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Primary moult of continental Black-tailed Godwits *Limosa limosa limosa* in the Doñana wetlands, Spain

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ABSTRACT

Capsule: Most Continental Black-tailed Godwits *Limosa limosa limosa* using the Doñana wetlands during post-breeding migration appear to begin moult before they arrive and suspend moult before they migrate onwards to West Africa.

Aims: We aim to describe the primary moult strategies and patterns in the Continental Black-tailed Godwits using the Doñana wetlands, a major passage and wintering area for waterbirds in southern Spain.

Methods: Individual godwits were captured, marked and their primary moult was scored in Doñana during the non-breeding season (June–March) in 2011 and 2012. Data from resightings of colour-marked godwits and birds equipped with satellite transmitters were used to estimate stopover duration during post-breeding migration (June–September) to determine if godwits move to West Africa before completing their primary moult.

Results: Average primary moult duration was estimated to be 84 days ± 9 se, during 29 June–21 September and did not differ between sexes. Only 2% of individuals were observed with suspended moult. We estimated stopover duration in Doñana to be 13 days ± 2 se before migrating to West Africa.

Conclusions: Most godwits stage for about two weeks in the Doñana wetlands during southward migration, moult their primaries and appear to suspend moult before crossing the Sahara. Others may complete their primary moult in Doñana, or elsewhere in Europe and overwinter in Doñana where increasing numbers of godwits have been detected in recent years. A few individuals may finish the moult in Doñana and migrate to West Africa late in the post-breeding season.

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The Continental European subspecies of the Black-tailed Godwit *Limosa limosa limosa* is a long-distance migratory wader that breeds exclusively in agricultural grasslands in northwest Europe (Gill *et al.* 2007, Kirby & Scott 2009). These godwits spend the non-breeding season along inland river deltas and rice fields in sub-Saharan West Africa (Zwarts *et al.* 2009, Hooijmeijer *et al.* 2013). However, an increasing fraction of birds also spend the non-breeding season in southwest Europe, especially in the Doñana wetlands in Spain, probably as a result of the creation of rice fields and fish pond habitats in recent decades (Márquez-Ferrando *et al.* 2011, Márquez-Ferrando *et al.* 2014). This now makes southern Spain a key non-breeding site where some godwits stay for the entire winter, while others might stop briefly during post-breeding migration or for a longer stay during pre-breeding migration. This flyway population has suffered a massive population decline of 75% over the past 40 years (Gill *et al.* 2007), and consisted of approximately 81,000 individuals in the winter of 2014/15 (Kentie *et al.* 2016). Although extensive research has been undertaken on godwits during spring migration and the breeding season (Masero *et al.* 2011, Groen *et al.* 2012, Kentie *et al.* 2013, Lourenço *et al.* 2010), less attention has been given to their post-breeding ecology, such as their post-breeding moult.

Moult is one of the most energetically demanding stages in the avian annual cycle and, as such, is thought to constrain long-distance migrants that must

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fit moult in between breeding and migration (Ginn & Melville 1983, Buehler & Piersma 2008, Barta *et al.* 2008, Dietz *et al.* 2015). Discovering where and when moult takes place during the annual cycle can, therefore, help us understand the energetic and time constraints faced by migratory birds and may help inform conservation efforts (Newton 2009, Bridge 2011, Conklin & Battley 2012, Barshep *et al.* 2013).

Several patterns of post-breeding moult are observed among waders using the East Atlantic flyway (Newton 2008). East Siberian populations of Dunlin *Calidris alpina* and Redeshank *Tringa totanus* moult at or close to the breeding areas before autumn migration, whereas Curlew Sandpiper *Calidris ferruginea* and Sanderling *Calidris alba* postpone their moult until they reach the West African wintering areas. Other species like the Black-tailed Godwit or Marsh Sandpiper *Tringa stagnatilis*, may split moult, partly in or near the breeding area and partly in the wintering areas (Prater *et al.* 1977, Remisiewicz 2011).

