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Colony attendance and moult pattern of Cory's Shearwaters (*Calonectris borealis*) differing in breeding status and age

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Migratory birds must fit three costly life-history events within the annual cycle, reproduction, moult and migration, to minimize their overlap and maximize survival and breeding success. However, some seabirds, such as Cory's Shearwater *Calonectris borealis*, overlap body moult and breeding, with flight feather renewal occurring in late chick-rearing. In contrast, the moult patterns of non-breeding adult (sabbatical) and immature Cory's Shearwaters, which also attend the colony during the breeding season, remain poorly understood. Furthermore, the potential implications of life-stage and breeding status trade-offs on moult status and colony attendance in non-breeders has rarely been investigated. Surveying different areas within one colony between June and September 2013 and 2014, we studied the age and breeding status composition of birds attending the breeding colony and scored moult of their body (breast and upper-neck), wing and tail feathers. We found that in addition to breeders (n = 165), 57.6% of the birds (n = 389) attending the colony were 4- to 10-year-old immatures (n = 132) and adult sabbatical shearwaters (n = 92). Sabbaticals and 8- to 10-year-old immatures (n = 28) were present at the colony during incubation, whereas only three sabbatical birds and no 8- to 10-year-old immatures were captured in late chick-rearing. Conversely, 4- to 7-year-old immatures arrived later in the season but were still present in late chick-rearing. Sabbatical and 8- to 10-year-old immatures were moulting body feathers at the same time as adult breeders, whereas, among 4- to 7-year-old immatures, older birds moulted earlier than younger birds. A larger proportion of sabbatical birds were replacing tail feathers compared with adult breeders. However, there was no evidence that sabbaticals or 8- to 10-year-old immatures differed in wing moult from adult breeders until August. Overall, our study shows that colony attendance by non-breeding adults and immatures is widespread in this population. The synchronous moult schedule of flight and body feathers across age groups at different life-history stages may suggest that this aspect of moult is controlled by environmental conditions.

Keywords: *Calonectris borealis*, moulting time, non-breeder, prospecting, seabird.

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Life-history theory predicts the occurrence of trade-offs between energy-consuming activities when resources are limited. Migratory birds, for example, must fit three important life-history events within the annual cycle, namely reproduction, moult and migration, the durations and timings of which characterize their routine, i.e. the scheduling of activities or behaviours over the annual cycle (McNamara & Houston 2008). Because each of these activities entails considerable costs, they are expected to be organized in such a way that they do not impair survival and breeding success (Kiat *et al.* 2019). Feather replacement entails direct nutritional and metabolic costs for growing new feathers (Lindström *et al.* 1993) but it may also impose indirect costs, such as impaired aerodynamic performance (Swaddle & Witter 1997, Achache *et al.* 2018) and thermoregulation (Chappell *et al.* 1989, Wolf & Walsberg 2000), as well as potentially increased predation risk (Slagsvold & Dale 1996). As a consequence, most long-distance migratory birds avoid moult coinciding with migration by delaying the former until they reach the wintering quarters or by starting moult shortly after the breeding season is completed (Newton 2008, Kiat *et al.* 2019).

In order to fine-tune the onset and extent of moult across the annual cycle, birds rely on environmental cues (Gwinner 2013). Photoperiod has been recognized as the primary external cue modulating the synchronization of seasonal activities such as moult (Gwinner 2013, Dawson 2015). For instance, the experimental decrease of photostimulation delays the initiation and rate of feather moult (Lesher & Kendeigh 1941, Dawson 2004, see within Danner *et al.* 2015). However, non-photoperiodic cues including food-resource acquisition can also modulate moult initiation, allowing birds to adapt to short-term environmental variability (Borras *et al.* 2004, Dawson 2008, Danner *et al.* 2015). Overall, the interplay between these cues would help to explain differences in the timing of seasonal activities observed between populations of a given species that probably must respond to different selection pressures (Arroyo *et al.* 2004, Helm & Gwinner 2006, Alonso *et al.* 2009, Gwinner 2013).

Procellariiform seabirds have developed a variety of moult strategies differing in their timings, extent and degree of moult–breeding overlap that represent exceptions to the broadly accepted inter-breeding feather renewal strategy reported in most other seabird species (Bridge 2006, Quillfeldt *et al.* 2015, Ryan *et al.* 2020). Moreover, Procellariiforms also have notably extended breeding periods and low development rates in pre- and post-embryonic phases, making them good models to study energy allocation decisions. Several species start to moult body, wing or tail feathers by the end of their breeding period whereas others partially overlap these activities (*Hydrobates pelagicus* Arroyo *et al.* 2004, *Calonectris borealis* Alonso *et al.* 2009, *Thalassarche melanophris* Catry *et al.* 2013a, *Puffinus yelkouan* Bourgeois & Dromzée 2014, *Stercorarius* spp. Graña Grilli & Cherel 2017) or completely overlap them (*Aethia pusilla* Bond *et al.* 2013, *H. pelagicus* and *Oceanodroma leucorhoa* Ausems *et al.* 2019). Furthermore, the ability of birds to modify their strategy depending on circumstances, as well as to suspend moult (Alonso *et al.* 2009, Ramos *et al.* 2009), allows species living in different environments and differing in size to migrate without the need to allocate nutrients to feather synthesis while maintaining high flight performance (Swaddle & Witter 1997, Hedenström & Sunada 1999).

