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Pattern of wing moult and its relationship to breeding in the Eurasian Stone-curlew *Burhinus oedicnemus*

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The timing, duration and pattern of the poorly documented wing moult in the Eurasian Stone-curlew *Burhinus oedicnemus* were described and related to the breeding cycle. Between 1998 and 2007, 141 birds were trapped in the Taro River Regional Park (Parma, Italy) both while incubating and during the post-breeding season. The timing of primary moult was estimated according to the method of Underhill & Zucchini (1988) and Underhill *et al.* (1990). Primary moult was very slow and overlapped most of the breeding season, beginning in early May and ending in October. Secondary moult was much more irregular and was not completed within a single moult cycle. Innermost and outermost secondaries were more likely to be shed than those at the centre of this tract. Juvenile secondaries were not shed during the first winter. The study provides the first detailed analysis of wing moult in the Eurasian Stone-curlew and suggests some useful ageing criteria based on the pattern of secondary moult. The extensive overlap between breeding and moulting is relatively uncommon compared to other waders. This could be interpreted as a way to maximize breeding success through renesting potential (up to 4 attempts), i.e. by spreading the cost of moult over a prolonged time period. A between-species comparison using independent contrasts was consistent with this hypothesis: species with a prolonged breeding season also showed considerable overlap in the timing of primary moult and breeding activities.

Key words: Eurasian Stone-curlew, *Burhinus oedicnemus*, wing moult, moult–breeding overlap, ageing criteria*s*

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INTRODUCTION

Moult in waders (Charadriiformes) has been generally investigated in depth for many species (e.g. Holmgren *et al.* 2001, Summers *et al.* 2004, Serra *et al.* 2006), but that of the Eurasian Stone-curlew *Burhinus oedicnemus* (hereafter Stone-curlew) remains poorly known. Indeed, current descriptions regarding this bird (Cramp & Simmons 1983, Ginn & Melville 1983) are based on small sample sizes, and they are not easily comparable to that of other species because they were made well before the latest statistical methodology designed for the analysis of moult data became available (Underhill & Zucchini 1988, Underhill *et al.* 1990). Furthermore, no information regarding the pattern of secondary moult is currently available, nor did these earlier studies report additional information that

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enables the moult to be reliably placed within the context of the species' annual cycle. This seems to be a particularly significant omission, because in this species the data at hand suggest a large overlap between breeding and moult (Cramp & Simmons 1983), which is relatively rare for birds in temperate areas, where seasons are marked and predictable (Jenni & Winkler 1994, Moreno 2004). Given that relatively few studies have investigated the costs and benefits of this overlap, and consequently the reasons for its higher frequency in tropical rather than in temperate species are poorly understood (Foster 1974, Jenni & Winkler 1994, Moreno 2004), it seems likely that an in-depth investigation of the moult strategy of the Stone-curlew could provide important information on this topic. The aim of this paper is to examine the timing, duration and pattern of wing moult in the Stone-curlew and to relate these parameters to the breeding cycle of the study population.

METHODS

Our study was performed during 1998–2007 in the Taro River Regional Park (Parma, Italy; 44.74°N, 10.17°E; total area 25 km^2), which hosts a relatively large breeding population of Stone-curlews (more than 80 pairs, Pollonara *et al.* 2001), mainly nesting along the dry gravel riverbed. 141 birds were caught either while incubating, using a fall trap over the nest (April–July, n = 101), or in the post-breeding season, using mist-nets placed near late summer-autumn roosts (August–November, $n = 40$). For 21 birds which were trapped more than once the first retrap within each year was considered as a first capture and thus included in the analysis. This gave a total of 166 records, 119 for the breeding season and 47 for the post-breeding season. All the considered birds were at least in their second calendar-year. Juvenile birds trapped in the post-breeding season, as recognized by their plumage characteristics (see Prater *et al.* 1977), were excluded from the analysis. In this regard it should be noted that post-juvenile moult of Stone-curlew is a 'partial moult', involving only body feathers, some rectrices and some great coverts, while post-breeding moult is usually described as a 'complete moult' (Ginn & Melville 1983).

