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The effects of annual cycle stages and life-history traits on feather abrasion

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Tissue wear in animals occurs consistently and can impair their functionality. In birds, abrasion – which reduces the feathered surface area – is caused by various factors. However, little is known about the underlying mechanisms, patterns and immediate consequences of feather abrasion. Given the lack of reliable and widely accepted methods for quantifying feather abrasion, we present the Minimum Convex Abrasion Area (MCAA), a novel approach for its measurement. This method facilitates the estimation of feather abrasion in both museum specimens and living birds, enabling an exploration of the factors influencing abrasion across different phases of the avian annual- and life-cycle. We analysed 283 feathers from 21 passerine species, revealing that the highest rate of feather abrasion occurs during the breeding season, with a significant reduction in feather surface area compared to other periods of the annual cycle. Surprisingly, migration periods, despite their high metabolic demands and long-distance movement, do not significantly contribute to feather abrasion. The timing of feather moult plays a pivotal role in influencing abrasion rates during the breeding season, with species that undergo moult nearer to the breeding season, during winter (pre-breeding moult), showing significantly lower abrasion rates than those moulting before the autumn migration (post-breeding moult), likely a result of the weakening of the feather structure over time. These findings highlight the importance of moult timing for feather abrasion rate and maintaining plumage integrity during the reproduction season. The application of the proposed abrasion measurement method is expected to facilitate better understanding of plumage function and properties, as well as bird moult strategies, thereby enhancing our comprehension of avian ecology, biomechanics, life-history traits and sexual selection, as well as their evolution.

Keywords Annual routine, Feather biomechanics, Migration, Minimum convex abrasion area, Moult timing, Passerines, Plumage wear

Abrasion is prevalent across a broad spectrum of natural materials, despite the development of various adaptations to reduce tissue wear[1]. The degree of abrasion and well as its underlying mechanism may substantially vary among different substances, tissues, taxa, environments and behaviours. Abrasion is identified as the process through which material is systematically diminished or abraded, either due to exposure to external agents such as air, water, acids, or radiation, or through friction or other forms of physical interaction with other entities. Abrasion through consumption of tissues by organisms (e.g., parasites) is also common. In response to abrasion, regeneration processes operate to preserve and restore tissue, allowing organisms to maintain their function after damage or wear. Complex biological systems work to repair and replace damaged tissues in animals[2]. For example, the skin, which serves as the primary immunologic barrier to the external environment, undergoes constant renewal through cell turnover processes[3,4]. Moreover, tissues such as bone and muscle possess the capacity for regeneration and recovery from injuries via self-repair mechanisms[5]. The ability to cope with tissue wear and to self-repair exemplifies biological flexibility and resilience, substantially contributing to animal fitness under diverse environmental conditions.

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Biomechanical considerations dictate that the flight surfaces in animals are delicate structures[6], thereby rendering them particularly susceptible to abrasion. Specifically, the wings and tails of bats, birds, and insects primarily evolved for locomotion[7,8], playing a critical role in daily survival activities such as foraging or escaping predators[9]. These surfaces, while enabling vital movement ability, are inherently prone to degradation over time due to their frequent and often strenuous use in various environments[10–12]. Therefore, among vertebrates, mechanisms were evolved to replace or repair these tissues[12,13], while among insects these damages are usually irreversible[14]. Nonetheless, behavioural changes to compensate for wing abrasion have evolved in both groups[15,16].

The renewal of flight feathers is essential for their function because feathers become abraded or lost with time due to exposure to radiation, parasites, physical friction and other environmental factors[12,17–19]. As a result, moult is one of the most important processes in the avian yearly cycle[12,20]. The case of avian plumage represents a unique scenario in the context of renewal following abrasion, as feathers are dead keratin-based structures that are incapable of self-regeneration by continuously renewing from their base like hair and claws that are also keratinous tissues. Consequently, the plumage renewal process must involve the shedding of old and worn feathers and the growth of new feathers in their place[12]. Nevertheless, research on feather abrasion is very sparse[21,22]. This is in sharp contrast to the importance of feather abrasion for understanding the biomaterial, biomechanical, ecological, life-history related and evolutionary aspects of bird plumage[23–25], as well as for the evolution of feather moult[12,26,27]. Plumage wear affects the feather's morphology, durability and colour[24,25,28,29] and hence may influences the bird's aerodynamic performance, as well as thermoregulation, visual signals and camouflage[24,29]. Furthermore, the limited scientific attention given to feather abrasion is likely due, at least in part, to the lack of effective methods for abrasion quantification. Although several approaches have been proposed in the past, they are either non-quantitative (e.g., anecdotal observations[30] or categorical scores[22,31] or require repeated measurements of the same individual (e.g., changes in feather length[32]), making them difficult to apply in practice. Therefore, there is a need to develop simple quantitative methods for assessing feather abrasion that would enable research into its causes and implications for avian biology and ecology.

