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Research paper

Moult and age determination criteria of the monk parakeet (*Myiopsitta monachus*)

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Abstract

Moult and age determination criteria of the monk parakeet (Myiopsitta monachus). Age determination of the invasive monk parakeet *Myiopsitta monachus* has been hampered by its juvenile plumage showing only subtle differences from subsequent plumages, and little is known about its moult. Here we examined three specific traits (grey patch on forehead, scalloped breast, and notch on primary P9) and three general juvenile traits (bill cornification, pale margins on wing feathers, and shape of flight feathers) and tested their potential as age determination criteria using 709 specimens of this parakeet collected from the metropolitan area of Barcelona in 2023 and 2024. We also studied five moult components: phenology, duration, extent, sequence, and intensity. Bill cornification, forehead patch, and scalloped breast (with continuous maturation) were exclusively associated with juvenile birds, while pale margins, shape of flight feathers (especially those of rectrices), and notch on P9 (all with discrete maturation) allowed us to age birds throughout the entire first annual moult cycle. The moult season stretched from March to November, although the mean moult duration was 168 days. Post-juvenile moult included the body and an average of 16 wing and tail feathers, while postnuptial moult was characterised by retention of several primary coverts, and frequently also of outer secondary coverts and inner primary coverts. The primary moult sequence was clearly divergent across tracts, with alula, tertials, and secondaries being less clearly so, while it tended to be convergent in rectrices. Moult intensity described a parabola for both primary and body feathers. We integrated this information in an age-determination protocol that may help increase our understanding of the population dynamics of monk parakeets.

Key words: Moult duration, Moult extent, Moult intensity, Moult phenology, Moult sequence, Psittaciformes

Resumen

Criterios de muda y determinación de la edad de la cotorra argentina (Myiopsitta monachus). La determinación de la edad de la cotorra argentina, *Myiopsitta monachus*, se ha visto dificultada porque su plumaje juvenil solo muestra diferencias sutiles con plumajes posteriores y su muda es poco conocida. Examinamos tres caracteres específicos (mancha gris en la frente, pecho festoneado y muesca en P9) y tres rasgos juveniles generales (cornificación del pico, márgenes claros en las plumas del ala y forma de las plumas de vuelo) y probamos su potencial como criterio de determinación de la edad utilizando 709 especímenes recolectados en el área metropolitana de Barcelona entre 2023 y 2024. También estudiamos cinco componentes de la muda: la fenología, la duración, la extensión, la secuencia y la intensidad. La cornificación del pico, la mancha en la frente y el pecho festoneado (con maduración continua) se asociaron exclusivamente a aves juveniles, mientras que los márgenes pálidos, la forma de las plumas de vuelo (especialmente de las rectrices) y la muesca en P9 (todas con maduración discreta) permitieron determinar la edad de las aves a lo largo de todo el primer ciclo de muda anual. La temporada de muda se extendió de marzo a noviembre, aunque la duración media de la muda fue de 168 días. La muda postjuvenil incluyó el cuerpo y un promedio de 16 plumas de las alas y la cola, mientras que la muda postnupcial se caracterizó por la retención de varias coberteras primarias y, con frecuencia, de secundarias externas y primarias internas. La secuencia de la muda primaria fue claramente divergente en la mayoría de tractos, aunque lo fue menos en el álula, las terciarias y las secundarias, mientras que tendió a ser convergente en las rectrices. La intensidad de la muda describió una parábola tanto para las primarias como para el cuerpo. Integramos esta información en un protocolo para la determinación de la edad de la cotorra argentina, que puede mejorar nuestra comprensión de su dinámica poblacional.

Palabras clave: Duración de muda, Extensión de muda, Intensidad de muda, Fenología de muda, Secuencia de muda, Psittaciformes

Introduction

Age is a key factor underlying numerous biological processes such as reproduction, post-juvenile dispersion, and survival (Martin 1995, Sutherland et al 2000). Age determination is therefore particularly relevant for the management of both threatened and invasive avian species. The age of free-ranging bird species is typically determined using conspicuous plumage characters that allow determining of several age classes, such as the circannual progression of immature and subadult (predefinitive) plumages until the acquisition of the adult (definitive) plumage in large gulls and raptors (Pyle 2008, Forsman 2016, Adriaens et al 2022). However, age determination for most bird species requires close examination of inconspicuous characters, such as iris colour, skull pneumatisation, and moult patterns (Chapin 1949, Wilson and Hartley 2007). All of these characters are based on the presence/absence of retained juvenile stages, although their usability and temporal applicability may differ widely among species and populations. While most juvenile traits change continuously until they reach full maturity (e.g., iris colour), moult exhibits two useful properties for age determination: i) it is a temporally delimited process of circannual periodicity, and ii) it produces stable and predictable patterns within circannual cycles (e.g., the retention of remiges and primary coverts during the post-juvenile moult in many species). This is not necessarily so, however, among annual cycles (Laesser and van Wijk 2017, Pyle and Schofield 2023).

Age determination in bird species for which there is no established protocol follow a heuristic iterative approach. This starts from a working hypothesis that is tested on the first individuals examined, then updated with new empirical knowledge acquired during the examination of more individuals, until the initial hypothesis or another hypothesis derived from this refinement process leads to the identification of diagnostic traits and accurate protocols. A reasonable starting hypothesis that focused on the bird's plumage considered that: i) juvenile plumage differs from subsequent plumages, ii) the moult that most bird species undergo shortly after fledging only replaces part of the juvenile plumage and therefore produces moult limits between the old juvenile feathers and the new feathers, and iii) that limits of this post-juvenile moult are predictable and resemble those of similar species. By defining traits that characterise the juvenile plumage and detecting post-juvenile-moult limits, it is possible to determine the age of birds until the start of the second annual moult cycle, that is, usually after the first potential reproductive season (Delhey et al 2020, Jenni and Winkler 2020a). Typical features that characterise juvenile feathers are shape (which tends to be shorter and narrower with more pointed tips in most taxonomic groups), colour (which tends to be duller with paler tips), and wear (which tends to be more faded and abraded). Typical post-juvenile-moult limits occur within wing coverts, tertials, and rectrices in passerines and near-passerines (Jenni and Winkler 2020b, Pyle 2022).

The monk parakeet *Myiopsitta monachus* is native to South America where it is considered an agricultural pest (Avery 2020, Pruett-Jones 2021). It was introduced through pet trade to North America and Europe in the 1960s, and rapidly shifted its reproductive and moult phenology from the austral to the boreal seasonality (Avery et al 2012). Its populations have grown exponentially (Postigo et al 2019, Borray-Escalante et al 2024), expanding from the original cities where escapees first established to other urban areas, with further spreading to rural habitats where they also cause agricultural damage (Senar et al 2016, Hernández-Brito et al 2020, Castro et al 2022). Awareness of the species' potential impacts has sparked great interest in developing optimal management strategies and accurate models to predict potential population outcomes under various biological and management scenarios (Büyüktahtakın et al 2015, Senar et al 2021). However, the effectiveness of these models is currently limited by gaps in key data, such as poor knowledge of age determination, which is vital to understand population dynamics and ensure the reliability of predictions (Oldekop et al 2023, Witting 2024). Age distribution affects reproductive rates, intra-specific competition, and survival (Gurney et al 1983, Pan et al 2018). Knowledge of the age structure of an invasive population also enables the design of better control strategies, tailoring interventions to the most vulnerable or productive age classes (Wells et al 2016).

Here we studied the moult of the monk parakeet with the aim of providing reliable age-determination guidelines throughout the year. Until now, age determination of free-ranging monk parakeets has been hindered by the lack of obvious diagnostic characters. In the field, its juvenile plumage shows only subtle differences with subsequent plumages (such as less grey on the juvenile forehead) (Avery et al 2012), and disappears as the post-juvenile moult proceeds. In the hand, the shiny blue-green wing and tail feathers are highly variable. The colour degradations within feather tracts are puzzling and blur the presence of potential post-juvenile moult limits. Because the post-juvenile (preformative) moult of monk parakeets is known to not include primaries (Navarro et al 1992, Avery et al 2012, Pyle 2022), monk parakeets moulting primaries will be adults. However, this information does not allow determination of the age of those that are not moulting primaries, regardless of whether or not the moult period is over.