Variation in moult strategies also occurs within the same population (Alonso *et al.* 2009, Grissot *et al.* 2019). For instance, the breeding status of individuals is a good predictor of the onset and intensity of moult (Hunter 1984, Furness 1988, Weimerskirch 1991, Alonso *et al.* 2009, Catry *et al.* 2013b, Ramos *et al.* 2018, Grissot *et al.* 2019). Specifically, failed breeders are able to reschedule moult by starting feather renewal ahead of successful breeders (Alonso *et al.* 2009, Williams 2012, Grissot *et al.* 2019). This empirical evidence corroborates physiological studies suggesting a control of moult by reproductive hormones where prolactin is assumed to play a key role (Dawson 2008). Prolactin secretion is influenced by photoperiod but baseline levels can be three times higher in breeding Cape Petrels *Daption capense* than in failed conspecifics (Angelier *et al.* 2013). Prolactin release can also be lower in non-breeding than breeding birds (see references in Dawson 2008), suggesting differences between sexually active and inactive individuals. Therefore, it is plausible to expect this in sabbatical birds, which are breeders present at a colony, that are not observed breeding for varying reasons, such as loss of partner, low body condition or late arrival (Campioni *et al.* 2016, Kappes *et al.* 2021). The sabbaticals' physiological preparation to moult and the timing of its occurrence (Alonso *et al.* 2009, Ramos *et al.* 2018) may differ from that of actively breeding conspecifics (Williams 2012).

Among non-breeders, immature birds (those that have never bred before) close to recruitment are individuals that, despite being physiologically mature and present in the colony at about the same time as adult breeders (Dias *et al.* 2011, Campioni *et al.* 2020), are not yet sexually active. Hence, if having fewer life-history constraints (e.g. no reproduction) increases flexibility in timing (Wingfield 2005) enabling an individual to invest more in self-maintenance activities such as moult (Catry *et al.* 2013b), and if the above considerations of the physiology of non-breeders applies also to immatures, then we might expect greater variation in moult timing in the latter group than in breeding individuals.

Despite the fact that immature birds do not have breeding-related duties, a timely arrival at the colony after spring migration may be critical to start attempts for mate/nest acquisition. Also, for both immature and sabbatical birds, an early departure from the colony may be important to relax pressure on moult schedule and start the following stages of migration sooner (Catry *et al.* 2013b). Hence, the arrival/departure time, frequency and duration of colony attendance may vary according to their breeding status and/or age-related needs. Furthermore, a regular attendance of the colony may be advantageous for reducing thermoregulation costs incurred during moult (Chappell *et al.* 1989, Wolf & Walsberg 2000). Notably, when on land, birds can be exposed to higher air temperatures and lower conductivity (Ancel *et al.* 2015), a condition potentially favourable to undertake body moult. Ultimately, seasonal patterns of colony attendance and moult are also related to food-resource availability/acquisition (Hatch 1979, 1989, Allard *et al.* 2008, Alonso *et al.* 2009, Danner *et al.* 2015), further suggesting a link between the two activities.

Here we studied the moult and colony attendance of Cory's Shearwater *Calonectris borealis*, a long-lived and long-distance migratory seabird, and compared them between individuals of different breeding status. Our study population, in Selvagem Grande Island, Northeast Atlantic Ocean, has been the object of a long-term study and a very large proportion of birds are of known breeding status and age. During the breeding season, a large number of birds attend the colony at night, including a large number of sabbatical and immature individuals (Granadeiro *et al.* 2009). At this stage, breeding adult Cory's Shearwaters have already started to moult body feathers and show an uncommon renewal of tail and flight feathers during late chick-rearing (Monteiro & Furness 1996, Alonso *et al.* 2009, Ramos *et al.* 2009). How moult progresses in sabbatical and immature birds that attend the colony, however, remains poorly understood.

We predict that both sabbatical birds and 8- to 10-year-old immatures will attend the colony from the onset of incubation but they will be the first birds to leave it in the late chick-rearing period. Given the broad temporal overlap between body moult and breeding (Monteiro & Furness 1996, Alonso *et al.* 2009), which suggests little energy trade-off between the two life-history events, we expect both groups of non-breeders to schedule their body moult at the same time as breeders (Monteiro & Furness 1996, Alonso *et al.* 2009). However, if the physiological preparation to moult varies between sexually active and inactive birds (Williams 2012), we predict also that sabbatical birds and 8- to 10-year-old immatures may show an advancement in the onset of moult of flight feathers with potential advantages in aerodynamic performance during migration.

Furthermore, since prospecting (visiting and sampling the quality of potential nesting areas; Reed *et al.* 1999) of the natal colony is a widespread strategy in this large population (Granadeiro *et al.* 2006), we expect a large number of immature Cory's Shearwaters of different ages to return to the colony long before recruitment. Because younger individuals show delayed migratory timing compared with older immatures (Campioni *et al.* 2020) and because in Procellariiforms age can affect the phenology of moult (Langstrom & Rohwer 1996, Dittmann & Becker 2003), we expect younger birds to arrive at the colony later and exhibit delayed moulting times in comparison to older immatures.

METHODS

Study area and colony attendance data collection

Fieldwork was carried out at Selvagem Grande (30°09′N, 015°52′W) in the Northeast Atlantic. The island harbours c. 30 000 Cory's Shearwater pairs (Granadeiro *et al.* 2006), and since 2004 has been the focus of a long-term monitoring study. Therefore, breeders and chicks from individually marked nests in four study plots have been systematically ringed, and demographic and breeding data have also been recorded. During the breeding seasons of 2013 and 2014, the study areas were visited regularly (approximately every day excluding periods of full moon (Granadeiro *et al.* 2009), and rain) on the same dates (from 13 June, i.e. immediately after laying onwards) to record the presence and breeding status of all birds attending the plots. Due to the high nest-site fidelity (Mougin *et al.* 1999), most breeding birds and new recruits have been ringed and controlled every year (if ringed in previous years). On the basis of this control, we were able to distinguish between successful breeding adults (individuals incubating an egg and rearing a chick), sabbatical birds (individuals that have bred in previous years and are present at the colony but not observed breeding in the current season (Campioni *et al.* 2016), see Introduction for a detailed explanation) and immature birds (individuals that have never reproduced before). Because most immature birds were ringed as chicks, we could determine their ages from the date of ringing. In this species, sexual maturity is only acquired at an average of 9 years (Mougin *et al.* 2000) and immature birds start visiting the colonies when they are 4 years old (Campioni *et al.* 2016).