Understanding plumage wear processes may also be critical for our understanding of the evolution of moult strategies and patterns, which include moult timing, frequency, extent and the identity of moulted feathers when the moult is incomplete. Specifically, breeding and migration represent demanding activities within the annual cycle, potentially incurring significant energetic and functional costs[33,34]. For instance, these activities, which involve extensive flight, may also have costs manifested in feather wear. Moreover, the advantage of having new, unworn feathers during certain periods of the year, when high performance is particularly required (e.g., breeding season or migration), may influence the evolution of moult strategies. For example, the winter moult that occurs in the non-breeding areas is a strategy whose significance has been debated in previous studies[35–38]. The benefit of renewing feathers closer to the breeding season, when high quality flight feathers are required due to food provision demands, may be a factor that maintains this strategy (winter moult) over long evolutionary time among long-distance migrants[36]. However, having this strategy may result in a trade-off as its cost may include post-breeding (autumn) migration with an abraded plumage, instead of breeding with worn feathers.

In this study, the term 'abrasion' is defined as the mechanical diminution of the feather's surface area, whereas 'wear' encompasses a broader range of effects including abrasion, as well as discolouration and degradation of the feather's structural integrity without a corresponding decrease in the feather's surface. Here, we used a new method to estimate the feather's abraded area using an assessment of the lost feather surface area due to abrasion. We describe the method, including materials, process and analysis, allowing us to estimate the level of feather abrasion. Estimated feather abrasion was tested in passerines to examine variation in abrasion between different annual-cycle stages and to test the effects of species-specific life-history traits. Using this method, we explore how the decrease in the feather's surface area as a result of feather abrasion is influenced by events in the annual cycle, as well as the species' life-history traits. We hypothesize that periods or traits requiring intense use of the feathers will lead to increased abrasion. Accordingly, we predict that breeding and migration seasons will cause greater abrasion compared to other periods in the annual cycle. Additionally, we hypothesize that the mechanical strength of the feather may decrease as abrasion intensifies. Therefore, we predict that longer migrations and increased nesting cycles will result in heightened feather abrasion. Additionally, since the moult strategy, (summer *versus* winter moult), influences the timing of plumage renewal relative to other events in the annual cycle[36,39], we hypothesize that this difference in timing may also affect plumage durability during various periods of the year.

Methods

Feather sampling

To examine the rate of feather abrasion throughout the annual cycle and under the influence of various yearly events (e.g., breeding and migration), we sampled outer tail feather (rectrix; R_6) from 21 passerine species in different periods of the annual cycle: (1) post-breeding period, before moulting and starting the autumn migration, (2) early wintering period, after autumn migration (only in migrant species which do not moult during this period), (3) late wintering period, before spring migration (only in migrant species which do not moult during this period), and (4) pre-breeding period, after spring migration. Although not required for the feather abrasion calculation method described below, newly grown feathers were also sampled shortly after moult and prior to any abrasion, in order to allow estimation of the percentage of abrasion. The described sampling design provided us with feathers that enabled assessment of the extent of abrasion at both the beginning and end of each defined period within the annual cycle for each species. To cover a variety of species, including migrants, and different periods of the annual cycle, we sampled feathers in the field in several countries: France, Spain, Germany, Israel, and The Gambia. Field data collection took place in 2016–2020. Additional data, which we could not collect during fieldwork, were collected in three ornithological collections: (1) Natural History

Museum (Tring, UK), (2) Natural History Museum Vienna (Vienna, Austria), and (3) Steinhardt Museum of Natural History, Tel Aviv University (Tel Aviv, Israel). A phylogenetic tree of the passerine species included in the study and their moult strategy (summer or winter moult) are provided in Fig. 1.

The sampled R_6 was used as an index for the bird's plumage abrasion using MCAA (minimum convex abrasion area), a method that measures the minimal missing feather area between the current outline of the given feather and a polygon enclosing the perimeter of the examined feather area. Although the degree of abrasion varies between different feathers in the bird's body[40], we assume a correlation in the abrasion rate among different feathers. This means that the abrasion rate of one feather can generally indicate the degree of abrasion of the entire bird's plumage. We selected this feather (R_6) because an important part of our sample is based on collecting feathers from live birds, and we were not interested in collecting feathers that are more vital for their flight. In addition, this feather represents a sufficiently large surface area for analysis. To calculate MCAA, each feather was photographed using an EOS 80D Canon DSLR camera, an EFS 18–135 mm Canon lens, and a Canon Macro Twin Lite MT-26EX-RT. Feathers were photographed against a uniform background (black or grey) in order to enable good distinction between the feather and its background, and a scale bar was placed next to each feather to allow calculating the MCAA. Using Adobe Photoshop (version 13.0), we manually drew a minimum convex polygon based on the outline of each feather (using Polygonal Lasso Tool) such that the points of the polygon are defined by the longest remaining 'tips' of the feather's outline (Fig. 2). Then, we summed the number of pixels found in-between the polygon and the feather outline. The number of pixels was converted to mm^2 using the scale bar that was positioned next to the feather and is included in the photo of each feather. We measured MCAA only for the distal 10 mm of each feather. In general, there is a difficulty to measure MCAA in the plumulaceous portion at the base of the feather and therefore this method is suitable only for the pennaceous part of the feather.