The stage of the moult of the remiges was described using the British Trust for Ornithology method (Ginn & Melville 1983) by allocating a score to each feather according to its state of growth (0 = old feather; 1 = feather in pin; 2 = brush to one-third grown; 3 = one-third to two-thirds grown; 4 = two-thirds to fully grown; 5 = new feather). For the purpose of the analysis the 10 innermost primaries (the vestigial eleventh was ignored), numbered from innermost to outermost, and the 12 outermost secondaries, numbered from outermost to innermost were considered. The timing and duration of moult was rigorously described only for the primaries, because they were completely replaced within one moult cycle (Cramp & Simmons 1983, Ginn & Melville 1983). Primary feather scores were converted to percentage mass grown using the percentage mass of each primary derived from Dawson (2005) and reported in Table 1 and the corresponding proportion of feather grown reported in Underhill & Zucchini (1988). The timing of primary moult was estimated according to the method of Underhill & Zucchini (1988) and Underhill *et al.* (1990). We restricted our analysis only to birds not yet

Table 1. Percentage mass of each primary feather in the Eurasian Stone-curlew derived from Dawson (2005, Figure 1).

Primary feather	% mass
1	4.5
2	5.0
3	6.0
4	7.3
5	8.9
6	11.0
7	12.6
8	14.2
9	15.1
10	15.4

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moulted or in moult (data type 5 of Underhill *et al.* 1990). We assumed that Stone-curlews moulting in our study area arrive with old primaries, but migrate away from this area soon after they have completed moult. This assumption is supported by the following two considerations. 1) Stone-curlews are recorded in our area from the beginning of February, well before the birds commence moult (Giunchi *et al.* pers. observ.). 2) The number of Stone-curlews recorded in the study area consistently decreased from the beginning of October, just when the moult cycle is completed or nearly completed (see below).

Because we lack data regarding secondary mass, the timing of secondary moult was described using moult scores. In order to speed-up the ringing procedures during incubation we did not record a secondary moult score for all birds (98 records were obtained for 89 individual birds).

By means of linear regression models we tested if the progress of secondary moult (sum of secondary moult scores) was affected by estimated onset date of primary moult, as expected, and by body mass (±1 g). Estimated onset dates *OD* were calculated as described in Newton & Rothery (2005): $OD = t - T \times PFMG$, where t = capture date (days), T = mean moult duration (days), and *PFMG* = percentage of primary feather mass grown. In all models, capture date was used as covariate. In order to meet the assumptions of linear models (normality and homoscedasticity) the dependent variable was transformed using the Box-Cox transformation (Sokal & Rohlf 1995). To select the model of maximal parsimony we used Akaike's Information Criterion corrected for small sample size (Burnham & Anderson 2002). All statistical analyses were performed using software R 2.6.0 (R Development Core Team 2007)

RESULTS

The parameters of primary moult estimated according to the Underhill-Zucchini model are given in Fig. 1. On the whole the fit of the model appears quite good, and most of the moult index

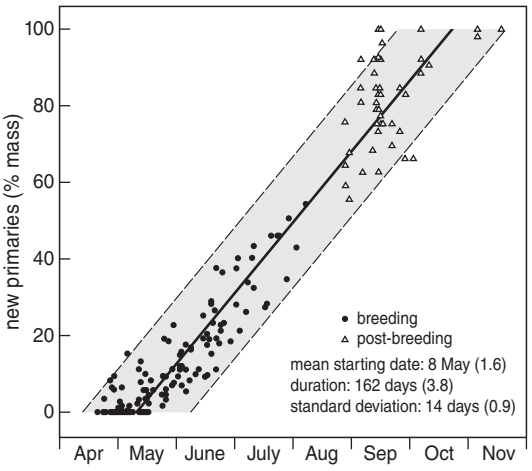


Figure 1. Relationship between the stage of primary moult and date. The solid line shows the mean rate of increase for the average bird, dashed lines are the 95% confidence intervals. Primary moult parameters are given with standard errors in parentheses.

values fall within the expected range of variation. As assumed by the Underhill-Zucchini model, the estimated onset dates (see Methods) did not show any obvious departure from the normal distribution (Shapiro-Wilk normality test, $W = 0.995$, $P = 0.93$). On average, primary moult started on 8 May and lasted more than five months, ending on 17 October. More than half of the moult process took place during the breeding season. Primaries were shed sequentially at a quite constant rate, except during the very beginning and the very end of the moult cycle (Fig. 2A). Usually only two, or sometimes three, feathers were growing at the same time during the whole process.

