

ANIMAL HEALTH AND WELL BEING

Describing the growth and molt of modern domestic turkey (*Meleagris gallopavo*) primary wing feathers

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Abstract

The use of feathers as noninvasive physiological measurements of biomarkers in poultry research is expanding. Feather molting patterns and growth rates, however, are not well described in domestic poultry. These parameters could influence the measurement of these biomarkers. Therefore, the objective of this study was to describe the juvenile primary feather molting patterns and feather growth rates for domestic turkeys. The 10 primary wing feathers of 48 female turkeys were measured weekly from week 1 (0 d of age) to week 20. Feathers were manually measured, and the presence or absence of each primary feather was recorded weekly. Generalized linear mixed models were used to investigate if feather growth differed between the primary feathers. The molting of the juvenile primary feathers followed a typical descending pattern starting with P1 (5 wk of age), while P9 and P10 had not molted by the end of the study (20 wk of age). The average feather growth rate was 2.4 cm/wk, although there was a significant difference between the 10 primary feathers ($P < 0.0001$, 2.1 to 2.8 cm/wk). Over time, feather growth followed a pattern where the growth rate reaches a peak and then declines until the feather is molted. The results of this study provide a critical update of patterns of molting and feather growth in primary wing feathers of modern turkeys. This can have implications for the interpretation of physiological biomarkers, such as the longitudinal deposition of corticosterone, in the feathers of domestic turkeys.

Key words: feather growth, *Meleagris gallopavo*, molting, primary feathers

Introduction

Feathers are critical derivatives of the avian integument, which are made primarily of keratin with a central shaft (rachis) and rows of parallel branches (barbs) rooted in a follicle (Dawson, 2015). Some feather types provide insulation, waterproofing,

or are a means for communication, whereas others, the flight feathers of the wing, provide aerodynamic lift for flight (Lucas and Stettenheim, 1972; Saino et al., 2013; Dawson, 2015). Feathers are a vital and defining part of a birds' biology, but they naturally become damaged or worn during the life of a bird

(Saino et al., 2013). Maintaining feather quality and performance comes at a high metabolic cost in the growth, maintenance, and replacement of feathers (Rubinstein and Lightfoot, 2014). Molting, the periodic replacement of feathers, is an essential process for birds but relatively little is documented about molting patterns and feather growth in domesticated poultry. Feather molting patterns in domestic chickens (Lucas and Stettenheim, 1972; Fisher, 2016), domestic turkeys, and wild turkeys have been documented but in older literature (Leopold, 1943; Williams, 1961; Williams and McGuire, 1971). In the interim, intensive breeding may have influenced these patterns. In addition, there are no studies that have provided information on the feather growth rate.

It is worth revisiting this area of research given the rise in popularity of using feathers as part of noninvasive techniques as indicators of nutritional (Strochlic and Romero, 2008; DesRochers et al., 2009) or physiological status (Greene et al., 2019). Nutritionally, feather growth requires a considerable protein investment; consequently, diet plays a significant role in feather maintenance. Diets low in protein have been demonstrated to reduce feather growth (Van Emous et al., 2014) and have the potential to affect molting pattern (Murphy and King, 1991). Physiologically, chronic challenges can also affect feather cover and quality. This will then affect the deposition of hormones and metabolites into the growing feather. For example, the circulating stress hormone, corticosterone, is believed to be deposited into growing feathers via the blood quill in a time-dependent manner (Harris et al., 2016). However, it is important to examine how feathers grow and how they are replaced so that inferences can be made about when the substance of interest was likely deposited and relate that to the growth pattern of the feather (e.g., potential stressors).

The objective of this study was to describe the molting pattern and feather growth rate of the juvenile primary wing feathers in domestic turkeys. Wing feathers were chosen as they are easily identifiable making repeated sampling within and between individuals consistent. This was done as part of a larger project aimed at developing novel welfare phenotypes in domestic turkey breeding (Malchiodi et al., 2019), where we are particularly interested in using feather corticosterone as a noninvasive measurement (Leishman et al., 2020).

