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Review

MOULT IN BIRDS OF PREY: A REVIEW OF CURRENT KNOWLEDGE AND FUTURE CHALLENGES FOR RESEARCH

LA MUDA EN AVES RAPACES: REVISIÓN DEL CONOCIMIENTO ACTUAL Y RETOS FUTUROS PARA INVESTIGAR

Iñigo ZUBEROGOITIA¹ *, Jabi ZABALA² and José Enrique MARTÍNEZ³

SUMMARY.—Moult is one of three major events in the annual cycle of birds. However, in contrast to breeding and migration, relatively few studies have been carried out on this topic. This is particularly the case with the large group of birds of prey and is partly a consequence of a general lack of appreciation of the relevance of moult within the life cycle of species. This factor is exacerbated by the difficulty in obtaining large enough sample sizes in this group, since some species are scarce and birds of prey are almost always difficult to trap. Nevertheless, moult is an energy-demanding process that takes longer than the breeding cycle and, contrary to the latter, it occurs every year. We stress the importance of the annual moult process for providing a “fixed image” of an individual’s biology and underline its utility in furthering knowledge of the life history of each species. In this review we first outline the basic definitions necessary for understanding the moult process, and discuss current information on the moult sequence of European birds of prey, as part of a comprehensive review of the mechanisms of the moult in each group. Secondly, we summarise the main methods used to study, analyse and understand the moult, and indicate how to use these to obtain relevant information. Thirdly, we explain the importance of the moult in the life cycle of birds of prey, and how we can use this information to advance our understanding of the ecology of each species. Finally, we include a view of possible strategies that may be used to improve future research, thanks to advances in knowledge of the moult process. —Zuberogoitia, I., Zabala, J. & Martínez, J.E. (2018). Moult in birds of prey: a review of current knowledge and future challenges for research. *Ardeola*, 65: 183-207.

Key words: arrested moult, definitive plumage, growth rate, moult cycle, moult score, moult sequence, prebasic moult, serial moult.

RESUMEN.—La muda es uno de los tres principales hitos en el ciclo anual de las aves. Sin embargo, al contrario que la reproducción y la migración, el número de estudios relativo a la muda es relativamente escaso. Esto es particularmente evidente en el caso de las aves rapaces, fruto de la falta general de apre-

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ciación de su relevancia en el ciclo vital de las especies. Este problema se ve incrementado por la dificultad de obtener tamaños muestrales suficientes, dado que algunas especies son muy escasas y la mayoría de las rapaces son difíciles de capturar. La muda es un proceso que demanda gran cantidad de energía y que suele durar más que el ciclo reproductor y que, al contrario que este, tiene lugar todos los años. Así, en este trabajo mostramos la importancia de los procesos de muda anual para obtener una “imagen fija” de la biología del individuo y subrayar su utilidad en el conocimiento futuro de la historia vital de las especies. En esta revisión primero describimos las definiciones básicas necesarias para entender el proceso de la muda y tratamos la información disponible sobre la secuencia de muda de las aves rapaces europeas, como parte integral de los mecanismos de muda de cada grupo. En segundo lugar, resumimos los principales métodos empleados para el estudio, análisis y comprensión de la muda y cómo utilizarlos para obtener una información relevante. En tercer lugar, explicamos la importancia de la muda en el ciclo vital de las aves rapaces y cómo podemos emplear dicha información para avanzar en el conocimiento de la ecología de las especies. Por último, incluimos una visión de posibles estrategias que podrían ser empleadas para mejorar estudios futuros gracias a la incorporación de los avances en el conocimiento de los procesos de muda. —Zuberogoitia, I., Zabala, J. & Martínez, J.E. (2018). La muda en aves rapaces: revisión del conocimiento actual y retos futuros para investigar. *Ardeola*, 65: 183-207.

Palabras clave: ciclo de muda, muda prebásica, muda retenida, muda en serie, plumaje definitivo, puntuación de la muda, secuencia de muda.

INTRODUCTION

Moult, breeding and migration are the three major events in the annual cycle of birds. However, moult has been proportionally much less studied (see Newton, 2009). This is partly a consequence of a general lack of appreciation of its importance to the annual cycle and population processes, and of how knowledge of moult strategies can contribute to conservation-driven research (Newton, 2009). Moult is an energy-demanding process that lasts for several months each year, in a regular fashion, throughout the life of each species of birds of prey. This process takes longer than the breeding cycle and, unlike the latter, it occurs every year in all species (Rohwer *et al.*, 2011). However, whereas studies exploring the ecological correlates and consequences of breeding and migration are abundant, only a few are focused on moult and its role in bird ecology. Obtaining comprehensive information on the moult state of a bird requires its capture; preferably more than once during each moulting event, and this can be very difficult with many species, particularly in birds of prey (see Bird & Bildstein, 2007).

Thus, lack of knowledge of moult is often a logistical problem. Nevertheless, there is recent increasing interest among ornithologists in revealing the evolution of moult in birds (see e.g. De la Hera *et al.*, 2012; Barshep *et al.*, 2013; Rohwer & Rohwer, 2013).

Sequential moult is the most widespread pattern across avian taxa. However, the time constraint on moulting in large birds cannot be overcome by growing more feathers simultaneously because of the size-related scaling of the power required for sustained flight and the maximum power available from the flight muscles (Schmidt-Nielsen, 1984; Rohwer *et al.*, 2009). For large birds, the difference between the power required for sustained flight and the maximum power available is relatively small, making flight with proportionately similar moult gaps than smaller birds impossible (Tucker, 1991). Therefore birds of prey, that fly while moulting, cannot compensate for the relatively slow growth of their remiges by replacing more primaries and secondaries simultaneously (Rohwer *et al.*, 2011; Zuberogoitia *et al.*, 2013; 2016a).

Intraspecific variation in moult sequence, duration and extent depends, among other

factors, on the breeding cycle; the age and sex of the bird; territory quality; the status (dispersive, floater, sedentary or migrant) of each individual; latitude; local weather and climatic variation (Ydenberg *et al.*, 2007; Newton & Dawson, 2011; Dietz *et al.*, 2013; Zubero-goitia *et al.*, 2016a). Moreover, it must be considered that, once grown, each feather will normally be retained for at least a year, during which it will deteriorate progressively, due to environmental conditions and individual behaviour (Zubero-goitia *et al.*, 2013). Feathers therefore act as a datalogger, in which the conditions experienced by the bird during feather growth have been recorded. Hence, a correct understanding of the moult sequence unveils valuable information about the life processes of a given individual or population.

Some of the above-mentioned factors (e.g. migratory behaviour) have also been suggested for modelling differences in moult duration between species (De la Hera *et al.*, 2012). However, unlike passerine birds, in which there are only a few deviations from the typical moult strategy (Kiat, 2017), birds of prey show several different moult patterns which may be analysed from an evolutionary point of view.

In this paper we provide an overview of moult sequences and patterns of birds of prey, focused mainly on European raptors and owls, and of how researchers are using this information to improve knowledge of the life histories of these species. We also identify prospects for this research field, including a set of methods to refine its study. We have tried to include most of the relevant scientific literature about moult in birds of prey. Unlike other biological traits of avian species, there is still a huge lack of basic knowledge on this topic and therefore we stress the moult as a future tool that can be used to complete the information necessary for understanding the life of birds of prey.

The review has four sections: (1) Moult in birds of prey, in which we introduce the basic

definitions required to understand the moult process and describe the different moult sequences of European birds of prey; (2) checking moult, where we describe methods used to study and analyse moult; (3) the moult and ecological implications, where we show the different factors affecting moult patterns and indicate how we can use them to develop interesting research; and (4) looking forward.

MOULT IN BIRDS OF PREY: AN OVERVIEW

Feathers

Feathers are special, lightweight structures consisting of keratin, a tough, inert protein. Unlike other keratinous structures, such as claws, feathers do not undergo continual growth. Once fully formed, feathers are dead structures in which damaged parts cannot be repaired. They deteriorate mainly through the actions of physical wear, sunlight, and feather parasites and must therefore be periodically renewed (Newton, 2009). Feathers can only be replaced by pushing out the old quill. This occurs long before the new feather is fully grown and functional (Jenni & Winkler, 1994). This is a major disadvantage since a significant reduction in plumage function results if there is a need to replace many feathers simultaneously (Jenni & Winkler, 1994). Birds require plumage to be in an optimal state, in order to efficiently develop key activities including flight, thermal insulation, courtship, etc. In the case of birds of prey, plumage condition also affects hunting ability, and plumage in a bad state can be fatal. Consequently, during the moult, feathers are generally replaced sequentially, in a fixed order, so that body insulation and (in most birds) flight are not severely hampered (Newton, 2009).

