

THE TIMING AND PATTERN OF MOULT OF FLIGHT FEATHERS OF EUROPEAN STORM-PETREL *HYDROBATES PELAGICUS* IN ATLANTIC AND MEDITERRANEAN BREEDING AREAS

Beatriz ARROYO*, Eduardo MÍNGUEZ**¹, Luis PALOMARES*** & Jesús PINILLA***

SUMMARY.—*The timing and pattern of moult of flight feathers of European Storm-petrel Hydrobates pelagicus in Atlantic and Mediterranean breeding areas.*

Aims: We describe the pattern and timing of moult in European Storm-petrels *Hydrobates pelagicus*.

Location: Benidorm Island (eastern Spain, Mediterranean Iberian coast) and Vizcaya (northern Spain, Atlantic Iberian coast).

Methods: Birds were caught with mist-nets set in breeding colonies and the state of flight feathers was scored. Primary, secondary and tail moult scores and the degree of moult asymmetry and an index of raggedness were calculated.

Results: Moulting in the primaries was ascendant, whereas in the secondaries it progressed from three different loci, and was irregular in the tail. During the breeding season, the level of raggedness was higher in the primaries than in the secondaries or the tail, but primary moult was significantly more symmetrical than in any of the other feather tracts. Primary moult started on average in late June in Benidorm, and in late July in Vizcaya. Secondary and tail moult in Benidorm started on average a month after onset of primary moult.

Conclusions: Average onset of primary moult differed among areas, being earlier in southern than in northern areas. These different patterns of moult among areas are probably due to differences in breeding phenology.

Key words: Atlantic, European Storm-petrel, *Hydrobates pelagicus*, Mediterranean, moult, phenology.

RESUMEN.—*Patrón e inicio de la muda en las plumas de vuelo del Paíño Europeo Hydrobates pelagicus en áreas de reproducción Atlánticas y Mediterráneas.*

Objetivos: Se describen los patrones, (secuencia, simetría e irregularidad) y las fechas de inicio de la muda en Paíños Europeos *Hydrobates pelagicus* durante la estación reproductora.

Localidad: Isla de Benidorm (este de España, costa mediterránea ibérica) e islotes de Vizcaya (norte de España, costa atlántica ibérica).

Métodos: Las aves se capturaron con redes en las colonias reproductoras y se categorizó el estado de las plumas de vuelo. Se calcularon las puntuaciones de la muda de las primarias, secundarias y de la cola, así como el grado de asimetría y un índice de irregularidad. Se estimó la fecha de comienzo de muda mediante un análisis *probit* usando una regresión binaria, codificando como 0 aquellas aves que no habían comenzado la muda y como 1 aquellas que sí.

Resultados: La muda de las primarias fue ascendente, mientras que en las secundarias progresó desde tres diferentes loci, y fue irregular en la cola. Durante la estación reproductora, el nivel de irregularidad fue mayor en las primarias que en las secundarias o la cola, pero la muda de las primarias fue significativamente más simétrica. La muda de las primarias comenzó de media a finales de Junio en Benidorm (fecha juliana media (DS, 176,0 (15,9, Tabla 1, Fig. 1) y a finales de Julio en Vizcaya (fecha juliana media (DS, 202,9 (10,2, Fig.2). Las secundarias y las plumas de la cola empezaron a mudarse en Benidorm un mes después de comenzar a mudar las primarias.

Discusión: El número de loci en las secundarias de las aves capturadas en el Mediterráneo fue menor al descrito en otros petreles. La estrategia de muda encontrada minimiza la asimetría en las zonas de las alas más alejadas del cuerpo, donde presumiblemente tendría un mayor coste aerodinámico. En promedio, el inicio de la muda de las primarias difirió entre zonas, ocurriendo antes en el sur que en el norte del área de distribución

* Centre for Ecology and Hydrology, Banchory, Hill of Brathens, AB31 4BW Scotland.

** Área de Ecología, Dpto. Biología Aplicada, Universidad Miguel Hernández, Avda. de la Universidad s/n, Edif. La Galia, E-03202 Elche, Alicante, Spain.

*** Centro de Migración de Aves, Sociedad Española de Ornitología/BirdLife, Melquiades Biencinto 34, E-28053 Madrid, Spain.