Materials and Methods

This study was approved by the University of Guelph Animal Care Committee (Animal Utilization Protocol 4105).

Subjects

Forty-eight 1-d-old female turkey poults were available as part of another study (van Staaveren et al., in preparation). Birds were individually wing tagged and housed at the Research Station of the University of Guelph, Ontario, Canada. For the first 2 wk, poults were housed in two floor pens (111 L × 140 W cm) with one dark brooder (35 × 42 × 35 cm) in each pen. Dark brooders (upside-down opaque plastic container with opening) were provided so poults had a dark place to rest. At 3 wk of age, poults were divided across 12 pens for a final group size of 3 to 4 poults per pen. Each pen was bedded with wood shavings and was equipped with two drinkers and one feed pan. Feed and water were available ad libitum. Standard commercial lighting and temperature protocols were applied (Hybrid Turkeys, 2020). It should be noted that as part of the main study, poults were

assigned to either a low (15% to 26% protein depending on the production phase, $N = 23$) or high (17% to 29% protein depending on the production phase, $N = 25$) isocaloric diet treatment. For more details regarding the dietary treatments, please refer to van Staaveren et al., (2020, in preparation). Diets were mixed by the Research Station, University of Guelph, Guelph, Ontario, Canada, to meet the nutrient recommendations by Hybrid Turkeys. Diets were randomly assigned to the birds in week 1 and maintained until the birds were euthanized at week 20. All birds were weighed on day 1 to determine their initial body weight and were weighed weekly throughout the experiment.

Feather measurements

Beginning at week 1 (1 d of age), the right wing of each bird was extended to visually inspect and measure the length of the primary feathers. The 10 primary feathers were numbered from 1 to 10 starting from the innermost feather to the tip of the wing as shown in Figure 1. The length of each primary feather was measured by placing a graduated rule at the base of the feather shaft, at the level of the skin, and measuring to the tip of the rachis (Wylie et al., 2003). A marking was made on the rachis of each primary at the level of the skin using a permanent marker at each weekly inspection. If the marking had not moved by the time of the next week's inspection, it was recorded that the feather had stopped growing. The markings were rechecked at every inspection until molt, and the interval length between the weekly markings was recorded and summed to calculate total feather length. This method avoided any damage at the tips of the feathers influencing the final feather length and growth calculation. The presence or absence of each primary feather was recorded weekly to track molting patterns. This process was repeated weekly until birds were euthanized in week 20 at the end of the experiment.

Statistical analyses

The average feather growth rate (cm/wk) was calculated as the final feather length divided by the total weeks of growth. Descriptive statistics (mean, SEM) of the growth and molting pattern of the 10 primary feathers were computed in SAS v9.4 (SAS Inst. Inc., Cary, NC). To determine if the average growth rate differed between the primary feathers (1 to 10), generalized linear mixed models were used in SAS while accounting for the different diet treatments (high or low protein) and including bird as the experimental unit. The average feather growth rate is presented as the LSMean ± SEM. Significance was determined as $P < 0.05$, and tendencies are reported at $0.05 < P < 0.10$. To visualize how feather growth changes over time, average weekly feather length ± SEM (cm) was plotted against time (wk).

Results

Feather development and molting pattern

The first six juvenile primary feathers were observable at 1 d of age, indicating growth in-ovo prior to hatch (Figure 1A). Primaries 8 and 9 were observable by week 3, and primary 10 was observable by week 4 as detailed in Table 1. The first juvenile primary was molted in week 5 and continued distally with the next respective primary molted approximately every week until the molt of primary 5 (Table 1). After the fifth primary molted, the rate of replacement slowed, and subsequent primaries were molted in 2- to 3-wk interval, except for primaries 9 and 10, which were not observed to molt during our study.