In this study we carried out a systematic search for juvenile traits from late May (when fledglings start flying; Senar et al 2019), including a trait that has remained largely overlooked: notches on outer primaries. We tested whether their development correlated positively with age, expecting to find this only in monk parakeets that had moulted their primaries at least once (i.e., after their first annual moult cycle). We then examined specimens for moult limits using the presence of juvenile traits within rectrices, tertials, and wing coverts. Since moult limits are frequently found in adults of many other non-passerine families (eg. Columbidae and Picidae; Pyle 2022), we considered that moult limits within primaries, primary coverts, or secondaries could also occur following an incomplete postnuptial (prebasic) moult. We collated this information with moult phenology and plumage wear, which is slight shortly after finishing moult but is expected to increase toward the dates when primary moult commences, especially on juvenile feathers, thereby facilitating identification of post-juvenile moult limits. From moult limits,

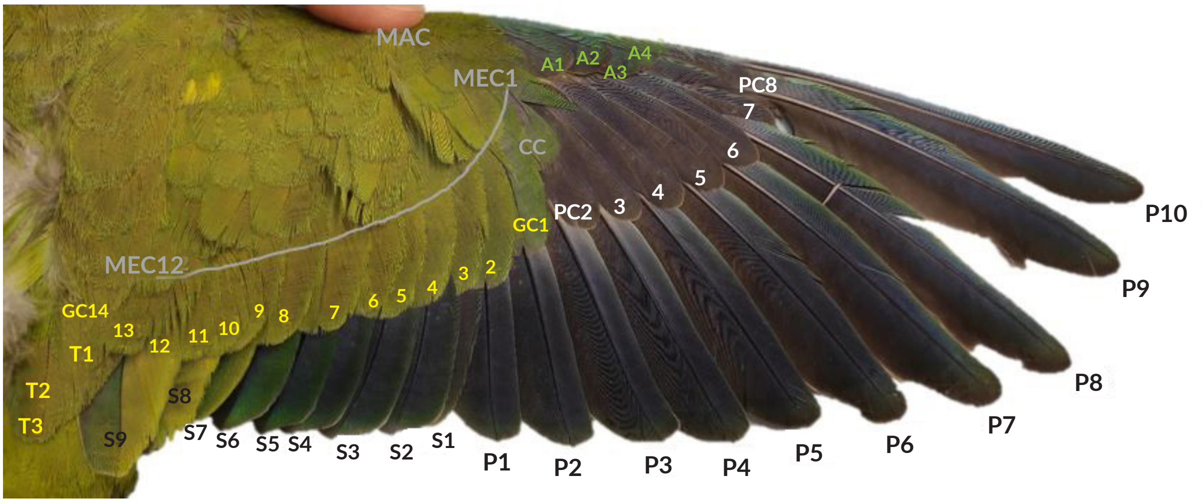

Fig. 1. Wing feather tracts and numbering used in this article. We followed numbering by Jenni and Winkler (2020b) save for the tertials, whose moult clearly differs from that of the secondaries. Rectrices were counted from the central pair (R1) toward the outer ones (R6). P, primary; S, secondary; T, tertial; GC, greater covert; PC, primary covert (PC1 and PC9 hardly visible); A, alula; MEC, median covert; MAC, marginal coverts; CC, carpal covert. The photo is from an adult monk parakeet labelled ICM112 (Pallejà, 5 January 2024).

Fig. 1. *Tractos de plumas del ala y numeración utilizada en este artículo. Seguimos la numeración de Jenni y Winkler (2020b) salvo para las terciarias, cuya muda difiere claramente de la de las secundarias. Las rectrices se empezaron a contar desde el par central (R1) hacia las externas (R6). P, primaria; S, secundaria; T, terciaria; GC, gran cobertora; PC, cobertora primaria (PC1 y PC9 apenas visibles); A, álula; MEC, cobertora mediana; MAC, cobertoras marginales; CC, cobertora carpal. La foto corresponde a una cotorra argentina adulta con la referencia ICM112 (Pallejà, 5 de enero de 2024).*

we defined moult extent and frequency of feather moult, thus allowing age determination of non-moulting birds.

To better understand how to use moult to calculate age of monk parakeets and interpret the final output of moult itself, we quantified three other moult components: duration, sequence, and intensity. Moult duration is linked to plumage quality mediated by timing of moult start, with late moulters tending to show plumage of lower quality (de la Hera et al 2010). Furthermore, juvenile feathers are generally of lower quality and become more worn and faded over time than adult feathers.

The long breeding season of monk parakeets in the study area (Senar et al 2019) might influence moult start and duration. Primary moult sequence in the monk parakeet starts by primary P6 and proceeds divergently (that is, in opposite directions from the focal primary (fig. 1), with secondaries and tertials also following a divergent pattern (Pyle 2013, 2022). We tested whether our specimens fitted this sequence, and we also defined the moult sequence of rectrices, alula feathers, and greater coverts. Additionally, we checked for evidence of serial moult or Staffelmauser (the simultaneous running of more than one moult wave following the same sequence), as observed in other Psittaciformes (Pyle 2013) and suspected to occur in some monk parakeets (Pyle 2022). Moult intensity is the amount of plumage growing at any given stage of the moult process, and it measures the investment in feather material over time. It may provide insight into the mechanisms of remex retention and predict moult extent within primaries and secondaries, which is common among non-passerines of similar size, including other Psittaciformes (Pyle 2022). We tested whether the moult intensity of the inner (P5 through P1) and outer (P7 through P10) primaries differed, expecting intensity to be greater in the latter because monk parakeets might retain inner primaries (Pyle 2022). At the end of this article, we provide a protocol to determine age.

Material and methods

We examined 709 specimens collected from 26 localities in the metropolitan area of Barcelona (within 55 km of the city centre). Specimens are lodged in the ornithological collections of the Natural Science Museum of Barcelona (MCNB) and the Institute of Marine Sciences (ICM-CSIC). The samples were collected after culling carried out in the vicinity between March 2023 and February 2024 (see Borray-Escalante et al 2023). We also included 11 monk parakeets captured and ringed in the MCNB between September 2023 and February 2024. We specified sample sizes used for each analysis where appropriate.

Monk parakeets have 10 primaries, nine secondaries, three tertials, and 12 rectrices. On the upper wing they have four alula feathers, nine primary coverts, 14 greater coverts, one carpal covert, 12 median coverts, and near 100 marginal coverts (fig. 1). We divided the rest of the contour plumage in head, upper and under parts, upper- and under-tail coverts, scapulars, and under-wing coverts. We scored the approximate percentage (expressed as a decimal) of marginal coverts and body feathers growing in within each group.

Juvenile traits

Birds that had not yet moulted their juvenile plumage were considered juveniles. We followed a moult-cycle terminology to name older birds. This system establishes

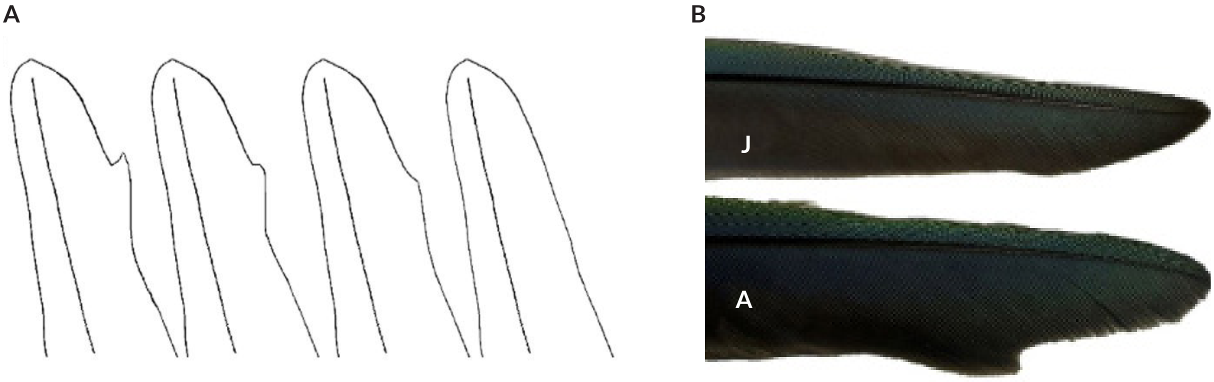

Fig. 2. A, categories of notch development defined in this article. From left to right: full (adult typical), medium, very little, null (juvenile typical). B, apical part of primary feather 9 of a juvenile individual (J) without a notch and of an adult (A) with a notch.

Fig. 2. *A, categorías de desarrollo de la muesca definidas en este artículo. De izquierda a derecha: completo (típico de los adultos), medio, muy poco, nulo (típico de los juveniles). B, parte apical de la pluma primaria 9 de un individuo juvenil (J) sin muesca y de un adulto (A) con muesca.*

the biological age of birds and it has a circannual duration. Each annual cycle is defined as the period between the onset of two consecutive postnuptial moults. The first cycle is an exception because it does not start with a postnuptial moult. Although juveniles obviously belong in the first annual cycle, we reserved the term 'first cycle' for birds between the start of the post-juvenile moult and the start of the first postnuptial moult. The term 'adult' designates birds after their first cycle. Unfortunately, no definition (or terminology) is free of contradictions because even birds of the same population are not synchronised. For example, two birds born on the same day but that started their first postnuptial moults six weeks apart would be aged using the moult-cycle terminology as first cycle and second cycle during these six weeks.

We checked for the presence of three juvenile features shared by many bird species: incomplete bill cornification, presence of pale margins on wing feathers, and shape of flight feathers (Jenni and Winkler 2020b, Pyle 2022). We also checked two specific plumage traits of juvenile monk parakeets: ill-defined forehead patch and scalloped throat and breast.

The inner vane of primaries P7 through P9 of monk parakeets frequently has a notch of variable size and shape. We scored its development according to four categories (fig. 2). We first obtained frequency of occurrence using 543 ringed nestling specimens of known age, tagged in the city of Barcelona during 2017 and 2019 (validation dataset). Notch development (null, little, or full) was only recorded after their recapture: 73 as juveniles and 29 as adults (17 were recaptured both as first-cycle and adults). We then tested whether differences in notch development in our specimen data correlated to bird age using chi-square tests.

Phenology and duration

Once we were able to determine the age of monk parakeets, we regressed the frequency of moulting birds per month (using polynomial regression with a span = 0.5). We regressed each of six wing-feather tracts (all except marginal and median coverts), the rectrices, and the body (N = 185 adults and 105 first-cycle).

We estimated population mean and standard error of moult start (SE_s) and end dates (SE_e) using generalised linear models with a binomial distribution and a probit link function (Rothery and Newton 2002): moult presence/absence ~ date. Moult duration was obtained from subtracting mean start date from mean end date. The standard error was calculated as:

$$SE=\sqrt{(SE^2_e + SE^2_s)}$$

We also made a rough estimate of moult duration of late moulters by subtracting the last date in active primary moult from the last test date of the last birds in the first stages of primary moult (see Moult sequence).