The duration of each examined period may differ between the different species, so we standardized the duration of the period based on the sampling dates by dividing the MCAA value by the number of days during which the abrasion occurred, thereby enabling comparison of abrasion rates across species and periods of the annual cycle. The assessment of the reduction in the sampled 10 mm tip of the feather area as a result of abrasion in a given period of the annual cycle was calculated as the value of the area reduced after the end of the period minus the value of the reduction before it began (mm^2; δ). This value was calculated per species if performed for the means of the individuals sampled. Alternatively, MCAA value was calculated for an individual and then the mean value per species from the previous period (or periods) was subtracted. In the latter case, when no or only small abrasion occurred, the low sample size for some species resulted in a negative value (22 out of 208 tested

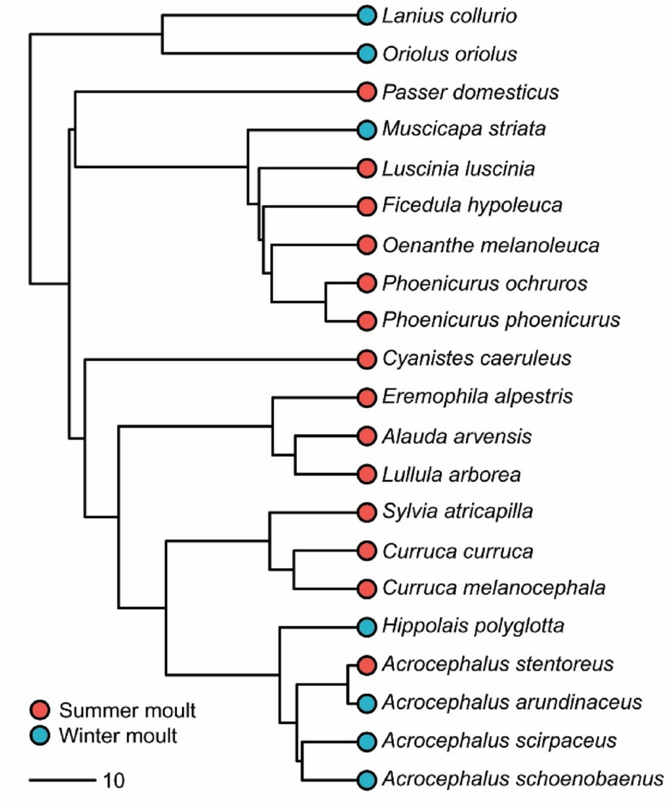

Fig. 1. The phylogenetic tree of the 21 species included in the analysis and their moult strategy (summer or winter). The tree is based on an analysis of global bird diversity[53,54]. The scale (bottom left) represents 10 million years.

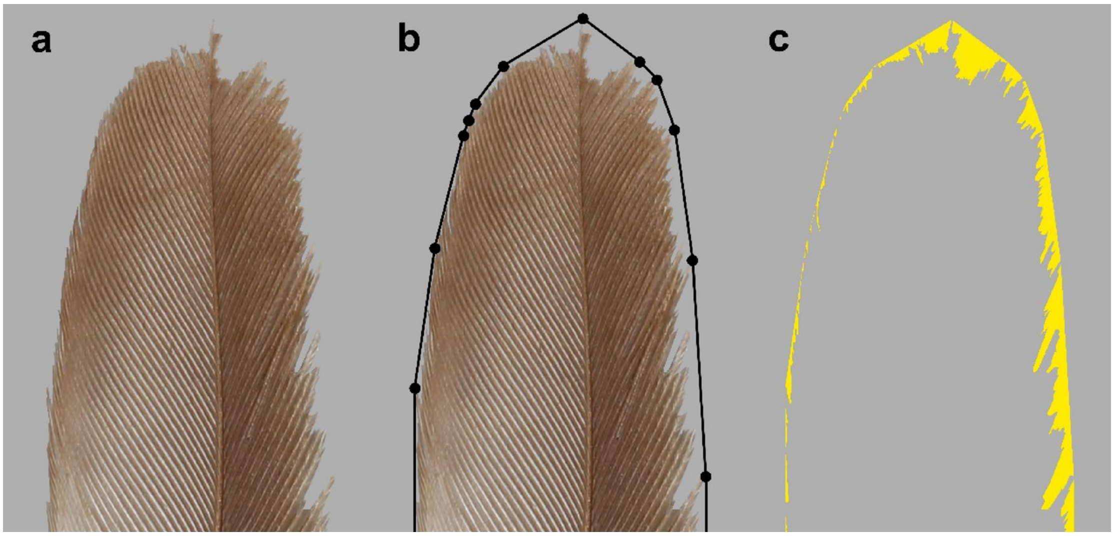

Fig. 2. Minimum convex abrasion area calculation (MCAA). (**a**) An abraded tertial feather of a Eurasian Reed Warbler (*Acrocephalus scirpaceus*). (**b**) A minimum convex polygon containing the feather area. (**c**) Minimum convex abrasion area which includes the area of the polygon minus the existing feather area and represents the minimum feather area that was lost as a result of brasion.

periods). In these cases, we converted the negative values to a minimal positive value (0.001 mm^2). An example which demonstrates the calculation performed at the species level for the breeding period: we calculated the mean abrasion in the post-breeding period (e.g., 8 mm^2) minus the mean abrasion in the pre-breeding period (e.g., 2 mm^2; $8-2=6$ mm^2) and divided by the number of days of the tested period (e.g., 60 days; 6 mm^2/60 days = 0.1 mm^2 per day). The value obtained is the mean feather area (mm^2 lost daily as a result of abrasion for each examined period in the annual cycle, breeding in this example. This value was multiplied by 30 days, an arbitrary value chosen in order to work with values on the scale of the investigated periods (tens of days) rather than one day.