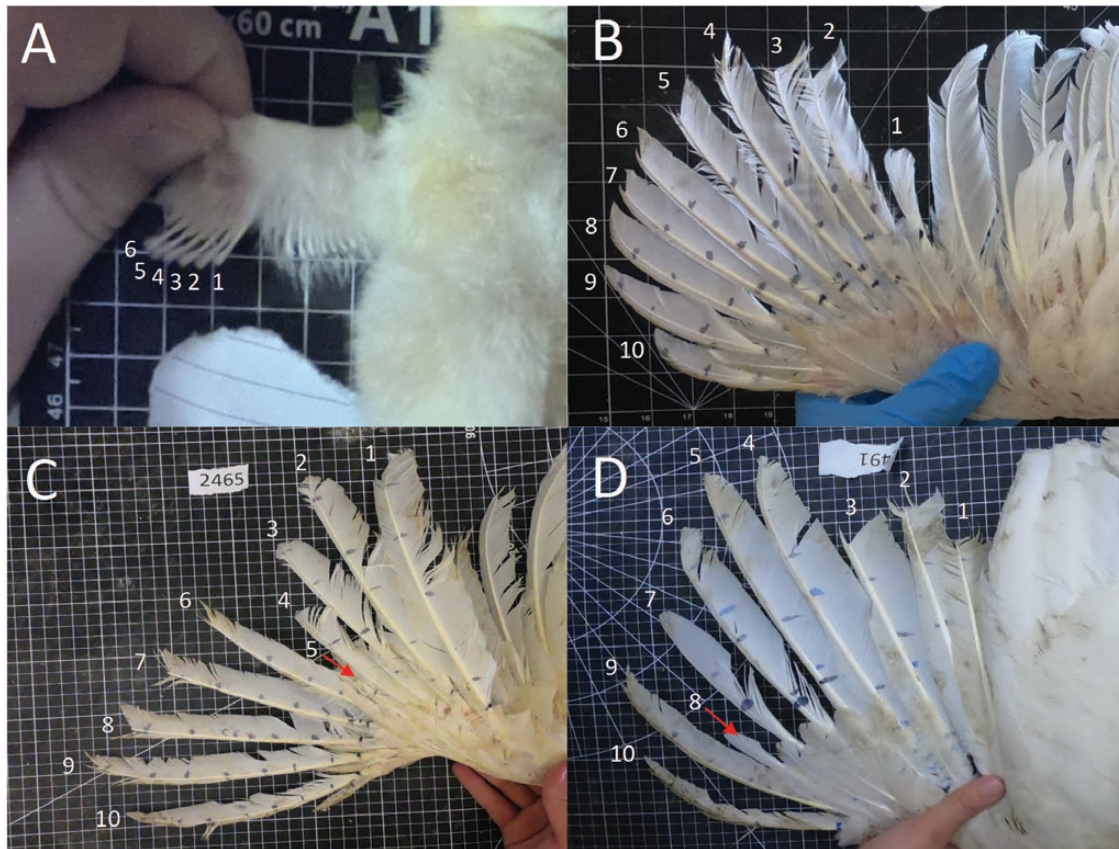


Figure 1. Image of a turkey hen right wing at one day of age (A), 7 wk of age (B), 12 wk of age (C), and 20 wk of age (D) showing the primary feathers measured in this study. Primaries are labelled from 1 to 10 from proximal to distal. The markings seen on the primaries were made at each weekly inspection.

Table 1. Age in weeks (wk) when the primary wing feathers (1 to 10) of turkeys ($N = 48$) were first observed, finished growing, or were molted, as well as the length of feather when the growth was completed¹