Birds were caught during incubation (between 13 June and 15 July; 2013: $n = 75$), early chick-rearing (between 25 July and 20 August; 2013: $n = 70$, 2014: $n = 182$) and late chick-rearing (between 10 September and 30 September; 2013: $n = 69$). They were caught by hand or with the help of a butterfly net when visiting the study plots. We measured the beak (culmen length: distance between anterior edge of nostrils and tip of the bill; bill height: measured at the foremost head feathering; and gonys: bill height at the gonys; see Granadeiro 1993) of all handled birds, which were then marked with nontoxic green/red (GÉNIA Penmark used on livestock and other animals) paint on the breast and tail to avoid resampling the same individuals (painting had no harmful effect on birds). We determined the sex of 100% of the birds employing a combination of two different methods. We used a discriminant function based on three bill measurements: culmen length, bill height and gonys (i.e. Discriminant score = 0.087 × Culmen length + 1.206 × Bill Height + 0.598 × Gonys + 40.063; Granadeiro 1993). Individuals with a discriminant score > 0.1 were classified as males, and those with a score < 0.1 were classified as females. For birds with intermediate values the sex was determined by other means: their distinctive vocalization during handling (Thibault *et al.* 1997) and cross-validating with nesting partners. In this way, sex classification accuracy was > 99% (Pérez *et al.* 2014). Finally, for 37 immatures where the discriminant function did not allow a high confidence in sexing, we employed standard molecular procedures using DNA (Fridolfsson & Ellegren 1999) extracted from blood samples.

Moult

In order to evaluate whether and to what extent birds were in active moult of body (breast and upper-neck) and tail (R1–R6) feathers, all individuals were inspected and scored for each body part as 1 if actively moulting or 0 if not. During early chick-rearing in 2014 and late chick-rearing in 2013 we also determined the number of wing and tail feathers of each bird using different scoring scales (0–5 based on Ginn and Melville (1983) and 0–3 based on Meier *et al.* (2017)) in each period. Hence, to homogenize the data we used the simplified criterion of Meier *et al.* (2017) modified from Ginn and Melville (1983). The moult score of wing (primaries and secondaries) and tail feathers was recorded as 0 = an old feather, 1 = a missing feather, 2 = a new feather in growth and 3 = a new fully grown feather. Breast and upper-neck moult were scored separately following Ramos *et al.* (2009), and a value of 1 was assigned when multiple feathers were growing and 0 if not. A tail + wing (primaries and secondaries) moult score was calculated by summing the scores for each feather (fully renewed score for tail = 18 and for wing = 30 + 66). Because in Cory's Shearwater the primary moult is descendent and secondary feather renewal is consistent and generally symmetric in the two wings (Monteiro & Furness 1996), only one wing was analysed (Ramos *et al.* 2009).

Ethics

Birds were manipulated for a period of 5–10 min and in strict accordance with good animal practices as defined by the current European legislation

(Directive 2010/63/EU; European Union 2010). All work including animal manipulation and ringing was approved by the relevant authority, Instituto das Florestas e da Conservação da Natureza (IFCN, Madeira), which provided the research permits (no. 1/2013; no. 5/2014 S) during the study period.

Data analysis

Colony attendance pattern was characterized by comparing the proportion of birds of different breeding status (breeders, sabbatical and immature birds) and ages (only for immatures) captured at night during incubation, early chick-rearing and late chick-rearing. Similarly, changes in immature age-group composition (4–7 years versus 8–10 years) among the three breeding phases was also tested. χ^2 tests were used for these comparisons, and it implies that our sampling effort was approximately uniform in the study areas and therefore that the number of individuals of each status captured was fairly proportional to its abundance in the colony.

The data on moult collected from birds examined in 2013 and 2014 were analysed together because there was no difference between years in the frequency of birds in active moult of breast (Pearson's χ^2 tests with Yates' continuity correction $\chi^2 = 0.0001$, $df = 1$, $P = 0.99$) and upper-neck feathers ($\chi^2 = 2.155$, $df = 1$, $P = 0.14$). In order to test for differences in the frequency of birds in active moult of breast, upper-neck, tail and wing feathers in relation to their breeding status, we used non-parametric statistics (i.e. χ^2 test and Fisher's exact test). Adult breeders were chosen as a reference group (because moult pattern is well understood) and used in pairwise comparisons with sabbatical birds and 8- to 10-year-old immatures, respectively.

Using the same pairwise arrangement we employed generalized linear models (GLMs) with quasi-binomial error distribution, to model the probability that a bird was in active moult (coded as 1) of breast and upper-neck feathers as opposed to no active moult (coded as 0). The models showed dispersion values that were slightly below or slightly over 1, so we decided to model the data using the quasi-binomial distribution. The quasi-binomial distribution is similar to the binomial distribution, but has an extra parameter φ (limited to $|\varphi| \leq \min\{p/n, (1-p)/n\}$) that attempts to describe additional/less variance in the data that cannot be explained by a binomial distribution alone (Zuur *et al.* 2009). GLMs allowed us to simultaneously test for the effects of breeding status (i.e. breeder versus sabbatical or breeder versus older immature) and date of sampling (Julian date as a continuous variable: 1 January = 1). The sex of the bird was also included in the GLMs to control for potential sex-related differences, although the work of Alonso *et al.* (2009) reported the lack of a significant effect. Due to the small number of birds moulting tail and wing feathers we could not model the probability of moulting in relation to the variable listed above, and therefore we used non-parametric tests to perform pairwise comparisons between birds of different breeding status (see above).

Furthermore, to test whether moult of the breast region was independent of the upper-neck moult among breeders, sabbatical birds and 8- to 10-year-old immatures, we used a χ^2 test of independence (Pearson's χ^2 test with Yates' continuity correction).

For immature birds aged between 4 and 10 years, the probability of moulting breast and upper-neck feathers was modelled running two GLMs with quasi-binomial error distribution including age, sampling date, years (2013 and 2014) and sex as explanatory variables.

Full GLMs were simplified using stepwise backward selection. This method selects variables on the basis of a chosen criterion (in our case $P < 0.05$). The algorithm selects a final model with only significant variables based on a correction choice of false discovery rate and Bonferroni correction (SignifReg package in R; Zambom & Kim 2018). All analyses were performed using the software R version 3.6.3 (R Core Team 2021).