Although some secondaries were replaced as early as at the end of May, i.e. less than one month after the beginning of primary moult, most secondaries were shed during the post-breeding period (Fig. 3). After controlling for capture date, the best predictor of the progress of secondary moult was the estimated onset date of primary moult, as expected (Table 2). The relationship between these two variables was negative (model coefficient was –0.015, SE 0.004, $P < 0.001$), thus indicating that

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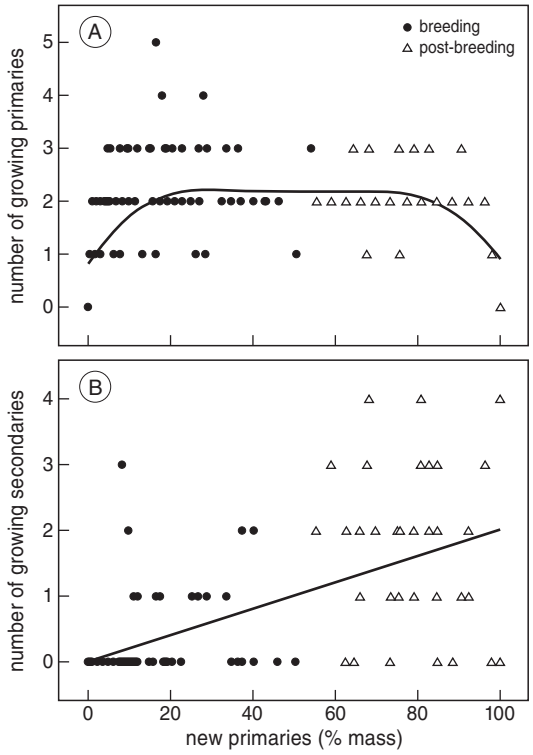


Figure 2. Relationship between the stage of primary moult and numbers of primary (A) and secondary (B) feathers growing simultaneously. Smoothing was calculated by means of a Gaussian kernel estimator and cross-validated choice of bandwidth (Bowman & Azzalini 1997).

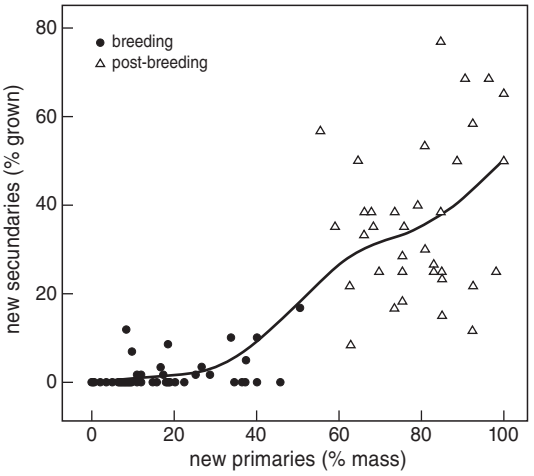


Figure 3. Relationship between the stage of primary moult and secondary moult. Smoothing as in Fig. 2.

Table 2. Analysis of the progress of secondary moult (feather score) using linear regression models evaluated using Akaike's Information Criterion for small sample sizes (AIC_c). k = number of parameters. ΔAIC_c = difference in AIC_c between a given model and the model with the lowest AIC_c. w_i AIC_c = AIC weights, which estimates the probability a specified model is the true model, given that one of the models being considered is indeed the true model.