Extent and frequency of feather replacement

We scored each feather on the left wing and the left half of the tail from parakeets that had completed the post-juvenile moult (N = 93): 1 when moulted (post-juvenile) and 0 when retained (juvenile). We scored marginal coverts as a decimal between 0 and 1. We estimated post-juvenile moult extent as the mean number and 95 % bootstrapped intervals of wing feathers and rectrices moulted. Frequency of feather replacement was computed as the mean score for each feather.

We assessed retention of primaries, secondaries, and primary coverts in 192 adult birds (that is, those that had undergone at least one postnuptial moult) based on their fade and wear.

Moult sequence

We scored the growth stage of rectrices, tertials, secondaries, primaries, alula feathers, and greater and primary coverts of 106 first-cycle and 186 adult monk parakeets (fig. 1). Because sequences within feather tracts may differ between partial and complete moults (Guallar

A  B 

Fig. 3. Juvenile (A) and adult (B) monk parakeets, Parc de la Ciutadella (Barcelona), 21 July and 9 September 2024, respectively.

***Fig. 3.** Juvenil (A) y adulto (B) de cotorra argentina, Parc de la Ciutadella (Barcelona), 21 de julio y 9 de septiembre de 2024, respectivamente.*

2024), we plotted sequence within rectrices, tertials, and greater coverts separately for first-cycle and older birds (the remaining feather-wing tracts were retained during the post-juvenile moult). To account for the differences in moult progress, we scored the growth stage of each feather on a continuous scale: 0 for old feathers, 0.5 for shed feathers that had not yet emerged, and 100 for fully grown feathers. For intermediate stages we took into account that feather length increases linearly (Winkler et al 1988). Thus, a feather grown up to 75 % of its full length was scored 75. This method was highly repeatable (see Guallar and Quesada 2023).

We determined moult sequence within feather tracts only when it could be clearly established, which implies that sequences from each individual were incomplete. We ordered growing feathers within tracts following Rohwer (2008): relative lengths of growing feathers indicate their sequence of replacement; when two feathers had equivalent lengths, we assigned them the same order along the sequence. We regarded primaries and secondaries growing in > 1 consecutive sequence as Staffelmauser (see Results). We estimated mean order within the sequence and 95 % intervals using Bayesian bootstrapping (applying 4,000 iterations), as implemented in the library bayesboot of the R environment (Bååth 2016). All analyses were carried out in R (R Core Team 2024).

Moult intensity

We computed body moult intensity as the percentage of feathers growing in on each part of the body defined above, and weighed by its weight relative to its accumulated mass. For this purpose, we used the weights obtained from a house sparrow model (Guallar and Quesada 2023). We regressed body moult intensity on date (polynomial regression with a span = 0.5).

We computed the raggedness index for the primaries (Bensch et al 1991) as:

$$\sum_i (100 - l_i)$$

where l_i = % growth of primary i. This index does not take into account either size or shape differences between primaries. We regressed raggedness on progress of primary moult, computed as $\sum_i l_i$ (polynomial regression with a span = 0.75).

Because monk parakeets tend to retain inner primaries (see Results) we tested whether outer primaries (P7 through P10) presented higher moult intensity than inner primaries (P5 through P1). We compared the length of growth or growing inner primaries with that of the outer primaries. To do so, we measured the length of each primary of an adult specimen (label ICM044), and considered that relative length was approximately constant across the adult population.

Results

Juvenile traits

Juveniles showed soft, slightly swollen, lateral bill teeth (fig. 3), and by late summer some had already lost these. Adult bills showed eroded layered bill edges whereas juvenile bills had smooth edges.

Wing feathers of the monk parakeets tended to have pale tips, especially on juvenile secondaries and primary coverts. Wing feathers became darker (e.g., bluer primary coverts) with narrower or absent pale tips in adults (fig. 4),

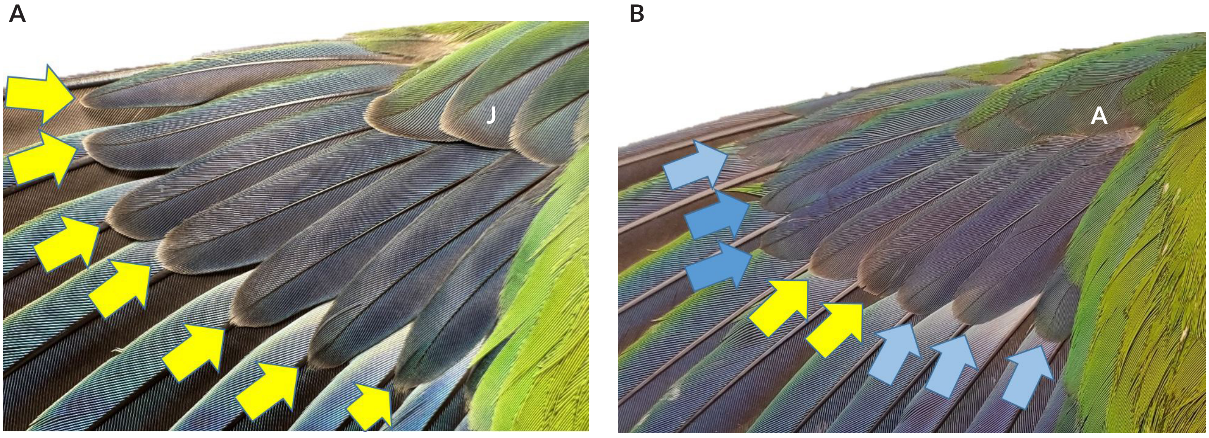

Fig. 4. Primary coverts. A, the primary coverts with pale tips, typical of a juvenile (J) monk parakeet. All feathers are similar. For clarity, the tips of the primary coverts have been marked with yellow arrows, indicating juvenile colouring. B, the primary coverts of an adult (A) individual. It can be observed that the individual has retained two juvenile feathers with pale tips (marked with yellow arrows), displays three inner feathers of a second generation (marked with light blue arrows), and two primary coverts typical of an adult, in the distal section, without pale tips and slightly bluer in colour (marked with dark blue arrows). The photos belong to free-ranging individuals captured during ringing sessions.

Fig. 4. Cobertoras primarias. A, las cobertoras primarias con puntas pálidas, típicas de un individuo juvenil (J) de cotorra argentina. Todas las plumas son similares. En favor de la claridad, las puntas de las cobertoras primarias se han marcado con flechas amarillas para indicar la coloración juvenil. B, las cobertoras primarias de un individuo adulto (A). Puede observarse que el individuo ha retenido dos plumas juveniles con puntas pálidas (marcadas con flechas amarillas), presenta tres plumas internas de una segunda generación (marcadas con flechas de color azul claro) y dos cobertoras primarias, típicas de adulto, en la sección distal, sin puntas claras y de un color ligeramente más azul (marcadas con flechas de color azul más oscuro). Las fotos pertenecen a individuos libres capturados durante sesiones de anillamiento.

although there was great variation, and for example, some juvenile feathers were indistinguishable from those of adults. Similarly, juvenile secondaries and greater coverts were shorter, narrower, and more or less tapered (adults tended to be square). Juvenile rectrices were pointed whereas adult rectrices were rounded (fig. 5). The combination of wear, shape, and colour facilitated detection of moult limits within the greater coverts, tertials, and rectrices (fig. 6). The juvenile forehead-patch was smaller and showed a variable green wash that blurred its edges, with barely any grey near the eyes (fig. 3). Juvenile throat and breast feathers had paler, and suede-colour centres, showing little contrast with the dull-white tips, whereas these were greyer with whiter edges in adults (fig. 7). They started blurring with the post-juvenile moult and disappeared in late autumn.

The frequency of a full notch on the adult P9 was smaller than expected by chance in juvenile P9 ($\chi^2_1 = 31.7$, p-value < 0.001), greater than expected by chance in adults ($\chi^2_1 = 46.7$, p-value < 0.001), and significantly greater in adults than in juveniles P9 ($\chi^2_1 = 37.3$, p-value < 0.001). Absence of a notch on P9 only occurred in juvenile and first-cycle parakeets (and one second-cycle), although sample size was small (validation dataset, table 2). Frequency of null versus full developed notch on P9 in adults did not differ between our dataset and the validation dataset ($\chi^2_1 = 0.4$, p-value = 0.540; N = 663 and 41, respectively); however, it was significantly lower for juvenile and first-cycle parakeets ($\chi^2_1 = 6.3$, p-value = 0.012; N = 584 and 74, respectively). The presence of a fully developed notch did not differ between the adult P8 and the juvenile P8 ($\chi^2_2 = 214.3$, p-value = 0.16), whereas the presence of a fully developed notch was significantly greater in the adult P7 than in the juvenile P7 ($\chi^2_2 = 14.3$, p-value < 0.001). Only about half of the adults developed a medium to fully developed notch on P7 (table 1).

Moult phenology

We found monk parakeets moulting primaries from April through November. Five individuals in April (N = 22) showed 3-5 fully-grown primaries, indicating that individuals within the study population may have already started moult in March. Conversely, we found monk parakeets starting primary moult as late as mid-July. Bimodality was also suggested by the curves of secondaries, rectrices, and alula feathers (fig. 8). Primary moult duration in our population was estimated at 168 (SE = 67.5) days. Mean start and end dates were 9 June (SE = 54.1 days) and 24 November (SE = 40.4 days). Latest start and end dates were 21 July (P6 = 40 %) and 24 November (P1 = 50 %).