Bird trapping and feather collection in Israel was done under a permit from the Israel Nature and Parks Authority (NPA permits A258, 40219 and 40722). Fieldwork at the Kartong Bird Observatory in The Gambia was undertaken with research permits from the Department of Parks and Wildlife Management (permits AHB 159/192/01(033) and AHB 159/192/01(120)). The birds handled and sampled in Spain have been carried out according to the Spanish regulations, under the permission of the current Ministry of Environment and the Aranzadi Science Society (permit A0391). Feather collection in Germany was done under a permit from the Landesamt für Umwelt and Landesamt für Arbeitsschutz, Verbraucherschutz und Gesundheit (LAU, LAVG Brandenburg: Beri-010-21, 2347-A-54-1-2020).

Statistical analysis

We used two different statistical methods. The first was carried out at the individual level and was intended to examine the effect of the yearly period on feather abrasion. The second was carried out at the species level and was intended to examine how species-specific traits affect the abrasion rate.

We used Generalized Linear Mixed Models (GLMM; family = gamma) to test the effects of the yearly period (autumn migration, wintering, spring migration and breeding; independent variable) on the level of feather abrasion (MCAA; dependent variable) of individual birds. We included two more fixed species-specific independent variables in this model: the species-specific migration distance and the number of annual nesting cycles as these may affect the abrasion during migration or breeding. Migration distance was calculated as the distance between the mid-wintering and the mid-breeding latitudes using distribution maps generated by BirdLife International (version 2019.1; see Kiat and Sapir[41]). The information regarding the number of nesting cycles was taken from Billerman et al.[42]. In addition, we included the "species" nested in "family" as a random factor to account for variance stemming from phylogenetic correlation[43]. Due to the challenge of sampling birds throughout the entire annual cycle, for most species we do not have abrasion data for all annual cycle periods. However, for all species that moult their feathers before autumn migration, we have abrasion data for both breeding and non-breeding seasons. Therefore, we repeated the analysis detailed above considering only two seasons (breeding *versus* non-breeding). This analysis could only include birds that moult in the summer ($n = 14$ species; Fig. 1) and could not include species that moult in the winter because moulting in these species occurs in the middle of this period, precluding calculating their feather abrasion during the non-breeding period. We used the R package 'lme4'[44] for GLMM. In each analysis, we compared the multivariate model described above to a null model using the Akaike Information Criterion, modified for small sample sizes (AICc[45,46]. The model statistics and selection were done through the R package 'MuMIn'[47]. R-square values were calculated using the R package 'rsq'[48].

We used a comparative approach to test the effects of three species-specific independent variables on the abrasion rate during the breeding period (dependent variable): (1) moult timing (summer *versus* winter), (2) migration distance, and (3) the number of annual nesting cycles. We tested the effects of two species-specific independent variables on the abrasion rate during the non-breeding period: (1) migration distance, and (2) the number of annual nesting cycles (univariate models), in this analysis, species that moult during the non-breeding period (winter moult) were not included due to the difficulty of examining abrasion in the period during which the moult takes place. Therefore, the effect of moult timing was not tested in this analysis. We did not include species that had less than three samples per period. Only one species (out of 22), the Western Olivaceous Warbler (*Iduna opaca*), was examined and excluded from the dataset due to an insufficient sample size. In both analyses described above, a species cannot technically be represented more than once in the sample, as in the case of the test of the annual cycle periods above. Consequently, we calculated the species-specific mean abrasion level as described above. Since species traits could be phylogenetically related, data from species that are closely related may not be statistically independent. Consequently, we alleviated this concern by analysing the data using the independent contrasts method which identifies evolutionarily independent comparisons[49]. To take phylogenetic non-independence into account, we applied Phylogenetic Generalized Least Square (PGLS) regression[50]. We explored the extent of phylogenetic non-independence by calculating the maximum likelihood value of Pagel's λ, a scaling parameter[51] using the R package 'caper'[52]. Pagel's λ ranges between zero (no phylogenetic signal) and one (phylogenetic signal that depends on branch lengths as in the analysis of phylogenetically independent contrasts) and is a multiplier of the off-diagonal elements of the variance-covariance matrix, which provides the best fit of the Brownian motion model to the tip data. Then, we corrected for the effect of shared ancestry by the maximum likelihood value of λ. We obtained the phylogenetic tree (Fig. 1) from a global analysis of bird diversity[53,54] using 1,000 trees that we generated using BirdTree.org version V2.iii[55]. The consensus tree was build using BEAST version 1.8.4. We used AICc for model selection as described above. A specific model was selected if its ΔAICc was larger than 2.00, compared with other models.

