the mystery of where they go between leaving the breeding grounds in August and arriving on the non-breeding grounds the following February/March. At least more

detailed counts at a finer temporal resolution are recommended at stopover sites along the migratory route in order to contribute to our understanding of their movements.

Overall, as the only component of a bird's annual cycle which cannot be missed if the individual is to survive to the next year, it is critical that a proper understanding of moult is obtained for each species. This study has highlighted the relative ease with which moult can be studied as compared to other components of a bird's life cycle and the insights that it can give to the biology of the species. Ultimately it has confirmed the major importance of studying and properly understanding moult in birds if they are to be conserved effectively.