This review of moult sequences and patterns is focused on flight feathers, including wing (remiges: primaries and secondaries) and tail

(rectrices) feathers, with particular emphasis on the first group. Primaries (PP) are numbered descendantly, from the carpal joint, P1, outwards to P10. The secondaries (SS) are those feathers attached to the ulna, and are numbered ascendantly from the carpal joint (S1) to the body (see Fig. 1 for an example). The number of SS varies between species, and depends greatly on the configuration of the wing, the size of the bird and, particularly, on the length of the forearm (Ginn & Melville, 2000). Small and medium-sized birds of prey usually have 13

SS. However, the longer the wing the more SS appear at the inner end. Old and New World vultures exhibit the largest numbers of SS, with as many as 25 in Griffon Vultures *Gyps fulvus* (Ginn & Melville, 2000; Zuberogoitia *et al.*, 2013). Bearded Vultures *Gypaetus barbatus* have a variable number of SS (19 or 20), possibly due to the absence of one of the innermost SS in some birds (Zuberogoitia *et al.*, 2016a). The rectrices (RR) are numbered in pairs, from the central feathers (RR1) outwards. Most birds of prey have six pairs of RR, although some ex-

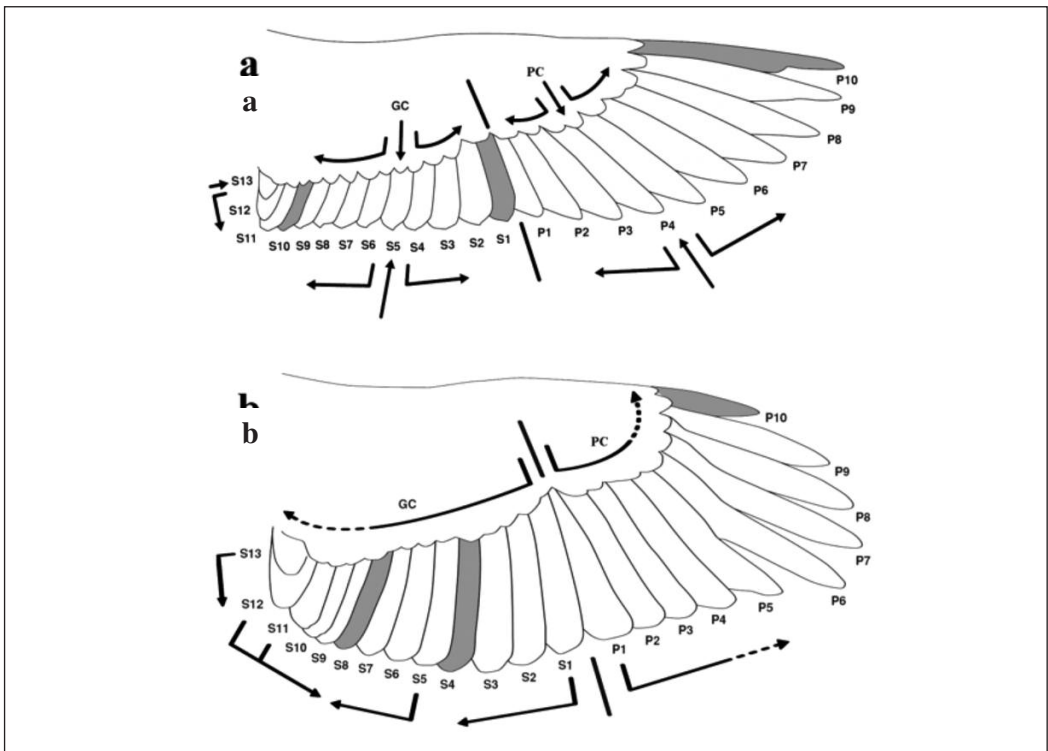


FIG. 1.—Moult sequence of (a) Falconids and (b) Accipitrids involved in one moult cycle. Black arrows show the moult foci and lateral arrows show the moult progression. Grey coloured feathers show the last-moulted feathers, which are normally those that are arrested in unfinished moult. GC Great Covert, PC Primary Covert, S Secondary and P Primary.

[Secuencia de muda de (a) Falcónidas y (b) Accipitridas sujetas a un ciclo de muda. Las flechas negras muestran los focos de muda y las flechas laterales muestran la progresión de la muda. Las plumas coloreadas de gris son las últimas plumas mudadas, que suelen ser las que son retenidas en las mudas incompletas. GC cobertora mayor, PC cobertora primaria, S secundaria, P primaria.]

ceptions exist (e.g. seven pairs in Egyptian Vultures *Neophron percnopterus*).

Differential quality and shape of juvenile versus adult feathers

Nestlings have a first cover of down which is termed the neoptile. Some species, mainly owls, show a second generation of downy plumage known as the mesoptile. During the first weeks of life nestlings are fed regularly by their parents and they exhibit a high increase in body mass (muscles and bones). The growth rate of the body changes significantly when the flight feathers start to appear because energy intake is redirected to feather growth, at the expense of corporal growth. Most of the energy intake is transformed into plumage and a smaller proportion is used to finish corporal development. Juvenile plumage is that formed when the downy cover grows out (Cieslak & Dul, 2006). This event is called the first prebasic moult (Wolfe *et al.*, 2014; Howell & Pyle, 2015).

The entire set of juvenile flight feathers is acquired during the nestling or parental dependence phase and the constituent feathers grow simultaneously. The complete growth of a juvenile flight feather takes about three weeks in the smaller species (e.g. Scops Owl *Otus scops* and Lesser Kestrel *Falco naumanni*), and three to four months in the largest ones (e.g., large eagles and vultures). In turn, adult feathers are moulted gradually and in restricted sets per moult cycle. As a result, juvenile feathers are weaker and looser in texture than adult feathers. Juvenile flight feathers are narrower, longer and more pointed at the tip than those of adults.

Moult terminology

Moult in birds is defined as the periodic shedding and replacement of feathers (Campbell & Lack, 1985). Replacement of all flight

feathers normally takes place annually (one moult cycle) in most small species and in some medium-sized birds of prey. However, other species, mainly large raptors, need more than one year to complete the replacement of all flight feathers. The whole process may take up to five years in some owls. The high variability of moult processes, depending on the particular species or group of birds, means that scientific moult terminology is quite confusing (e.g., Wolfe *et al.*, 2014; Howell & Pyle, 2015). We therefore describe here some of the terms used, in accordance with the above references.

- **Prebasic moult:** The replacement of feathers that occurs approximately annually in most birds. Prebasic moults are complete in most small birds, but are incomplete in large birds, and therefore they delineate moult cycles (Shugart & Rohwer, 1996).
- The **first prebasic or prejuvenile moult** results in the juvenile plumage. The prejuvenile moult usually occurs soon after hatching and often replaces natal down. The prejuvenile moult is ubiquitous (occurring in all birds) and complete in extent (developing a complete, new set of feathers). This is not a flight feather moult, thus we will not refer to it in this review, although it is necessary to explain the process in order to understand the following terminology.
- The **second prebasic moult** starts during the second calendar year (hereafter cy) of the bird (one year old), when it starts to replace the juvenile feathers, and it finishes in the same moult cycle, when the bird stops the annual moult. Most species start the prebasic moult during the breeding season and finish it before winter, within the same calendar year. Prebasic moults are repeated every year during the rest of the life of each individual and are numbered according to the age (cy).

- **Moult cycle:** The period between the start and finish of the prebasic moult.
- **Seasonal moult cycles:** This term is employed in the current article for the first time. Some migratory raptor species moult in two periods: the post-breeding period and the wintering period. Together, these two seasonal stages constitute the same prebasic moult and the same moult cycle, and they usually take place in different calendar years (e.g. July-September/January-February).
- **Complete moult:** When all flight feathers of the same generation have been replaced.