We employed the Wilcoxon rank sum test to assess the validity of integrating field-collected samples with museum specimens gathered decades ago, which constitutes a sample that is not normally distributed (Shapiro-Wilk normality test; $W = 0.91$, $P < 0.001$). The analyses were performed using R version 4.2.2 (R Development Core Team 2023).

Results

Feather abrasion in relation to annual cycle stages

We measured the R_6 MCAA of 208 periods (autumn migration = 38, wintering = 13, spring migration = 43 and breeding = 114; Table 1) belonging to 21 passerine species (Fig. 1) to uncover whether feather abrasion significantly varies between four periods (autumn migration, wintering, spring migration and breeding). Our

	Examined periods (number of feathers tested)				Origin of the examined samples (M = museum specimens, F = field samples)
	Breeding	Autumn Migration	Wintering	Spring Migration	
Oenanthe melanoleuca	6	3	4	7	M
Luscinia luscinia	3	5	4	4	M
Ficedula hypoleuca	5	4	5	6	M
Acrocephalus arundinaceus	7	5		7	M
Lanius collurio	7	7		5	M
Muscicapa striata	7	7		7	M
Oriolus oriolus	5	7		7	M
Acrocephalus schoenobaenus	[5] 5				F
Acrocephalus scirpaceus	[7] 6				F
Acrocephalus stentoreus	[4] 7				F
Alauda arvensis	[5] 5				M
Curruca curruca	[6] 6				F
Curruca melanocephala	[6] 7				F
Cyanistes caeruleus	[7] 5				F
Eremophila alpestris	[5] 5				M
Hippolais polyglotta	[3] 6				F
Lullula arborea	[5] 5				M
Passer domesticus	[6] 5				M + F
Phoenicurus ochruros	[5] 3				M
Phoenicurus phoenicurus	[4] 4				M
Sylvia atricapilla	[7] 5				F

Table 1. Sample sizes and the origin of examined samples, shown by species and examined periods. Values shown in square brackets indicate additional feathers collected prior to the respective period, which were used to calculate abrasion during that period (see detailed explanation in the methods section).

analysis indicates that the rate of reduction in the feather area as a result of abrasion is not constant throughout the annual cycle. During the breeding season, the abrasion rate is significantly higher compared to the two migration seasons and the wintering period (GLMM; $P = 0.026$; ΔAICc compared to the null model = 63.91, model $r^2 = 0.20$, fixed $r^2 = 0.18$; Table S1). During the breeding period, the 10 mm tip of the feather lost 1.76 ± 1.26 mm^2 of its surface (2.79% of the inspected feather surface; per 30 days) due to abrasion (mean ± SD; $n = 114$ samples), while during the two migration and wintering periods, only 0.46 ± 0.78 mm^2 (0.74% of the inspected feather surface; per 30 days) was lost ($n = 94$ samples; Fig. 3a). Similarly, among the 14 species that moult in the summer, we found that the abrasion rate during the breeding season is significantly higher than during the non-breeding period, without distinguishing between different non-breeding periods throughout the year (GLMM; $P < 0.001$; ΔAICc compared to the null model = 271.92, model $r^2 = 0.29$, fixed $r^2 = 0.16$; Table S1). In these species, during the breeding period, the 10 mm tip of the feather lost 2.13 ± 1.55 mm^2 of its surface (3.37% of the inspected feather surface; per 30 days) due to abrasion ($n = 72$ samples), while during the non-breeding period, only 0.13 ± 0.09 mm^2 (0.21% of the inspected feather surface; per 30 days) was lost ($n = 77$ samples; Fig. 3b).

The effects of life-history traits on feather abrasion

An analysis that included the abrasion rate only during the breeding season among 21 passerine species as the dependent variable showed that the degree of feather abrasion differed between the two moult timing strategies. Species that undergo moult nearer to the breeding season, in the wintering areas ('winter moult'; pre-breeding moult), had significantly lower abrasion rates than species that moult in the post-breeding period, before the autumn migration (PGLS; 'summer moult' $P = 0.039$, $r^2 = 0.21$; $\lambda = 0.00$, ΔAICc = 2.13, Akaike weight = 0.64 Table S2). During the breeding period, summer moult species lost 2.27 ± 1.05 mm^2 (3.64% of the inspected feather surface; per 30 days) due to abrasion (mean ± SD; $n = 14$ species), while winter moult species, lost only 1.34 ± 0.44 mm^2 (2.02% of the inspected feather surface; per 30 days; $n = 7$ species; Fig. 4). In our dataset, migration distance and the number of annual nesting cycles were not found to be associated with abrasion rate during the breeding period (PGLS; $P = 0.56$ and 0.78, $r^2 = 0.02$ and 0.00; Akaike weight = 0.08 and 0.07 respectively, Table S2). The same was found for the non-breeding period, with no evidence for an association between abrasion rate and either migration distance or the number of annual nesting cycles (ΔAICc < 1.83 compared to the null model; PGLS; Table S2).