First-cycle parakeets started wing and tail moult in June. Moult was largely finished in December. We found monk parakeets of all ages moulting body feathers throughout the year although frequency decreased during winter (see also Moult intensity). Juveniles showed a fresh plumage during summer, whereas most adults looked worn during this season, coupled with the circannual moult cycle (fig. 8). During winter, monk parakeets in their first-moult cycle usually appeared more worn than adults.

Extent and frequency of feather moult

The partial post-juvenile moult appeared to include all the body plumage (we were unable to detect juvenile feathers after December) and a variable number of marginal,

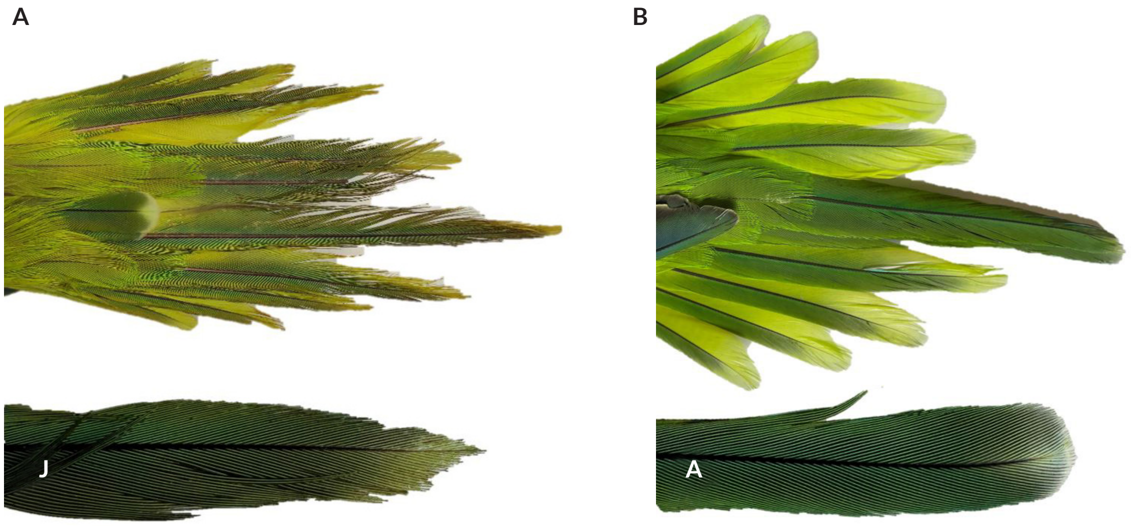

Fig. 5. Rectrix shape. A, the tail of a first-cycle parakeet showing pointed rectrix tips typical of juveniles. The left central rectrix is growing in, displaying the rounded tip typical of an adult. Below, the apical part of a juvenile feather with its characteristic pointed shape. Note also the pronounced feather wear. B, the tail of an adult individual, showing the rounded rectrix tips typical of adults. Below, the apical part of an adult feather with its characteristic rounded shape. Individuals captured in Parc de la Ciutadella on 3 November and 2 October 2024, respectively.

Fig. 5. *Forma de las rectrices. A, la cola de una cotorra de primer ciclo en la que se pueden observar las puntas puntiagudas de las rectrices, típicas de los juveniles. La rectriz central izquierda está en crecimiento y presenta la punta redondeada, típica de un adulto. Debajo, la parte apical de una pluma juvenil con su característica forma puntiaguda. Nótese también el marcado desgaste de la pluma. B, la cola de un individuo adulto en la que se pueden observarlas puntas redondeadas de las rectrices, típicas de los adultos. Debajo, la parte apical de una pluma de adulto con su característica forma redondeada. Individuos capturados en el Parc de la Ciutadella el 3 de noviembre y el 2 de octubre de 2024, respectivamente.*

Table 1. Percentage of notch on primaries P7, P8, and P9 of first-cycle and older monk parakeets (N = 584 and 663, respectively). Notch development classified according to four groups. We collapsed medium and full developed notches to allow direct comparison with the validation test (see table 2).

Tabla 1. *Porcentaje de presencia de la muesca en las primarias P7, P8 y P9 de primer ciclo y ciclos posteriores en la cotorra argentina (N = 584 y 663, respectivamente). Clasificación del desarrollo de la muesca según cuatro grupos. Sumamos las muescas de desarrollo medio y completo para permitir una comparación directa con la prueba de validación (véase la tabla 2).*

	P9		P8		P7	
	1st-cycle	Older	1st-cycle	Older	1st-cycle	Older
Null	87	7	25	2	59	17
Little	1	0	3	0	28	28
Medium	6	1	24	7	10	36
Full	6	92	47	91	3	19
Medium and Full	12	93	72	98	13	55

median, and greater coverts, tertials, and rectrices (also including the alula feather in one case A2). The smallest extent of post-juvenile moult included only 40 % of marginal coverts, while the largest extent of moult included all secondary coverts, two tertials, and four rectrices. The mean extent [95 % bootstrapped intervals] = 15.9 [14.3, 17.5] feathers per wing and 0.7 [0.4, 0.9] per tail side. Frequency of wing feather moult decreased outwardly: feathers closer to the body were prioritised over distal feathers (fig. 9). The central rectrices were those that moulted most frequently (fig. 9).

The postnuptial moult was incomplete. A variable number of primary coverts were always retained, the amount decreasing significantly with increasing age: from 7-9 during the first postnuptial moult to as few as four in subsequent moult cycles (0.63 ± 0.1 primary coverts per annual cycle; fig. 10 and 11). One to a few juvenile primary coverts were retained until the fourth cycle. Apparently, the outermost primary covert was that most often replaced and PC8 was the least replaced in second-cycle parakeets (42 % and 0 %, respectively; N = 19). Of 198 monk parakeets, we found 25 individuals which retained 1-3 innermost primaries (12.6 %) and 63 which retained 1-6 outermost secondaries (31.8 %). Primaries and secondaries were retained more frequently as they were closer to P1 to S1, respectively. The number of moulted primaries decreased significantly with age (0.66 ± 0.31 primaries per annual cycle; fig. 10), whereas the number of secondaries did not vary significantly as age increased (fig. 10).

Moult sequence

During postnuptial moults, primaries and alula feathers showed clearly divergent sequences (within each tract), while those in tertials and secondaries were less clear. The

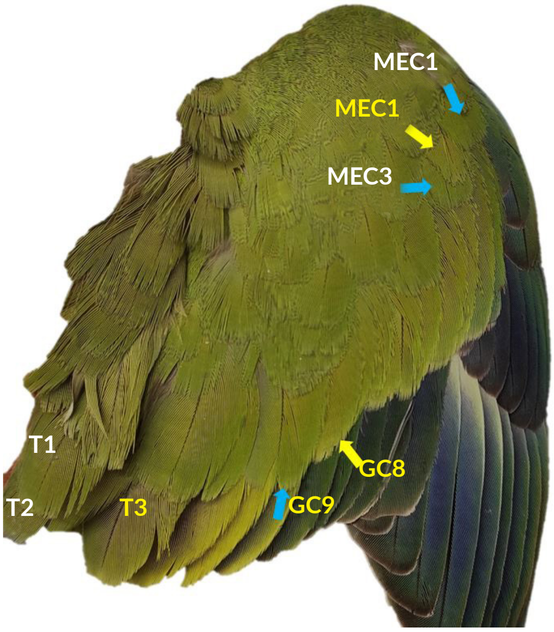

Fig. 6. Limits of post-juvenile moult in the individual labelled ICM109 (Pallejà, 5 January 2024). Median covert MEC2, eight outer greater coverts (GC1-GC9, and the carpal) and outer tertial T3 are juvenile (marked in yellow); in white with blue arrows we have marked moulted feathers in post-juvenile appearance. The remaining remiges, primary coverts, and alula feathers are juvenile; marginal coverts are post-juvenile. Note that the post-juvenile coverts and tertials are a slightly darker green with fresh square tips.

Fig. 6. Límites de muda postjuvenil en la cotorra con la referencia ICM109 (Pallejà, 5 de enero de 2024). La cobertera mediana MEC2, ocho grandes coberteras externas (GC1-GC9, incluida la carpal) y la terciaria externa T3 son juveniles (marcadas en amarillo); en blanco con flechas azules hemos marcado las plumas mudadas con apariencia de postjuvenil. Las restantes rémiges, las coberteras primarias y las álulas son juveniles; las coberteras marginales son postjuveniles. Nótese que las coberteras y las terciarias postjuveniles son de un verde ligeramente más oscuro con ápices cuadrados nuevos.

latter were therefore often blurred by the presence of an extra focal node among the outer secondaries. Rectrices tended to follow a convergent sequence (starting from R1 and R6 finishing and merging at medial rectrices on each half of the tail), with strong asymmetry between tail sides (fig. 12). Sequence within the greater coverts was ill-defined, although the carpal tended to moult last, whiles some innermost coverts seemed to be first (fig. 13B). Moult of primary coverts was decoupled from that of primaries and showed an ill-defined divergent sequence across annual cycles (N = 66 lumping all adults; fig. 8-12B). All wing and tail tracts tended to be activated at the early stages of the primary moult (fig. 8). Retained innermost primaries could be moulted at this stage (two cases), recalling Staffelmauser. Likewise, moult of retained outermost secondaries (three cases) could be resumed during the start of primary moult, although they could also be activated later as part of a continuous outward sequence, or forming a second outward wave. During post-juvenile moults, tertials showed an inward direction, greater coverts suggested an outward direction, and rectrices did not show any clear direction (fig. 13).