RESULTS

Colony attendance pattern

In the breeding seasons of 2013 and 2014, during night surveys, we captured 389 Cory's Shearwaters of different breeding statuses and ages. We found that the attendance patterns during the three phases differed significantly among the three groups ($\chi^2 = 66.1$, $df = 4$, $P < 0.001$). A substantial number of sabbatical birds ($n = 92$) and immatures (of all age classes; $n = 132$) attended the colony together with breeding adults ($n = 165$). Indeed, sabbatical birds and 8- to 10-year-old

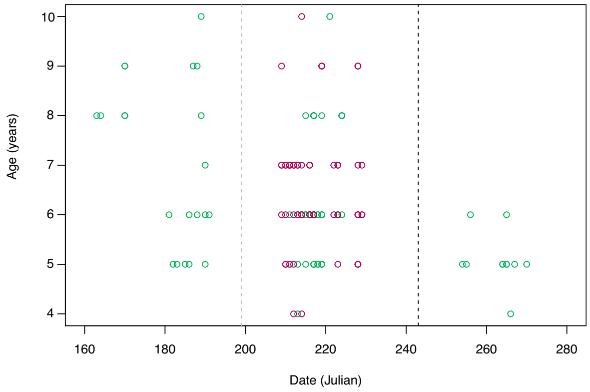

Figure 1. The age of immature Cory's Shearwaters (n = 132) captured at night in the study colony between mid-June and late September in 2013 (green points) and 2014 (red points). Vertical lines indicate the beginning of the chick-rearing (light grey dotted line) and late chick-rearing (black dotted line) periods. Julian date 1 = 1 January. Note that the absence of red symbols before the beginning of chick-rearing and after late chickrearing is because no visits at night were made.

immatures were already present in June, but their relative abundance decreased significantly in September (late chick-rearing) in relation to that of breeders (Fig. 1 and Table 1). The age of immature Cory's Shearwaters attending the colony ranged between 4 and 10 years (4–7 years: n = 104; 8–10 years: n = 28). Among them, 8- to 10-year-old individuals were observed as early as mid-June (incubation) whereas it was only between the end of July and August that 4- to 7-year-old immatures began to be observed in the colony (χ^2 = 12.3, df = 2, P < 0.002). Younger birds were still present in September during late chick-rearing (Fig. 1).

Birds in active moult of feathers

In the breeding seasons of 2013 and 2014, we examined the moult stage of 285 Cory's Shearwaters including adult breeders, sabbatical birds and 8- to 10-year-old immatures. Overall, between June and September, we found that 251 (89%) and 169 (59%) individuals were in active moult of breast and upper-neck feathers, respectively (Table 1, Fig. 2). Only 16 (6%, n = 285) and 5 (2%, n = 188) Cory's Shearwaters were renewing tail and wing feathers, respectively (see Tables 1 and 2 for details).

Pairwise comparisons of adult breeders versus sabbatical birds and of adult breeders versus 8- to 10-year-old immatures showed that there were no significant differences in the number of breeders and sabbatical birds nor of breeders and immatures (Table 2), which between June (incubation) and September (late chick-rearing) were actively moulting breast feathers (Table 1, Fig. 3) and upper-neck feathers (χ^2 tests all P > 0.4, Table 2). Moreover, birds renewing breast feathers had a higher probability of being in active moult of

Table 1. Number of Cory's Shearwaters of differing breeding status in active moult of body (breast and upper-neck) and tail feathers during different phases of the breeding season of 2013 and 2014.

Moult	Breeding status	Incubation	Early chick-rearing	Late chick-rearing
Breast	Breeder	10	92	42
	(165)	(12)	(104)	(49)
	Immature (8–10 years)	10	16	–
	(28)	(10)	(18)	(0)
	Sabbatical bird	34	44	3
	(92)	(39)	(50)	(3)
Upper-neck	Breeder	6	59	27
	(165)	(12)	(104)	(49)
	Immature (8–10 years)	4	12	–
	(28)	(10)	(18)	(0)
	Sabbatical bird	21	39	1
	(92)	(39)	(50)	(3)
Tail	Breeder	2	1	2
	(165)	(12)	(104)	(49)
	Immature (8–10 years)	0	1	–
	(28)	(10)	(18)	(0)
	Sabbatical bird	4	7	0
	(92)	(39)	(50)	(3)

Total number of birds attending the colony at night and inspected for moult is given in parentheses.

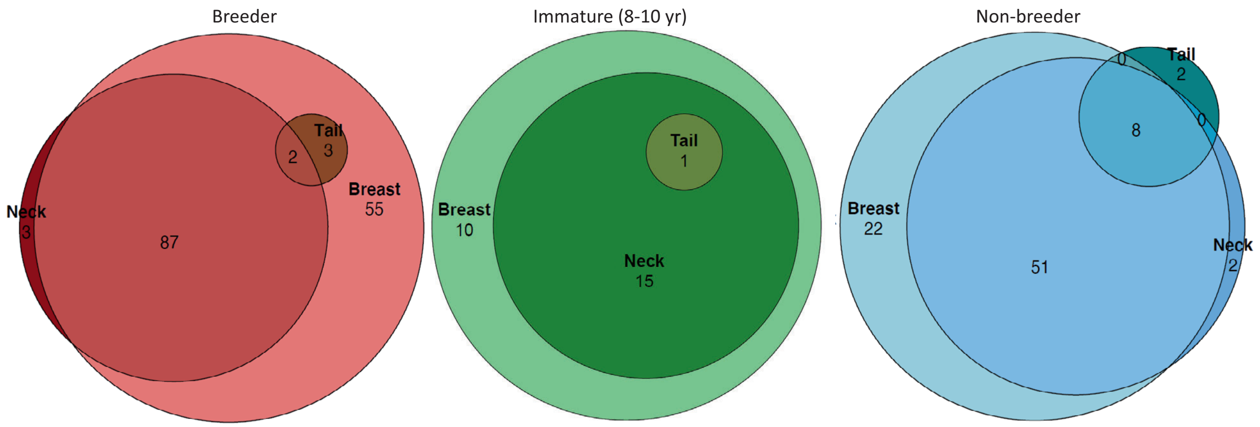

Figure 2. Euler plots of the number of Cory's Shearwaters of differing breeding status in active moult and simultaneously replacing breast, upper-neck (Neck) and tail feathers during the breeding season. The circumference of the circles is proportional to the number of birds in moult.