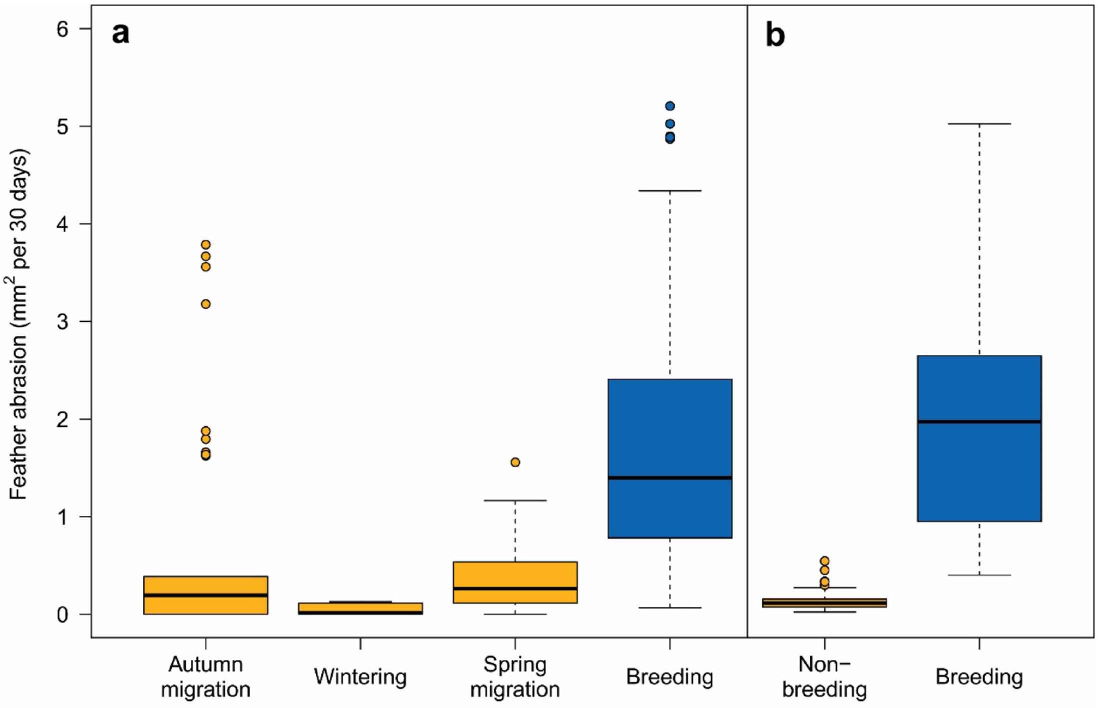

Fig. 3. The difference in feather abrasion between periods throughout the annual cycle. The results indicate that abrasion during the breeding season is significantly higher than non-breeding period, which includes autumn and spring migrations and the wintering period, (**a**) for all species, represented separately, and (**b**) combined as non-breeding period, for species moulting in the post-breeding period (summer moult). The boxplots display the minimum, 1st and 3rd quartiles, median and maximum of each tested period.

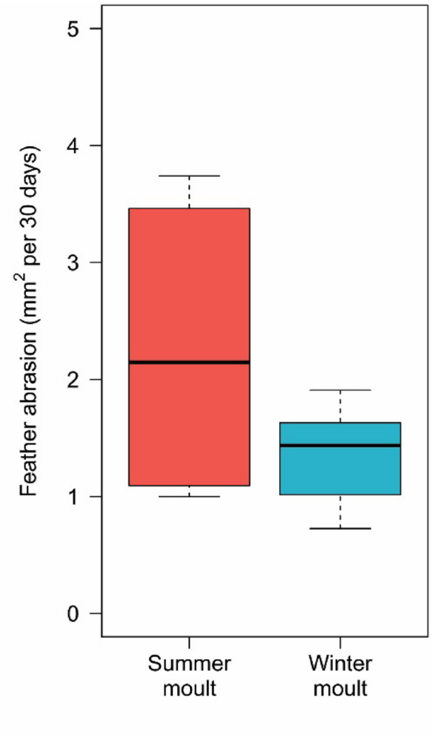

Fig. 4. The difference in feather abrasion during the breeding season between species moulting in the post-breeding period (summer moult) and species moulting in the pre-breeding period (winter moult). The results indicate that abrasion during the breeding season is significantly higher among summer moult species. These species renew their plumage long before the breeding season, which in turn may affect the abrasion rate. This finding may show the advantage of moulting in the pre-breeding period among long-distance migrants wintering in the tropics and the southern hemisphere. The boxplots display the minimum, 1st and 3rd quartiles, median and maximum of each tested period.

Validity of utilizing museum specimens for abrasion research

To examine the validity of using museum specimens and field samples together, an analysis comparing abrasion rates from these two data sources was conducted. No difference in abrasion rates was found between museum specimens ($n = 59$) and field samples ($n = 55$) in the breeding season, validating the use of both data sources (Wilcoxon rank sum test; $W = 1433$, $P = 0.28$). Feathers of museum specimens are not expected to undergo increased abrasion, even after prolonged storage periods.