Table 2. Percentage of notch on primary P9 as a function of age obtained from monk parakeets of known age used for validating observed values shown in table 1 (N = 85).

Tabla 2. Porcentaje de presencia de la muesca en primarias P9 en función de la edad obtenido a partir de cotorras argentinas de edad conocida para validar los valores observados en la tabla 1 (N = 85).

	1st-cycle	2nd-cycle	3rd-cycle	4th-cycle	5th-cycle	6th-cycle
Null	69	5	0	0	0	0
Little	5	0	0	0	0	0
Full	26	95	100	100	100	100

Moult intensity

Adult body-moult intensity showed bimodality, with a main period in summer and a secondary period in spring, peaking at 14 % in mid-September and 7 % in early June, respectively. First-cycle body-moult intensity showed a single period, peaking at 12 % in early October. Both tailed off during winter at values barely above 0 % (fig. 14). Of 150 cases, only six values were over 20 %. We could not confirm the moult of juvenile-body feathers during winter.

Primary raggedness showed a near-parabola shape with a maximum of 13 % at about 38 % progress (fig. 15). Maximum values reached 26 %, and up to four primaries grew in simultaneously (two primaries in 28 % cases). One parakeet interrupted primary moult after replacing only primary P6. 14 parakeets retained up to 2 inner primaries. Moult intensity was greater than expected in outer primaries than in inner primaries (71 of 97 cases; χ^2_2 = 13.9, p-value < 0.001).

Discussion

Juvenile traits

Juvenile plumage traits that are retained during the entire first moult cycle (therefore, showing discrete maturation) have the greatest potential for age determination. Such traits include the shape of rectrix tips, pale tips on primary coverts, and, especially because of its 'user-friendly' quality, notch development on primary P9. Primary notches are enigmatic structures: their function remains obscure as does their maturation, since some nestlings already produce fully developed notches, while some individuals may not reach full maturation until the third annual moult cycle (table 2). Primary notches of various degrees are present in multiple bird groups (eg., Anatidae, Columbidae, Tyrannidae; Pyle 2008, 2022) and might have a communication function (Niese and Tobalske 2016) although we have not seen parakeets clapping their wings or heard them making a distinctive noise. Aerodynamic improvement is an alternative and non-exclusive function. Primary notches are known to

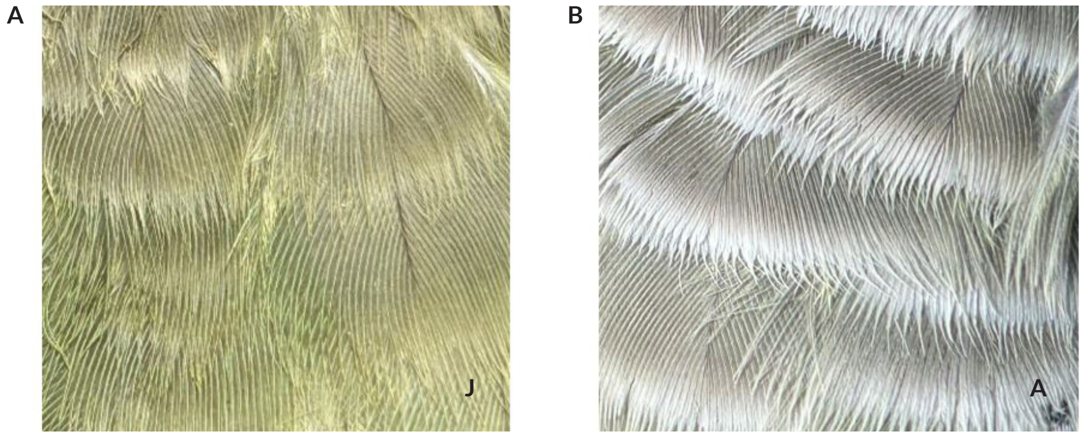

Fig. 7. Upper left: upper breast feathers of a juvenile with paler, suede-colour centres, showing little contrast with the dull beige tips. On the right, throat feathers of an adult that are greyer and have whiter edges than those of juveniles.

Fig. 7. *A la izquierda, plumas de la parte superior del pecho de un juvenil con el centro más pálido y amarillento, en las que se observa poco contraste con las puntas de color blanco beige apagado. A la derecha, plumas de la garganta de un adulto, que son más grises y con bordes más blancos que las de los juveniles.*

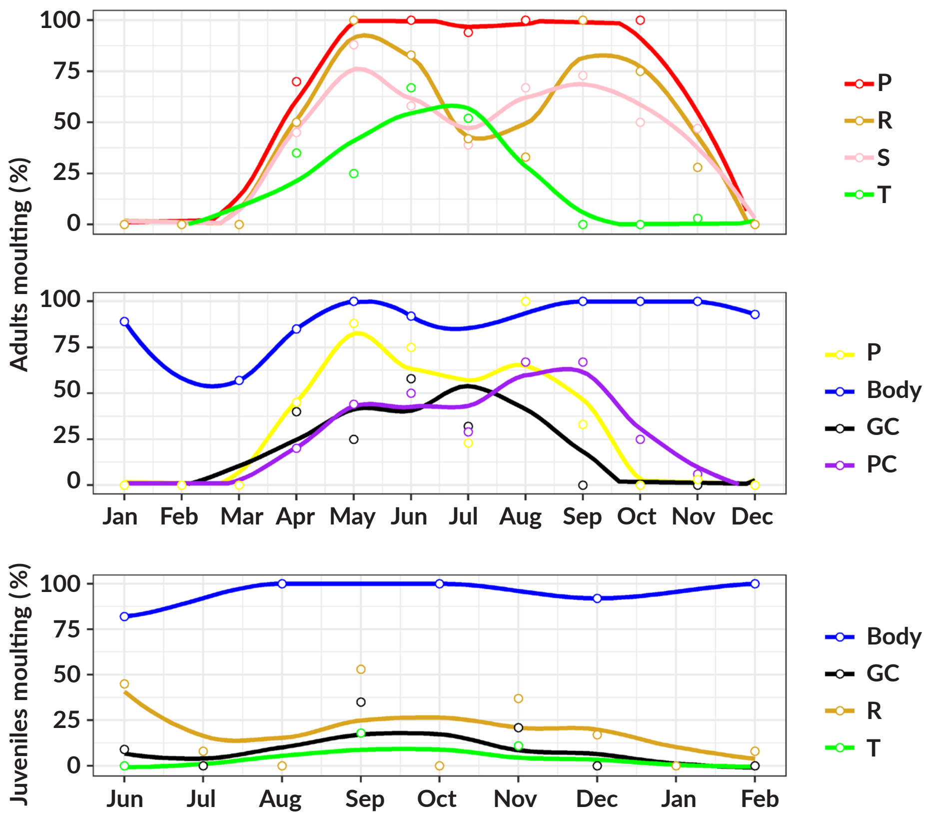

Fig. 8. Moult phenology of the monk parakeet. Upper two panels adults (N = 96), lower panel juveniles (N = 72). R, rectrices; rest of feather-tract nomenclature follows fig. 1. Dots are mean monthly values. Confidence intervals not shown for clarity.

Fig. 8. *Fenología de la muda de la cotorra argentina. Los dos paneles superiores corresponden a los adultos (N = 96) y el panel inferior a los juveniles (N = 72). R, rectrices; el resto de la nomenclatura de los tractos de las plumas sigue la de la fig. 1. Los puntos son las medias mensuales. Los intervalos de confianza no se muestran en favor de la claridad.*

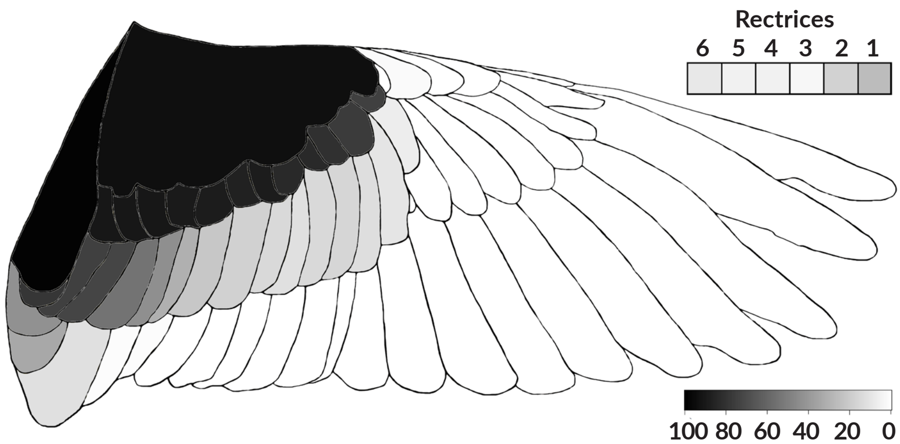

Fig. 9. Frequency (%) of wing- and tail-feather post-juvenile moult (upper right wing and left half of tail).