¹ Corresponding author: E-mail: eminguez@umh.es

(Fig. 3). Estas diferentes fechas de comienzo de la muda entre áreas pueden ser debidas a diferencias en la fenología reproductora. Sin embargo, los resultados sugieren que el periodo entre la fecha de puesta y el comienzo de la muda de las primarias es menor en las poblaciones sureñas.

Palabras clave: Atlántico, fenología, *Hydrobates pelagicus*, Mediterráneo, Muda, Paño Europeo.

INTRODUCTION

Moult is one of the most energetically demanding activities in the avian annual cycle (Payne, 1972; Murphy & King, 1992), together with reproduction and, in migratory species, migration. Timing of these activities is usually adjusted to minimise the overlap in their energetic demands (Pietiäinen *et al.*, 1984; Murphy & King, 1992; Espie *et al.*, 1996; Hemborg *et al.*, 2001). Thus, onset and rate of moult might be constrained by the timing of breeding and/or migration (Yuri & Rohwer, 1997). For species that spend most of the time flying and that forage on the wing, like Procellariiformes (Warham, 1990), the constraints are not only the energy to replace the feathers, but the extra costs in flying with gaps in the wing (Tucker, 1991; Swaddle & Witter, 1997). Thus moult of flight feathers in Procellariiformes often takes a longer time than in other birds of similar size (Cramp & Simmons, 1977; Warham, 1996).

The European Storm-petrel *Hydrobates pelagicus*, is unusual among migratory Procellariiformes in starting wing moult during breeding (Warham, 1996). Nevertheless, relatively little is known about moult in the European Storm-petrel (Baker, 1993; Amengual *et al.*, 1999; Bolton & Thomas, 2001), and no studies have assessed quantitatively whether moult patterns vary among populations. The main study on moult of this species (Scott, 1970) was based in birds breeding on Skokholm, south Wales, where fledging occurs mainly in October, after which birds undertake long migratory flights to southern Africa (Cramp & Simmons, 1977). In Northern Spain, the peak of fledging for this species occurs in early September (Mínguez *et al.*, 1992), and birds presumably also migrate south after breeding. European Storm-petrels breeding in the Western Mediterranean sea fledge their broods mainly in August (Mínguez, 1994), and might be partially sedentary or perform only short migratory trips (Cramp & Simmons, 1977, Hashmi & Fliege, 1994).

In this study we describe the patterns of moult based on data obtained during the reproductive season on Atlantic and Mediterranean Spanish breeding sites. Moult onset, sequence, symmetry and raggedness for each feather tract are included.

METHODS

Study areas

The study took place on Benidorm Island, eastern Spain (38°30' N, 0°08'E) where about 400 pairs of European Storm-petrel breed (Mínguez, 1994), and in four different breeding colonies on the islets in Vizcaya, Basque country, (Northern Spain) between Cape Villano (43°27'N, 2°56'W) and Cape Ogoño (43°25'N, 2°39'W), (Mínguez *et al.*, 1992; Franco *et al.*, 2004). In Benidorm, 211 birds were caught between 9-12 July 1994, and 521 birds between 13-16 July, 22 July and 5-8 August 1995. Additionally, moult was recorded in 88 breeding birds removed from monitored nesting burrows (42 in 1994 and 46 in 1995). In the Basque coast, 221 birds were mist-netted between 11 July and 24 August 1990-91. All birds were ringed. Birds were caught with mist-nets set in breeding colonies. No play-back of vocalisations was used, since the use of tape lures increases the catch rate but decreases the proportion of local breeders (Mainwood, 1976; Furness & Baillie, 1981; Fowler *et al.*, 1982).

Moult data

The state of each flight feather was scored from 0 to 5, where 0 represents an old feather, 1-4 represent progressions of feather growth, and 5 a fully grown new feather (Ginn & Melville, 1983). Primaries were numbered descendantly from 1 (the innermost) to 10 (the outermost); secondaries, including the tertials, were numbered ascendantly from 1-13 (1 being the outermost); and rectrices were numbered des-

cendantly from 1 (innermost) to 6 (outermost), for each side of the tail. Moulting of the vestigial outermost primary (P11) was not recorded. The Primary Moulting Score (PMS) was calculated for each bird as the sum of the moulting scores of the ten large primaries in one wing, and the range of PMS was thus 0-50 (Ginn & Melville, 1983). Similarly, we calculated a Secondary Moulting Score (SMS, range 0-65), and a Tail Moulting Score (TMS, range 0-30) for each bird. Primary moulting was recorded in all birds, but secondary or tail moulting only in a sample of Benidorm birds. In the Vizcaya islets, only primary moulting scores were analysed (no trapped birds had started secondary moulting, and tail moulting was not recorded). Sample sizes thus vary according to feather tract. When moulting scores differed between wings of the same bird, an average of the two scores was used in analyses. However, we also calculated for each bird the degree of moulting asymmetry, as the absolute value of the difference in score between both wings for each tract. We categorised birds as symmetric (if asymmetry score was 0), or asymmetric (asymmetry score > 0).