Table 2. Number of Cory's Shearwaters in active moult through the whole breeding season.

Moulting	Breeder	Sabbatical	χ^2/Fisher's test	Immature (8–10 years)	Fisher's test
Breast	143 (165)	81 (92)	$\chi^2 = 0.015$, $P = 0.90$	26 (28)	$P = 0.74$
Upper-neck	89 (165)	61 (92)	$\chi^2 = 3.22$, $P = 0.07$	16 (28)	$P = 0.99$
Tail	5 (165)	11 (92)	$\chi^2 = 5.25$, **$P = 0.02$**	1 (28)	$P = 0.55$
Wing	4 (130)	2 (51)	$P = 0.98$	0 (7)	$P = 0.69$

Note that the number of birds moulting wing feathers is calculated only for the early chick-rearing (August) and late chick-rearing (September) phases. Total number of birds examined is given in parentheses. Statistical comparisons were made comparing breeder versus sabbatical and breeder versus immature (8- to 10-year-olds) using χ^2 tests and Fisher's exact tests. Bold type indicates $P < 0.05$.

upper-neck than those that were not renewing breast feathers (χ^2 test: $\chi^2 = 27.40$, $df = 1$, $P < 0.001$) resulting in 57% birds ($n = 285$) simultaneously moulting both body regions (Fig. 2).

On the other hand, the number of sabbatical birds moulting tail feathers was significantly higher than that of breeders (χ^2 test: $\chi^2 = 5.49$, $df = 1$, $P = 0.019$) but no difference was found between breeders and old immatures (8–10 years old; Tables 1 and 2: χ^2 test $P > 0.50$). Similarly, for each pairwise comparison, we did not find any difference in the number of birds moulting wing feathers between breeders and sabbaticals and between breeders and immatures (8–10 years old; Tables 2 and 3).

The results of the GLMs led to similar conclusions, indicating that in either comparison (breeder versus sabbatical and breeder versus 8- to 10-year-old immature) the probability of being in active moult of breast or upper-neck feathers was not affected by the breeding status, sex or the sampling date on which birds were examined (Table 4, models 1–4).

In the same breeding seasons, among birds examined at night, there were also 104 immatures with ages between 4 and 7 years. Of those birds, 84 (81%) and 38 (36.5%) individuals were actively moulting breast and upper-neck feathers, respectively, whereas only five (4.8%, $n = 104$) and two (3.3%, $n = 60$) were renewing tail and wing feathers, respectively. The probability of being in active upper-neck moult increased with age and over the breeding season (Table 4, model 6) with older immatures being in active moult of upper-neck feathers in larger numbers than younger birds. Conversely, model selection retained Year as an explanatory variable when we modelled breast moult (Table 4, model 5; Fig. 4).