Model[a]	k	ΔAIC_c	w_i AIC_c
Capture + Onset[b]	4	0.00	0.71
Capture + Onset + Mass	5	1.80	0.29
Capture	3	11.52	0.00
Capture + Mass	4	12.76	0.00

[a]Capture: capture date. Onset: estimated onset date of primary moult (see Methods). Mass: body mass at capture.
[b]AIC_c=164.4, residual SE = 0.56, adjusted R^2 = 0.81, $P < 0.001$.

birds starting primary moult earlier tended to show a higher percentage of moulted secondaries, even though the recorded variability was quite high. On the other hand, body mass did not seem to have any effect.

It should be noted that up to c. 80% of secondaries were replaced during the study period, thus indicating that the post-breeding moult of this population was incomplete. Indeed, most birds (55 out of 63 examined individuals, or 87.3%) trapped early in the breeding season (April–May) showed at least two different generations of feathers, the newest secondaries seemingly moulted at the same cycle of primaries, while older ones probably retained from the previous moult cycle.

It is interesting to note that among those individuals that could be precisely aged by means of colour-ringing, all birds with at least two generations of secondaries were at least in their third calendar-year, while no second-calendar birds showed any detectable lack of homogeneity within the secondary tract (Table 3). This highly significant

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Table 3. Number of generations recorded in the secondary tract in relation to the age of birds captured while incubating (Fisher's Exact Test, $P < 0.001$).

Age	No. of generations 1	2+
second calendar-year	3	0
> second calendar-year	0	17

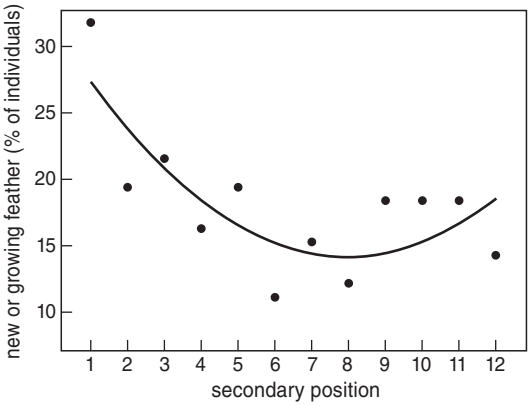


Figure 4. Percentage of birds with new or growing feathers in each considered secondary position. A quadratic regression line shows the underlying trend ($y = 0.3x^2 - 4.3x + 31.4$, $R^2_{adj} = 0.53$, $n = 98$).

association suggested that juvenile secondaries were not shed during the first winter. According to our data second-calendar birds could be identified by the age pattern of secondary feathers and/or by the presence of juvenile secondaries, which are usually narrower and more pointed than adult ones. Moreover, juvenile primaries (especially the tip of the 2–3 outer ones) of these birds are rather pointed, paler and much more worn than secondaries.

As observed for primaries, the moult rate of secondaries was quite slow, and usually no more than three secondaries were growing simultaneously (Fig. 2B). The moult sequence of secondaries was much more irregular than that of primaries. However, the percentage of birds with new or growing feathers in each position clearly indicated that innermost and outermost secondaries were shed more often than feathers belonging to the centre of this feather tract (Fig. 4).

DISCUSSION

As mentioned in the Introduction, this paper represents the first detailed description of the wing moult of the Stone-curlew, and thus it helps to fill a significant gap in the information regarding the biology of this species. Concerning primary moult, the fit of the Underhill-Zucchini model turned out to be quite good, and parameters were estimated with an acceptable precision, even though the sample size was only moderately large. While significant differences in the timing of wing moult among populations should be expected, as reported for other waders (e.g. Dunlins *Calidris alpina*, Holmgren *et al.* 2001), our estimates compare well to the data reported in the literature, although published ranges are based on small numbers of birds. Contrary to what is reported in Cramp & Simmons (1983) and Ginn & Melville (1983), we did not record any evidence regarding suspended moult (sensu Ashmole 1962), nor serially descendant moult following moult suspension. Given that most available moult data come from northern populations (e.g. BTO moult cards, Ginn & Melville 1983), it could be hypothesised that this moult strategy is more widespread in the northern part of the species' range, while at southern latitudes Stone-curlews could be favoured by a relatively long season of fair weather, which should guarantee enough time to complete the moult cycle. This hypothesis is supported by data from other waders, such as the Grey Plover *Pluvialis squatarola*, in which the frequency of birds with moult suspension is relatively high at higher latitudes (5–40%; Serra *et al.* 2006 and references therein) and near zero in south-eastern India (Balachandran *et al.* 2000).