The moult of primary flight feathers ('primary moult') usually spans the period of time required to replace all other flight feathers combined and is thus commonly used to indicate the duration of the moult process in general (Ginn & Melville 1983). Most godwits from the Dutch breeding population initiate the primary moult around June after breeding, but then suspend moult while still close to their breeding areas, and presumably resume and complete it at their non-breeding sites in West Africa (van Dijk 1980). It is known that many godwits stop in the Netherlands, Belgium, France, Portugal, Spain or Morocco during southward migration (Hooijmeijer *et al.* 2013). However, we know very little about the incidence of primary moult during this period, with the bulk of our knowledge coming from a few individuals captured along the coast of Morocco more than 40 years ago (Pienkowski *et al.* 1976).

Here, we determine the timing and extent of the primary moult in the continental Black-tailed Godwits using the Doñana wetlands in southwest Spain, and describe the moult patterns observed.

Methods

Study area

The Doñana wetlands, located in the Guadalquivir estuary (Figure 1), are one of the most important wintering quarters for waterbirds in Europe (Rendón *et al.* 2008), as well as an important stopover and staging area for many other long-distance migrants (García-Novo & Marín-Cabrera 2005). Waterbird habitat availability is determined by rainfall during autumn and winter, when the flooded area within the wetlands can reach up to 30,000 ha (García-Novo & Marín-Cabrera 2005). However, in recent decades, many birds have begun to use man-made habitats around the natural wetlands, such as rice fields, fish farms and saltpans (Rendón *et al.* 2008, Toral *et al.* 2011). These man-made habitats offer alternative resting and feeding sites, especially during the dry season (Kloskowski *et al.* 2009). According to the observation of colour-ringed godwits in Doñana, very small numbers of the Icelandic subspecies (*Limosa limosa islandica*) also occur in Doñana during the whole non-breeding period, with around 20% of colour-marked individuals being Icelandic and 80% from the nominate population (Márquez-Ferrando *et al.* 2011).

Fieldwork and laboratory analyses

During the non-breeding season (June-March) of 2011 and 2012, we captured 51 adult Black-tailed Godwits (October 2011 $n = 9$; January 2012 $n = 3$, March 2012 $n = 1$, July 2012 $n = 24$, September 2012 $n = 13$ and October 2012 $n = 1$), at the fish ponds of Veta la Palma fish farm, which is part of the Doñana wetland complex (Figure 1). Godwits were captured using mist-nets during the night and early morning. All individuals were weighed and their total head, bill-length, tarsus, tarsus-toe and wing were measured to the nearest millimetre. Individuals ($n = 48$) were marked with a numbered metal ring, four plastic colour-rings and a coloured flag to enable visual identification in the field. Two of the godwits captured had been previously marked in the Netherlands with a similar colour scheme. We scored moult stage according to Ashmole (1962). Each primary feather, from the innermost (P1) to the outermost (P10), was scored on a scale from 0 (old feather) to 5 (fully grown new feather), with values 1–4 describing consecutive stages of feather growth (Ginn & Melville 1983). To determine individual sex and subspecies (Lopes *et al.* 2013), we took a 0.2 ml blood sample from each individual for molecular DNA analysis. Subspecies determination was done by polymerase chain reaction (PCR) amplification of the mtDNA region with the primer pair L438 and H772 according to Höglund *et al.* (2009). Sequences were obtained from an ABI PRISM 3130 genetic analyser (Applied Biosystems, New Jersey, US) and results were visualized and edited with BioEdit (Hall 1999) and Geneious software (v 7.0.5; Kearse *et al.* 2012). Molecular sexing was done by PCR, using the primers CHD-P8 and CHD1-M5