Discussion

Feather wear may affect the functions of the plumage, including its colouration, thermoregulation capacity and aerodynamic performance. A better understanding of temporal variation in feather abrasion and its underlying drivers is expected to enhance the study of feather biology, with implications for various aspects of plumage ecology and evolution, including feather moult, long-distance migration, breeding success, and bird survival. We devise the MCCA method as a standardized, easy to use tool for expanding our knowledge of feather abrasion. This method examines the reduction in feather area by summing the value of the minimum feather area that was lost as a result of abrasion. Although theoretically, feather abrasion may occur uniformly along the feather margins and thus reflect a low MCAA value even in cases of substantial abrasion, our observations and findings indicate that this was not the case in the examined sample – MCAA values increased with time since moult. Additionally, comparison between the measured abrasion and the actual feather abrasion showed a strong correlation between the values (Figure S1), supporting the use of MCAA as a valid comparative index. While we encourage scientists and ornithologists to apply this method for characterizing feather abrasion and studying different aspects of this process, we also recommend considering species-specific habitat use and behaviour, as these may affect abrasion patterns.

The effects of the annual cycle on feather abrasion

Among the passerines studied, feather abrasion was significantly higher during the breeding season (Fig. 3). This finding aligns with our hypothesis and previous results[54,56], and is likely due to intensive foraging associated with the high rate of food provisioning to the young during this period. These findings may represent a proposed mechanism that drives the trade-off between current and future reproduction[57,58]. Increased investment in current reproduction (e.g., food procurement for more offspring) is predicted to lead to a functional cost and therefore to a decrease in future reproductive output[59,60]. For example, previous studies have suggested that abrasion rates are linked to differential workload, a hypothesis partially supported by abrasion varying directly with experimentally reduced, but not increased, chick numbers[22]. The functionality that could decline due to high feather abrasion includes the ability to escape predators and to acquire food resources for self-maintenance, and thus it is expected to reduce future reproductive output. This is especially relevant for long-distance migrants which moult in the wintering areas and thus are forced to migrate with worn feathers during the autumn migration. In this group of species, obtaining food resources for survival and flight performance during migration could be impaired due to high feather abrasion, which may affect the duration of the migration[61].

Contrary to our prediction, and unlike during the breeding period, migration was not found to be a period when feather abrasion is high. We note that foraging in the species examined occurs within dense vegetation in reeds or forests (e.g., *Acrocephalus arundinaceus*, *Ficedula hypoleuca* and *Cyanistes caeruleus*), or on the ground (e.g., *Alauda arvensis* and *Eremophila alpestris*). The friction of the feathers against plant parts during foraging is likely a major cause of the increased abrasion during the reproduction period. In addition to the friction against plants or the ground, the time spent in nests, which are often constructed from hard plant materials, may also contribute to the elevated feather abrasion found in this period. In contrast, it appears that migration flight in the open air, which does not involve intense friction with objects in the bird's habitat, does not lead to significant feather abrasion, even over thousands of kilometers of prolonged active flight. However, previous studies suggested that the durability of the flight feathers might be adapted to withstand the challenge of their lengthy journeys. Specifically, Kiat and Sapir[62] found that the lifespan of nest-grown feathers until their projected replacement is a strong predictor of feather quality, suggesting that feather quality, which is determined when the feather grows, is adapted by the expected duration of the use of each feather. Similarly, we propose that the feathers of birds that undertake long-distance migration are more durable when generated during the nesting (for juveniles) and moulting (for adults) periods, resulting in the lack of positive relationship between migration distance and feather abrasion rate. Indeed, this hypothesis has been tested and confirmed for a few passerine species in previous research[63,64].

The effects of the life-history traits on feather abrasion

The findings of this study indicate that moult strategy is a key life-history trait influencing feather abrasion during the breeding season. In contrast, the dataset used in this study and the analysis conducted did not reveal any effect of migration distance on feather abrasion. Species that undergo moult nearer to the breeding season, in the overwintering period, had lower rates of abrasion compared to species that moult earlier, during the post-breeding season (summer moult; Fig. 4). This suggests that feathers exposed to the environment and are in use for a longer duration are less durable and abrade more during the breeding season. A similar result was described by Flinks and Salewski (2012) in wing feathers, in which the remiges wore down more as the feathers aged. However, they found that rectrices, which were the focus of the current study, had constant abrasion over time, regardless of the feather's age[65]. The current study's findings reveal that rectrices underwent more abrasion in species that their feather's age was older, compared with species whose feathers were relatively fresh. It should be noted that Flinks and Salewski (2012) examined feather length, and the difference in the methods used for quantifying feather abrasion could account for the discrepancy in the findings of the two studies.

Notably, our findings did not show a direct relationship between migration distance and the degree of feather abrasion, despite previous findings that may suggest greater feather durability in long-distance migrants[63,64]. Nevertheless, migration indirectly affects feather abrasion through its influence on moult strategy. Winter moult occurs only among long-distance migratory species, in the tropics or the southern hemisphere non-breeding areas[35,36]. Long-distance migratory species that moult in the post-breeding season showed similar abrasion rates to resident species that moult in the same season, indicating that the timing and strategy of moult are crucial factors in feather abrasion dynamics rather than migration distance per se. Note that the periods during which MCAA was measured in relation to breeding or migration in this study may be broader than the specific event examined, and therefore may also include abrasion that occurred before or after the breeding or migratory period; consequently, our analysis can be regarded as a seasonal comparison rather than comparing between short-term events.