One of the remarkable features of the pattern of moult here described is the extensive overlap between breeding and moulting. Indeed, especially

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in temperate regions, birds tend to delay moult until breeding has (nearly) finished (Morton 1992, Hemborg 1999, Hemborg *et al.* 2001, Arroyo *et al.* 2004), in order to reduce the overlap between two energy-demanding activities (Jenni & Winkler 1994, Moreno 2004 and references therein). European waders (families Haematopodidae, Recurvirostridae, Charadriidae, Scolopacidae) show various degrees of overlap between breeding and moult, but usually this overlap includes less than a quarter of the breeding period. The case of Stone-curlew here documented is noteworthy, because in our population (but see also Cramp and Simmons 1983) this overlap extends over most of the breeding season, excluding its very beginning. Primary moult is also quite slow (>5 months) compared to other wader species, which usually complete their moult cycle in less than 4 months; longer moult cycles are usually associated with moult suspension. It could be hypothesized that this slow and constant rate facilitates the overlap between breeding and moult by spreading the costs of moult homogeneously over the whole period and by avoiding the detrimental effects on feather quality of rapid moult cycles (Dawson *et al.* 2000, Serra 2001). It is interesting to note that, while usually avoided in most temperate species, an extensive moult–breeding overlap is relatively common among tropical birds (Foster 1974, Moreno 2004), where it is associated with small clutches and long breeding seasons (Foster 1974).

We tested whether a prolonged breeding season correlates with an extended moult–breeding overlap using literature data of 41 Palearctic wader species (Appendix 1). Indeed, moult–breeding overlap was positively correlated only with the length of the breeding season, using both the raw data and phylogenetically independent contrasts (Table 4). Female body mass and clutch mass were related to each other, but not to moult–breeding overlap (Table 4). Foster (1974) proposed that the above-mentioned set of traits is a means by which tropical birds may maximise their breeding output in areas where nesting success is strongly dependent on renesting potential. According to this hypothesis, the high nest predation in the tropics (Ricklefs 1969) may select for the capacity to renest repeatedly both by reducing the investment in single clutches and by prolonging the breeding season, thus favouring moult–breeding overlap. It is difficult to determine if the observed correlation between moult–breeding overlap and length of the breeding season in Palearctic waders could be explained by considering the selective effect of predation rate on renesting potential. Indeed the available data do not take into consideration the significant variability among populations both regarding breeding phenology (e.g. Cramp & Simmons 1983) and timing and duration of primary moult (e.g. Pienkowski *et al.* 1976, Underhill 2003). Moreover, it seems likely that other factors, such as ecological (e.g. latitude of breeding grounds, local climate, nutritional constraints) and physiological (e.g. activity of the immune system) constraints, should be taken into account (see also Moreno 2004). Testing these hypotheses is beyond the scope of this paper.

It should be noted, that among waders, the Stone-curlew represents a clear outlier, both considering the extent of the moult–breeding overlap (about 90% of the breeding season) and the strongly reduced parental investment in single clutches (c. 19% of female body mass). Moreover,

Table 4. Correlations between the length of the breeding season (in months), clutch mass, female body mass and extent of primary moult–breeding overlap (in months) in Palaearctic waders. Upper diagonal part: Spearman rank partial correlation using species level data (n = 41). Lower diagonal part: Spearman rank partial correlation using phylogenetically independent contrasts (n = 40). See Appendix 1 for the species and data used.