An index of raggedness (Haukioja, 1971) was calculated for each feather tract (primaries, secondaries and tail), using the sum of values for each feather of the tract. Each feather was scored with values ranging from 0 to 4 according to their moulting score, where 0 indicates a feather of full length (whether old or new), 4 indicates a feather at the first stage of growth (moulting score 1), 3 a feather with moulting score 2, 2 a feather with moulting score 3, and 1 a feather with moulting score 4. For each individual, the sum of raggedness scores from both sides (left and right) of each tract was used as an overall index of raggedness.

Analyses

We determined the order in which secondary feathers or tail feathers were moulted by calculating the accumulated scores for each numbered feather, and ranking each according to their accumulated scores (Arroyo & King, 1996). The relative order in the accumulated moulting score indicates feathers that are more advanced in the moulting process, and thus that were moulted earlier. The relationship between raggedness and initial moulting score was analysed with linear relationships.

The variation of moulting scores with date is non-linear. We obtained an estimate of the mean and standard deviation of the moulting start date for each population or feather tract using a binary regression with response probability linear on a probit scale (using the PROBIT procedure in SAS 8.0). The intercept (a) and slope (b) of such a regression are related to the mean and standard deviation of the start date distribution as $x = -a/b$ and $SD = 1/b$ (Rothery & Newton, 2002). For such analyses, birds were coded as 0 (not having started moulting) or 1 (having started moulting). No differences in moulting onset were found between years, when controlling for date (PROBIT, Chi-square = 0.01, $P = 0.89$), so data from both years were combined for analyses. Date is expressed as Julian date, with 1 = 1 January, throughout the paper.

RESULTS

Moulting patterns: sequence, raggedness and moulting symmetry

Moulting in the primary feathers was ascendant except in two birds, where P2 was dropped before P1. Moulting in the secondaries progressed from three loci. It started at S12, and was followed quickly by S5. Moulting from both centres was centrifugal (progressing simultaneously inwards and outwards), but proceeded apparently more quickly outwards from S12 (as moulting scores were higher on S11 than S13), and inwards from S5. Moulting at the third centre, S1, only started after at least two feathers had been dropped from the other two centres. Pattern for tail moulting varied among individuals, but in general started with T2, followed closely by T1. T6 was moulted on average after T3, and T4 and T5 were usually the last to be moulted.

Raggedness increased with increasing state of moulting (linear regression, $F_{1,703} = 46.7$, $P < 0.001$ for primaries; $F_{1,263} = 302.4$, $P < 0.001$ for secondaries; $F_{1,251} = 11.4$, $P < 0.001$ for tail feathers). For birds that had started moulting in each feather tract, 65% of birds had asymmetric primary moulting (up to 12 points difference, $n = 705$), 72% had asymmetric secondary moulting (up to 11 points differences, $n = 264$), and 92% had asymmetric tail moulting (up to 10 points difference, $n = 253$).

Moult timing

Primary moult on Benidorm started on average on 25 June (mean Julian date \pm *SD*, 176.0 \pm 15.9, from the intercept and slope of the PROBIT analyses; Table 1 and Fig. 1). Excluding from the analyses the birds trapped in the nesting burrows, average date of onset of moult was 168.3 \pm 19.2. Secondary moult started on average one month later (202.4 \pm 6.8), as did tail moult (207.7 \pm 18.4).

Birds in the Vizcaya islets started moult on average almost a month later than in Benidorm (22 July, mean Julian date \pm *SD*, 202.9 \pm 10.2, Fig. 2). The proportion of birds in moult during the breeding season in Benidorm Island, Basque colonies and Wales (Scott, 1970) is compared in Fig. 3.