Feather	Age observed, wk	Age completed, wk	Age molted, wk	Total feather length, cm ²	Total feather length range, cm ³
1	1 ± 0.0	5 ± 0.14	5 ± 0.00	9.3 ± 0.22	6.4 to 10.7
2	1 ± 0.0	6 ± 0.22	6 ± 0.07	12.4 ± 0.28	9.0 to 19.8
3	1 ± 0.0	7 ± 0.27	8 ± 0.06	15.5 ± 0.18	13.1 to 18.9
4	1 ± 0.0	8 ± 0.27	9 ± 0.04	18.1 ± 0.25	14.0 to 22.2
5	1 ± 0.0	9 ± 0.31	10 ± 0.08	20.8 ± 0.26	18.1 to 26.0
6	1 ± 0.02	10 ± 0.34	12 ± 0.07	23.2 ± 0.35	15.6 to 27.3
7	2 ± 0.05	11 ± 0.41	14 ± 0.07	26.5 ± 0.35	19.3 to 30.4
8	3 ± 0.07	12 ± 0.49	17 ± 0.09	27.3 ± 0.28	20.7 to 29.6
9	3 ± 0.09	14 ± 0.57	20 ⁴	26.9 ± 0.28	22.0 to 30.4
10	4 ± 0.12	14 ± 0.60	20 ⁴	20.4 ± 0.32	15.3 to 26.4

¹Data are displayed as mean ± SEM.

²Total calculated length of the feather when growth was completed.

³Minimum to maximum total feather length.

⁴Primary feathers 9 and 10 had not molted yet by the end of the experiment at 20 wk of age.

Growth rate

The overall average feather growth rate was 2.43 ± 0.068 cm/wk; however, the average feather growth rate was different between the 10 primary feathers ($P < 0.0001$, Figure 2). Primaries 7 and 8 had the highest average feather growth rate, whereas primary 10 had the lowest feather growth rate. The remaining primary feathers 1 to 6 and 9 were intermediate, with minor differences among each other. When visualizing feather growth, we found that initial feather growth is rapid, reaches a peak, and then gradually declines before the feather is molted (Figure 3). Although not statistically

significant, there was a tendency for the feather growth rate in the low protein treatment to be lower (2.40 ± 0.0298 cm/wk) than birds in the high protein treatment (2.47 ± 0.0318 cm/wk, $P = 0.0985$).

Discussion

Feather development and molting pattern

While (Leopold, 1943) reports the first seven primaries being observable on a day-old female poult, we generally only

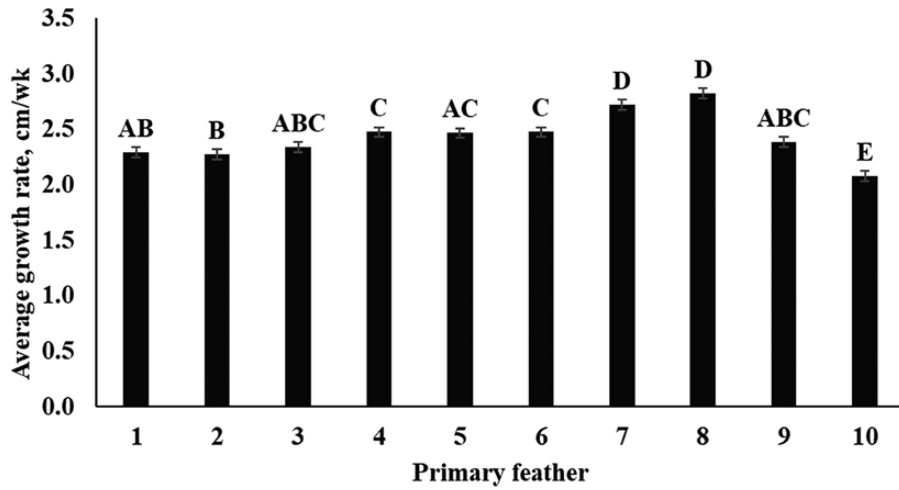


Figure 2. Least square means (LSM) ± SEM for feather growth (cm/wk) in primary wing feathers (1 to 10) in turkeys. Columns that do not share a letter are significantly different from each other ($P < 0.05$).

