

PRIMARY FEATHER MOLT AND DEVELOPMENT PATTERNS IN FLAMMULATED  
OWLS (*PSILOSCOPS FLAMMEOLUS*) OF THE PIKES PEAK REGION

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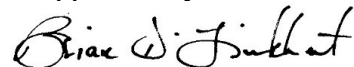
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## ABSTRACT

Molting is a process that involves periodically replacing feathers in all avian taxa. This process is energetically expensive, and for this reason molt has evolved in most birds to avoid significant temporal overlap with other energy-taxing processes, such as mating and migration. Although the molt sequence of flight feathers varies by species and age class, if the pattern of a particular species is understood, it can provide insight into energetic tradeoffs and facilitate conservation efforts. The Flammulated Owl (*Psiloscops flammeolus*) is a small, territorial raptor that breeds in the montane forests of western North America and migrates to Mexico and Central America during the winters. While more is known about the breeding and migration processes, feather molt patterns in the species have not yet been studied. In analyzing nine consecutive years of molt observational data collected from Flammulated Owls in their summer breeding grounds in the Pike National Forest, Colorado, I sought to determine the general timeline and sequence of molt in this population among different sex and breeding classes. Additionally, I quantified growth patterns in hatch year birds to clarify the extent to which migration may exert strong selective pressure on development in this species. My results showed that all individuals exhibit one sequential prebasic molt annually that begins in the late breeding season and continues just prior to fall migration. While this pattern appears the same regardless of sex and breeding status, these factors seem to have an effect on the proportion of individuals in molt at any given time within the molt timeline. I found that over two-thirds of non-breeding males were observed molting their primaries at the time of capture compared to about one-third of both breeding males and females – a pattern I hypothesize to be the result of differences in energy allocation. Furthermore, since migratory behavior can impact aspects like behavior, morphology, and energy allocation – all of which can have strong effects on development – understanding the

molt and development patterns of a species can provide valuable insight into evolutionary differences between migrant and resident populations.

## INTRODUCTION

Among avian taxa, identifying birds goes far beyond simply determining the species; it can also include sexing and aging individuals, among other factors. Identifying the age and sex of a bird is critical in the study of many areas of avian ecology and evolution, such as life history evolution, reproductive ecology, and behavioral ecology. However, this identification process is generally complicated due to the significant variation in size, plumage, and molt sequences that differ with each species and age/sex class (Pyle 1997). Moreover, while many age determination techniques have been developed for the other four vertebrate classes, few techniques have emerged to accurately determine the ages of adult birds (Klomp and Furness 1992).

Comprehending the age structure of any population is a crucial component of life history and is necessary for the future conservation of species. Having the ability to construct a pyramid to depict the age structure of a population provides an indicator to anticipate future population growth or decline. More specifically to avian taxa, prior studies have suggested that consistently monitoring the age structure of territorial pairs in long-lived bird species may have a predictive capacity, and this could serve as an early warning sign for changes in the health of the population (Balbontín et al. 2003; Ferrer et al. 2003). For example, a study conducted on Floreana Island in the Galápagos assessed male age structure in the endangered Medium Tree Finch (*Camarynchus pauper*) and found relatively few fully mature males compared to younger individuals (O'Connor et al. 2010). Since mature males exhibit higher pairing and fledging success compared to their younger counterparts (Kleindorfer 2007; Kleindorfer et al. 2009), the scarcity of the older males has a negative influence on the nesting outcomes and contributes to the

declining population. Therefore, an increase in the proportion of non-breeding or lower fecundity individuals in a population, particularly in species with deferred maturity, may result in decreased density of breeding pairs and overall productivity.

Expanding techniques for determining age structure is also useful for research in reproductive ecology. After hatching year (AHY) males in populations of long-lived avian species, such as raptors, are comprised of territory holders and “floaters,” which are sexually mature individuals that neither defend a territory nor breed (Brown 1969). These individuals have the ability to enter the reproductive population as breeders whenever a breeding area or possible mate becomes available (Penteriani et al. 2005; 2006; 2008). In the case of territorial birds, the potential mate can be the owner of a suitable breeding territory. While floaters themselves are not territory holders, they can put a strain on the territorial individuals – especially breeders – who must spend increased time and energy attempting to expel floaters from territories. This in turn may compromise the ability of territory holders to defend their territories without reducing territory size (Sunde and Bølstad 2004).

One hypothesis regarding the cause for floaters suggests that in avian populations, some individuals that are excluded from territories form a reserve supply to control breeding densities by replacing territorial birds when they die (Howard 1920; Nice 1941). This hypothesis was later expanded upon in a model classifying three levels at which territoriality affects the dispersion patterns of individuals; Level 1 describes sufficiently low density with an abundance of favorable habitats whereas Level 3 describes fully saturated habitats that allow for a surplus of floaters (Brown 1969). Thus, in many studies of bird populations, territorial behavior was shown to regulate the number of territory holders that have the immediate potential for breeding (e.g., Knapton and Krebs 1974; Manuwal 1974; Franklin 1992). In populations where territorial

behavior is common, if a population decline were to occur, it would first be observed as a reduction of the number of floating individuals due to increased recruitment of floaters into the breeding class. Therefore, if the quantity of floaters is substantial, then the number of territory holders would be seemingly stable before a decline is observed. Since many habitats are suffering from increasing levels of deforestation and degradation, the breeding status of birds can likely be used as an indicator of population health. Having the ability to age birds and infer their breeding status is becoming more necessary now than ever before.

Age determination of live birds should be based on combinations of all available characteristics of the individual in order to compare these aspects to the description of age/sex classes of the species. One such method involves collecting morphometric mensural data, such as the ranges of the wing chords, tail lengths, exposed culmens or other bill-length metrics, bill depth, tarsus length, and mass (Pyle 1997). However, while these measurements can provide insight about avian populations, they do not always reveal the exact age of a bird, and sometimes they are only useful in distinguishing between juvenile and adult.

One common means of distinguishing age classes of a wide variety of land birds involves identifying patterns of plumage replacement from one molt cycle to the next. All AHY birds undergo at least one molt annually, although many species molt twice, and a few species even molt three times a year (Payne 1972). This process requires distinguishing primary feathers from the current and previous molts and having knowledge of molt timing (DeLong 2004). Since a bird's plumage always contains feathers that were replaced in its most recent molt as well as feathers retained from earlier plumages, several molts with unique characteristics that show age-specific patterns in the plumage have been identified among North American land birds: the prejuvenal molt generates the juvenal plumage, the preformative molt occurs during a bird's first

fall and produces the adult plumage, and all ensuing molts are prebasic and occur annually throughout the remainder of the bird's lifetime (Pyle 1997; Froelich 2003). The distinguishing features of these various types of molt are what allow birds to be classified as hatch years, second years, and so forth. Some species will even exhibit additional molts in their annual cycle called prealternate molts, although these typically do not display replacement patterns that can be used to distinguish different age classes (Pyle 1997; Howell 2003).