Juvenile plumage is moulted in either a single or several moult cycles (years) depending on the species, until the “definitive” (mature) plumage aspect is acquired. Mature plumage is fully developed after the completion of second or third prebasic moult in most passerine birds, the fourth or fifth prebasic moult in most gulls, and later in some larger bird species (Pyle, 2008; Howell, 2010). Some species go through an intermediate step, showing a “subadult” plumage (e.g. Bearded Vulture; Bonelli’s Eagle *Aquila fasciata*). In these cases, juvenile birds need one or more moult cycles to reach the subadult plumage. Subadult feathers are different in colour, size and pattern from both juvenile and adult feathers. Later, the subadult plumage is replaced in one or more moult cycles until the definitive adult plumage is acquired. Once the moult has started, each individual exhibits variable plumage coloration between cycles, depending on the differential wear of the feathers over time.

In raptors, as in all birds, moult proceeds in different directions through different parts of the wing (Edelstam, 1984). The sites from which the moult originates are known as “moult foci”. The use of more moult foci, or moult centres, may permit a more rapid moult while reducing the size of gaps between feathers. Moult in large birds, which need

more than one year to replace all their flight feathers, often involves more than one moult centre and occurs in “waves” termed “serial moult” (e.g. Edelstam, 1984) or “Staffelmauser”. “Staffelmauser” is a German word meaning “staggered moult”, introduced by the German ornithologists Stresemann and Stresemann (1966). Serial moult in medium-sized and large raptors typically begins with an incomplete second prebasic moult, during which primary replacement proceeds distally from P1, as in smaller birds, but then arrests before all feathers are replaced. The bird thus retains its juvenile outer primaries for another moult cycle, the third prebasic moult, which equates to an additional year. The third prebasic moult begins where the previous moult left off the year before, while another sequence commences again from P1, resulting in two “waves” of simultaneous primary replacement (Pyle, 2006). As with the primaries, subsequent moults of secondaries begin where the preceding moult arrested. At the same time new waves begin, although not always commencing at all foci every year and, as we will see, there is high variability between species.

Growth rate

Few works have focused on the growth rate of flight feathers in birds of prey. Feather growth rates are strongly influenced by feather size and feather type, and there is also an association with body size (Rohwer *et al.*, 2009; De la Hera *et al.*, 2011, 2012; Rohwer & Rohwer, 2013). It takes about 50-65 days for a single flight feather to grow in Common Buzzards *Buteo buteo* and Black Kites *Milvus migrans* (Ontiveros, 1995); 50-60 days in Spotted Owls *Strix occidentalis* (Forsman, 1981) and 100-125 days in California Condors *Gymnogyps californianus* (Snyder *et al.*, 1987) and White-backed Vultures *Gyps africanus* (Houston, 1975). The mean growth

velocity of primaries is 4.6 ± 0.8 mm/day in Black Kites and 4.6 ± 0.5 mm/day in Common Buzzards, whereas the rates in secondaries and rectrices are slightly slower. The average rate for regenerating primaries is 4.2 mm/day in Spotted Owls. Five Ospreys *Pandion haliaetus*, retrapped within short periods, showed average feather growth rates of 5.7 mm/day for primaries, 3.1 mm per/day for secondaries and 3.2 mm per/day for rectrices (Prevost, 1983). The average growth velocity of California Condor primaries, despite their larger size, is quite similar, at 4.3–6 mm/day, and 4.4 mm/day has been reported for captive White-backed Vulture remiges (Houston, 1975). The longest feathers showed the highest growth rates.

Arrested moult/retained feathers/ incomplete moult

Some individuals keep interspersed feathers from a previous generation (showing a higher degree of wear) in the position where new ones should be. In fact, it is common to find retained, non-moulted feathers in birds of prey (Pyle, 2005a). Zuberogoitia *et al.* (2009) described that, during the breeding season of European Sparrowhawks *Accipiter nisus*, when the chicks are fledging (in July), 18.75% of the breeding females and 55.5% of the breeding males suspended the moult. The period during which some individuals were found to have stopped moulting coincided with that of peak food demand by nestlings. Pyle (2005a) defines the contrasts caused by these interruptions as “suspension limits”, and such instances can be identified in the plumage even after a long period of time. Following these recesses the moult is resumed and usually follows the normal sequence. However, in some cases the feather at which the moult stopped is retained, and the sequence jumps to the next quill. We suspect that this phenomenon may not be restricted to

the breeding season, and that when an individual is not able to obtain sufficient resources to keep up with energy demands it suspends the moult, resuming the process when conditions improve. In fact, during winter, when the moult is finished, it is relatively common to find retained quills in most species. These are evidenced by clear signs of wear in the primaries, secondaries or rectrices moulted in the previous moult season. There is also obvious wear separation between generations, that is those arrested and those moulted in the current year. The presence of retained, non-moulted quills allows us to be more specific when determining the age of a bird, adding an additional year in appropriate cases. The number of retained feathers can also help to evaluate the life history of an individual during the previous year. Moreover, if the retained feather is of the juvenile type, it provides a useful “zero reference” with regard to the year in which the individual was born.

The ability to replace damaged feathers outside the moult schedule

Rohwer *et al.* (2011) suggested that in Laysan Albatrosses *Phoebastria immutabilis* and Black-footed Albatrosses *P. nigripes*, those primaries that drag along the sand of the atolls where the birds breed, thus becoming severely abraded, are replaced more often. In the same context, Brommer *et al.* (2003) showed that Ural Owls *Strix uralensis* replace the outer primaries more frequently, suggesting that the allocation of position-specific energetic costs may benefit large birds. Zuberogoitia *et al.* (2013; 2016a) found that adult vultures replace some feathers more often than others, indicating that certain feathers may be more important for soaring and gliding. The same authors also noted that vultures are able to provoke the replacement of damaged feathers facultatively, prior to scheduled moult

dates. Zuberogoitia *et al.* (2013) described that adult griffons select the damaged quills requiring removal by considering the degree of wear and the feathers' position on the wing. The vultures then force these feathers to fall out, by pecking them repeatedly. Ellis *et al.* (2016) also documented this behaviour, in Golden Eagles *Aquila chrysaetos*, and suggested the existence of a neurophysiological mechanism for preferentially replacing damaged feathers. Even juvenile vultures are able to force the replacement of certain primaries, thus bypassing the habitual moult sequence (Zuberogoitia *et al.*, 2013). This capacity would explain the relatively good plumage condition observed in Griffon Vultures, above all in adults, despite the fact that these birds need at least two years for a complete moult and that they are involved in continuous disputes whilst feeding, with consequent deterioration of their plumage.

Importance and consequences of symmetry in the moult

Fluctuating asymmetry (i.e. random deviations from perfect symmetry in bilateral characters) has received increasing attention from ecologists in recent decades (Brommer *et al.*, 2003). Asymmetry in feathers is thought to reduce flight performance and symmetrical wings are therefore crucial for hunting success (Thomas, 1993). However, Thomas (1993) focused his attention on fluctuating asymmetry in the size of the wings and tail, which differs from the asymmetry found in the moult sequence. Basically, the moult tends to be symmetrical between both wings and tail in those species that develop a simple moult pattern consisting of one moult cycle. However, asymmetry increases in proportion to the complexity of the moult pattern and the age of the individual (Zuberogoitia *et al.*, 2005; 2013, 2016a). The ability to carry out selective replacement of damaged feathers and/or

arrest the moult process increases asymmetry. This is more evident in long-lived birds. The high degree of symmetry that individuals are able to maintain, and the cost that a loss of symmetry has in terms of a reduction in individual survival probability, strongly suggest that developmental homeostasis in partial moult is maintained by (stabilising) survival selection (Brommer *et al.*, 2003). However, Brommer *et al.* (2003) did not obtain significant conclusions about the consequences of asymmetry on the biology of an individual. Nonetheless, they stressed its potential value for ecological and evolutionary research.

Moult Sequence/moult pattern

The sequence of flight feather replacement is fairly constant in each species of bird and is often similar throughout larger taxonomic units (Miller, 1941). Falconids replace the primaries centrifugally, from P4 to the innermost (P1) and the outermost (P10), and the secondaries from two foci (S5 and S13) (Zuberogoitia *et al.*, 2002; Pyle, 2005b; Fig. 1a). Accipitrids, and some owl species, replace the primaries from the innermost (P1) to the outermost (P10), and the secondaries from three foci (S1, S5 and S10) (Miller, 1941; Stresemann & Stresemann, 1966; Martínez *et al.*, 2002; Zuberogoitia *et al.*, 2013, 2016a; Fig. 1b). Strigiforms, however, show high inter-genus variability and most genera follow unique sequences.