***Fig. 9.** Frecuencia (%) de la muda postjuvenil de las plumas del ala y de la cola (dorso del ala derecha y mitad izquierda de la cola).*

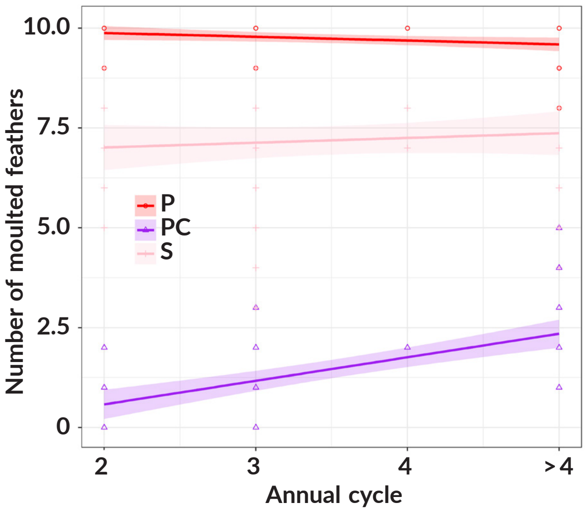

Fig. 10. Linear regression of number of moulted primaries, secondaries, and primary coverts on moult cycle. Feather-tract nomenclature follows fig. 1.

***Fig. 10.** Regresión lineal del número de plumas primarias, secundarias y coberteras primarias mudadas en función del ciclo de muda. La nomenclatura de los tractos de las plumas se muestra en la fig. 1.*

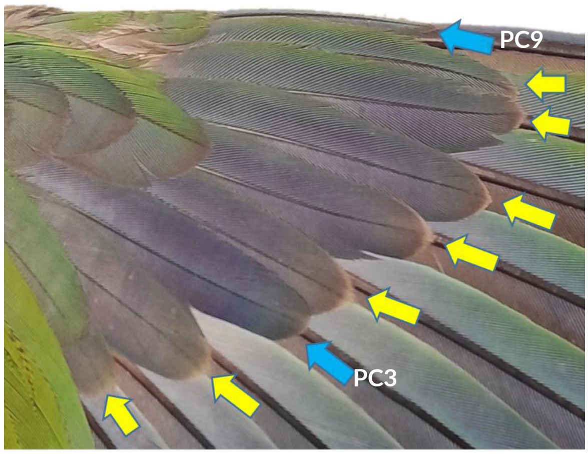

Fig. 11. Moult limits within the primary coverts of the individual labelled ICM152 (L'Hospitalet de Llobregat, 3 November 2023). PC3 and PC9 recently moulted (blue arrows), rest juvenile, duller with whitish tips (yellow arrows).

***Fig. 11.** Límites de muda en las coberteras primarias de la cotorra con la referencia ICM152 (L'Hospitalet de Llobregat, 3 de noviembre de 2023). PC3 y PC9 recientemente mudadas (flechas azules), el resto son juveniles, más opacas con ápices blanquecinos (flechas amarillas).*

increase flight performance in Galliformes (Drovetski 1996) and might help dampen vibration during flight (Deng et al 2023). Moreover, the degree of maturation could vary with year or site as suggested by differences found between juveniles of our two independent samples.

Moult study

Our moult study corroborates previous results on phenology, postnuptial extent, and sequence conducted in other geographical areas where the species are native or also introduced. Despite latitudinal differences, monk parakeets in the metropolitan area of Barcelona (41-42°) show the same 6-month shift in moult phenology as those in Miami, Florida (25.5-27°) with respect to their native geographical range (Avery et al 2012). The primary-moult season lasts about eight months, one month longer than in their native geographical range (Aramburú 1995). This long period overlaps with the four-month

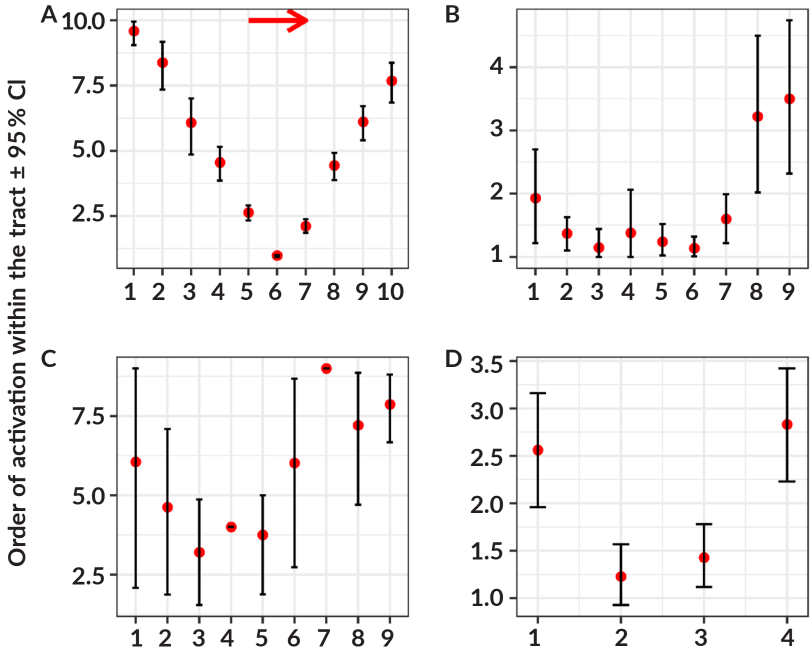

Fig. 12. Moult sequence in adult monk parakeets (sample-size ranges in parentheses): A, primaries (N = 12-41); B, primary coverts (5-14); C, secondaries (N = 2-15); and D, alula feathers (N = 16-22). The red arrow indicates distal direction from the body's longitudinal axis. The red dots show mean order within the tract's moult sequence. Wider 95 % bootstrapped intervals indicate greater variation within the tract's sequence.

Fig. 12. Secuencia de muda en los adultos de cotorra argentina (el rango de tamaño se muestra entre paréntesis): A, primarias (N = 12-41), B, cobertoras primarias (5-14), C, secundarias (N = 2-15) y D, álula (N = 16-22). La flecha roja indica la dirección distal respecto al eje longitudinal del cuerpo. Los puntos rojos indican el orden medio dentro de la secuencia de muda del tracto. Los intervalos de bootstrap del 95 % indican una mayor variación dentro de la secuencia del tracto.

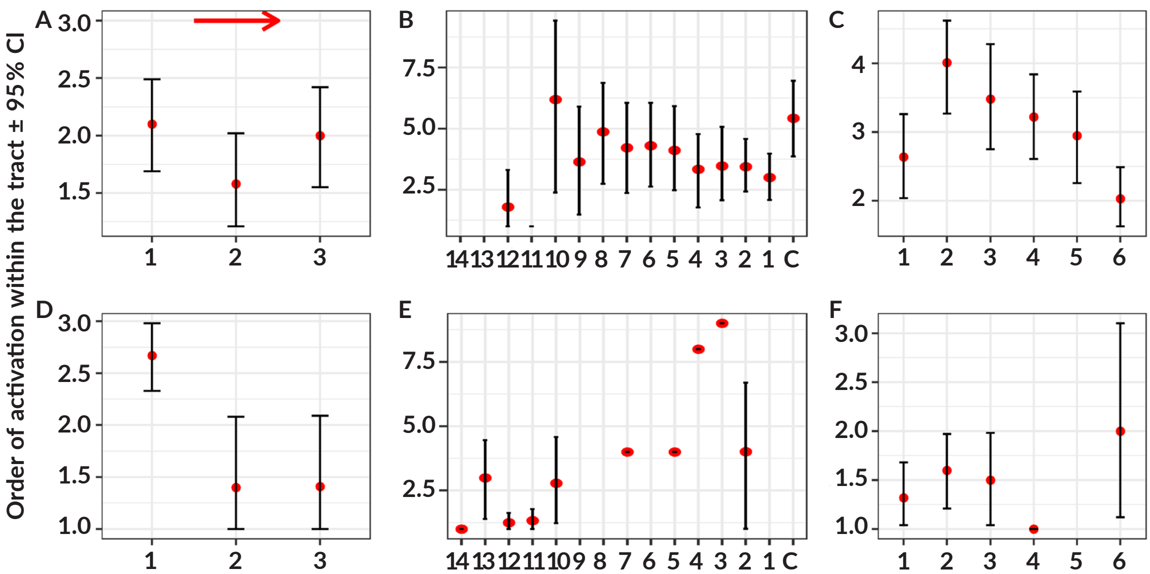

Fig. 13. Moult sequence in the monk parakeet. Upper row adults, lower row first-cycle birds (sample-size ranges within parentheses): A, D, tertials (Na = 17- 22, Nfc = 5-6); B, E, greater coverts (Na = 1-18, Nfc = 0-4); C, F, rectrices (Na = 17-36, Nfc = 0-22). The red arrow indicates the distal direction from the body's longitudinal axis. The red dots show mean order within the tract's moult sequence. Wider 95 % bootstrapped intervals indicate greater variation within the tract's sequence.

Fig. 13. Secuencia de muda en la cotorraargentina. Fila superior adultos, fila inferior aves de primer ciclo (rango de tamaño de muestra entre paréntesis): A, D, terciarias (Na = 17-22, Nfc = 5-6); B, E, grandes cobertoras (Na = 1-18, Nfc = 0-4); C, F, rectrices (Na = 17-36, Nfc = 0-22). La flecha roja indica la dirección distal respecto al eje longitudinal del cuerpo. Los puntos rojos indican el orden medio dentro de la secuencia de muda del tracto. Los intervalos de bootstrap del 95 % indican una mayor variación dentro de la secuencia del tracto.