DISCUSSION

Feather loss during moult decreases flight performance, and increases flight costs (Tucker, 1991; Swaddle & Witter, 1997). The secondaries and the tail are the feather tracts that provide much of the lift required for flight (Newton & Marquiss, 1982), so it may be especially important to minimise gaps in those tracts. In accordance with this hypothesis, raggedness scores in the secondaries and tail were lower in comparison with those of primaries, particularly when moult and breeding were still overlapping, as in Benidorm Island in July-August. The presence of several loci of moult in the secondaries is a common pattern in birds with long wings (*e.g.* Edelstam, 1984), including Procellariiformes (Mayaud, 1950; Stresemann & Stresemann, 1966), and may reflect the need of minimising big gaps in that tract, when several feathers are moulted simultaneously. However, the number of loci observed in European Storm-Petrels in the Mediterranean was lower than that described in other petrel species (Stresemann & Stresemann, 1966), which suggests that the constraints may be lower in this species, or at least in Benidorm birds.

Moult symmetry was higher in the primaries than in the secondaries or tail feathers. Asymmetry in flight feathers has associated aerodynamic costs, and reduces manoeuvrability (Thomas, 1993; Swaddle *et al.*, 1996). Additionally, costs of asymmetry, particularly in tracts asso-

ciated to locomotion, should be increasingly greater when occurring away from the centre of gravity (Møller & Swaddle, 1997). The higher level of symmetrical moult in the primaries in relation to secondaries or tail feathers supports the prediction that birds try to minimise asymmetry where the functional importance of the feather is greatest, *i.e.* in the feathers furthest away from the body axis (Møller & Swaddle, 1997).

Moult of European storm-petrels started on average 27 days later in Vizcaya than in Benidorm. Additionally, onset of moult in Wales was on average one month later than in the Vizcaya islets (Scott, 1970; Fig. 3) and even more in Scotland (D. Okill, *pers. obs.*). Age and reproductive status are well known to influence onset of moult: breeding birds moult on average later than non-breeding birds (*e.g.* Arroyo & King, 1996; Bolton & Thomas, 2001; Struwe-Juhl & Schmidt, 2003). Our sample mainly included birds of unknown status. Therefore, regional differences may have appeared also if the sample of Benidorm included proportionally more breeders than the sample in Vizcaya islets. However, methods of trapping in both areas were similar, breeding densities in both study areas are also similar, and the proportion of birds with different brood patches was similar between both areas (own *unpubl. data*). The sample in Benidorm included birds trapped in the nest, which was not included in Vizcaya islets. However, analyses excluding those birds only emphasized the results. Amengual and collaborators (1999) also found in Cabrera Archipelago that Mediterranean European Storm-petrels moult their primaries during the breeding period. Thus, we are confident that our results indicate true regional differences in onset of moult.

Onset of moult is usually related to breeding phenology (Newton & Marquiss, 1982; Morton, 1992; Hemborg, 1999). In storm-petrels, moult usually starts late in the breeding season or even after the end of it (Mayaud, 1950; Scott, 1970). For European Storm-petrel, the peak of hatching occurs in mid June in Benidorm (Mínguez, 1994), in early July in the Vizcaya islets (Mínguez *et al.*, 1992), and in early August in southern Wales (Scott, 1970). Differences in the onset of moult are therefore partly related to variations in the breeding phenology between areas, as described for other species