In small and some medium-sized accipitrids, some owls, and all falconids the moult of all flight feathers is usually completed in one year (one moult cycle). However, medium-sized and, more particularly, large accipitrids and certain owl species need more than one year (more than one prebasic moult) to complete the replacement of all flight feathers. In the case of accipitrids, the basic pattern is followed in an orderly way during the second prebasic moult. During subsequent prebasic moults the process

becomes complicated, due to the overlapping of different moult waves (serial moult), and the capacity of some species to voluntarily replace damaged feathers. In fact, adult specimens of medium-sized and large accipitrids show a chaotic moult pattern, which some authors describe as an irregular and variable sequence (Stresemann & Stresemann, 1960; Cramp & Simmons, 1980; Schumtz, 1992; Herremans, 2000). Similarly, certain owl species complete the moult in two or more years, with some taking over five years (Martínez *et al.*, 2002; Korpimäki & Hakkarainen, 2012). In addition, some species are long-distance migrants, which start moulting in the breeding grounds and continue in the winter quarters, thus showing seasonal moult cycles.

Almost all birds of prey, except the genus *Bubo*, prioritise moulting the primaries during the second prebasic moult. The moult of secondaries usually starts when the primary moult is already advanced. Moreover, second cy individuals of those species that require more than two moult cycles to replace the juvenile plumage usually moult very few secondaries, if any, during the second prebasic moult.

Falconids– Complete moult in one moult cycle, starting at P4

Most falconids start moulting P4 and S5 during the breeding season and finish moulting P10 and S1 in the autumn (mainly October; Fig. 1a; Zuberogoitia *et al.*, 2002; Leonardi, 2015).

Falconids– Complete moult in one moult cycle, two seasonal moult cycles, starting at P4.

Most of the species in this group are late-breeding migrants that moult a few PP and some SS whilst at the breeding grounds, arrest the moult for migration, and finish moulting in their winter quarters. Forsman (2016) states that Eurasian Hobbies *Falco subbuteo* and Eleonora's Falcons *Falco eleonora* moult flight feathers in their winter quarters. However, breeding females from

southern populations moult P4 (also even P3, P5 and P6) and sometimes S5 (S4 and S6) during the last few days of nestling care, as seen in both Eurasian Hobbies (northern Spain, own, unpublished data; Gabriel de Jesús pers. comm., 2017) and Eleonora's Falcons (Canary Islands, Sagardía, pers. comm., 2012). The interval between the last feather moulted in summer-autumn and the first feather moulted in winter is longer than one month, and determination of the focus of the suspended moult is feasible, due to differential wear between adjacent feathers.

Some widespread species show varying behaviour between different populations, depending on the latitude. Most Peregrine Falcon *Falco peregrinus* populations from low latitudes are sedentary, those from medium latitudes are partial migrants, and those breeding in arctic grounds are long-distance migrants (White *et al.*, 2013). Sedentary or partial migrant populations show a continuous moult pattern in a single seasonal moult cycle, while nordic peregrines (e.g. *F. p. calidus*) moult in two seasonal moult cycles; they start on the breeding grounds, arrest the moult to migrate, and finish in the winter quarters (Wegner & Kersting, 2016; Olle & Estrada, 2017).

Accipitrids– Complete moult in one moult cycle, starting at P1

Most sedentary and short-distance migrants in the category of small and medium-sized accipitrids follow the pattern in Figure 1b. They start moulting at P1 during the breeding season. When PP moult is advanced (P4-P6) they start moulting SS at S1, followed by two foci in SS (S5 and S11-13). P10, S4 and S8 are the last flight feathers to be moulted and are also the most frequently retained feathers from the previous year.

Medium-distance migrant populations of some species (e.g. Red Kites *Milvus milvus*) complete the moult in their winter quarters if they have not finished before migration. However, in such cases, the number of feathers

involved is small. The affected birds do not halt the moult process, finishing in October–November in only one seasonal moult cycle, in a similar fashion to local populations.

Owls– Complete moult in one moult cycle, starting at P1

Some small and medium-sized owl species (e.g. Little Owl *Athene noctua*; Short-eared Owl *Asio flammeus*; Long-eared Owl *Asio otus*; Martínez *et al.*, 2002) follow exactly the same pattern as the above-mentioned accipitrids (Fig. 1b).

Accipitrids– Complete moult in one moult cycle, two seasonal cycles, starting at P1

Certain medium-sized migratory species start moulting during the breeding season, with some PP and a few SS being affected (they also follow the pattern of Fig. 1b). Some species stop the moult before migrating (e.g. Honey Buzzard *Pernis apivorus*), although others continue moulting during migration (e.g. Montagu's Harriers *Circus pygargus*, Arroyo & King, 1996). All of them complete the moult in their winter quarters.

Owls– Complete moult in one moult cycle, two seasonal cycles, starting at P1

Scops Owls moult the innermost PP, and in a few cases some of the SS, after the breeding season. They then arrest the moult for migration, and finish it after arriving at the wintering grounds (Martínez *et al.*, 2002).

Accipitrids– Complete moult in multiple moult cycles, starting at P1

Common Buzzards, for example, need two moult cycles to complete the replacement of all flight feathers, following the same sequence as for other medium-sized raptors (Zuberogoitia *et al.*, 2005; Fig. 2a). This species, and others that need more than one year to complete the replacement of all flight feathers (e.g. vultures, which need two or three moult cycles; Fig. 2b), demonstrate se-

rial moult (Clark, 2004), although not all individuals follow this pattern in the third prebasic moult. Most individuals resume the moult sequence where they finished in the second prebasic moult, and only a small proportion start a new wave, moulting P1 and/or P2 (Zuberogoitia *et al.*, 2005; 2013, 2016a). In fact, the moult sequence during the second, third, and fourth prebasic moults is orderly (moulted feathers form a homogeneous block) and there is high symmetry between both wings. Serial moult is more evident in later years and, together with other individual factors, contributes to the asymmetry and chaotic appearance of the moult in adults.

Accipitrids– Complete moult in multiple moult cycles, multiple plumages, starting at P1

Some species change the juvenile plumage to an intermediate, subadult plumage in two or three moult cycles (e.g. Bonelli's Eagle, Vincent-Martin & Ponchon, 2013; Golden Eagle, Liguori, 2004 and Watson, 2010; White-tailed Eagle *Haliaeetus albicilla*, Forsman, 2016; Bearded Vulture, Zuberogoitia *et al.*, 2016a). Subadult quills usually have a different colour and pattern to juvenile and adult feathers. Subadult quills are also shorter than juvenile feathers but are still slightly longer than adult feathers. This can be observed mainly in the secondaries. Adult, definitive plumage appears when subadult feathers are moulted in subsequent cycles. However, some adult feathers (mainly innermost PP) appear early on, in the third or fourth prebasic moult, due to the serial moult effect. Such feathers contrast strongly with adjacent, subadult quills.