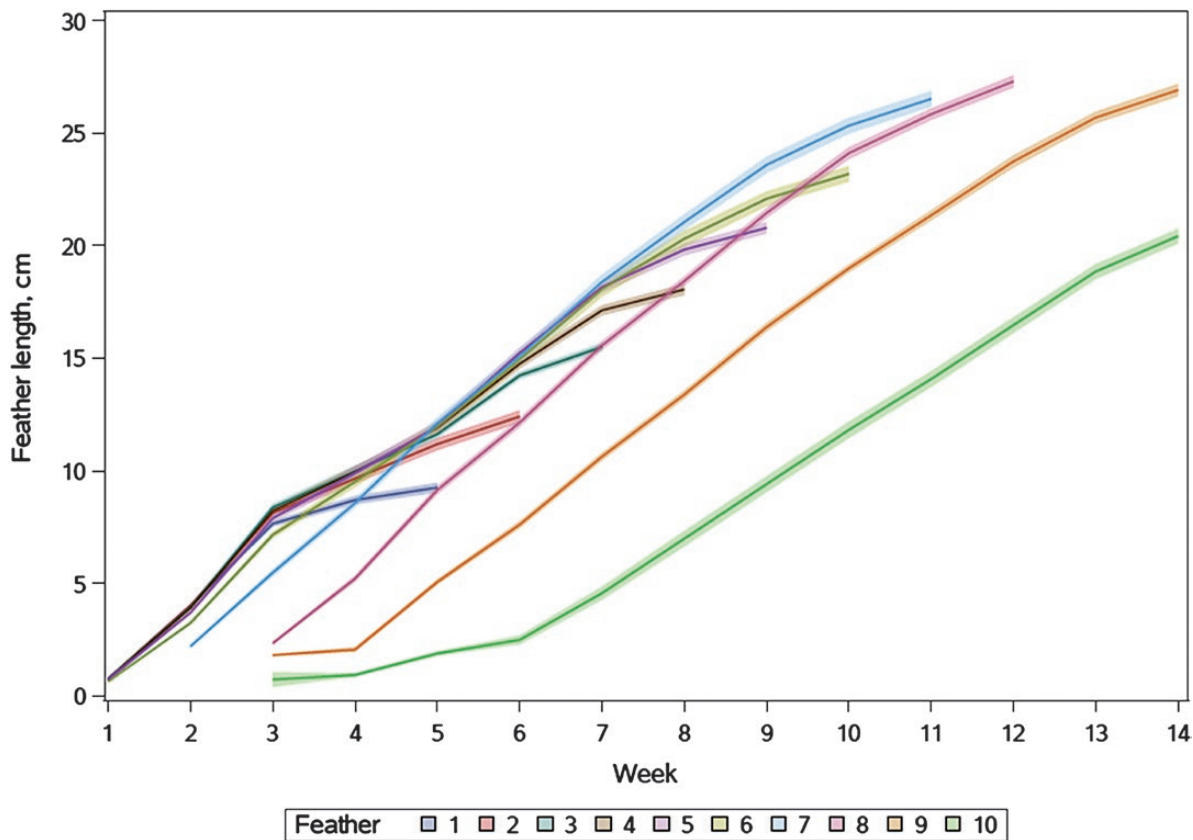


Figure 3. Average turkey hen primary feather (1 to 10) length ± SEM (cm) plotted against time (week) ($n = 48$). Feather length is plotted until the completion of feather growth. The shaded band represents mean length ± SEM for each week.

observed primaries 1 to 6 at 1 d of age. Only one poult in our study had an observable seventh primary at 1 d old; however, it was observable on all other individuals by week 2 (7 d of age). Six primaries at hatch are also in line with reported characteristics of domestic chickens, although there is variation between breeds (Lucas and Stettenheim, 1972). All juvenile primary feathers were observable by 4 wk of age, demonstrating that

the juvenile primary feathers are all present within 1 mo. In the wild, turkeys nest on the ground and have precocial young, meaning that feather growth is typically rapid and completed sooner than altricial species such as songbirds (Chen et al., 2019). This rapid feather development could be important from a biological perspective for the various functions mentioned previously, in particular, the use of space. For example, it is

shown that chickens kept for egg laying start moving vertically (i.e., perches and ramps) at 2 wk of age and rely on their wing feathers for this purpose (Kozak et al., 2016; Leblanc et al., 2016, 2018). These behaviors are likely not as essential for turkeys in commercial conditions; however, turkeys are known to perch, particularly at younger ages (1 to 5 wk of age; Martrenchar et al., 2001).