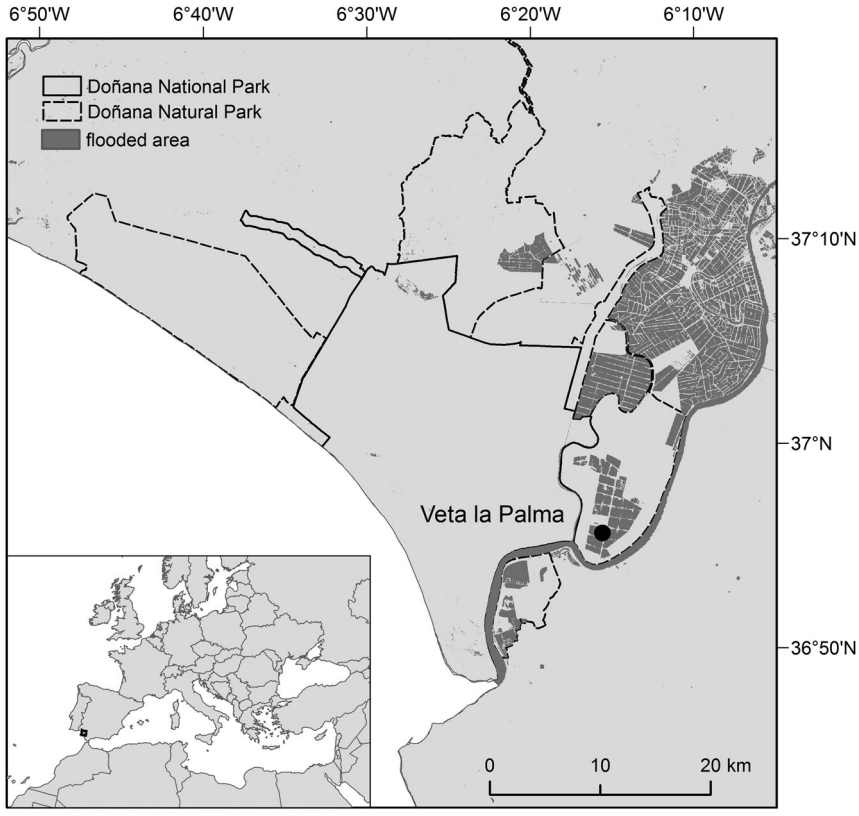

Figure 1. Doñana National and Natural Park. The map shows the flooded area based on a Landsat image from August 2012. Only anthropogenic habitats keep water during the dry season (June–September) in post-breeding migration.

following the protocols by Ellegren (1996) and Griffiths *et al.* (1998). Blood samples were not available for four individuals after subspecies determination, so these individuals were sexed on the basis of their body size (Schroeder *et al.* 2008).

To determine whether godwits migrate from Doñana to non-breeding sites in West Africa prior to the completion of primary moult, we estimated the staging duration of those individuals that were assumed to leave Doñana. To do that, we searched for colour-marked godwits (captured between July and September 2012, $n = 30$), at least twice a week until late November 2012. Marked godwits not seen in Doñana during October and November were assumed to have left the site. Individuals seen in October were assumed to be wintering there (Kentie *et al.* 2017). Because the sample size of individuals assumed to have left Doñana was small ($n = 20$), the power of a mark-recapture analysis using resightings ($n = 30$) would have been insufficient to provide robust estimates of stopover duration. We, therefore, estimated the Minimal Staging Duration (MSD) for each individual, calculated as the number of days between the day of capture and the last day of sighting during July–September 2012. To supplement these data, we also present staging duration from eight adults godwits carrying satellite transmitters captured in Extremadura, Spain, in January 2013, which made a stop in Doñana during southward migration in 2013 (Senner *et al.* in review). Briefly, satellite transmitters were attached using a leg-loop harness and 2 mm nylon cord and were programmed to transmit for 10 hours and recharge for 48 hours (Senner *et al.* 2015). For these individuals, we were thus able to identify their true staging duration to within 1 day, estimated as the number of days present in Doñana.

Statistical analyses

For each bird, we calculated the Proportion of Feather Mass Grown (PFMG) using the moult scores and relative masses of primaries for Bar-tailed Godwits *Limosa lapponica*, a closely related species for which this information was available (Underhill & Joubert 1995). Closely related species of a similar wing shape have similar relative primary masses (Underhill & Joubert 1995), and such substitution introduces a negligible bias (to the fourth decimal place) into the calculated PFMG value and estimated moult parameters (Burman 2016). To determine moult parameters (duration, mean start date and standard deviation in start date) of the *limosa* subspecies, we

excluded individuals molecularly assigned to the *islandica* subspecies ($n = 5$) and individuals with suspended moult ($n = 1$).