Studies have shown that molt sequences can be examined through at least two key methodologies. One way to estimate the age of primary flight feathers is to assess the amount of porphyrin pigments present when viewed under an ultraviolet light. Porphyrins are characterized by pyrrole rings that incorporate nitrogen and are used as a plumage pigment in 13 orders of birds, including owls (Gill 1995, McGraw 2006). Because porphyrins are easily destroyed by sunlight (UV) exposure, they are most abundant in new feathers (Weidensaul et al. 2011). Therefore, a new feather comes across as much brighter when viewed under a blacklight than does an older feather. Another method of determining molt sequences is by examining feather wear. This term is used to describe the fraying and abrasion that feathers undergo as a result of exposure to solar irradiation as well as through physical abrasion against foliage and branches. Thus, feathers exposed for a longer time period should show more wear than feathers replaced (molted) more recently as a result of longer periods of exposure (Froelich 2003).

While molt always involves periodically replacing old flight feathers with new ones each year across all avian taxa, this process has variations among species and age classes. Some of these variations include a biannual molt, a split molt between seasons, or even molting a few primaries at stopover sites along the migration pathway (Hedenström 2007). Moreover, at least in the case of most birds of prey, once grown, each feather is usually retained for at least a year,

throughout which it will deteriorate (Zuberogoitia et al. 2013). No matter which variation of molt pattern a bird uses, it always has to balance the energetics of the process with other life history demands.

Breeding, molt, and migration are crucial to the continued existence of migratory avian species and, at the same time, are among the most energetically demanding processes in the annual cycle of most birds. For this reason, each process has adapted to avoid significant temporal overlap with the other processes (Kendeigh 1949; Farner 1964). Thus, the duration and extent of molt is restricted by the energy invested in the other two factors (Pietiäinen et al. 1984; Rohwer et al. 2011). With regard to long-distance migrants, having intact wings is crucial in making a successful migration. Consequently, molting of the wing and tail feathers typically occurs with minimal temporal overlap with migration (Berthold 1975).

Because migratory birds rarely molt during migration due to energetic constraints, two major molt patterns exist: post-breeding molt, which occurs while still in the breeding area, and post-migration molt, which occurs on the wintering grounds (Jenni and Winkler 1994). Other research found that as migration distance increases, molt in Sylviid warblers was more likely to occur after fall migration in the wintering grounds (Norman 1997; Hall and Tullberg 2004). Furthermore, populations that breed at higher northern latitudes have a tendency to interrupt their post-breeding molt more frequently than southern populations. Some northerly or late-breeding species, such as the American Redstart (*Setophaga ruticilla*), will even begin migration and stop along the route to molt (Norris et al. 2004). Regardless of the molt strategy employed by avian populations, each has adapted its own way to successfully complete each process while accounting for the energy required.

Energy allocation controls nearly all aspects of a bird's life, and only a certain amount of time and energy can be allotted to the three crucial annual processes exhibited in migratory species. Compared to resident birds that may begin reproduction early in the calendar year and extend the duration of molt, molt in migratory individuals and populations usually begins at a younger age, occurs earlier in the season, and is of shorter duration (Zuberogoitia et al. 2013). In birds of prey, molting requires a greater length of time than in passerines (Newton 2009), so the process typically begins earlier in the season during incubation or early chick rearing. A period of hunger resulting from increased food demand in offspring is associated with a deceleration in the molt process and causes some birds, mostly males, to arrest this process in order to meet the needs of their offspring (Pyle 2005; Zuberogoitia et al. 2009). Furthermore, molting typically starts sooner in individuals that complete the breeding process earlier, have an early nest failure, or are nonbreeding for a particular season, because these birds have more energy available to allocate towards feather replacement (Cieslak and Dul 2006). Thus, earlier molt may serve as an adaptation for migration so that individuals can migrate earlier and be more successful in the subsequent reproductive season. Similarly, studies have found that having larger broods leads to fewer flight feathers being molted (Karell et al. 2013). These processes highlight a critical ecological trade-off; the more time, and therefore energy, birds spend caring for their young, the less time they have for molting. In contrast, if they spend more time molting to replace worn feathers from their wings, breeding may not be possible in the following season (Rohwer et al. 2011).

The timeline of the molt process as related to an individual's breeding status begs the question: *how do individual variations in the breeding and molt timeline of neotropical migratory birds affect the timing of migration?* One study conducted by Stutchbury et al. (2011)



tested whether late nesting and molt of Wood Thrushes (*Hylocichla mustelina*) imposed carry-over effects on the timing of fall migration and arrival at the wintering grounds. They found that late nesting individuals had a delayed molt and departed the breeding grounds later. However, despite this initial delay in migration, these later-molting birds did not seem to arrive any later to their wintering grounds than earlier breeders, because stopover duration was highly variable later in migration. Therefore, while there may be strong carry-over effects from the wintering grounds to spring migration, a significant reproductive effort later in the season does not necessarily inflict time restrictions that postpone winter habitat acquisition.

Understanding the molt sequence of an avian species can have important conservation implications. Previous research has demonstrated that molt may be used as a proxy for assessing territory quality (Espie et al. 1996), which is inherently difficult to measure. Having another method beyond the usual indicators of territory quality (e.g., occupancy, breeding success, productivity) can be of value. For example, one study illustrated that male Merlins (*Falco columbarius*) that occupied high quality territories had higher molt scores than individuals in lower quality territories (Espie et al. 1996). This suggests that having plentiful food to fuel the obligatory annual processes proves to be advantageous in that it enables individuals to molt at a faster rate or start earlier than their equivalents who do not have the same access to these resources. Not only can molt serve as a potential indicator of territory quality, but it can also indicate other life history stages that may not be easily quantifiable. For instance, one investigation demonstrated a delayed molt onset in European Storm Petrels (*Hydrobates pelagicus*) with irregular weather events (Zuberogoitia et al. 2016). Other studies examined various environmental effects and illustrated the impact that disturbance can have on the life history of bird species as interpreted through molt patterns (e.g., Barshep et al. 2013). In the face

of a changing climate, better understanding how anthropogenic effects influence aspects of avian lives is critical to ensuring their futures.

One neotropical migrant that has to manage ecological trade-offs is the Flammulated Owl (*Psiloscops flammeolus*). This insectivorous nocturnal raptor is territorial and breeds in the montane Ponderosa Pine ecosystems of western North America while migrating to Mexico and Central America for the winter (Linkhart et al. 2016). While more is known about the breeding and migratory processes of this species, feather molt sequences in the species have not yet been extensively studied. To the extent of current knowledge, Flammulated Owls only exhibit one (prebasic) molt annually; no prealternate molts have been documented in the wintering grounds of the species (Pyle 1997; Howell 2003; Linkhart and McCallum 2020). Furthermore, once mature, Flammulated Owls are suspected have either a complete or nearly complete Definitive Prebasic molt that occurs during the summer and fall prior to migration with primaries usually molting from July to September. Primaries seem to be molted from the innermost to outermost feather (P1-P10), usually symmetrically on both wings with no more than three primaries in molt simultaneously (Dawson 2015; Linkhart and McCallum 2020; Linkhart unpubl. data). In sum, further research is necessary to confirm any suspected molt patterns of Flammulated Owls and make any distinctions between age classes.