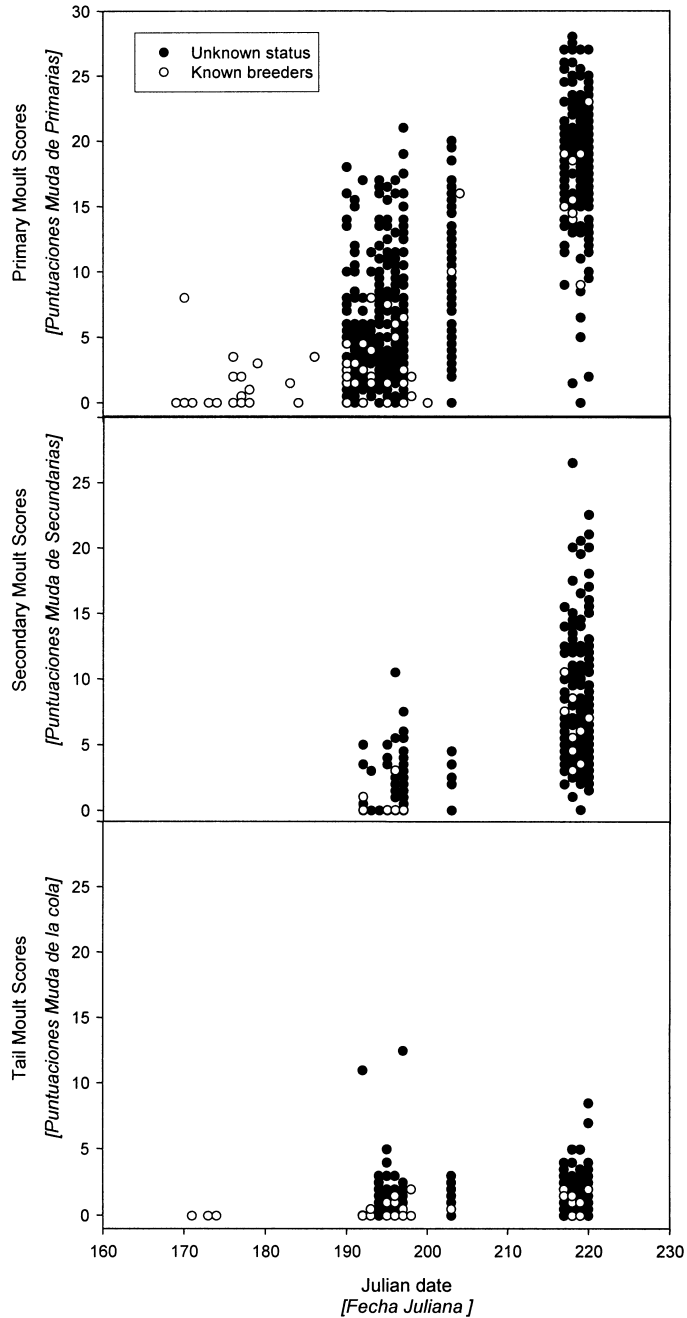


FIG. 1.—Primary, Secondary and Tail Molt Scores in European Storm-petrels in Benidorm Island in relation to Julian date. Data from birds removed from breeding burrows indicated with white circles (known breeders), birds trapped with mist-nets outside the colony with black circles (unknown status).
 [Valores de muda de primarias, secundarias y cola en Paños Europeos de la Isla de Benidorm en relación con la fecha Juliana. Los datos recogidos de aves reproduciéndose en sus madrigueras se indican con círculos blancos, las aves atrapadas con redes japonesas fuera de la colonia con círculos negros.]

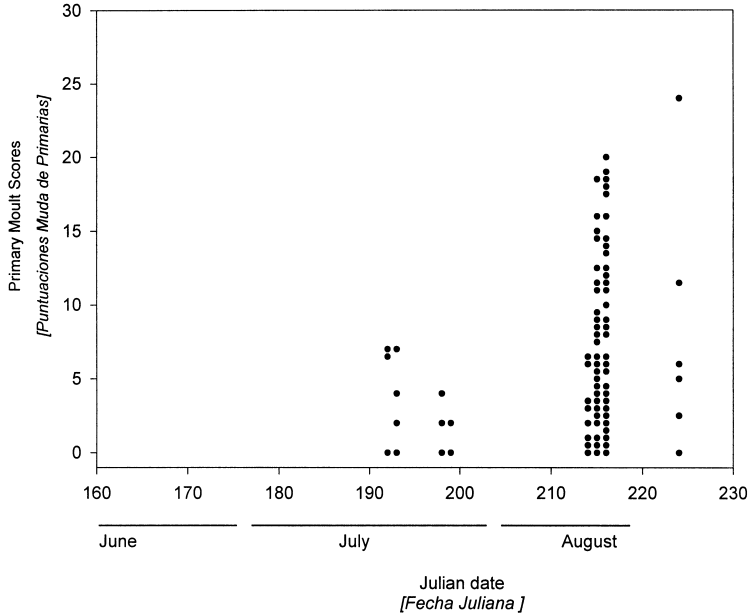


FIG. 2.—Primary Moulting Scores in European Storm-petrels mist-netted outside breeding colonies in Vizcaya in relation to Julian date.
 [Valores de muda de primarias en Paños Europeos atrapados con redes japonesas fuera de las colonias de cría en Vizcaya en relación con la fecha juliana.]