We used the package 'moult 2.0' (Erni *et al.* 2013) in R 3.3.1 (R Development Core Team 2016), which implements the Underhill–Zucchini moult models (Underhill & Zucchini 1988, Underhill *et al.* 1990) to estimate moult parameters. Our sample consisted of moulting birds and birds that had completed moult, but not pre-moult birds, thus the data were type 4 for the moult model (Underhill *et al.* 1990). We used the date of capture calculated as the day number from 1 June. To determine sex differences in moult, we compared models where sex was or was not a covariate of moult duration and start date (Remisiewicz *et al.* 2014). We ranked these models using Akaike Information Criterion corrected for small sample size (AIC_c) and their respective model weights (w_i; Burnham & Anderson 2002). We estimated the daily growth rate (% PFMG/day) by dividing the relative mass of all primaries (100%) by the estimated duration of moult (Remisiewicz *et al.* 2009). Using that daily growth rate, and the average staging duration of godwits staging at Doñana from the literature (Hooijmeijer *et al.* 2013), and in this study for each individual we estimated the maximum PFMG at departure (Burman 2016), assuming it was caught on the first day at arrival in Doñana, stayed there for the longest described time, and moulted at a constant rate.

Results

We used moult data from 45 Continental godwits (hereafter 'godwits') in primary moult analyses (Figure 2). The earliest moulting birds captured after the breeding season were two females on 2 July (Figure 2). One weighed 292 g and had shed its first three primaries (P1–P3), the other weighed 293 g, and had already replaced its first two inner primaries (P1, P2) and with the P3–P6 in active moult. The latest moulting individuals were caught on 19 September with moult nearly complete (Figure 2). All godwits captured in October had completed their primary moult. The single bird with suspended moult was a female caught on 25 July, which had replaced four inner primaries (Figure 2) and had a body mass of 339 g.

The mean primary moult duration was estimated at 84 days ± 9 se, from 29 June to 21 September (Table 1, Figure 2a). We did not find differences between sexes in moult parameters since the model with the highest w_i was the one in which sex did not have any effect on moult parameters (Table 2). Two other models

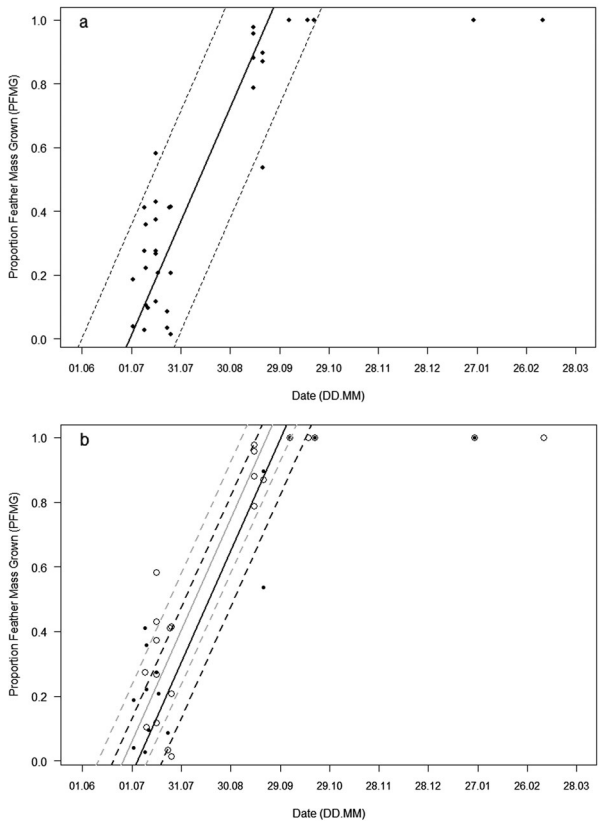

Figure 2. PFMG in adult Continental godwits captured in Doñana Wetlands in 2011–12. Continuous lines indicate the mean progress of moult and dashed lines the 95% confidence intervals. (a) PFMG in godwits with active or complete primary moult = black circles; PFMG in godwits in suspended moult = asterisk (n = 1); (b) PFMG in males = open circles and grey lines (n = 30); PFMG in females = black circles and black lines (n = 15) based on the model 2 (Table 2).

had ΔAIC_c scores <2, but they were considered less parsimonious as they had one additional parameter compared to the best supported model (Arnold 2010). Because the results were inconclusive, and because sex differences in the timing of moult could exist (Cramp & Simmons 1983), we present moult estimates from the best model that showed the differences between the sexes (model 2 in Table 2). According to that model, males started moult on average a week earlier than the females, but the duration and the standard deviation of moult were similar for both sexes (Figure 2(b)).