	Breeding season	Clutch mass	Female body mass	Overlap
Breeding season	-	–0.11	0.16	0.53**
Clutch mass	–0.22	-	0.71**	–0.06
Female body mass	0.22	0.70**	-	0.20
Overlap	0.44*	0.08	0.21	-

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as expected for an open-nester (Lack 1968, Ricklefs 1969, Martin & Li 1992, Bennett & Owens 2002), nest survival of the Stone-curlew is relatively low (only 40–60% of the nests produce at least one hatchling, Giunchi *et al.* unpubl. data), and this species has a very high potential for renesting (4 attempts per year, both considering replacement and second clutches, see also Vaughan & Vaughan Jennings 2005). Females usually replace their lost clutches in less than 15 days (Nethersole-Thompson & Nethersole-Thompson 1986; Giunchi *et al.* unpubl. data). This evidence is obviously only circumstantial, but the observed pattern is intriguing and surely deserves further investigation, possibly comparing data belonging to different populations of Stone-curlew.

Even though the moulting process began while birds were still breeding, most of secondary feathers were moulted during the post-breeding season. As observed for primaries, moult rate of secondaries was slow, and this could explain why apparently only some of these feathers were replaced on the breeding grounds. Indeed, the data at hand suggest that Stone-curlews shed secondaries before starting autumn migration and probably arrested this process at the end of primary moult (the last record of birds actively moulting secondary feathers was from the beginning of October). Even though we have no data regarding moult on the wintering grounds, moult suspension seems unlikely since we did not record any birds showing secondaries distinctly younger than the not yet moulted primaries. Interestingly, juveniles do not replace their secondary feathers until their second year of life, and thus they could be easily recognized as having homogeneous secondary feathers till late spring.

To our knowledge, this is the first time that partial moult of secondary feathers has been described in Stone-curlew, even though this feature is not uncommon among medium-large waders (see e.g. the Golden Plover *Pluvialis apricaria*, Cramp & Simmons 1983) and may be selected for to spread the costs of moult over a long time period (see Herremans 2000 and references therein). In the Stone-curlew this strategy could be facilitated also by secondaries needing less quick replacement due to moderate abrasion (Giunchi *et al.* pers. observ.), given the limited rubbing against vegetation (our Stone-curlews inhabit open habitat), and the reduced sun exposition (in folded wing, secondaries are completely concealed by long tertials and scapulars). Secondary moult shows large between-individual variation both in the number of retained feathers, varying between 2 and 10 (median 6.5, $n = 24$), and in its sequence, although it tended to follow the pattern recorded for other waders (Prater *et al.* 1977). This between-individual variation may come about by timing differences, as birds starting moult earlier may have more time to complete the moult of both primaries and secondaries (note that the progress of secondary moult and the onset of primary moult were significantly correlated). Moreover some degree of complementary moult could not be excluded, because in only a few cases we were able to distinguish three generations among old secondaries. Unfortunately, we have too few data regarding the reproductive output of the observed birds to test if parental investment might constitute a severe constraint on wing moult, as otherwise observed for other species (e.g. Pietiaeinen *et al.* 1984, Hemborg & Lundberg 1998). Clearly the resource allocation between current reproduction and moult in the Stone-curlew deserves further investigations.

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SAMENVATTING

In het Regionale Park Taro (ten westen van Parma, Italië) komt de Griel *Burhinus oedicnemus* talrijk voor. In de zomers van 1998–2007 werden er 141 vogels gevangen om het ruistadium van de vleugelpennen vast te stellen. De rui van de handpennen begon begin mei en eindigde pas in oktober, daarmee een groot deel van de broedtijd overlappend. De rui van de handpennen verliep volgens een vast patroon, de vervanging van de armpennen was veel onregelmatiger. Bovendien werd binnen een zelfde seizoen slechts een deel van de armpennen geruid, waarbij vooral de middelste pennen werden overgeslagen. Vogels hadden daarom armpennen van verschillende leeftijd. Omdat jonge vogels hun armpennen pas na de eerste winter begonnen te vervangen, bood dit de mogelijkheid vogels in hun tweede kalenderjaar van oudere vogels te onderscheiden. Gelijktijdig ruien en broeden, zoals Grielen doen, is betrekkelijk ongewoon onder steltlopers. Door de rui over een lange periode uit te smeren kunnen de energetische kosten per tijdseenheid mogelijk verlaagd worden. Dit zou een aanpassing kunnen zijn om binnen een zelfde seizoen enkele broedpogingen te doen. Steun voor deze veronderstelling komt uit een vergelijking tussen 41 steltlopersoorten: hoe langer het broedseizoen duurt, des te groter is de overlap van rui van de handpennen en broedactiviteiten. (DH)