In this study, I analyzed nine consecutive years' worth (2011-2019) of Flammulated Owl molt observations collected to further investigate the molt pattern of this species. These data included observations based on blacklight and/or primary wear scores and were taken by summer research crews during the months of May through September in central Colorado. Furthermore, the molt pattern in some well-documented species, like the Northern Saw-whet Owl, can be utilized to age individuals to a certain extent. On the other hand, the molt patterns of other small,

migratory Strigidae, such as the Burrowing Owl (*Athene cunicularia*), Whiskered Screech Owl (*Megascops trichopsis*), and Elf Owl (*Micrathene whitneyi*), have been identified, but due to their near-complete annual molts, accurate aging is not possible by means of this technique (Weidensaul 2011; Slack 1992; Pyle 1997). Thus, since the general molt pattern of Flammulated Owls is not well understood, I aimed to gather more insight into this pattern and determine if assessing age in this manner is possible with the current data.

Moreover, I examined the development of hatch year (HY) Flammulated Owls throughout the nestling phase to investigate energy tradeoffs that may be revealed by primary growth rate in these individuals. By understanding the growth rate of flight feathers in HY birds, we can gain a better understanding of tradeoffs in molt for long-distance migrants (Ricklefs 1968). I concentrated on the primary feather growth rate of these individuals, especially those whose measurements were recorded on a daily basis during the nestling period, and I modeled this growth rate to better comprehend the feather development of all life stages of the Flammulated Owl. Because Flammulated Owl females begin incubation following when they lay the second-to-last egg in the clutch (clutch size = 2-3), asynchronous hatching occurs (Reynolds and Linkhart 1987; Linkhart unpubl. data). Therefore, I differentiated between the older and youngest siblings (runts) of the monitored broods to analyze potential variations in primary growth rate while investigating how energy allocation may affect growth and development from the first year.

In sum, I sought to better understand three primary questions. (1) Is primary molt pattern a reliable indicator of sex and age class in Flammulated Owls? I hypothesized that the Flammulated Owl molt pattern would be similar to other small, migratory owls. (2) How does the Flammulated Owl molt pattern differ across sex and breeding status? With energetics

controlling an organism's life history, I predicted that the molt process would commence in the late nestling/early fledgling period and terminate prior to fall migration. I also hypothesized that breeders would have more energy constraints and would molt fewer primary feathers than non-breeders. (3) What insights regarding energy tradeoffs are revealed by growth rate in primary feathers of HY birds? I predicted that the primary growth rate of HY owls could provide further insight into energetic tradeoffs especially with regard to older siblings versus runts of broods.

## **MATERIALS AND METHODS**

### *Study Area & Forest Composition*

Molt data were collected annually each summer from 2011-2019 across four study sites: Hotel Gulch, Missouri Gulch, Hayman Fire, and Trout Creek, located in or near the Manitou Experimental Forest on the Pike National Forest in central Colorado (*Fig. 1*). The study sites were about 500 ha each and were composed of (1) mixed conifer forests with ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) on ridgetops and south- and west-facing slopes; (2) quaking aspen (*Populus tremuloides*) in moist lower slopes and drainage bottoms; (3) quaking aspen mixed with blue spruce (*Picea pungens*) in moist lower slopes and drainage bottoms; and (4) Douglas-fir mixed with blue spruce on north-facing slopes of higher elevations. Elevation ranged from approximately 2,550 to 2,855 m (Linkhart and Reynolds 2007). Each year, an average of three to six territories were occupied by breeding pairs, while three to seven territories were occupied by unpaired males (Linkhart and Reynolds 1997). The number of defined territories in each study area ranged from 12-18.

### *Nest Discovery and Owl Capture*

Other owl researchers previously defined territory boundaries of male Flammulated Owls in each study area using spot-mapping and radiotelemetry (see Linkhart et al. 1998). As Flammulated

Owls are secondary cavity nesters, other researchers and I located their nests each summer by examining the contents of cavities in all previously enumerated cavity trees using cameras fixed on the ends of extendable Hastings poles. The process of nest finding started at the beginning of incubation in late May and continued until the young fledged in mid- to late-July. We also determined some nest locations at night by observing common nesting behaviors, such as prey deliveries between males and females and listening for courtship and nesting vocalizations (Linkhart and Reynolds 2007).

We captured and banded AHY birds at nests or in mist nets erected near the periphery of territories using playbacks of territorial song (also known as lure nets). Since sexual dimorphism in Flammulated Owls is not very pronounced, there were several ways on which we behaviorally distinguished males and females. First, the timing of nest activities was a big clue; the female would stay in the nest cavity throughout the incubation and post-hatching periods until the young were homeothermic, and during this sensitive period, the male would be the only one delivering prey to the nest (Reynolds and Linkhart 1987). Second, the prominent male territorial behaviors also served as obvious indicators of sex; territorial males would sing throughout their home ranges and would sometimes chase out intruders (Linkhart 1984; Linkhart et al. 1998; Reynolds and Linkhart 1990). Lastly, males and females have an array of different vocalizations, so we could distinguish them based off of their sounds (Linkhart and McCallum 2020).

In order to band and measure young birds, we waited until they had grown enough plumage to be homeothermic, typically 12-13 days after hatching, then climbed the nest tree using a ladder or tree hooks to reach the cavity and manually extract the nestlings. We mostly handled nestlings during the daytime hours to minimize the impact at night when the adults are most active, and we placed all nestlings back in the cavity after we finished processing. While

we did most HY processing during the day, sometimes we banded and measured the young upon fledging the nest – especially when the nest cavities were inaccessible for nestling extraction.

### *Primary Molt Sequence*

Upon capturing AHY Flammulated Owls at either their nest sites or in lure nets, we used an ultraviolet light examination as one method of assessing the primary feather molt pattern (*Fig. 2*) (as described in Weidensaul et al. 2011). We rated feather fluorescence on a scale of zero to three where zero reflected the oldest feathers showing the dullest pink color (least amount of Porphyrin) and three reflected the newest feathers with the brightest pink color (greatest amount of Porphyrin). We recorded new feathers that were growing in as “in molt.”

The other technique we used to assess the Flammulated Owl feather molt pattern was recording primary wear observations upon capture (*Fig. 3*). Primary wear describes the degree of fraying and abrasions in primary feathers due to exposure (Froehlich 2003). Since wear can be used to help identify molt limits among feather generations, we rated wear on a scale of zero to three where zero reflected the newest feathers with no visible wear and three reflected the oldest, very worn feathers.