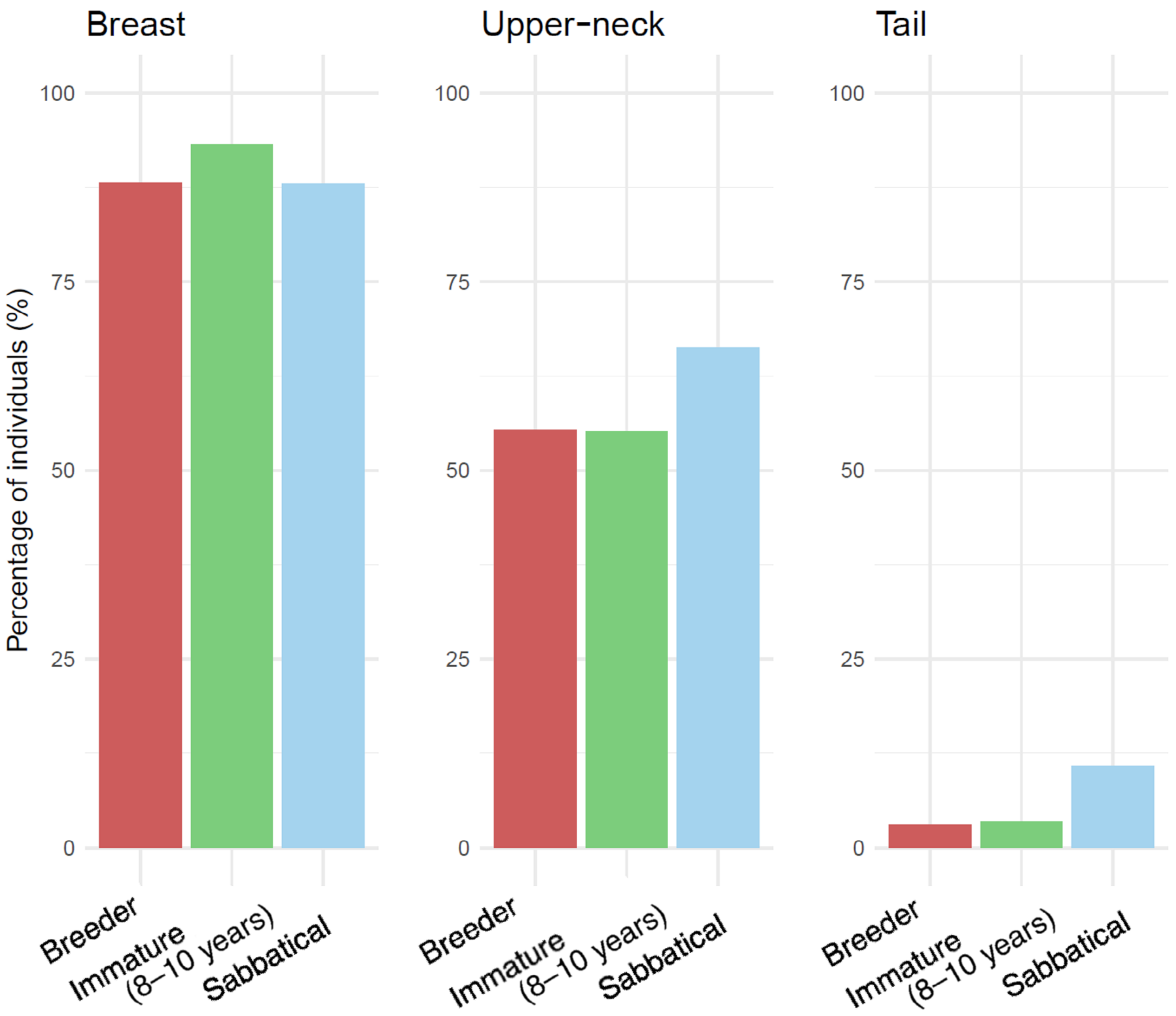

Figure 3. The proportion of Cory's Shearwaters of differing breeding status in active moult of breast, upper-neck and tail feathers during the breeding season (June–September).

Moult score and wing feather moult

In August (early chick-rearing) only two of the 50 sabbatical birds were moulting their primary feathers and none of the breeders and immatures (4–10 years old) showed any evidence of wing feather moult. In September three breeders with old chicks had started to moult some secondary feathers and two (4–6 years old) immatures had primary/secondary feathers in active moult, most of which were in pin (score = 2, see Supporting information, Fig. S1). However, moult scores for any bird never exceeded 8 (Table 3).

DISCUSSION

In this study we investigated the group composition (i.e. breeding status and age) and moult pattern of Cory's Shearwaters attending the colony of Selvagem Grande, Northeast Atlantic, during the breeding season. Our main results show that colony attenders are individuals of different breeding status and age. Notably, 57.6% of birds captured at night were adult birds in their sabbatical year and immatures with age between 4 and 10 years. Although they attended the colony from June to September, the relative abundance of non-breeders

Table 3. Moult score and number of Cory's Shearwater of different breeding status in active moult of wing (primaries, secondaries) and rectrix feathers during chick-rearing and late chick-rearing.

Breeding status	Moult score	Rectrix	Primary	Secondary
Breeder	0	127	130	127
	2	3	0	1
	4	0	0	2
Sabbatical bird	0	44	49	51
	1	6	0	0
	2	1	1	0
	8	0	1	0
Immature 8- to 10-year-old	0	6	7	7
	1	1	0	0

changed significantly during the study period. Furthermore, a large proportion of sabbatical and 8- to 10-year-old immatures were in active moult of body feathers, showing a pattern broadly similar to adult breeders (Table 1). In contrast, in 4- to 7-year-old immatures the onset of upper-neck moult was positively correlated with age. As expected, and in line with previous knowledge on breeding Cory's Shearwaters (Monteiro & Furness 1996, Ramos *et al.* 2009), body feather moult occurred consistently throughout the whole breeding season (June–September). Conversely, the number of sabbatical and older immature birds replacing wing feathers was marginal and, contrary to our predictions, none of them was observed to initiate primary moult in the early chick-rearing phase (August). Furthermore, between June and August, there was a significant difference in the number of sabbatical birds replacing tail feathers compared with breeders (Table 2).

Night-time captures of birds between June and September showed that, as in other seabird species (Wood *et al.* 2021), there is a substantial number of adult birds that, for different reasons, are not observed to breed (Giudici *et al.* 2010) but that keep attending the breeding colony. Despite being free from breeding-related duties, sabbatical birds have several needs to fulfil. Their return and the time spent in the colony in activities such as territorial defence (Calladine & Harris 1997, Danchin & Cam 2002, Phillips *et al.* 2005), finding a mate or prospecting new nest-sites may ensure reproduction in the future. As expected, most sabbatical birds were also actively moulting body feathers, which confirms that this activity is timed to occur during the breeding season and is unrelated to the bird's breeding status. Contrary to our prediction, sabbatical birds did not advance the onset of wing moult in August, but they might have done it by September, namely when major differences in primary replacement between breeders and failed breeders have been observed (e.g. 75% failed breeders versus 8% successful breeders; Alonso *et al.* 2009). Unfortunately, because in September we only captured three sabbatical birds (and no 8- to 10-year-old immatures), we were not able to assess the progress of wing and tail moult beyond August.

We collected evidence that sabbatical birds are able to moult tail feathers when breeders are known to suspend moult, i.e. in June–July. Apparently, rectrix renewal starts on the wintering grounds and is advanced but not completed in March–May; it is then suspended and concluded in most birds by September (Monteiro & Furness 1996, Ramos *et al.* 2009). Overall, though our results are not conclusive, they provide some support to the idea that non-breeders (including sabbatical birds or failed breeders) of several seabird taxa present some degree of flexibility in scheduling moult (Hunter 1984, Furness 1988, Barbraud & Chastel 1998, Alonso *et al.* 2009). One of the mechanisms that could be responsible for such flexibility is the physiological preparation to moult mediated by a less fixed hormonal control in non-breeders compared with the more rigid reproductive hormonal control of breeders (Dawson 2008, Williams 2012).

Previous evidence from Cory's Shearwaters showed that 8- to 10-year-old immatures return to the natal area at about the same time as breeding adults (Campioni *et al.* 2020). In accordance with our expectation and in line with the findings of Campioni *et al.* (2020), we found that 8- to 10-year-old immatures were attending the colony from June onwards. For these birds close to recruitment, an early arrival and a regular attendance at the nesting ground can be critical to ensure the success of future breeding attempts. During this time, immatures have been suggested to acquire environmental and social information, and to engage in mate finding and nest prospecting, all activities with potential implications for successful recruitment (Campioni *et al.* 2017).

During late chick-rearing (September) colony attenders were mostly 4- to 7-year-old immatures whereas 8- to 10-year-old immatures were absent and sabbaticals were less present compared with

Table 4. Summary of predictors used for modelling the probability of moulting of breast and upper-neck feathers for breeders and non-breeding adults (Models 1 and 2), breeders and older immatures (8- to 10-year-olds; Models 3 and 4), and the probability of immature birds (4- to 7-year-olds) being in active moult in relation to their age, sex, sampling date and year (Models 5 and 6).