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Appendix 1. Palaearctic waders considered in the analysis (n = 41) belonging to seven families (del Hoyo *et al.* 1996). Variables were derived from Cramp & Simmons (1983): (1) length of the breeding season (accuracy by 0.5 months): period of egg laying and caring for young, excluding outliers (early eggs and late broods); (2) modal clutch mass (by 1 g); (3) modal female body mass (by 1 g); (4) extent of the overlap (by 0.5 months) between primary moult and the breeding season (excluding outlying data for the onset and termination of primary moult). Analyses were performed by means of the Spearman rank partial correlation both using species level data and phylogenetically independent contrasts (Felsenstein 1985). These contrasts were calculated by considering the phylogenetic tree reported in Thomas *et al.* (2004), randomly resolving all multichotomies. Analyses were performed using the R-package APE 2.0-2 (Paradis *et al.* 2004).

Species	Family	Breeding season (months)	Clutch mass (g)	Female body mass (g)	Moult–breeding overlap (months)
Burhinus oedicnemus	Burhinidae	5	84	449	4.5
Haematopus ostralegus	Haematopodidae	4.5	140	616	2.5
Himantopus himantopus	Recurvirostridae	3	88	180	0.5
Recurvirostra avosetta	Recurvirostridae	4	129	325	1
Vanellus spinosus	Charadriidae	5	64	148	3
Vanellus vanellus	Charadriidae	5	100	217	3
Charadrius hiaticula	Charadriidae	5	46	65	2
Charadrius dubius	Charadriidae	5	31	39	2
Charadrius alexandrinus	Charadriidae	4	27	60	1.5
Eudromias morinellus	Charadriidae	3.5	48	116	1.5
Pluvialis apricaria	Charadriidae	3.5	139	191	3
Pluvialis squatarola	Charadriidae	3	140	220	0.5
Cursorius cursor	Glareolidae	4.5	28	128	0
Glareola nordmanni	Glareolidae	2.5	44	96	0
Glareola pratincola	Glareolidae	3.5	30	74	1
Dromas ardeola	Dromadidae	4.5	45	325	3
Numenius arquata	Scolopacidae	3.5	300	788	1
Numenius phaeopus	Scolopacidae	3	200	398	0
Limosa lapponica	Scolopacidae	2.5	148	273	1
Limosa limosa	Scolopacidae	3.5	162	315	1.5
Scolopax rusticola	Scolopacidae	5	100	320	1.5
Gallinago media	Scolopacidae	3.5	82	190	1.5
Gallinago gallinago	Scolopacidae	4.5	68	112	1
Lymnocryptes minimus	Scolopacidae	3	56	68	2
Tringa hypoleucos	Scolopacidae	3.5	48	50	0
Arenaria interpres	Scolopacidae	2	72	115	0
Limicola falcinellus	Scolopacidae	2.5	36	39	0
Philomachus pugnax	Scolopacidae	3	88	118	1
Calidris minuta	Scolopacidae	2.5	25	31	0
Calidris alpina	Scolopacidae	2.5	40	55	0
Calidris maritima	Scolopacidae	2	52	70	0
Calidris temminckii	Scolopacidae	2.5	24	28	0
Phalaropus fulicaria	Scolopacidae	2	31	61	0.5
Phalaropus lobatus	Scolopacidae	2.5	25	35	0
Tringa glareola	Scolopacidae	3	56	60	0
Tringa erythropus	Scolopacidae	3	98	157	2
Tringa totanus	Scolopacidae	4	89	135	1
Tringa nebularia	Scolopacidae	3.5	145	200	0.5
Tringa stagnatilis	Scolopacidae	3.5	56	76	0
Tringa ochropus	Scolopacidae	3	62	85	1
Tringa cinerea	Scolopacidae	2.5	52	75	0

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