Future research directions

In this study, we introduced a new method for assessing the abrasion of pennaceous feathers, highlighting the advantages of this method over previous approaches (Table 2) and presenting an analysis that examined how feather abrasion varied throughout the annual cycle and under the influence of several important factors. This method could represent an opportunity for advancing research on feather abrasion. Numerous questions relating to bird ecology, evolution and life-history properties could be addressed through the application of the minimum convex abrasion area (MCAA). Feather abrasion may vary depending on multiple factors, such as habitat, climate[1], sex[22,31], age, species, flight type or foraging strategy (e.g., as in bats[11]), which affect feather function. Only very few studies have demonstrated the need for feather replacement (e.g., in seasonal acquisition of plumage colouration[66,67], as opposed to many studies dealing with constraints (e.g., constraints due to age, long-distance migration, geographic distribution or body size[68–70]. By applying MCAA, it is possible to assess whether the replacement of certain feathers twice a year (e.g., through pre-breeding partial moult) includes feathers that are more exposed to abrasion compared to other feathers of the birds thus improving plumage performance trough feather moult. It may also be of interest to attempt estimating the abrasion in well preserved fossilized samples of Mesozoic birds, an extinct paraphyletic group whose feather-related studies have garnered attention in recent decades[71–73].

MCAA provides an assessment of feather abrasion from a specific aspect, but other aspects of wear are not yet adequately addressed, and it would be interesting to examine them in future studies. For instance, it is assumed that a feather might lose thickness and become thinner, which could affect the feather's durability and

Abrasion measurement method	Disadvantages	References
Anecdotal observations	● Do not provide an accurate assessment of the abrasion level.	Averill (1923)
Categorical scores	● Do not provide an accurate assessment of the abrasion level.	Merilä and Hemborg (2000), Vágási et al. (2011)
Wing or tail length reduction	● Relevant only for the longest feather in the wing or tail. ● Determined mainly by the length of the rachis, the more durable part of the feather. ● Does not provide an accurate assessment of the abrasion level of the main feather surface. ● Largely affected by the initial wing/tail length, and hence, requires measurements data of fresh wing/tail as a comparative reference.	Francis and Wood (1989), Flinks and Salewski (2012)
Feather length reduction	● Determined mainly by the length of the rachis, the more durable part of the feather. ● Does not provide an accurate assessment of the abrasion level of the main feather surface. ● Largely affected by the initial feather length, and hence, requires measurements data of fresh feathers as a comparative reference.	Barrowclough and Sibley (1980); tested also in the current study
Feather area reduction	● Largely affected by the initial feather area, and hence, requires measurements data of fresh feathers as a comparative reference.	Barrowclough and Sibley (1980)
Feather mass reduction	● Determined mainly by the mass of the rachis, the heavier part of the feather. ● Largely affected by the initial feather mass, and hence, requires measurements data of fresh feathers as a comparative reference.	Tested in the current study
MCAA	● Refers to the minimum abrasion area, and thus, in highly abraded feathers, the difference between the measured and the actual feather abrasion may be large. ● Measuring the plumulaceous portion of the feather, near its base, is difficult or impossible.	Presented at the current study

Table 2. Comparison of seven methods for quantifying feather abrasion.

the MCAA. Furthermore, sun radiation likely does not directly affect MCAA but may be an important factor in feather wear[74]which is probably important among species of open and arid habitats or in aerial species such as swallows (Hirundinidae) and swifts (Apodidae). This effect on the feather could be examined in future research by assessing changes in feather colour and mechanical durability. Although not documented in our findings, theoretically, abrasion may occur uniformly along the feather margins, in which case MCAA values would not accurately reflect the extent of feather wear. In such cases, future users of this method should compare the area reduction of the examined abraded feather to the mean area of that specific feather type immediately after moult.

Conclusions

This paper presents a new method for measuring feather abrasion. The simplicity of the method, together with the ease and accuracy of its application, demonstrates its utility in the laboratory and in the field for measuring feathers from both dead and live birds. We found that the breeding season is the period during which feather abrasion is the highest. Contrary to our expectations, migration, despite being a demanding activity in the avian annual cycle, does not result in substantial feather abrasion. Notably, the timing of feather moult influences abrasion intensity during the breeding season. The future application of this method will enable a comprehensive examination of plumage functions, feather properties, and moult strategies, thereby enhancing our understanding of avian biology, ecology, and life-history traits.

Data availability

The data that support the findings of this study are available in the Open Science Framework (OSF): https://osf.io/be95j/.

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Author contributions

Y. Kiat and N. Sapir conceived the ideas and designed methodology; Y. Kiat, Q. Dupriez, O.J.L. Fox, R. Paz, H.J. Eilts and C. Talabante collected the samples and data; Y. Kiat and G. Pyo digitized the samples; Y. Kiat analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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