Accipitrids– Complete moult in multiple moult cycles, two seasonal cycles, starting at P1

This pattern applies to medium-sized migratory raptors. These are trans-Saharan migrant species that breed late in Europe, moulting some primaries and secondaries

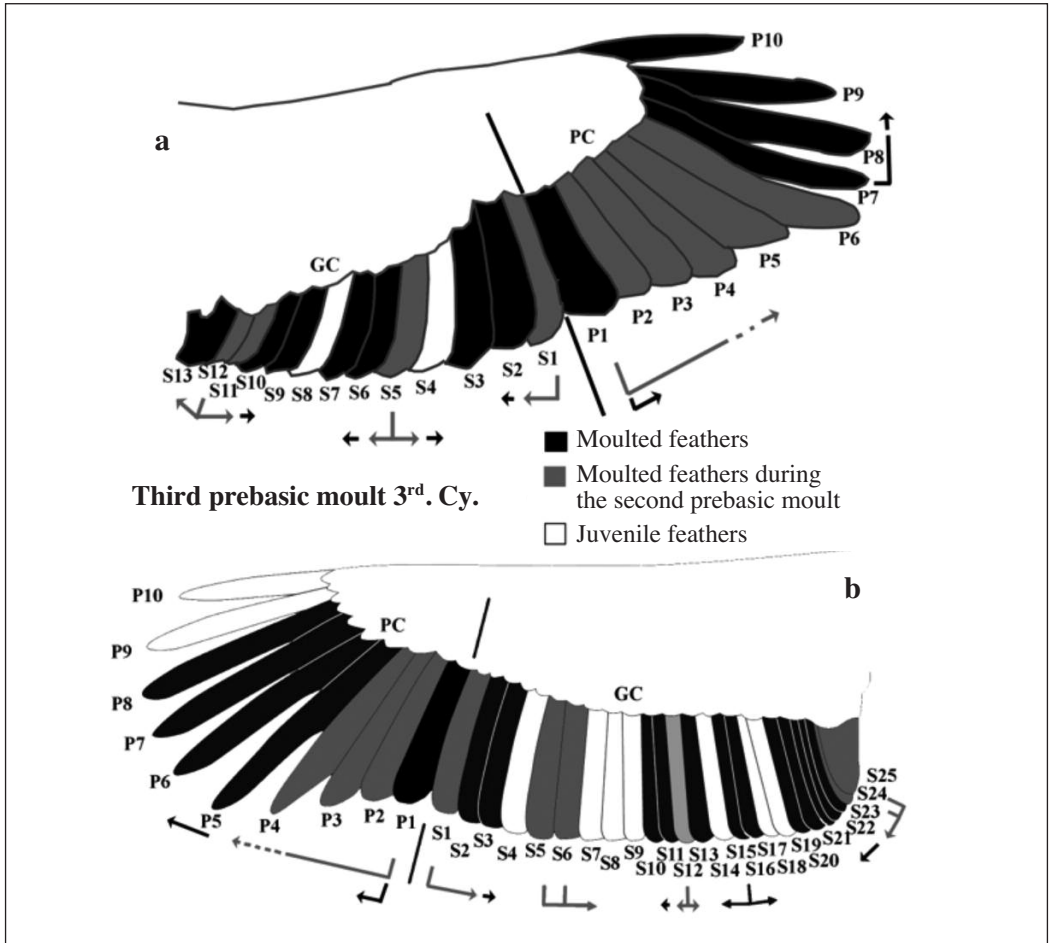


FIG. 2.—Moult sequence of (a) medium-sized accipitrids and (b) large accipitrids, which need two or more moult cycles to complete the replacement of all feathers of the same generation. Figures show the typical moult sequence of individuals that have finished the third prebasic moult (3rd cy in winter or 4th cy in spring). Arrows show the foci and the progression of the moult. Grey coloured feathers and arrows show the feathers and progression of moult during the second prebasic moult (2nd cy); black feathers and arrows belong to the third prebasic moult (3rd cy); and white feathers are juvenile, retained ones from the first prebasic, prejuvenile moult (1st cy). Calendar year (cy). GC Great Covert, PC Primary Covert, S Secondary and P Primary.

[Secuencia de muda de (a) Accipitridas medianas y (b) Accipitridas de gran tamaño, que requieren dos o más ciclos de muda para completar el reemplazo de todas las plumas de la misma generación. Las figuras muestran la típica secuencia de muda una vez finalizada la tercera muda prebásica (3^{er} ac en invierno o 4^o ac en primavera). Las flechas muestran los focos de inicio de muda y la progresión de la misma. Las plumas y flechas coloreadas de gris indican las plumas mudadas y la progresión de la muda durante la segunda muda prebásica (2^o ac); las plumas y flechas negras muestran la tercera muda prebásica (3^{er} ac); y las plumas y flechas blancas son aquellas juveniles, retenidas de la primera muda prebásica, prejuvenil (1^{er} ac). Año calendario (ac). GC cobertora mayor, PC cobertora primaria, S secundaria, P primaria.]

before departure. Some of them, for example Ospreys and Steppe Buzzards *Buteo buteo vulpinus*, arrest the moult before migrating and continue the sequence in the winter quarters (Edelstam, 1984; Herremans, 2000). However, other species are able to moult while migrating (e.g. Booted Eagle *Hieraaetus pennatus*, Short-toed Eagle *Circaetus gallicus*; Forsman, 2016; unpublished pers. data). Some individuals of these species winter in southern Europe, or behave as sedentary species, expending less energy and time than birds that migrate to central or southern Africa (García-Dios, 2016; Sayago, 2011). We hypothesise that this behaviour may permit them to save energy and advance more quickly in the moult sequence than would be expected. This theory remains to be tested, although some of our data suggest it may be true. In the same context, juveniles of some of these species spend their first two years in their wintering grounds. For example, Prevost (1983) showed that juvenile Ospreys start the second prebasic moult during the first autumn of life (some months after hatching), whilst in their winter quarters. Moult then continues uninterrupted until the age of 22-29 months, before their departure to breeding grounds. These juvenile Ospreys complete the moult in one year, and even show serial moult, which causes some of the innermost primaries to be moulted twice.

Owls– Complete moult in multiple moult cycles

Contrary to raptors, Strigiforms show high variability in moult patterns, depending on both the start point of the moult and the direction. As we have mentioned above, certain owl species fall within some of the described P1 groups (Fig. 1b). These owls display a simple moult pattern. “Simple” because they follow an orderly schedule, and there is only one moult cycle, although some migratory species (e.g. Scops Owls) need two seasonal

cycles. However, most owl species need multiple moult cycles to complete the replacement of all flight feathers, and some of them require more years than any other raptor species. Another differential characteristic is the fact that most owls do not demonstrate serial moult patterns. Owl moult follows an orderly sequence, resuming where the previous moult left off the year before.

Strix owls: starting at P5

The moult sequence starts at P5 (P4 in Ural owl *Strix uralensis*; see Pietiäinen *et al.*, 1984) and continues outwards to P10 (Fig. 3a). Some birds do not manage to moult these six primaries in one prebasic moult, but others are able to moult even more quills. In the latter cases, the sequence continues at P4 and moves inwards to P1. Secondaries show two foci (S10, S5 and sometimes S1/S2), which develop centrifugally (e.g. Ural Owl, Pietiäinen *et al.*, 1984; Tawny Owl, *Strix aluco*, Martínez *et al.*, 2002; and Great Grey Owl, *Strix nebulosa*, Solheim, 2011). During the third prebasic moult, *Strix* owls continue where the previous moult finished, and this schedule follows systematically. However, the differential wear of some feathers causes some of them to be replaced more often than others (Brommer *et al.*, 2003), mainly in adult birds.

Barn owls: starting at P6

Barn owls start the second prebasic moult with P6 and continue centrifugally with P7 and P5, although a few individuals are able to shed three primaries during the first cycle (Lenton, 1984; Taylor, 1993; Martínez *et al.*, 2002; Fig. 3b). Secondaries show two/three foci (S12, S2 and S6), from which moult continues centrifugally. During the third prebasic