Dependent variables	Tested predictors	β	se	*Z*	*P*
Breeders and sabbatical birds					
Probability moulting – breast (0/1)					
Model 1	Intercept	**2.104**	**0.746**	**2.822**	**0.005**
GLM	BS non-breeder	−0.075	0.452	−0.167	0.86
(*n* = 257)	SEX male	−0.059	0.396	−0.150	0.88
	JULIAN DATE	−0.0002	0.008	−0.027	0.98
Probability moulting – upper-neck (0/1)					
Model 2	Intercept	**−0.189**	**0.486**	**−0.389**	**0.698**
GLM	BS non-breeder	0.593	0.304	1.952	0.052
(*n* = 257)	SEX male	−0.214	0.261	−0.819	0.414
	JULIAN DATE	0.007	0.005	1.265	0.207
Breeders and immatures					
Probability moulting – breast (0/1)					
Model 3	Intercept	**2.50**	**0.88**	**2.83**	**<0.001**
GLM	BS non-breeder	−0.368	0.883	0.451	0.65
(*n* = 193)	SEX male	−0.003	0.482	−0.006	0.99
	JULIAN DATE	−0.006	0.009	−0.598	0.55
Probability moulting – upper-neck (0/1)					
Model 4	Intercept	−0.173	0.544	−0.318	0.75
GLM	BS non-breeder	0.248	0.445	0.558	0.59
(*n* = 193)	SEX male	−0.159	0.304	−0.536	0.59
	JULIAN DATE	0.006	0.006	1.048	0.29
Immature (4- to 7-year-old)					
Probability moulting – breast (0/1)					
Model 5	Intercept	**−0.781**	**0.936**	**−0.834**	**0.406**
GLM	SEX male	0.723	0.653	1.108	0.271
(*n* = 104)	AGE	−0.148	0.421	−0.352	0.725
	JULIAN DATE	0.025	0.012	1.136	0.074
	YEAR 2014	**1.537**	**0.604**	**2.546**	**0.012**
Probability moulting – upper-neck (0/1)					
Model 6	Intercept	**−8.733**	**2.617**	**−3.338**	**<0.001**
GLM	SEX male	0.291	0.647	0.451	0.653
(*n* = 104)	AGE	**0.834**	**0.308**	**2.701**	**0.008**
	JULIAN DATE	**0.039**	**0.013**	**2.919**	**0.004**
	YEAR 2014	−0.327	0.529	−0.617	0.538

Coefficient estimates β, standard error of the mean (se), *Z* and *P* values are shown. Sample size (*n*) is shown in parentheses. Predictors in bold type were those retained in the final model by the backward selection procedure (see Methods for more details).

earlier in the season. For sabbatical birds, this pattern is supported by unpublished evidence indicating that they leave the colony, on average, 3 weeks before successful breeders (P. Catry & J.P. Granadeiro unpubl. data), whereas for immature birds it is in line with the findings of Campioni *et al.* (2020). Both groups may take advantage of their weak bonds to the colony for departing earlier and moving into more productive waters where wing and tail moult can start and/or progress (Alonso *et al.* 2009, Ramos *et al.* 2009).

The attendance at the natal colony by immatures of different ages (range: 4–7 years) suggests that natal prospecting is a common behavioural strategy in this population. In agreement with our expectation and in line with previous observations in this and other seabird species, younger immatures arrived later compared with older individuals (Halley et al. 1995, Dittmann & Becker 2003, Campioni *et al.* 2020; Fig. 4). Similarly, younger immatures were also less likely to be in active moult of upper-neck feathers compared with older individuals, possibly indicating some delay in scheduling seasonal activities. In support of our results, Dittman and Becker (2003) observed young immature Common Terns *Sterna hirundo* to