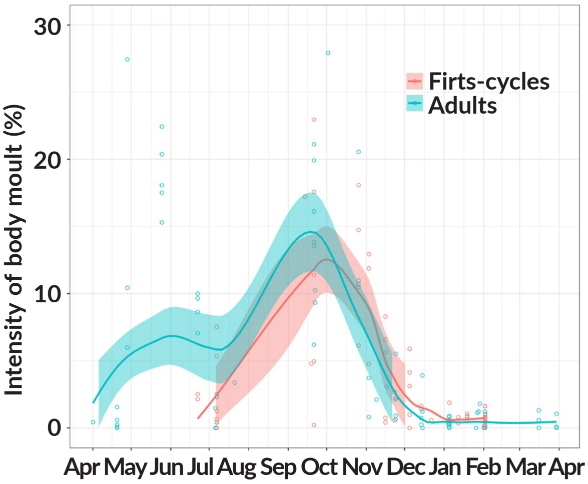

Fig. 14. Variation of body moult intensity throughout the annual cycle in monk parakeets (N = 283).

Fig. 14. Variación de la intensidad de la muda corporal a lo largo del ciclo anual en las cotorras argentinas (N = 283).

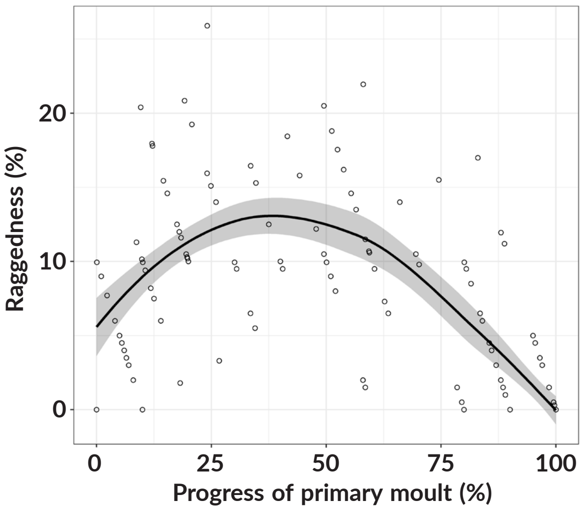

Fig. 15. Dynamics of primary raggedness during the moult of adult monk parakeets (N = 184).

Fig. 15. Dinámica del 'raggedness' de las primarias durante la muda de las cotorras argentinas adultas (N = 184).

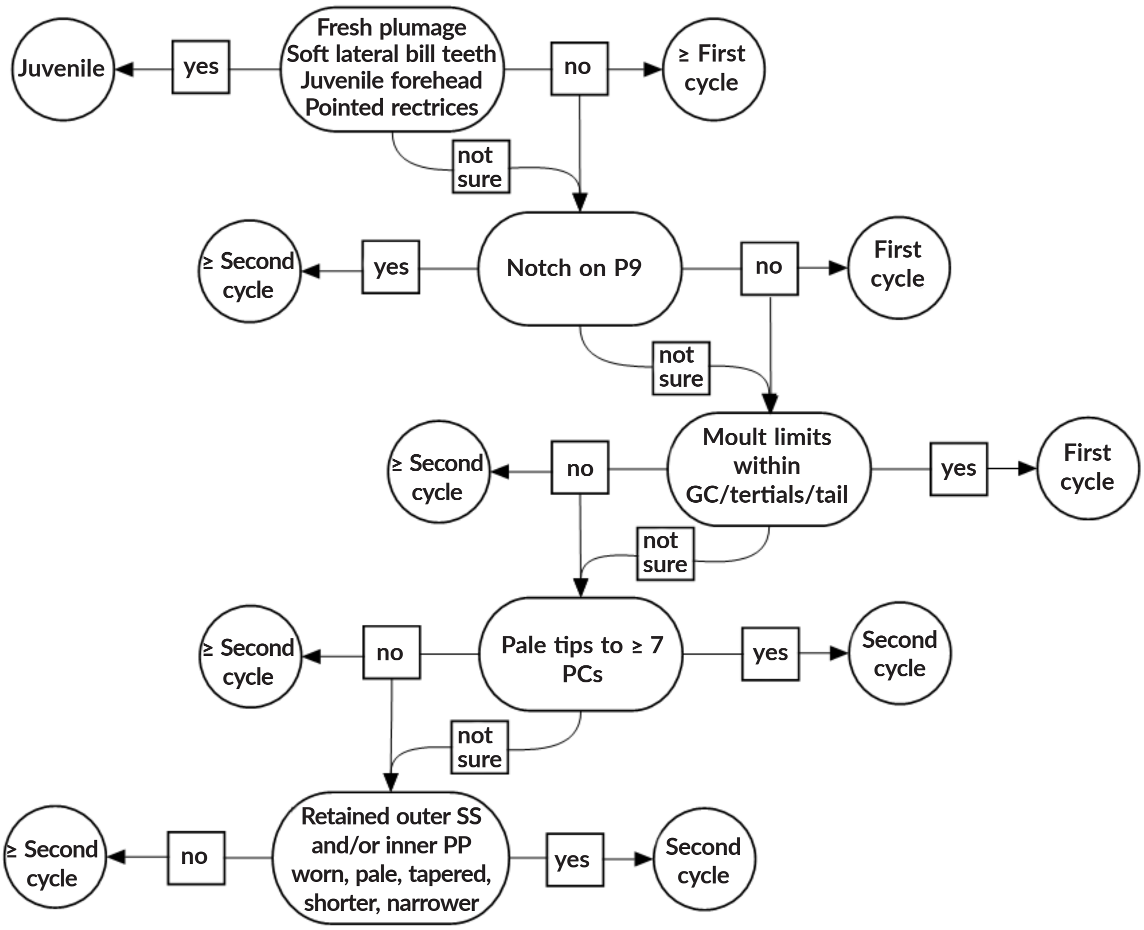

Fig. 16. Protocol to age monk parakeets.

Fig. 16. Protocolo para determinar la edad de las cotorras argentinas.

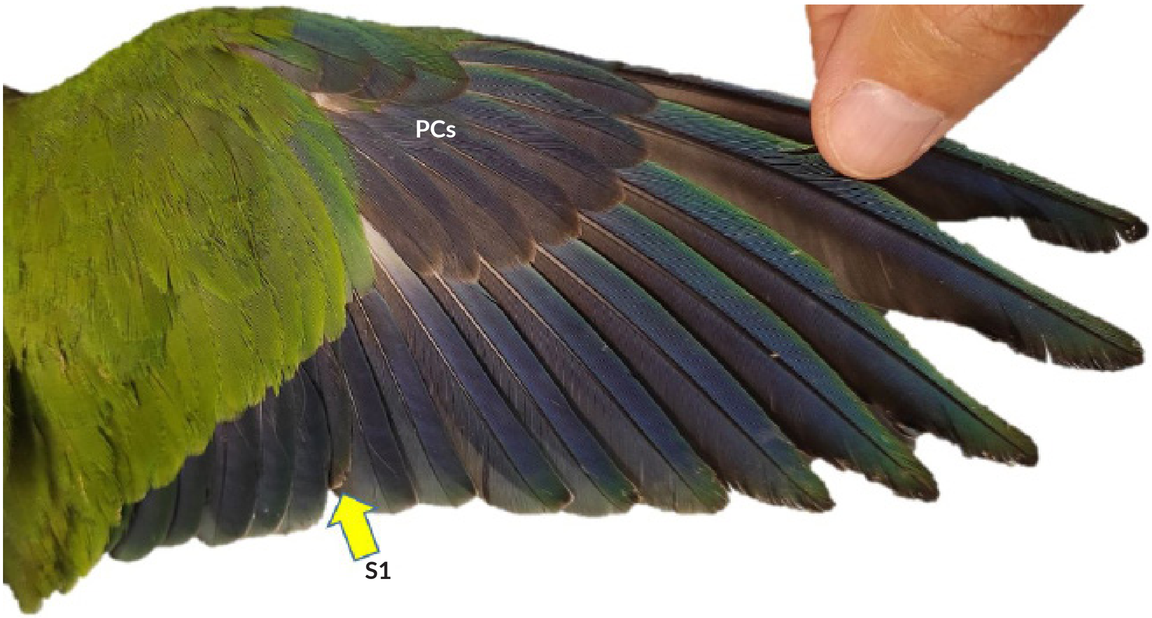

Fig. 17. Retention of juvenile secondary S1 (yellow arrow) and of primary coverts PC1 to PC8 (PCs) in the individual labelled ICM92 (Jardí Botànic de Barcelona, 27 January 2024). Note that S1 is shorter, narrower and worn, and has a pale tip.

Fig. 17. *Retención de la secundaria S1 (marcada con una flecha amarilla) y de las coberteras primarias PC1 a PC8 (PCs) juveniles en la cotorra con la referencia ICM92 (Jardí Botànic de Barcelona, 27 de enero de 2024). Nótese que la S1 es más corta y más estrecha, está desgastada y presenta la punta pálida.*

period during which monk parakeets may start moult, approximately coinciding with the first and last clutches laid (figs. 8 and 14; Senar et al 2019). This could reflect differences in breeding strategy: monk parakeets that skip their first potential breeding season (45 % in Barcelona) may start early, and breeders that lay two clutches (56 % in Barcelona) could be late moulters (Senar et al 2019). Discrepancies between the estimate of the population's moult duration and the moult duration estimated using only late moulters could arise from biases in our sample (e.g., an imbalance between data on start- and end-moult dates for early and late moulters). The post-juvenile moult does not include primaries (Navarro et al 1992), although it has a far greater extent than previously proposed (Pyle 2022). The postnuptial moult extent is incomplete (Pyle 2022), with frequent retention of inner primaries and outer secondaries. As in Picidae, the moult extent of primary coverts increases with age (Pyle and Howell 1995, Pyle and Schofield 2023). It is worth mentioning that moult decoupling between primaries and their accompanying primary coverts is only known for woodpeckers and kingfishers (Pyle 2022). However, we were not able to find a pattern of primary-covert replacement to predict the distribution of new moulted coverts from the first postnuptial moult onward. Moult sequence within remex tracts also coincides with previous descriptions (Avery et al 2012, Pyle 2013, 2022). The sequence of wing-feather tracts included in the post-juvenile moult differs from those in adults, likely driven by variability in moult extent (Guallar 2024).