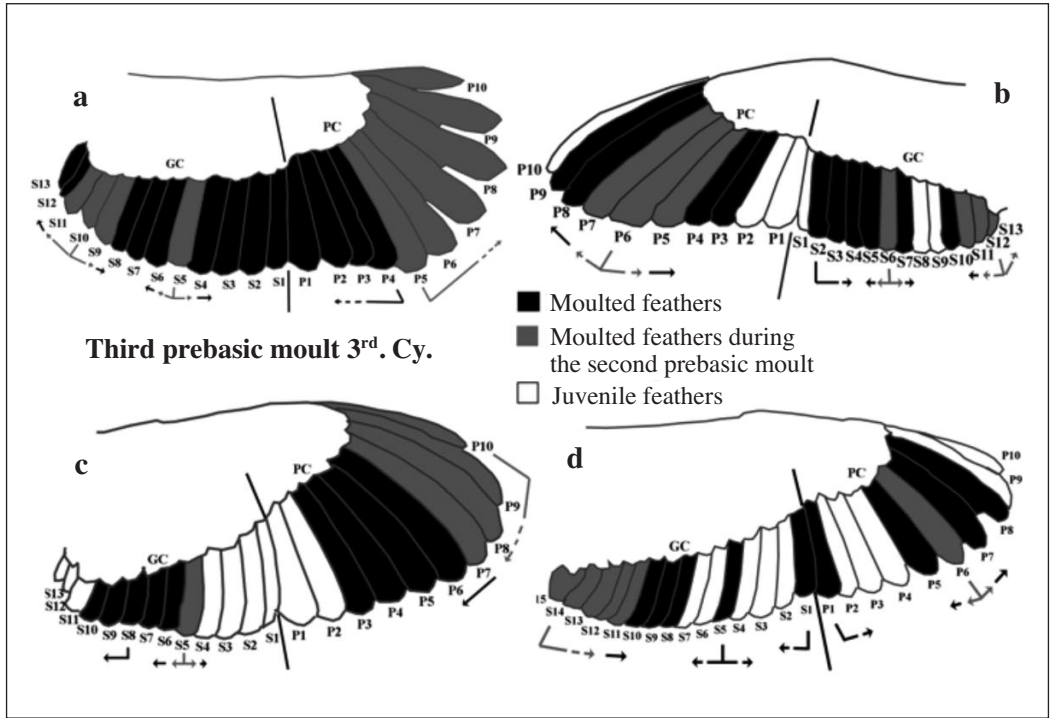


FIG. 3.—Moult sequence of (a) *Strix* owls, (b) *Tyto* owls, (c) Boreal Owl, and (d) *Bubo* owls. Figures show the typical moult sequence of individuals that have finished the third prebasic moult (3rd cy in winter or 4th cy in spring). Arrows show the foci and the progression of the moult. Grey coloured feathers and arrows show the feathers and progression of moult during the second prebasic moult (2nd cy); black feathers and arrows belong to the third prebasic moult (3rd cy); and white feathers are juvenile, retained ones from the first prebasic, prejuvenile moult (1st cy). Calendar year (cy). GC Great Covert, PC Primary Covert, S Secondary and P Primary.

[Secuencia de muda de (a) género *Strix*, (b) género *Tyto*, (c) mochuelo boreal y (d) género *Bubo*. Las figuras muestran la típica secuencia de muda una vez finalizada la tercera muda prebásica (3^{er} ac en invierno o 4^o ac en primavera). Las flechas muestran los focos de inicio de muda y la progresión de la misma. Las plumas y flechas coloreadas de gris indican las plumas mudadas y la progresión de la muda durante la segunda muda prebásica (2^o ac); las plumas y flechas negras muestran la tercera muda prebásica (3^{er} ac); y las plumas y flechas blancas son aquellas juveniles, retenidas de la primera muda prebásica, prejuvenil (1^{er} ac). Año calendario (ac). GC cobertora mayor, PC cobertora primaria, S secundaria, P primaria.]

moult the sequence follows on from where the previous moult finished, P8, P4 and P3. The sequence is completed in the fourth prebasic moult (4th cy), with the moult of P9, P10 and P1. There is high inter-individual variability in the number of remiges shed during each moult cycle.

Boreal Owl: starting at P10

Boreal Owls *Aegolius funereus* can take up to five moult cycles to complete the replacement of all the juvenile feathers (Hörmfeld *et al.*, 1985; Korpimäki & Hakkarainen, 2012). During the second prebasic moult, Boreal Owls

start moulting at P10 and the sequence continues inwards (Fig. 3c). The number of primaries moulted each year depends on age, sex, latitude, breeding status, weather and rodent cycles (Korpimäki & Hakkarainen, 2012). Some individuals show serial moult, starting a new wave at P10 while still moulting the innermost primaries (Martínez *et al.*, 2002).

Large owls: exceptional cases

In all the cases described above, the moult of flight feathers starts in the primaries. However, Eagle Owls *Bubo bubo* and Snowy Owls *Nyctea scandiaca* are totally different (Martínez *et al.*, 2002; Solheim, 2012). In the second prebasic moult the process normally starts with the central pair of rectrices and the shedding of the innermost secondaries (SS13-15). In favourable conditions, second cy owls are able to continue moulting further secondaries, following an ascendant order (outwards). Additionally, some individuals are able to moult P6/P7 (Fig. 3d). During the third prebasic moult, owls continue where they finished the year before, shedding P6 and continuing with P7 and P8 and advancing in an orderly manner with SS from a new focus at S1. They continue the moult of PP centrifugally during the following prebasic moults, although a new focus starts from P1 outwards, and P3 and P4 are the last moulted primaries. Some birds may take up to five years to complete the replacement of all flight feathers of the same generation.

METHODS FOR ASSESSING MOULT

Once in hand, a bird of prey is firstly given an overall check, to review the general appearance of the plumage. Juveniles have uniform plumages, with all flight feathers showing the same wear level, colour and pattern. By contrast, from the onset of the

second prebasic moult onwards, individuals show heterogeneous plumage due to differential feather wear. The main rule when recording moult is to keep in mind the predictable moult sequence of the species. Knowing when and how the moult of each feather is going to occur will help the correct identification of feathers. For example, the first flight feather(s) moulted in a Peregrine Falcon is always P4 and the last should be S1, P1 and P10. Between these extremes there should be a gradual difference in colour and wastage from the newest feather to the oldest. If checking a peregrine in winter we should first examine P4, which should be the oldest feather at this time. If any other quill shows a more worn pattern, then it is a retained feather that has not yet been moulted or is not going to be moulted. This is especially useful to identify several feather generations in large species.

In some species it is very difficult to detect subtle changes in the worn feathers. This is particularly true for owls, especially older birds, which are able to conserve all their flight feathers in an excellent state. However, researchers can now use black ultraviolet (UV) light fluorescence to check moult in owls (for more details see Weidensaul *et al.*, 2011). In owls, new feathers are covered by porphyrins, which are natural pigments that fluoresce brightly when exposed to UV light. Porphyrins are easily destroyed by exposure to sunlight, and are hence most abundant in new feathers. Under UV light, positioned 15 cm away, the ventral surfaces of newly-moulted flight feathers fluoresce an intense magenta colour. This effect is brightest in the proximal third of the feathers, and fainter or absent from the distal third (Supplementary material appendix 1, Figure A1). The older the feather the less magenta is present, hence it is possible to detect the moult sequence by comparing the magenta composition of the feathers. Feathers replaced during the previous moult cycle lack porphyrins and do not

show the magenta colour. This method is very good for checking the moult of some species (e.g. Tawny Owl, Supplementary material appendix 1, Figure A1) but lacks enough resolution for others (e.g. Barn Owl).

Field photography

The study of moult entails trapping and handling (and associated disturbance) of birds of prey. Thus, the use of field photography could be considered as a non-invasive study technique. Despite this, the use of high quality photographs of wild birds of prey to create moult cards has scarcely been used since the first articles were published (Snyder *et al.*, 1987). The current level of sophistication and widespread use of digital photography among ornithologists has created a huge databank of high-quality pictures from which moult state can be safely inferred (Supplementary material appendix 1, Figure B1). Zuberogitia *et al.* (2016a) used this method to increase the number of moult cards for a species that is difficult to handle (Bearded Vulture). This technique has also been used to increase sample sizes for scarce, endangered species or those that are difficult to trap (see Ryan, 2013; Vieira *et al.*, 2017).

Moult in captive birds

The moult sequence is the same for birds in captivity as for wild individuals, at least for small and medium-sized species that complete the moult in one cycle. However, the onset, duration and end date of the moult may be different (see e.g. Hörnfeldt *et al.*, 1985; Chandler *et al.*, 2010). Captive birds are fed daily and their energy demands: for flying, hunting, mating or defending the nest and the territory, differ from those of wild birds (Cieslak & Kwiecinski, 2009). Moreover, climatic conditions in captivity vary less than those experienced in the wild, hence less energy is re-

quired to maintain basal metabolism. For example, most falconers know how to induce a peregrine or goshawk to finish the moult by the first weeks of September, by increasing both the quantity and quality of food and keeping the bird in stable light and temperature conditions, whereas a wild individual does not finish until at least a month later.