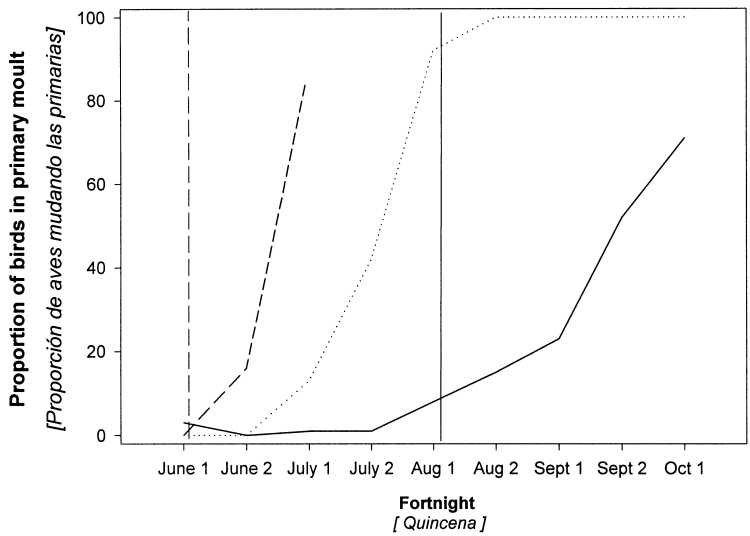


FIG. 3.—Cumulative proportion of trapped European Storm-petrels where primary moulting had started in Benidorm Island, Vizcaya islets (this study) and Wales (Scott, 1970). Vertical lines indicate the average hatching date in each site.
 [Proporción acumulada de Paños Europeos atrapados cuando la muda de las primarias ha comenzado en la Isla de Benidorm, islotes de Vizcaya (este estudio) y Gales (Scott, 1970). Las líneas verticales indican la fecha de puesta promedio en cada sitio.]

TABLE 1

Summary of fitted binary regression Probit analyses for the start of moult and the date when reaching PMS 20 in European Storm Petrels (see text for details).

[Resumen de los ajustes de los análisis de una regresión Probit entre el comienzo de la muda y la fecha en la que PMS 20 se desarrolló en Paños Europeos (véase el texto)].

Feather tract (site) [Zona de plumas (lugar)]	Onset (Started/Not started) [Comienzo (iniciada/ sin iniciar)]		PMS 20 (Reached/Not reached) [PMS 20 (desarrollada/ no desarrollada)]	
	a ± SE	b ± SE	a ± SE	b ± SE
Primaries (Benidorm) [Primarias (Benidorm)]	11.07 ± 3.089	-0.063 ± 0.016	27.42 ± 3.032	-0.125 ± 0.014
Primaries (Vizcaya) [Primarias (Vizcaya)]	19.89 ± 2.252	-0.099 ± 0.011	21.72 ± 5.538	-0.092 ± 0.025
Secondaries (Benidorm) [Secundarias (Benidorm)]	29.44 ± 2.579	-0.146 ± 0.013		
Tail (Benidorm) [Cola (Benidorm)]	11.30 ± 1.020	-0.054 ± 0.005		

(Yuri & Rohwer, 1997). However, our results also suggest that there was a shorter gap between average hatching date and the average onset of primary moult in southern than in northern populations.

Migratory constraints might also play a role explaining these differences in moult timing. Migratory birds have to face both time and energetic constraints to moult, and non-migrants may be able to start moult sooner after breeding, and complete moult earlier in the non-breeding season (O'hara *et al.*, 2002). It is not known whether the Mediterranean populations of European Storm-petrels are migratory. Large movements of European Storm-petrels out of the Mediterranean occur in autumn (Cramp & Simmons, 1977), which suggests that at least some of the birds migrate. However, birds also occur in the Mediterranean in winter, and it is likely that part of the population is sedentary or disperses short distances (Hashmi & Fliege, 1994). In the Basque region, Storm-petrels were actively moulting the secondaries in December (E. Mínguez, *pers. obs.*) and in Wales it was suggested that no complete secondary moult was achieved at the end of the winter (Scott, 1970). The latter also supports the idea that moult is constrained because of migration in northern areas, whereas this constraint is mitigated in the Mediterranean, allowing a larger overlap between moult and breeding.