### *Molt Patterns of Known Age Birds*

Furthermore, I sought to determine if identifying patterns based on age class was possible with the current data. From 2011-2019, we recorded 553 observations on patterns of molt based off of ultraviolet light and/or primary wear assessments. These observations were made up of 371 unique individual owls. Among these 553 observations, 91 were of known age birds, although, the majority of these individuals were HY individuals (identified by the presence of juvenal plumage) captured in late August or September prior to their first fall migration. Only 16 observations made up adult owls of the following age classes: 7 second year owls, 2 third year

owls, 2 fourth year owls, 3 fifth year owls, and 2 sixth year owls. Individuals that made up these 16 observations were all previously banded during their hatch year and recaptured in one of the study sites in subsequent years. For the 462 observations of unknown age birds, I estimated age based on banding year. Because Flammulated Owls are territorial, it was common to recapture breeding individuals in the same areas for many consecutive years which helped to give a sense of their age. For instance, an un-banded AHY individual must be at least in its second year, while a bird first banded in 2015 as an AHY and recaptured in 2018 must be at least in its fifth year. Finally, I sorted the known age bird data by year while looking for potential similarities in molt pattern among individuals of the same age and tried to compare this with birds of unknown age.

#### *Molt Patterns Across Sex and Breeding Classes*

In addition to examining potential differences in Flammulated Owl molt pattern among age class, I analyzed the data for possible effects of sex and breeding status on molting. To sex each bird, we recorded the presumed sex while in the field and later confirmed it with analysis of individual blood samples. On the other hand, breeding class was not always as easy to quantify as sex. The only definitive way to distinguish an individual's breeding status was only applicable to individuals of whose nests and/or mates were also discovered. While the breeding status of un-banded birds caught in lure nets is often unknown, we presumed birds to be male floaters if they were non-territorial (i.e., they flew into the vicinity of the capture net without vocalizing) and had a heavier mass than breeding males that was not quite as heavy as breeding females (mean mass of breeding males =  $53.4 \pm 3.35$  g; breeding females =  $63.1 \pm 7.49$  g) (Reynolds and Linkhart 1987; Linkhart unpubl. data). While floaters are also suspected to be younger individuals who have not yet established their own territory, the exact age that a male becomes a breeder is unknown and likely depends on environmental conditions and other population

demographics. Thus, I was able to distinguish male floaters from breeders based on behaviors recorded in past field notes.

Among the Flammulated Owls primary feather observations, the data were comprised of the following 375 observations: 273 breeding males, 71 breeding females, and 31 male floaters. In addition, 104 observations consisted of birds whose breeding status was ambiguous, and 74 observations accounted for HY birds. I compared molt patterns among male and female breeders and male floaters using pivot tables within my data spreadsheet to examine the molt pattern exhibited within these demographic groups. Finally, I used Minitab18 (<https://www.minitab.com/en-us/>) to run an ANOVA followed by a Tukey-Kramer test to make pairwise comparisons among molt differences between breeding males, breeding females, and floater males.

#### *Hatch Year Growth Parameters*

We quantified nestling growth in one to three broods annually from 2003 to 2019. Throughout these 17 years, we monitored a total of 83 owlets across 35 nests by visiting the nest cavities almost daily via an extendable ladder. The average duration from hatching to fledging in Flammulated Owls is  $23 \pm 1.1$  nights (Reynolds and Linkhart 1987), and all measurements were collected until fledging occurred. Since egg clutches hatch asynchronously, the youngest owlet in each brood is typically 3-5 days younger than its 1-2 siblings (mean clutch/brood size =  $2.5 \pm 0.1$  eggs/owlets) (Linkhart and Reynolds 1987; Linkhart et al. 2007). Predictably, brood members also often fledge asynchronously so that the brood is separated into two groups with one or more days between the owlets fledging the nest (Linkhart and Reynolds 1987).

I quantified primary growth by means of frequent remige measurements in the nestlings. We removed all owlets once remiges began protruding from the shafts, typically starting around



the seventh or eighth day, we measured the length of the fifth and sixth left primary feathers to the nearest millimeter. We accomplished this by positioning a small ruler at the base of each feather and flattening it to record the length. Prior to fledging, we also banded the owlets and collected blood samples to be used for sexing and genetic analysis. Until the nestlings were grown enough to band, each owlet was marked on the head with a different colored permanent marker for easy identification.

### *Data Analysis*

If exact hatching date was unknown, I extrapolated based off field observations to infer the rough age of each owlet upon its first measurement and all subsequent measurements. Within each brood of three, I also recorded which of the nestlings was the runt in order to investigate potential impacts of hatching order on primary growth rate. I modeled the nestling growth rate based off of 80 individuals, 16 of which were runts. Furthermore, I calculated the mean daily P5 growth rate and the mean P5 length at fledging for each group in order to quantify possible differences in growth rate. Finally, I ran a two-sample t-test to determine if there was a significant difference in P5 length at fledging between the older siblings and runts.

## **RESULTS**

### *Primary Molt Sequence*

Based on observations of 553 AHY owls, of which 122 had at least one primary in molt, I found that primary molt began later in the breeding season (usually late June/early July) and continued just prior to fall migration (*Fig. 4*). I assumed that any instance of a primary found to be missing or growing in on either or both wings was in molt, although the majority of molt observations were symmetrical. While all observations, regardless of whether or not molting was noted, took place between the months of May and September, the owls were only observed to be molting

between late June and September. However, the majority of the total observations (66%) were in June and July due to the schedule of the research crews. 5% and 22% of observations took place in May and September, respectively. Less than 8% of observations occurred in August, and nearly all of them were on or after August 18<sup>th</sup>. I found a total of 295 left primary feathers observed to be in molt, and they were broken up as follows: 31 in June (10%), 167 in July (57%), 37 in August (13%), and 60 in September (20%). No primaries were observed to be molting in May or in early- to mid-June (prior to June 21). Of the 10 primaries on each wing in Flammulated Owls, when they were molting, they molted an average of 2.38 primaries simultaneously (range = 1-6).

#### *Primary Molt Sequence Timeline*

I found that AHY owls seemed to exhibit a sequential molt pattern in which they began by molting their inner-most primaries first then molted their outer-most primaries later in the season prior to fall migration. This finding was exhibited by the primary molt observation data I analyzed that indicated the following: of the 39 P1 molt observations, 8 were in June and 41 were in July; of the 64 P2 observations, 16 were in June, 47 were in July, and 1 was in August; of the 49 P3 observations, 7 were in June, 41 were in July, and 1 was in August; of the 26 P4 observations, 25 were in July and 1 was in August; of the 17 P5 observations, 15 were in July and 2 were in August; of the 8 P6 observations, 7 were in July and 1 was in August; of the 8 P7 observations, 1 was in July, 5 were in August, and 2 were in September; of the 22 P8 observations, 9 were in August and 13 were in September; of the 30 P9 observations, 9 were in August and 21 were in September; and of the 32 P10 observations, 8 were in August and 24 were in September (*Fig. 5*). In addition to these molt observations, my findings were strengthened by the molt scores that often indicated when feathers were newly grown based off of the primary

wear and level of brightness under a UV light. For instance, most birds showed lower molt scores in June, and these scores gradually increased until all primaries were molted in September. Additionally, the outer primaries tended to experience more exposure than the inner primaries, which led to fewer Porphyrins and more physical wear upon examination following spring migration. On the other hand, it is significant to note that the inner primaries typically experienced less exposure and therefore had more Porphyrins and less physical wear. Thus, an observation in early June often revealed moderate blacklight and wear scores (ratings about 1.5-2 for blacklight and 0.5-1 for wear) for the inner primaries that progressively showed fewer Porphyrins and more wear through the middle and outer primaries (ratings up to 0-1 for blacklight and 2-3 for wear). On the contrary, an observation in September usually revealed moderate to high Porphyrins and little wear (ratings about 2-3 for blacklight and 0-0.5 for wear) for all primaries except the outer primaries that were in molt or about to molt (P8, P9, P10). Overall, the molt scores showed a wave-like pattern as more primaries were molted in chronological order over the course of three months on the summer breeding grounds.