Our results in the current domestic turkey show a descending molting pattern, in which feathers are replaced sequentially from proximal (primary 1) to distal (primary 10). The distinct sequential molting pattern of the primary feathers serves to sustain the natural function of feathers for protection and flight (Dawson, 2015). For this reason, wing feathers are typically not replaced all at once but are regrown in a symmetrical pattern. This is different compared with, for example, waterbirds, whose flight feathers are less critical and may molt simultaneously since they can still obtain food and protection from predators on the water (Dawson, 2015). All juvenile primary feathers, except for primaries 9 and 10, had molted by the time our study ended at 20 wk of age. In wild turkeys, primaries 9 and 10 are reported to be retained throughout the winter season, which indicates that they molt much later than primaries 1 to 8 (Leopold, 1943; Williams, 1961).

The development and molting pattern of the juvenile primary feathers in turkeys appear relatively similar to older reports (Leopold, 1943; Lucas and Stettenheim, 1972). This suggests that domestication and almost 80 yr of genetic selection for growth and reproductive traits in turkeys have not drastically altered the timing, development, and molt of feathers, reinforcing the fact that maintaining adequate feather cover and quality is important for domestic turkeys.

Growth rate

The average feather growth rate was relatively consistent between the 10 primary feathers (2.08 to 2.82 cm/wk); however, differences between the feathers were observed. These differences were only minor and could be expected since the time to completion of the feather increases from primaries 1 to 10, while all feathers grew to a similar size (Lucas and Stettenheim, 1972). For example, the final length of primary 10 is similar to primary 5 but has a much longer period in which feather growth is completed. Therefore, its overall growth rate must be lower (Lucas and Stettenheim, 1972). Interestingly, Wylie et al. (2003) recorded the length of domestic turkey poult secondary wing feathers at the end of a 6-wk experimental period and estimated an average growth rate of approximately 3.05 cm/wk. This is close to the average growth rate calculated across primary feathers (2.4 cm/wk) in the current study.

This is the first longitudinal description of feather growth reported for domestic turkeys. Our study is unique in that the length of the primary feathers is measured over time on the same individuals, which allows us to describe how feather growth changes as the birds age. The rate of feather growth was not constant each week. Instead, we found that the feather growth rate was the highest soon after the feather's emergence; it reached a peak, and then the growth rate gradually decreased until growth was complete. Very few other studies describe feather growth in domesticated poultry. Relevant work was completed by Gous et al. (1999, 2019) who modeled the growth of feathers in broilers; however, this is presented as total feather weight per pound of body weight and not as a length rate. That said, the pattern of growth is

similar to that found in our study, though within a different age range and species.

Finally, while not the main aim of the current study, we had to account for dietary differences as part of another study (van Staaveren et al., in preparation), as it is known that nutrition can impact feather growth and feather quality (Urdaneta-Rincon and Leeson, 2004; Van Emous et al., 2014). We only observed a tendency for birds in the low-protein treatment to have a slightly slower feather growth compared with birds on the high-protein diet. This could possibly be a consequence of feather growth being very costly in terms of protein utilization and energy (Strochlic and Romero, 2008). Apart from this limited difference in feather growth, turkeys on the low- or high-protein diets in the current study did not differ in production performance parameters, such as body weight, average daily feed intake, average daily gain, and feed conversion ratio (van Staaveren et al., in preparation). Wylie et al. (2003) suggested that modern turkeys preferentially partition dietary protein to feather growth over muscle growth when dietary protein is limited, compared with traditional turkeys whose feather growth was affected more by low-protein diets. This suggests that feather growth is still a priority in modern turkeys and may not be as affected by low-protein diets compared with wild or traditional breeds.