ACKNOWLEDGEMENTS.—Jon King inspired this project and participated actively throughout it. Benigno Asensio, Paco Cantos, Txuso García, Félix Martínez, Stefano Mazzeletti, Alfredo Ortega, Rosa Rodríguez and Sol Sotillos helped with fieldwork. We also thank the Conselleria de Medio Ambiente de la Generalitat Valenciana for permission to work on Benidorm Island, and the British Ecological Society for financial support in 1995. We thank Mike Harris, François Mougeot and Mick Marquiss for comments on a previous version of the manuscript, and two anonymous referees commented and improved this version.

BIBLIOGRAPHY

- AMENGUAL, J. F., GARGALLO, G., SUÁREZ, M., BONNIN, J., GONZÁLEZ, J. M., REBASSA, M. & McMINN, M. 1999. The Mediterranean Storm Petrel *Hydrobates pelagicus melitensis* at Cabrera archipelago (Balearic Islands, Spain): breeding moult, biometry and evaluation of the population size by mark and recapture techniques. *Ringing & Migration*, 19: 181-190.
- ARROYO, B. E. & KING, J. R. 1996. Age and sex differences in molt of the Montagu's Harrier *Circus pygargus*. *Journal of Raptor Research*, 30: 161-184.
- BAKER, J. K. 1993. *Identification Guide to European Non-Passerines*. BTO Guide 24. BTO, Thetford.
- BOLTON, M. & THOMAS, R. 2001. Molt and ageing of Storm Petrels *Hydrobates pelagicus*. *Ringing & Migration*, 20: 193-201.
- CRAMP, S. & SIMMONS, K. E. L. (Eds.) 1977. *The Birds of the Western Palearctic, vol. 1*. Oxford University Press. Oxford.