#### *Molt Patterns of Known Age Birds*

The AHY known age bird data was relatively sparse with only 7 second year owls, 2 third year owls, 2 fourth year owls, 3 fifth year owls, and 2 sixth year owls. Of the 16 known age individuals, only eight of them were observed to be molting at least one primary feather at the time of observation, and no age-based molt pattern was apparent (*Fig. 6*). Furthermore the only ages that contained a wider range of observation distributions (from at least July and September) were the second- and third year owls, and a chi-square test of goodness-of-fit test indicated that there was not a significant difference in primaries molted between these two groups [ $\chi^2(1, N = 18) = 0.112, p = 0.738$ ]. Taken together, these results suggest that with the current data, molt

pattern is not a reliable indicator of age in Flammulated Owls. However, given this sample size limitation and the fact that the observations stemmed from a wide range of dates from May to September, I could not definitively pinpoint a common pattern for any given age. Based on the primary wear/UV light scores and observations of molt, I suspected that the primary molt sequence was the same for every age class, however, the timeline may have varied slightly among individuals. Among each of these age classes, primary molt appeared to begin in late June or early July and terminate in September. While the sample sizes were too small to draw any conclusions, the data ostensibly showed that second year, third year, and fifth year owls molt all ten primaries in one season. Although data are lacking for observations of P5-P7 in molt, the molt scores from late August and September for these age classes indicated high levels of Porphyrins and little wear on these feathers implying that they were recently molted as well. Pre-migration fall observations were absent for fourth- and sixth year owls, therefore no assumptions about age-based molt patterns could be made.

#### *Molt Patterns Across Sex and Breeding Classes*

In order to analyze for possible effects that sex and breeding status may have on molting, I looked at the differences between 152 total observations of breeding males, 71 of breeding females, and 31 of floater males. I only incorporated observations taken on or after June 21<sup>st</sup> as this is the earliest date in which Flammulated Owls have been observed to be beginning their annual molt process. A one-way between subjects ANOVA indicated that there was a significant effect of sex and breeding status on the proportion of individuals in molt [ $F(2, 238) = 5.94, p = 0.003$ ]. Post hoc comparisons using the Tukey HSD test indicated that the mean proportion of male floaters observed to be in molt ( $M = 0.772, SD = 0.461$ ) was significantly different than the male breeders ( $M = 0.335, SD = 0.474$ ) as well as the female breeders ( $M = 0.310, SD = 0.466$ ).

However, the male and female breeders did not significantly differ from each other in this regard. Taken together, these results suggest that breeding status has more of an effect on molt, with non-breeders more likely to be observed molting than breeders, whereas sex does not appear to have any significant impact (*Fig. 7*).

Based off of 53 molt observations in breeding male Flammulated Owls, I found the general timing of primary feather molt to be similar to the molt pattern exhibited across all AHY observations of the species. Primary feather molt peaked in July when 60.17% of owls examined were observed to be in molt (*Fig. 8*). Like the overall molt pattern, breeding male Flammulated Owls seemed to begin the process later in the breeding season (late June-early July) and continued until just prior to fall migration in September. Furthermore, the June molt observations are lower because molt did not begin until later in the month with the earliest observations beginning on June 21<sup>st</sup>. Significant data were lacking for August and September in which I presume much more primary molt to have occurred than what the data portrayed, however, more data collection is needed to confirm this. In terms of timing of the primary molt process, the pattern exhibited in breeding males also seemed to be in line with the general sequential pattern of molt discussed earlier; Most P1, P2, and P3 feathers molted in late June and July, P4, P5, and P6 molted in July and early August (inferred with some data missing for August), and P7, P8, P9, and P10 molted in late August and September (*Fig. 9*).

According to 22 observations of primary molt in breeding female Flammulated Owls, they too began molting later in the breeding season and continued throughout the rest of their time on the breeding grounds. While data are lacking from June because this is a very sensitive time in the breeding process when the females must incubate eggs and remain with young nestlings until they are homeothermic, it appeared that they started to molt in early July – and

possibly late June for some individuals – as inferred by the earliest recorded molt scores in early July. The earliest record of a female Flammulated Owl in molt was on July 7<sup>th</sup>, and she was molting her first primaries. The earliest observations for P2 and P3 in molt were on July 9<sup>th</sup> and 10<sup>th</sup>, respectively. The data showed that nearly all of the female primary molt observations occurred in July, however, this was also when nearly all of the field work was done (*Fig. 10*). The limited data available from August and September made a strong case that female Flammulated Owls did continue to molt during this time as corroborated by the molt scores. Thus, in order to confirm any potential findings, further data must be collected. In terms of the primary molt timeline, the data revealed that P1-P5 molt peaked in July and P8-10 molt peaked in September (*Fig. 11*). By extrapolating the molt scores in September, I inferred that August is a peak month for P5-P8 molt given the lack of data for these feathers. This finding also helped to show that the molt pattern was sequential for breeding Flammulated Owl females and males.

The non-breeding and non-territorial, or floater, male Flammulated Owls ostensibly exhibited the same molt pattern as the male breeders. Despite not having a nest to tend to, the floater males still began molting in late June, with the earliest recorded molt observation also being June 21<sup>st</sup>, and likely continued molting until fall migration. However, more data are needed to confirm the extent of the molt timeline for this group. The main distinction between the molt pattern in the male breeders versus the floater was likely only the difference in quantity of individuals observed in molt. A sample size comprised of 31 total observations and 18 molt observations in floaters revealed that primary molt reached a climax in July with 72.73% of observations recorded during this time (*Fig. 12*). It is important to note that the one September observation was presumed to be a floater because he was previously banded as a known age, seemingly non-territorial individual. In terms of the overall timeline of the individual primary

molt sequence, like the breeders, it was also sequential beginning with P1 in late June/early July and finishing with P8, P9, and P10 in September prior to migration. The data revealed that P1-6 molt peaked in July and P8-10 molt peaked in September, however, data from August and September are needed to confirm this finding (*Fig. 13*). Overall, the molt patterns exhibited among the three sex/breeding classes indicate that the pattern is likely similar for all AHY individuals.