Only 13% of birds captured between July and September ($n = 4$) wintered in Doñana. For the 67% of birds ($n = 20$) that were assumed to migrate to Africa, mean staging duration was estimated to be 4 days ± 2 se. The rest ($n = 6$) were seen in November, so were excluded from the estimation of staging duration. The eight individuals tracked with satellite transmitters stayed in Doñana for 13 ± 2 days (mean ± se) during

Table 1. Moult parameters for Black-tailed Godwits caught in Doñana wetlands during 2011–12 (see Figure 2a) estimated using a moult model for type 4 data (Underhill & Zucchini 1988). 95% CI = 95% confidence interval for the moult start date, se = standard error.

Moult parameters					Sample size			
Mean Start date (se)	End date (se)	Duration of moult in days (se)	sd of Start date (se)	95% CI	Pre-moult	Active moult	Post-moult	% PFMG/day
29 Jun (6.14)	21 Sep (6.14)	84 (8.63)	15 (5.46)	30 May–28 Jul	0	33	12	0.0119

Table 2. Moult models used to determine the effect of sex on moult parameters in adult Black-tailed Godwits in Doñana wetlands during 2011–12. The formula for each model has five parts, in order: (1) PFMG: moult indices for each individual; (2) Day: day of each individual capture, from 1 June; (3) covariate for the duration of moult; (4) covariate for the mean start date of moult and (5) covariate for the standard deviation in start date. Position of the 'sex' indicate the moult parameter affected by sex; 1 indicate the moult parameter assumed equal between sexes. The models were ranked by corrected Akaike's Information Criteria for small samples size (AIC_c), k is the number of estimated parameters in the model, ΔAIC_c gives the difference in AICc from the model with lowest AICc, w_i is the Akaike weight. The models with $\Delta AIC_c < 2$ are given in bold face.

Model no	Model formula	k	AICc	ΔAICc	w_i
Model 1	**PFMG ~ Day | 1 | 1 | 1 |**	**3**	**188.23**	**0.00**	**0.35**
Model 2	**PFMG ~ Day | 1 | sex | 1 |**	**4**	**188.75**	**0.52**	**0.27**
Model 3	**PFMG ~ Day | sex | 1 | 1 |**	**4**	**188.97**	**0.74**	**0.24**
Model 4	PFMG ~ Day | sex | sex| 1 |	5	191.29	3.07	0.08

June–August 2013 (Table 3). The godwits with the names 'Amsterdam' and 'Amalia' briefly stopped in Extremadura and a small wetland near Seville before arriving in Doñana.

The estimated average advancement of the primary moult of godwits arriving in July, by the time they leave Doñana, did not exceed 74% of the new primary feather mass grown, with an average staging duration of 13 days (this study) (Figure 3). With an average staging duration of 24 days, (from Hooijmeijer *et al.* 2013), the birds would have reached up to 87% (± 16% sd) of the primary feather mass grown (Figure 3). Considering the stage of moult at which these birds were caught at Doñana, they would require 63 ± 14 days (mean ± sd) in Doñana to complete primary moult.

Table 3. Staging duration of Black-tailed Godwits with satellite transmitters visiting Doñana wetlands during their post-breeding migration in 2013.

Individual name	Staging period	Staging duration (days)
Amalia	1 Jul–15 Jul 2013	14
Amsterdam	11 Jul–5 Aug 2013	25
Badajoz	26 Jun–9 Jul 2013	13
Bissau	15 Jun–1 Jul 2013	16
Lisboa	27 Jun–7 Jul 2013	10
Madrid	24 Jun–1 Jul 2013	7
Nouakchott	8 Jul–13 Jul 2013	5
Paris	26 Jun–6 Jul 2013	10