Recording and analysing moult

Moult Score

Ginn and Melville (2000) and Newton (2009) suggested a standard recording system according to the growth stage of primaries and secondaries: old feathers are scored as 0, fully grown new ones as 5, and growing feathers as 1-4 for intermediate stages of development. These individual moult scores were then summed to give an overall moult score of between 0 and 50 (for 10 PP) and 0 and 65 (for 13 SS). Rohwer (2008) also showed how to assign scores indicating direction of replacement and points where waves of moult started or will stop, which is really interesting. Combining these scores across individuals yields a moult summary table, the starting point for determining the rules of feather replacement. In this procedure, growing primaries and secondaries are scored as decimal fractions of their full length, varying from 0.1 to 0.9 (Rohwer & Wang, 2010; Rohwer & Broms, 2013), and they have also changed the moult score system used in Europe. However, the problem of summarising moult in summary tables where two or three feather generations must be considered was not normally addressed. Following Zuberogitia *et al.* (2013), feathers scored as 0 are also recorded as A (juvenile), K (moulted in the previous moult season), M (moulted two years previously) and O (moulted three years previously). In future, it would be valuable that moult cards of birds of prey include: 1) the numbers of growing feathers examined at

each locus, 2) the direction of replacement between adjacent feather pairs, 3) nodal and terminal feathers marking points of initiation or re-initiation of moult following arrests, and 4) the age of the feathers.

Timing of Moulting. Underhill-Zucchini models

The timing of primary and secondary moult can be analysed using models developed by Underhill and Zucchini (1988) and Underhill *et al.* (1990), implemented in the “moult” package (Erni *et al.*, 2013) for R. Moulting index (the ratio between the sum of moult scores at any one time and the total moult scores of all feathers, with values between 0 and 1) is used as the response variable. Date, converted into Julian days, is the vector on which moult indexes are observed. With this data (moult index and date) it is possible to build basic models that make use of non-moulted as well as moulting birds, fitting the model using the maximum likelihood method (Newton, 2009). These models give estimates of moult duration, average start date (from which average end date can be calculated), and the standard deviation of the start date. It is possible to select five basic levels or types for analysis of the moult data: Type 1 – Where the entire population is considered: those individuals that are not yet moulting, those in moult, and birds which have completed moult. In this case the value used does not matter. Type 2 – The entire population is considered but moult scores are required. Type 3 – Only birds in moult are considered. Type 4 – Birds in moult and those that have completed moult are considered. Type 5 – Birds that have not started moult and that are in moult are considered. However, these models cannot be applied to those many birds of prey with incomplete or stepwise moults. Thus, these likelihood models cannot be applied to tropical species that moult year-round, and they sometimes fail to work for species with distinct moult seasons. Nevertheless, Zuberogoitia *et al.* (2016a) modelled the moult of Bearded Vul-

tures using the data type 1, requiring only information on whether an individual has not yet started moult, is in moult, or has completed moult, coded as 0, 0.5, and 1, respectively, using only the current year’s moulting feathers for analyses.

Explanatory variables

The moult package (Erni *et al.*, 2013) goes further, by enabling exploration of the effects of explanatory variables (e.g. sex, age, different geographical populations, years, rainfall; Barshep *et al.*, 2013 and Zuberogoitia *et al.*, 2016a,b) on: 1) moult duration, 2) start date and 3) the standard deviation of the start date (Erni *et al.*, 2013). As the authors suggest, these covariates can overlap, and quadratic terms, interactions, etc. can be added to either part, using the standard R notation for model formulae. Dietz *et al.* (2015) investigated the effect of body mass and geographical latitude on primary moult duration with linear and quadratic models, using a non-phylogenetic conventional ordinary least squares regression (OLS) and a phylogenetic generalised least square regression (PGLS) in R. Dietz *et al.* (2013) also used the moult package for some analyses. Since the package does not allow a comparison of nested groups they also used general linear models (GLM) for testing differences between age categories within sex, and between males and females within an age category, employing a series of models that estimated a combination of the variables (duration, start date and SD of start date) separately for both age category and sex and calculating AIC values.

Using moult for ageing

In species achieving a complete moult in one moult cycle, a high proportion of individuals can be aged as either in their second

cy (in second-basic plumage) or older (at least third-basic plumage; Pyle, 2005a). However, it is possible to go further, through analysis of feather retention patterns. An individual with adult plumage but with some retained juvenile feathers is aged as second cy in autumn or third cy in spring. If the retained feathers are adult (i.e., two generations of adult feathers), the individual will be aged as at least third or fourth cy (3rd cy+ in autumn/4th cy+ in spring).

For those species taking more than one moult cycle to complete the replacement of all feathers of the same generation, the minimum age of individuals can be determined up to their 5th cy (fifth-basic plumage). This is achieved by examining the number of generations present among the primaries and secondaries, and looking for retained feathers (see e.g. Martínez *et al.*, 2002; Pyle, 2005a; Zuberogoitia *et al.*, 2013). In some species showing multiple different plumages (i.e., juvenile, subadult and adult) birds can be aged beyond their 5th cy (see e.g. Zuberogoitia *et al.*, 2016a). Moreover, if the moult pattern and the trend in the asymmetry of both wings are known it is possible to go further in ageing certain species (e.g. Common Buzzard <http://depredadoresdebizkaia.blogspot.com.es/2013/01/busardo-ratonero-tercera-mudana.html>).

THE MOULT OF BIRDS OF PREY AND ITS ECOLOGICAL IMPLICATIONS

Trade-offs between moult, breeding, migration and wintering

The processes of breeding, flight feather moult, and migration all require extra food above the needs of daily maintenance. Normally, each stage requires high amounts of energy that determine mutually exclusive activities (Hedenström, 2006). Moult is usually timed to minimise peaks in energy demands during either reproduction or migration, and

the duration and extent of moult is constrained by the energy invested in either of the latter two factors (Pietiäinen *et al.*, 1984). In addition, many birds demonstrate a quiescent period in winter, during which they are neither breeding, moulting or migrating (Newton, 2009).

Moulting and breeding are both energetically demanding activities. Hence moult in passerines is usually delayed until breeding has finished (Hemborg & Lundberg, 1998; Hinsley *et al.*, 2003). However, birds of prey require long periods for moulting, and therefore moult normally starts during incubation (several weeks earlier in females than males) or during the first weeks of chick rearing (Schumtz, 1992; Newton, 2009; Zuberogoitia *et al.*, 2016a). In birds of prey, the division of breeding duties between the sexes is more marked than in most other birds (Korpimäki & Hakkarainen, 2012). In most species, except vultures, females perform most or all of the incubation, brooding and feeding of the nestlings, while males provide most or all of the food for the family (Newton 1979, 1986; Cramp & Simmons, 1980; Krüger, 2005; Zuberogoitia *et al.*, 2018). A period of hunger, due to increased demand for food on the part of offspring, is mostly associated with a deceleration in the process of feather loss and also causes some birds, mainly males, to arrest the moult process in order to meet their offspring's requirements (see Newton & Marquiss, 1982; Espie *et al.*, 1996; Cieslak & Dul, 2006; Zuberogoitia *et al.*, 2009). Hence, the more time spent rearing young, the less time there is for moult. Reciprocally, a longer moult, to clear worn feathers from the wing, may make breeding in the next season impossible (Rohwer *et al.*, 2011). The number of moulted remiges has also been found to decrease with increasing brood size (Pietiäinen *et al.*, 1984; Karell *et al.*, 2013). Equally, birds losing their broods early, or not commencing breeding at all in

the given season, tend to have a more advanced moult (Cieslak & Dul, 2006).

Photoperiodic responses in birds differ with latitude and more northerly breeders tend to moult faster (Orell & Ojanen, 1980; Morton & Morton, 1990, Bojarinova *et al.*, 1999). Late-moulting birds will also have shorter days in which to accumulate energy stores for overnight feather growth (Murphy & King, 1990), and may face dwindling food supplies and falling temperatures. Later breeding has been associated with reductions in adult reproductive success and survival (e.g. Siikamäki *et al.*, 1994; Nilsson & Svensson, 1996), and conflicts between the requirements of breeding and moulting have been suggested as explanatory factors (Hinsley *et al.*, 2003). Birds of prey, however, have corrected this problem and show differential moulting processes depending on the latitude of the breeding grounds. Smaller raptor and owl species normally finish their moult before the post-breeding migration or before winter (for sedentary species). However, late-breeding species (e.g. Eurasian Hobby, Scops Owl) or populations (e.g. arctic peregrines; Wegner & Kersting, 2016) replace their feathers in two seasonal moult cycles: starting on their breeding territories and finishing at the wintering grounds.