#### *Nestling Primary Growth and Development*

I analyzed the daily growth rate of the left fifth primary throughout the nestling period from a total of 80 owlets (64 older siblings and 16 runts) representing 35 broods between 2003 and 2019. These measurements began when remiges first emerged from the shafts around eight days after hatching and continued daily until nestlings fledged, typically 22 to 24 days after hatching. The average fifth primary growth rate during the nestling period following emergence from the shafts, based off of all nestling daily observation data, was 3.74 mm per day (SE = 0.25). The average fifth primary length at time of fledging was between 63 and 67 mm depending on the age at fledging. However, growth rates differed between the older siblings and the runts with the runts having an average fifth primary growth rate of 3.32 mm per day (SE = 0.44) compared to 3.90 mm per day (SE = 0.21) in the older siblings. Furthermore, based off of an independent samples t-test to compare the fifth primary length at fledging, I found that there was a significant difference for older siblings ( $M = 65.316$ ,  $SD = 4.988$ ) compared to runts ( $M = 57.333$ ,  $SD = 6.745$ );  $t(45) = 4.023$ ,  $p = 0.0001$  (*Fig. 14*). These results suggest that hatching order in a brood did have an impact on fifth primary growth rate during the nestling period. Specifically, the runts had a slower primary growth rate than their older counterparts.

## DISCUSSION

While the timeline and sequence of molt in Flammulated Owls appeared to be consistent across sex and breeding class, I did find a significant difference in the proportion of floater males in molt compared to male and female breeders. This finding is in line with my hypothesis that more non-breeders should be molting primary feathers because they have more energy to allocate to their physical condition by not having to care for young. This prediction may be related to the concept of suspended molt described in some species, such as the European Sparrowhawk (Zuberogoitia et al. 2009). The 2009 study by Zuberogoitia et al. found that during the breeding season when the chicks were fledging, 18.75% of breeding females and 55.5% of breeding males suspended their molt, and this period coincided with the peak food demand by nestlings. Molt is usually resumed after these halts; however, current Flammulated Owl molt data is comparatively sparse for previously captured breeders after their young fledge, and re-capturing the same floaters at later points in the season has proved to be a challenge. Furthermore, distinguishing between male breeders and floaters after young have fledged can also be difficult, because after the breeding season ends and territory boundaries dissolve, distinguishing whether an un-banded male is a breeder or a floater becomes nearly impossible. Therefore, despite the logistical challenges, more data are needed for individuals of all sex and breeding classes – particularly for late July and August to further delve into how these factors affect the proportion of individuals molting their primaries.

Moreover, this lack of data for August, particularly early- to mid-August, almost certainly affected my results. Therefore, based off of September observations revealing newly molted feathers and previous studies of similar species, contrary to my results, I believe that August is an important month for primary molt in Flammulated Owls. With more data collected



during this time in the future, I anticipate that a much higher proportion of AHY Flammulated Owls will be molting their primaries since the birds no longer have nests to attend to and they are preparing for the physical demands of fall migration. As body temperatures and metabolic rates of molting birds have suggested that molt increases energy demands (Newton 1968), post-breeding individuals should have more energy to distribute towards replacing their primary feathers than breeding individuals.

Despite the energetic toll that molt takes, molting does not appear to physiologically create a huge strain on the energy resources of birds. In fact, studies have shown that birds do not lose body mass during this time, but rather, their body weight increases right before or during the time in which the greatest number of feathers are growing in (King et al. 1965; Holmes 1966). This gain is related to the growth of feather papillae due to increased lean dry weight, fat, and water content of the growing feathers and blood volume (King et al. 1965; Newton 1968; Evans 1969). Stored body fat also increases slightly suggesting that molt does not strain the energy resources in birds (Payne 1969; Payne and Landolt 1970). Thus, the temporal separation of breeding and molting can prove to be an adaptive strategy in the annual cycle.

Furthermore, temporal constraints on molting and breeding should be reduced in non-migratory populations. Previous research has shown that molt-breeding overlap is more likely to occur in non-migratory populations than in migratory populations (Rohwer et al. 2009). When a molt-breeding overlap occurs, birds exhibit a prolonged, low intensity molt growing few primaries at once to reduce energetic demands thus allowing both processes to occur simultaneously (Foster 1975). Additionally, these individuals tend to have a slightly smaller clutch size compared to those that do not overlap the two activities. Larger birds, especially migratory individuals, that complete their molt in one season must speed up the process by either

increasing the growth rates of their primaries or by growing more feathers simultaneously. Thus, since resident species are more likely to spread out the molt process over a longer time, the daily increase in energy need for molt is relatively less than that of the migratory individuals (Payne 1972; Rohwer et al. 2009). Therefore, the duration of primary molt has been shown to be inversely related to the intensity of molt, and all birds must make an ecological trade-off with regard to their physical condition and the time they have to put towards molting. Of the 10 primaries on each wing in Flammulated Owls, they molted an average of 2.38 primaries simultaneously. While there was clearly some overlap, they molted over a longer period of time of almost three months. Molt patterns are likely different in resident Flammulated Owl populations in Mexico and Central America who do not need to allocate energy towards migrating twice a year, but data are needed to confirm this hypothesis. Further research is needed to investigate how differences in energy allocation needs distinguish the life history strategies of migratory versus resident populations of Flammulated Owls.

There are other components besides migratory status that contribute to the energetics of Flammulated Owls as well that may have an impact on primary molt. Just like previous studies have shown that breeding individuals of some avian species may start the molt process slightly later than non-breeders and have higher instances of suspended molt (Thomsen 1971; Zuberogoitia et al. 2009), factors like brood size and nest failure may have indirect impacts on molt. Research has found that the number of molted remiges decreases as brood size increases (Pietiäinen et al. 1984; Karell et al 2013). Similarly to floaters who do not breed in a given season, breeders whose nests fail early also tend to have a more advanced molt (Cieslak and Dul 2006). Future research should analyze the relationship between these factors and molt in Flammulated Owls to provide further insight into these evolutionary tradeoffs.

My results also showed that the molt process of Flammulated Owls commenced near the end of the breeding season, or about the time the young fledged, and terminated just prior to fall migration. This timeline was the same regardless of sex and breeding status of the individual. This finding shows that with the current data, there are no indications that sex or breeding status impacts the timing of onset or termination of primary molt in Flammulated Owls. The pattern based on my results confirmed that Flammulated Owls complete their Definitive Prebasic molt on or near breeding grounds between the months of June and September. The primary molt sequence and timeline of Flammulated Owls seemed similar to some other Strigidae with migratory populations, such as the Elf Owl and Burrowing Owl, who begin molting primary feathers in late June/early July and molt distally from the inner (P1) to outer (P10) primary (Poulin et al. 2020; Ligon 1968). Moreover, previous research on Burrowing Owls has shown that non-breeding individuals can begin the molt process in June whereas breeding individuals begin in mid-July (Thomsen 1971). This finding may hold true for Flammulated Owls as well, however more data are needed, especially for non-breeders, to confirm this.