Feathers can act as a longitudinal record of chronic challenges through the development of a bird (e.g., disease, food shortage, high stocking density, and heat stress), as highlighted by the recent interest in assessing welfare in poultry through feather hormones and metabolites, such as feather corticosterone (Von Eugen et al., 2019; Nordquist et al., 2020). However, the period of feather growth is often unknown, so it is unclear what stage of life the measured feather corticosterone values reflect in these studies. Our findings can assist in identifying the most probable time periods when the metabolites of interest were deposited. For example, if a metabolite is measured from the complete length of turkey juvenal primary 1, this should reflect the average circulating level during the first 5 wk of life. However, if a metabolite is measured in juvenal primary 9, this should reflect the average circulating level during weeks 3 to 14 of life. This pattern may be an important factor when deciding which feather to use for measurement depending on the experimental design and to make inferences about certain stressors (Leishman et al., 2020). Furthermore, our findings reinforce the need to use the same primary consistently across individuals when measuring feather metabolites to ensure it reflects the deposition over the same period. Alternatively, as suggested by Kennedy et al. (2013), studies could homogenize multiple feathers from an individual to capture some of the variations between feathers.

One limitation of the study is that due to our weekly measurements, we cannot be specific about when feathers are molted within a certain week, and the molting pattern described may not necessarily capture all the individual variation in molting pattern. Furthermore, the manual measurement of feathers in the same individuals is time consuming (Saino et al., 2013). Ptilochronology was suggested as an alternative technique for estimating feather growth rate whereby a pair of alternating light and dark bands on feathers are thought to represent feather growth over a 24-h period (Saino et al., 2013). However, we were unable to differentiate growth bars on the primary feathers of domestic turkey due to a lack of pigmentation that is required to distinguish growth bars. This could explain why ptilochronology has not been reportedly used for domestic poultry and confirms that feather growth measurements for domestic poultry with white feathers will likely continue to be performed manually. It

would be interesting to determine if the technique would work in domestic birds with pigmented feathers, such as bronze-feathered or heritage turkey breeds.

Conclusions

This study provides an updated account of the molting patterns of the primary wing feathers and is the first to report the feather growth rate of juvenile primary feathers in domestic turkeys. The primary feathers followed a typical descending molting pattern with feathers molting as early as 5 wk of age (primary 1) or later than 20 wk of age (primaries 9 and 10). The pattern of molting was well conserved over years of genetic selection in modern turkeys, possibly due to the crucial role of wing feathers in bird physiology. Weekly feather growth varied slightly between the 10 primary feathers but was, on average, 2.4 cm of growth per week. Interestingly, the pattern of feather growth had initial rapid growth, which reached a climax, and then slowed down until the feather is molted. This information provides an important perspective on new noninvasive welfare indicators in poultry, such as longitudinal deposited feather corticosterone during the feather growth period.

Acknowledgments

We would like to acknowledge Emma Hyland, Isabelle Kwon, Jeff Li, Cristian Mastrangelo, and Jacob Maxwell for their help with data collection. Additionally, we would like to thank the staff at the Arkell Research Facility at the University of Guelph for their assistance during the experiment. This project was funded by the Government of Canada through Genome Canada and the Ontario Genomics Institute (OGI-133). This study was part of the project entitled "Application of genomic selection in turkeys for health, welfare, efficiency and production traits" funded by the government of Canada through the Genome Canada Genomic Application Partnership Program and administered by Ontario Genomics (recipients: B.J.W. [Industry] and C.F.B. [Academic]). We would also like to acknowledge NSERC Discovery Grant and Hybrid Turkeys for their financial support. The funders had no role in the design of the study and collection, analysis, and interpretation of data and in writing the manuscript.

Conflict of interest statement

The authors declare that J.M. and B.J.W. were employees at Hybrid Turkeys at the time of the study. All remaining authors declare that they have no known competing financial interests or personal relationships that influence the work reported in this paper.

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