- EDELSTAM, C. 1984. Patterns of moult in large birds of prey. *Ann. Zool. Fennici*, 21: 271-276
- ESPIE, R. H. M., JAMES, P. C., WARKENTIN, I. G. & OLIPHANT, L. W. 1996. Ecological correlates of molt in Merlins (*Falco colombarius*). *The Auk*, 113: 363-369.
- FOWLER, J. A., OKILL J. D. & MARSHALL, B. 1982. A Retrap Analysis of Storm Petrels Tape-lured in Shetland. *Ringling & Migration*, 4: 1-7.
- FRANCO, J., ETXEZARRETA, J., GALARZA A., GOROSPE G., & HIDALGO, J. 2004. Seabird populations. In: A. Borja & M. Collins, M. (Eds.): *Oceanography and Marine Environment of the Basque Country*, pp. 515-529. Oceanography Series nº 70. Elsevier. Amsterdam.
- FURNESS, R. W. & BAILLIE, S. R. 1981. Factors affecting Capture Rate and Biometrics of Storm Petrels on St Kilda. *Ringling & Migration*, 3: 137-148.
- GINN, H. B. & MELVILLE, D. S. 1983. *Moult in Birds*. B.T.O. Guide 19. Tring: British Trust for Ornithology.
- HASHMI, D. & FLIEGE, G. 1994. Herbstzug der Sturmschwalbe (*Hydrobates pelagicus*) in der Meeresenge von Gibraltar. *Journal für Ornithologie*, 135: 203-207.
- HAUKIOJA, E. 1971. Processing moult card data with reference to the Chaffinch *Fringilla coelebs*. *Ornis Fennica*, 48: 25-32
- HEMBORG, C. 1999. Sexual differences in moult-breeding overlap and female reproductive costs in pied flycatchers, *Ficedula hypoleuca*. *Journal of Animal Ecology*, 68: 429-436.
- HEMBORG, C., SANZ, J. J. & LUNDBERG, A. 2001. Effects of latitude on the trade-off between reproduction and moult: a long-term study with pied flycatcher. *Oecologia*, 129: 206-212.
- MAINWOOD, A. R. 1976. The movements of Storm Petrels as shown by ringing. *Ringling & Migration*, 1: 98-104.
- MAYAUD, N. 1950. Nouvelles précisions sur la mue des procellariens. *Alauda*, 18: 222-233.
- MÍNGUEZ, E. 1994. Censo, cronología de puesta y éxito reproductor del Paño común (*Hydrobates pelagicus*) en la isla de Benidorm (Alicante, E de España). *Ardeola*, 41: 3-12.
- MÍNGUEZ, E., ELIZONDO, R. S., BALERDI, M. & SABBAN, P. 1992. Statut, distribution, taille de la population et phénologie de la reproduction du Pétrel tempête *Hydrobates pelagicus* dans la communauté basque (Espagne). *L'Oiseau et R.F.O.*, 62: 234-246.
- MØLLER, A. P. & SWADDLE, J. P. 1997. *Asymmetry, developmental stability, and evolution*. Oxford University Press. Oxford.
- MORTON, M. L. 1992. Control of postnuptial molt in the mountain white-crowned sparrow: a perspective from field data. *Ornis Scandinavica*, 23: 322-327.
- MURPHY, M. E. & KING, J. R. 1992. Energy and nutrient use during molt by white-crowned sparrows *Zonotrichia leucophrys gambelii*. *Ornis Scandinavica*, 23: 304-313.
- NEWTON, I. & M. MARQUISS. 1982. Molt in the Sparrowhawk. *Ardea*, 70: 163-172.
- O'HARA P. D., LANK D. B. & DELGADO F. S. 2002. Is the timing of moult altered by migration? Evidence from a comparison of age and residency classes of western sandpipers *Calidris mauri* in Panama. *Ardea*, 90: 61-70.
- PAYNE, R. B. 1972. Mechanics and control of moult. In: D. S. Farner & J. R. King (Eds.): *Avian biology*. Academic Press. New York
- PIETIÄINEN, H., SAUROLA, P. & KOLONEN, H. 1984. The reproductive constraints on moult in the Ural Owl (*Strix uralensis*). *Annales Zoologici Fennici*, 21: 277-281.
- PIMM, S. 1976. Estimation of the duration of bird moult. *Condor*, 78: 550.
- ROTHERY, P. & I. NEWTON, 2002. A simple method for estimating timing and duration of avian primary moult using field data. *Ibis*, 144: 526-528.
- SCOTT, D. A. 1970. *The breeding biology of the Storm Petrel*. Unpubl. D. Phil. Thesis, University of Oxford.
- STRESEMANN, E. & STRESEMANN, V. 1966. Die Mauser der Vogel. *Journal für Ornithologie*, 107: 1-447.
- STRUWE-JUHL B. & SCHMIDT R. 2003. Flight feather moult of White-tailed Eagle (*Haliaeetus albicilla*) in Schleswig-holstein, Germany. *Journal für Ornithologie*, 144: 418-437.
- SWADDLE, J. P. & WITTER, M. S. 1997. The effects of moult on the flight performance, body mass, and behaviour of European starlings (*Sturnus vulgaris*): an experimental approach. *Canadian Journal of Zoology*, 75: 1135-1146.
- SWADDLE, J. P., WITTER, M. S., CUTHILL, I. C., BUDDEN, A., & MCCOWEN, P. 1996. Plumage condition affects flight performance in Common Starlings: implications for developmental homeostasis, abrasion and moult. *Journal of Avian Biology*, 27: 103-111.
- THOMAS, A. L. R. 1993. The aerodynamic costs of asymmetry in the wings and tails of birds: asymmetric birds can't fly round tight corners. *Proceedings of the Royal Society London, Series B*, 254: 181-189.
- TUCKER, V. A. 1991. The effect of molting on the gliding performance of a Harris' Hawk (*Parabuteo unicinctus*). *The Auk*, 108: 108-113.
- WARHAM, J. 1990. *The Petrels. Their ecology and breeding systems*. London: Academic Press.
- WARHAM, J. 1996. *The behaviour, population biology and physiology of the petrels*. London: Academic Press.
- YURI, T. & ROHWER, S. 1997. Molt and migration in the Northern Rough-winged Swallow. *The Auk*, 114: 249-262.

Beatriz Arroyo did a PhD on the breeding ecology of Montagu's Harriers, subsequently worked in France with ecology and conservation of steppe birds (including little bustards and harriers), and is currently working in Scotland on raptor conservation issues. She is a bird ringer since 1986. **Eduardo Mínguez** has been studied bird ecology, mainly in breeding ecology on seabirds, during the last 15 years. With experience in

management for conservation of Mediterranean islands, he is currently lecturer on Conservation Biology. **Luis Palomares** is a bird ringer and **Jesús Pini-lla** is ornithologist and bird ringer. Currently he is responsible of the *Spanish Migration Centre*.

[Recibido: 29-01-04]

[Aceptado: 14-09-04]