With the current extent of known age bird observation data, I could not come to any definite conclusions about whether or not an age-based molt pattern is exhibited in Flammulated Owls. More observations are needed for all years across a range of dates (June-September) in order to draw conclusions. However, given the feathers molted in second year, third year, and fifth year owls, I suspect that all ten primaries are molted annually in each individual. While significant molt observation data are lacking for P5-7 in these three age classes, I suspect that they were molted in August based off the September molt scores for these seemingly new feathers. The only observations for fourth year owls come from one male breeder whose primaries were observed on two separate occasions: once in the early nestling period and once in

the late nestling period. Upon the first observation, he was molting his first primary, whereas upon the second observation three weeks later, he was molting his third primary and had seemingly just finished molting his second primary based off of its molt score. Whether or not he continued to sequentially molt his remaining primaries following this last observation remains unknown. Furthermore, the only observations for sixth year owls come from one male breeder whose primaries were observed on two separate occasions: once in the early nestling period and once in the mid-nestling period. While no primaries were observed to be in molt for this individual, I believe he would have started to molt not too long after the second observation was taken.

Research on other owl species shows that knowing the secondary molt pattern – in addition to the primary molt pattern of a species – can aid in identifying an age-based molt pattern. Observations suggest that secondary molt of Flammulated Owls begins around the time P5 is dropped (about early- to mid-August) and likely commences with the innermost secondary (S12) and progresses outward (Linkhart and Reynolds 1987). While outer secondaries likely begin molting not too long after, starting with S1 and progressing inwards, more observational data are needed to confirm this. Northern Saw-whet Owls exhibit molting foci at S1, S12, and S5 (Evans and Rosenfield 1987), and Flammulated Owls likely exhibit a similar pattern (Bloom 1983). Furthermore, Northern Saw-whet Owls have been shown to molt their remiges in blocks so that one can reliably tell the age of an individual up to its third year based on how many new, old, and very old blocks are exhibited (Evans and Rosenfield 1987; Pyle 1997). For instance, a second-year bird shows a pattern which consists of a solid block of old feathers (both primaries and secondaries) in the middle of both wings. These blocks may or may not have one skip, or new feather, within the block of old feathers on one or both wings (Mackentley et al. 2019).

Thus, since other Strigidae have age-distinguishable molt patterns that are dependent on examining the condition of other remiges, future observations of feather molt in Flammulated Owls should note the conditions of secondaries in addition to primaries. Only when these data are sufficient will we be able to establish if an observational age determination is possible for individuals.

With regard to primary growth and development of nestlings, I found that the average growth rate of the fifth primary during the nestling period was 3.74 mm per day, with the older siblings having a faster growth rate of 3.90 mm per day compared with the runts whose growth rate averaged 3.32 mm per day. Since later-hatched young are innately smaller than their older siblings, they are competitively disadvantaged from the start. Previous research has found that differences in competitive ability can determine the food distribution among siblings (Gottlander 1987; Parker et al. 1989). The most competitive nestlings tend to position themselves closest to the feeding parent, so naturally, parents typically feed these young first (Greig-Smith 1985). Thus, the late-hatched young often become runts since their initial size differences remain constant or increase throughout the nestling period (O'Connor 1975). Among species in which the fledging spread is roughly equal to the hatching spread, such as the European Bee-eater or the Flammulated Owl, there is less selection for simultaneous fledging than in species that exhibit asynchronous hatching and synchronous fledging where having better developed wings at fledging is crucial to survival (Lessells and Avery 1989; Linkhart and McCallum 2020; Nilsson and Svensson 1996). European Bee-eaters also have a significantly reduced wing growth rate in runts compared to their older siblings, so my results suggest that this pattern holds true for Flammulated Owls as well. Because the difference in competitive ability between the youngest and older siblings of a brood often becomes very large, the runts do not always acquire enough

energy and will subsequently die (Ricklefs 1965; Stouffer & Power 1991). In my data, the sample size for older siblings was far greater than that of the runts, partially due to this reason, as well as because the clutch size for Flammulated Owls is two or three owlets, so many broods lacked runts. Because of this discrepancy, more primary growth observations are needed for the runts to confirm my findings.

Going forward, researchers should continue to expand the current dataset of HY individuals re-captured post-fledging. I initially attempted to quantify the remige growth rate from the time of fledging until migration departure using the von Bertalanffy model (Ricklefs 1967). However, re-capture data for HY birds are quite sparse with just five individuals who were each captured once after fledging. In order to accurately fit a logistic growth curve to model the primary development of HY Flammulated Owls, we must have enough data to serve as a baseline, and not enough data have been published on similar studies in order to extrapolate this model. Moreover, as my results provide a strong basis that the growth rate of runts is slower than the growth rate of the older siblings during the nestling stage, we do not know how long this decelerated growth rate continues into the fledgling stage, nor do we know when the runts might catch up to their siblings in terms of growth. Thus, once the sample size of HY re-captures – ideally based off of both runts and older siblings – is sufficient, then estimating the age of any HY based off of its fifth primary length may be possible.

Gaining a comprehension of a species' molt pattern can have important implications for conservation. While further research is needed in this area, Espie et al. (1996) found a correlation between higher territory quality and higher molt scores in male Merlins. If this is the case in other avian species, molt may be used as a tool to further investigate the population ecology of Flammulated Owls. Future research should compare territory quality over time (as measured by

occupancy of both breeders and non-breeders) and examine the molt scores of individuals in presumably high quality compared to low quality territories. Additionally, as the onset and duration of molt may serve as an indicator of disturbance events (Barshep et al. 2013), future Flammulated Owl work should focus on comparing events like drought, fire, and abnormal temperatures to gain further insight into the impacts these events may have on the population. Finally, a major limitation of remigial observations across all avian taxa is that it is highly subjective. In order to address this issue and add to the current knowledge of remigial molt in Flammulated Owls, I recommend increasing the use of high-resolution photography to serve as an additional resource to accompany the recorded molt scores (Zuberogitia et al. 2017). Especially in a species like the Flammulated Owl that is not easy to trap, adding high-resolution photos of the wing under both regular and UV light would provide a clear visual representation of remigial conditions and would thus minimize discrepancies in the molt scores as recorded by different researchers. Lastly, improving the documentation of remigial molt in Flammulated Owls would better facilitate the sharing of information so that researchers can examine differences across populations and continue investigating knowledge gaps that remain.