In long-distance migrants flight feather moult rarely overlaps with breeding or migration. However, most species start moulting during the last part of the breeding season and stop before migration, resuming the moult in winter quarters (Herremans, 2000; Chandler *et al.*, 2010). The replacement of some primaries before migration may enable the birds to exploit a food resource during a period of the year when other pressures are not high. It may also enable the replacement of the remaining primaries, on the wintering grounds, to take place at a more leisurely rate than otherwise (Mead & Watmough, 1976). However, as we have already commented, some species are able to continue moulting

during migration (e.g. Booted Eagle, Short-toed Eagle, Montagu's Harrier). The migratory flight of harriers seems to be slow and generally takes place at relatively low altitudes. They combine flapping and gliding with hunting along the way (Brown, 1976). This mode of migration may allow harriers to continue moulting slowly while migrating, as they are not obligate soaring birds, for which gaps in the wings would represent higher energetic costs (Arroyo & King, 1996).

By contrast, large, sedentary species may extend the time devoted to moult, but suspend moult in winter to save energy, in order to survive during adverse weather periods and build enough reserves to start reproduction early (Zuberogoitia *et al.*, 2013).

Individual experience and status

Age-related differences in moult may be expected between individuals that have not yet entered the breeding population, and should be especially prominent in long-lived species with delayed sexual maturation. During the first years of life, juveniles of all species pass through critical stages that affect the moult process (e.g. dispersion, foraging experience, first migration, floating). Juveniles require more energy to obtain the same food intake as territorial adults. Experience and knowledge of the territory mark the difference, and this is reflected in the moult. Although most birds of prey do not breed during the second cy, and hence are not then limited by the energy demands required to develop the breeding cycle, juveniles normally start moulting later than adults and they moult fewer flight feathers than adults during the moult cycle. This is especially evident in large species. Immature vultures, for example, need three moult cycles to complete the moult, while adults are able to finish a complete moult in two moult cycles (Zuberogoitia *et*

al., 2013; 2016a). However, subadult birds (3rd, 4th and 5th cy) start moulting earlier than adults, although they are still not able to moult more feathers than adults (Zuberogoitia *et al.*, 2016a). As birds gain experience they can mobilise more energy, which enables them to moult earlier and change more quills than juveniles.

Age-related plumage care

New quills usually contrast strongly with old feathers in both juvenile and subadult birds. This is made more obvious by the fact that, as we have mentioned above, feathers are different during the first stages of the life of a bird of prey, particularly in large raptors. However, the older an individual, the more difficult it is to detect differences between two generations of flight feathers. We suspect that individuals are able to improve feather care, and that this ability may be related to survival probability.

Territory quality

Individuals inhabiting a rich territory may have a greater food intake and feed more frequently than those located at a lower quality site. This parameter (territory quality) is usually difficult to measure. Occupancy, breeding success, and productivity are the commonest factors used to model it. We suggest that moult may be used as another relevant tool for assessing territory quality. In this regard, Espie *et al.* (1996) showed that male Merlins *Falco columbarius*, inhabiting higher quality territories had higher moult scores, suggesting that they were able to moult at a faster rate, or start earlier, than their counterparts in lower quality territories. This example suggests that moult may be used as a novel tool to study population ecology.

Applications of moult in ecological studies

Unfortunately, few studies of moult in birds of prey go further than the classical objective of ageing an individual. As Newton (2009) suggested, the lack of knowledge of basic moult in raptors prevents major investment in other research projects. Nevertheless, it should be possible to develop a trend in which moult can be used to test the biological and ecological parameters of birds of prey. By way of an example, Karell *et al.* (2013) suggest that the colour polymorphism of Tawny Owls is likely to covary with physiological and behavioural traits, due to genetic pleiotropy between genes regulating pigment production and those regulating physiological and behavioural functions. The authors show that both male and female brown Tawny Owls moult significantly more primary feathers than grey individuals, irrespective of age or reproduction decisions in the year of moult. The benefits of moulting additional feathers may override putative costs and instead improve performance. In the studied population, brown adult Tawny Owls have a lower survival probability than grey birds, especially under adverse winter conditions (Karell *et al.*, 2011).

This type of analysis using birds of prey as models is scarce in the literature but nowadays there is increasing interest in exploring the relationship between moult and ecological processes in other groups of birds. For instance, moult can serve as an indicator of other life-history stages that cannot be quantified directly. Zuberogoitia *et al.* (2016b) showed a relationship between delayed moult onset of European Storm Petrels *Hydrobates pelagicus* and particular episodic weather events. Barshep *et al.* (2013) quantified the effects of environmental factors on the start and duration of moult in the Curlew Sandpiper *Calidris ferruginea*, demonstrating that disturbance at a certain stage within the annual cycle of migratory birds can alter the next

biological event, through carry-over effects. They demonstrated that when moult started later the duration was often shorter, but that late completion of moult might have fitness consequences, probably jeopardising survival. Rohwer *et al.* (2011) suggested that, if feather quality is the currency linking trade-offs in reproductive performance between seasons, birds with worn feathers should have reduced breeding success. In fact, by studying two species of albatrosses, they related the failure to replace all primaries every two years to a lower success rate in the breeding season following the failure. The likelihood of attempting to breed during that season was also reduced.

Determination of individual condition

If we know the moult pattern, age and gender determinations, and breeding cycle of each species we can assess the health status of an individual prior to its being handled. This is very useful for wildlife rehabilitation centres (WRC), where birds of prey are usually admitted all year round in multiple circumstances. If we know the moult pattern and the average extent of the moult on a certain date, we can distinguish between an acute or chronic cause of admission, where this is not readily apparent.

LOOKING FORWARD

In recent decades there has been increasing interest in determining the moult sequence and related traits of raptors and owls. Consequently, the number of published papers on this topic has increased considerably in recent years, although there is still a dearth of knowledge that prevents researchers from going further. Unfortunately, there is a lack of sufficient expertise for carrying out proper studies of moult in most birds of prey species.

One of the main reasons why moult data is not considered more widely is that checking raptor moult is a skill that many researchers lack.

In this review we have summarised current knowledge of the moult of birds of prey, and we propose the need for further studies to complete basic information on the moult of some species. We also consider it important to increase the use of high-resolution photography, in order to accelerate the collection of moult data for scarce or difficult-to-trap species. As a subsequent step, moult cards could be useful tools in a new generation of ecology and evolution research. It is very interesting, for example, that most raptor species follow two basic moult patterns (Falconids and Accipitrids), but owls show at least five totally different moult patterns, which are unique to each genus. We must also consider that, currently, we only partially know the moult sequence of a limited number of species, mainly European and North-American birds of prey. There is still a huge gap in knowledge of tropical species and those of other less-studied regions. This lack of information obscures potentially interesting data and limits model variations (see e.g. Kang & Hur, 2016).

An example of how moult data could be applied in future studies arises from the work of Margalida *et al.* (2013). They examined the movement patterns of pre-adult, non-breeding Bearded Vultures born in the wild Pyrenean population and in the reintroduced populations of the Alps and Andalusia. They showed that birds from the wild and reintroduced populations differed in their movement patterns, with shorter dispersal in the former. However, the authors failed to postulate which of these behaviours would be advantageous for the target populations since they lacked data on response variables (e.g. breeding success), which is needed to evaluate individual condition. We consider that, by using field photographs of the birds,

it might be possible to obtain individual moult cards. The response variable (moult scores) could then be modelled with fixed factors, such as the origin of the population, sex, or age; and with covariates, such as dispersal area, movement patterns and dispersal distance

This method is also valid for testing the life strategies of different populations or for comparing different habitats (see e.g. Hinsley *et al.*, 2003). For example, some species, mainly large raptors and owls, do not breed every year, and knowledge of moult scores might permit other hidden responses to be evaluated (see e.g. Rohwer *et al.*, 2011). Moreover, moult scores and related factors (onset, standard deviation of the start date and moult duration) may be useful for comparing the inter-annual effects of climatic conditions on target populations (see e.g. Zubero-goitia *et al.*, 2016b).

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SUPPLEMENTARY ELECTRONIC MATERIAL

Additional supporting information may be found in the on-line version of this paper. See volume 65(2) on www.ardeola.org

Appendix 1, Figure A1. Left wings of Tawny Owls, lit by normal flash (left) and UV torch (right).

Appendix 1, Figure B1. Molt sequence of a 4th cy Bonelli's Eagle in flight, photo taken in January

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