Body moult apparently protracts throughout the year, although it does not occur in all parakeets during winter (fig. 8). Winter body-plumage moult is slack (fig. 15), and not necessarily the protracted tail of the single annual moult. It may be accidental replacement, repeated replacement of worn feathers, such as that undergone by some North American sparrows (Willoughby 1991), or even steady year-round production of powder feathers (Stettenheim 2000). The primary moult sequence follows a norm different to that of the typical complete moult sequence of passerines (Jenni and Winkler 2020a), and its interaction with moult intensity suggests interesting regulatory and output consequences. Primary moult intensity increases during the replacement of the central primaries (fig. 15), suggesting that a tighter control could be exerted on the outermost and innermost. Our results suggest that moult intensity of inner and outer primaries could be regulated separately. This mechanism might be activated to save energetic resources or when the favourable period for moulting is ending, thus being a strategy to adjust moult while it is underway. By decreasing moult intensity of inner primaries, monk parakeets might regulate their retention. This contrasts with what was observed in captive budgerigars *Melopsittacus undulatus* (a species that exhibits the same moult sequence), which replaced inner primaries faster than outer ones (Wyndham 1981), perhaps because these captive birds were not undergoing any constraints. Under these conditions, the moult of inner primaries would proceed faster because of their shorter length. Retention of inner and not outer primaries may have evolved to tackle the greater wear undergone by the more exposed outer primaries, or because of the greater aerodynamic impact associated with moult of inner prima-

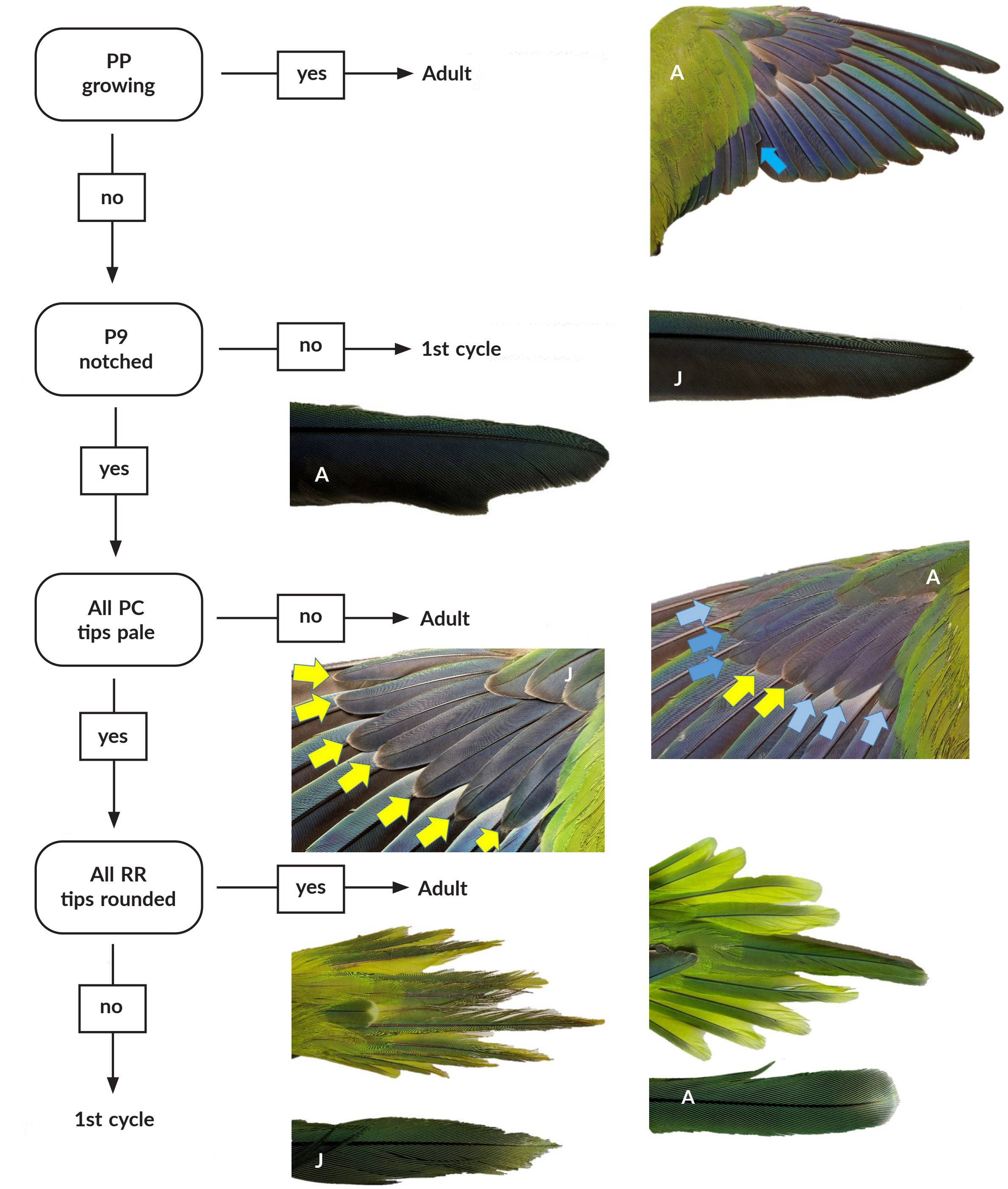

Fig. 18. Simplified protocol to age monk parakeets for field use. First-cycle here includes juveniles. Adults are second-cycle birds or older.

Fig. 18. *Protocolo simplificado para determinar la edad de las cotorras argentinas para su uso en el campo. Aquí, las cotorras de primer ciclo también incluyen los juveniles. Los adultos son las cotorras de segundo ciclo o mayores.*

ries (Hedenström and Sunada 1999). The advantages of Staffelmauser of retained remiges are unclear, and although this would provide benefits by reducing gaps on the inner wing (Tucker 1991, Pyle 2005) it could also be a tool to avoid retention of these feathers for more than one annual cycle, in which case they would undergo excessive wear.

Age determination

Age determination of free-flying monk parakeets has been limited to birds undergoing primary moult (Navarro et al 1992). Rectrices with 'truncated' tips and the presence of 'moult gradients' among secondaries (gradual fading due to large shedding lags between consecutive secondaries) have been proposed to identify adults (Pyle 2022). Here, we provide a protocol that integrates information on juvenile traits and moult arranged in five dichotomous keys (fig. 16). It leads from the identification of juveniles (top) to the identification of monk parakeets beyond the second moult cycle (bottom). When identification at one key is either negative or not granted, go down to the next key. The following points should be taken into account:

1. Juvenile features become less clear as the moult season advances. Once the post-juvenile moult is complete (fig. 8), only juvenile traits that are retained throughout the first annual moult cycle can be used. These traits associate with juvenile features of retained flight feathers, such as colour, shape, and size. From this key onward, it is highly recommended to check more than one character.

2. Up to 26 % of birds may present a full notch on P9 before the first postnuptial moult (fig. 2), whereas up to 5 % of adults may completely lack this (tables 1 and 2). Consequently, absence of notch on P9 indicates that the bird is most probably a juvenile or first-cycle.

3. Moult limits are generally subtle, and difficult to detect on birds with either high-quality juvenile plumage or worn plumage. The juvenile plumage of some birds already presents a full notch on primary P9, with primary coverts nearly lacking pale tips, and no clearly pointed rectrices.

4. Primary coverts that have moulted moulted during the first postnuptial moult vary from none to two (PC9 and a central one). In subsequent postnuptial moults, more than one primary covert is moulted, although we did not find a clear pattern of replacement over time. Some juvenile primary coverts will be retained until at least the fourth cycle. Stepwise moult of primary coverts potentially allows determination of the age of third, fourth, and (indeterminate) older parakeets with caution because some parakeets may retain all of them during their first postnuptial moult. Parakeets with at least one juvenile primary covert can be aged by counting the number of primary-covert generations present: two adult generations besides the juveniles would correspond to a third cycle (or fourth cycle if the parakeet had retained all primary coverts during its first postnuptial moult). Absence of juvenile primary coverts will identify parakeets in their fifth cycle or older.

5. Retention of juvenile secondaries and primaries after the postnuptial moult allows identification of birds in their second annual-moult cycle (fig. 17).

No data are required to identify first-cycle birds from older birds but it is useful information for specimens. Age determination is more difficult during the moulting season because of the presence of juveniles and adults that have not yet started to moult. In winter, no monk parakeets have remaining juvenile plumage, and all of them have already finished moult (except for a 'baseline' body; fig. 8). Fig. 18 provides a simplified protocol to determine the age of monk parakeets.

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Author contributions
S Guallar, **M Illa** and **JC Senar** designed the study. **J Baucells**, **L Cardador**, **J Navarro** and **JC Senar** provided and manage the collection of the specimens. **S Guallar**, **A Manzanilla** and **M Illa** recorded the data of the specimens. **S Guallar** and **JC Senar** analysed the data. **S Guallar** wrote the paper with input from all co-authors. All authors read and approved the final manuscript. **JC Senar** and **L Cardador** contributed funding and materials.

Conflicts of interest
Authors declare no conflict of interests.

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