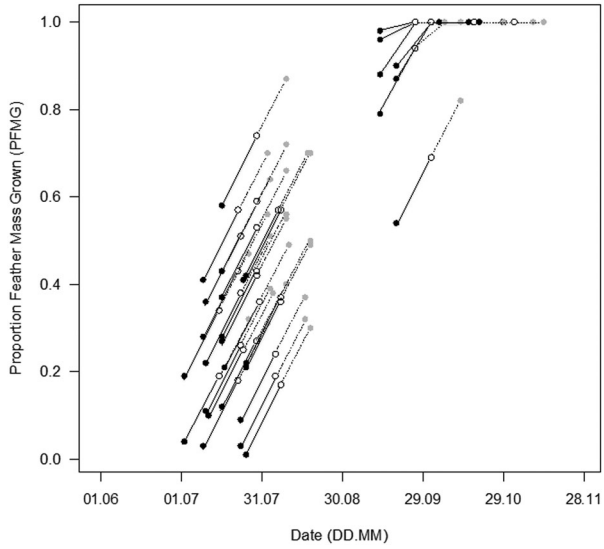

Figure 3. The estimated PFMG that adult godwits captured in Doñana Wetlands in 2011–12 would reach at departure, assuming the estimated mean daily growth date (%PFMG/day) of 0.0119 ± 0.0619 (mean ± se) (Table 1) and an staging duration in Doñana of 13 days (our study) and of 24 days (Hooijmeijer *et al.* 2013). Black symbols = actual PFMG of godwits at capture; white symbols = estimated PFMG after 13 days; grey symbols = estimated PFMG after 24 days. Wintering birds caught in November–January with completed moult were not included in the figure.

Discussion

In this study, we estimated that post-breeding primary moult in the Continental Black-tailed Godwit population takes 84 days to complete, two weeks shorter than previous estimates estimated by van Dijk (1980) and Pienkowski *et al.* (1976). Although only 2% of the godwits captured in Doñana were in suspended moult, our results suggest that most birds may actually suspend moult at a medium or advanced stage (between P4 and P7) prior to departure to the West African sites, since most individuals captured in July (86%) had already completed the moult of primaries P4–P7.

The MSD estimated using resighting information (4 days) was shorter than that documented using satellite transmitter data (13 days), likely biased by our small sample or because some birds were already in Doñana for a while before their capture. However, one satellite-

tagged godwit stayed only for 5 days (8–13 July 2013). This suggests that some birds do not stay as long as 13–24 days in Doñana, and so probably do not proceed far with their moult.

Regarding sex differences, our results suggest that if the sexes differ in moult timing, it would rather be the males that start moult before females, which is contrary to what is mentioned in Cramp & Simmons (1983). Sex differences in the timing of post-breeding moult in waders was previously explained by sex differences in parental care, where the sex tending the offspring longest usually begins moult later (Figuerola & Bertolero 1995, Barshep *et al.* 2013, Dietz *et al.* 2013). However, in godwits both sexes take care of the chicks (Cramp & Simmons 1983). To clarify this, information on the moult patterns of a higher number of individuals will be required.

The variation observed in primary moult score among individuals and the staging durations estimated in post-breeding migration suggest that individual godwits using Doñana wetlands may adopt several moult strategies:

(1) *Suspension of moult in Doñana before crossing the Sahara*. Moulting some primaries at staging sites before long migratory flights, and completing it at the final destination, is a strategy observed in some wader species breeding at intermediate latitudes, e.g. some British Grey Plovers *Pluvialis squatarola* that use the East Atlantic flyway (Serra *et al.* 2006, Remisiewicz 2011). Such a strategy may enable individuals to profit from temporary high-quality feeding conditions when they are encountered, and thus to potentially bear the cost of both moult and migration (Pienkowski *et al.* 1976, Swann & Baillie 1979). The continental female Black-tailed Godwit caught in Doñana in July with suspended moult and body mass of 339 g was potentially able to undertake a non-stop flight of approximately 3000 km, according to the predictions of flight range models (Lourenço & Alves 2014). Such high body masses may indicate that Doñana provides good refuelling conditions that enable godwits to gain fuel sufficient for non-stop flights to Senegal or Guinea-Bissau (Hooijmeijer *et al.* 2013).

(2) *Completion of moult in Doñana or elsewhere before migrating to West Africa.* The fact that 25% of individuals that did not winter in Doñana were captured in September with advanced moult (Figure 3) suggests that some individuals might complete moult in Doñana, and then cross the Sahara in a later post-breeding migration (end September). However, we suggest this strategy is used by a small part of the population only, as not many godwits are present in Doñana late in the season (Márquez-Ferrando *et al.* 2011).

(3) *Completion of moult in Doñana or elsewhere in Europe and no onwards migration to West Africa*. This is suggested by our observations of birds that were present in Doñana in the post-breeding season or winter. Indeed, the increasing numbers detected in Doñana in October (when moult must be finished) (Márquez-Ferrando *et al.* 2011) may suggest that many individuals might arrive from elsewhere in Europe with completed moult.

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