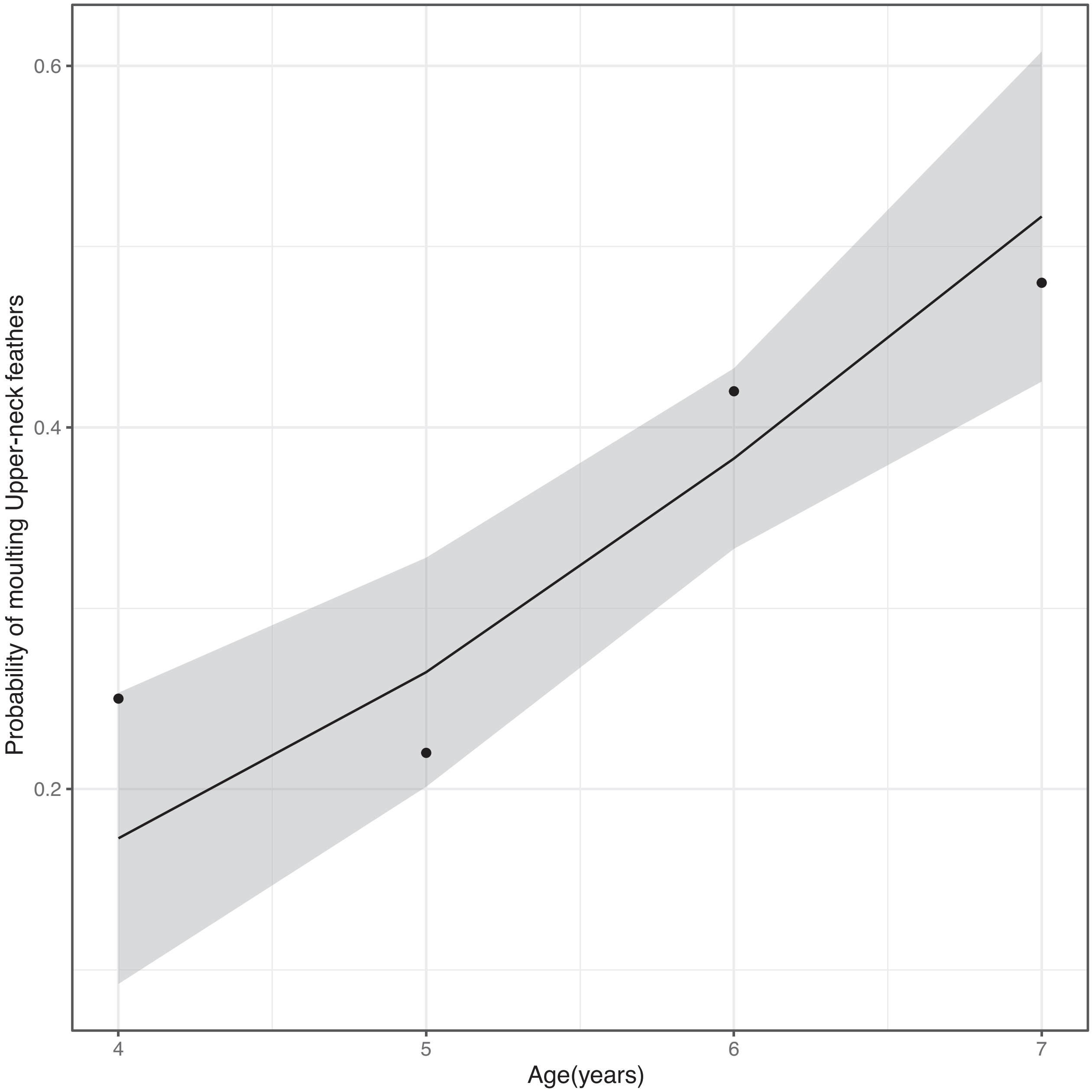

Figure 4. Predicted probability of immature (4- to 7-year-old) Cory's Shearwaters being in upper-neck moult, accounting for Julian date (see Table 4, Model 6). The curve (shaded area: standard error) shows the quasi-binomial relationship between age and probability of being in moult and black points represent the probability of moulting for each age class.

return later to the colony and to defer primary moult compared with older conspecifics, thus speculating that their hormonal activity could be modulated in order to delay the start of moult.

Temporal consistency of different life-history stages (and across age groups) in active moult of body feathers might suggest that this aspect of moult is controlled by environmental conditions (or timed to help birds adapt to adverse environments), but further research is needed to test this hypothesis more thoroughly. Body feathers are known to play a key role in thermoregulation, insulation and waterproofing, all functions that are extremely important in pelagic seabirds (King & Farner 1961, Chappell *et al.* 1989, Wolf & Walsberg 2000). During body moult, feather insulation is not as effective and birds may have to increase the production of internal heat to compensate. Hence, it is reasonable to assume that there might be a selective advantage to moult body feathers during the warmest time of the year (Vezina *et al.* 2009) or when the thermal environment is less harsh (Piersma 1988). Because thermal conditions linked to weather (i.e. wind and rain) and water temperature can significantly increase heat loss (Lustick & Adams 1977, Webster & Weathers 1990, Kelly *et al.* 2002, Viain & Guillemette 2016) it is likely that Cory's Shearwaters have almost completed body moult before departing on their trans-oceanic migration toward the windy and relatively cooler regions of the South Atlantic Ocean. The body moult pattern of Cory's Shearwater is similar to that described for the closely related migratory Scopoli's Shearwater *Calonectris diomedea* (Ramos *et al.* 2009) and it is also consistent with the body feather renewal exhibited by the Yelkouan Shearwater *P. yelkouan* (Bourgeois & Dromzée 2014). However, in contrast to the former species, the Yelkouan Shearwater does not experience remarkable changes in the thermal environment between the breeding and the non-breeding seasons (i.e. it overwinters in the Mediterranean) and, despite this, still renews body feathers in the fixed temporal window between incubation and late chick-rearing (Bourgeois & Dromzée 2014), suggesting a generally consistent correlation between breeding time and body moult time.

Overall, the information available on body feather renewal in Procellariiformes is scant and its chronology is often poorly understood (but see Monteiro & Furness 1996, Warham, 1996, Ramos *et al.* 2009, Battam *et al.* 2010, Bugoni *et al.* 2015, Cherel *et al.* 2016,). For instance, some studies provide information on Arctic moulting species, such as the Blue Petrel *Halobaena caerulea* or the Thin-billed Prion *Pachyptila belcheri* (Cherel *et al.* 2016) showing that they replace body feathers gradually over several months, mainly during non-breeding (Warham 1996, Battam *et al.* 2010, Bugoni *et al.* 2015, Cherel *et al.* 2016). A protracted body moult during non-breeding could minimize effective insulation losses that may be energetically costly for seabirds when they increase time spent on low-temperature waters (e.g. Antarctic waters; Cherel *et al.* 2016). Indeed, it is a plausible explanation for species breeding in colder regions, but it might be less applicable to species occurring in subtropical/temperate zones, such as Cory's Shearwaters, which instead seem to concentrate body feather renewal during the extended breeding season in the boreal summer months when water temperature may be relatively higher.

Overall, our study shows that the attendance and prospecting of the nesting/natal colony by non-breeders is a widespread behavioural strategy in Cory's Shearwater at Selvagem Grande. In general, non-breeding birds attending the colony showed a body moult schedule highly consistent with that of adult breeders, suggesting no influence of breeding status on moult timing over the study period.

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AUTHOR CONTRIBUTIONS

Letizia Campioni: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft. **Sofia Bolumar Roda:** Formal analysis; visualization; writing – original draft. **Hany Alonso:** Data curation; investigation; methodology; writing – review and editing. **Paulo Catry:** Conceptualization; funding acquisition; investigation; methodology; resources; validation; writing – review and editing. **José Pedro Granadeiro:** Conceptualization; funding acquisition; investigation; resources; supervision; validation; writing – review and editing.

ETHICAL NOTE

None.

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CONFLICT OF INTEREST

The authors declare they have no conflicts of interest.

Data Availability Statement

The data in this study are available on request from the authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Frequency of occurrence of tail- and wing-feather moult for a sample of breeders, sabbatical birds and immatures.