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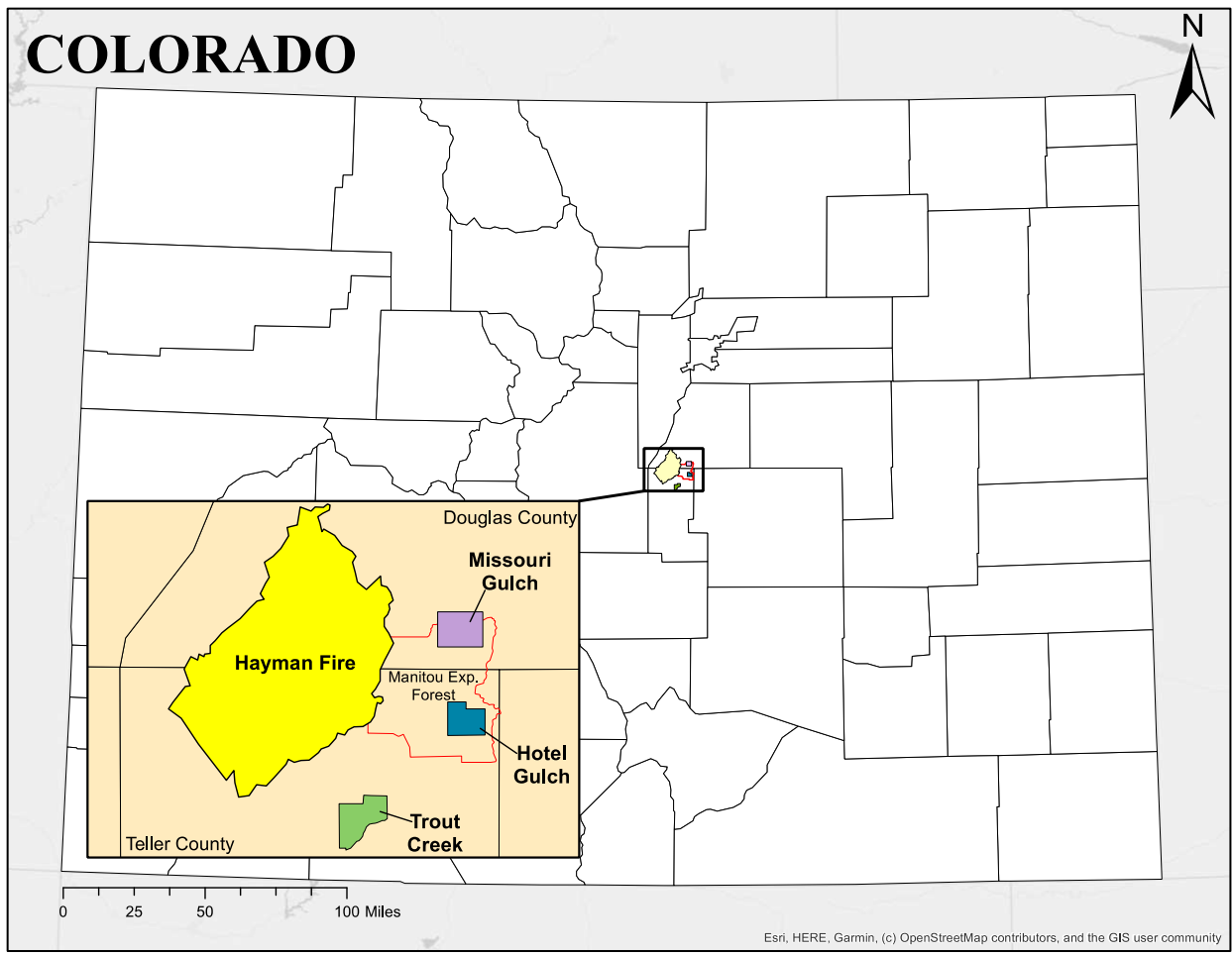
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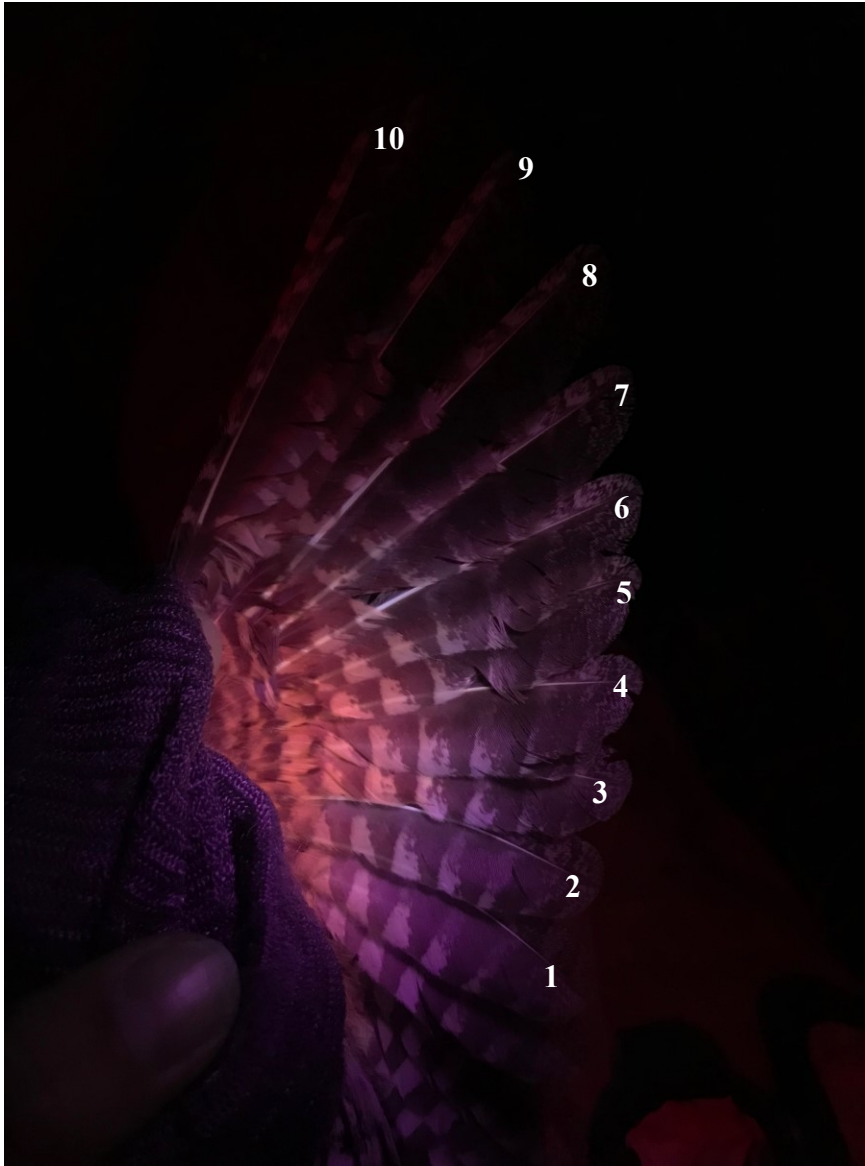
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**Figure 1.** Hotel Gulch, Missouri Gulch, Hayman Fire, and Trout Creek study areas are located in and near the Manitou Experimental Forest of Pike National Forest in Douglas and Teller Counties, Colorado. Each study area is made of Flammulated Owl territories with each territory typically occupied by one breeding pair. The extent of the Manitou Experimental Forest is indicated by the red outline.

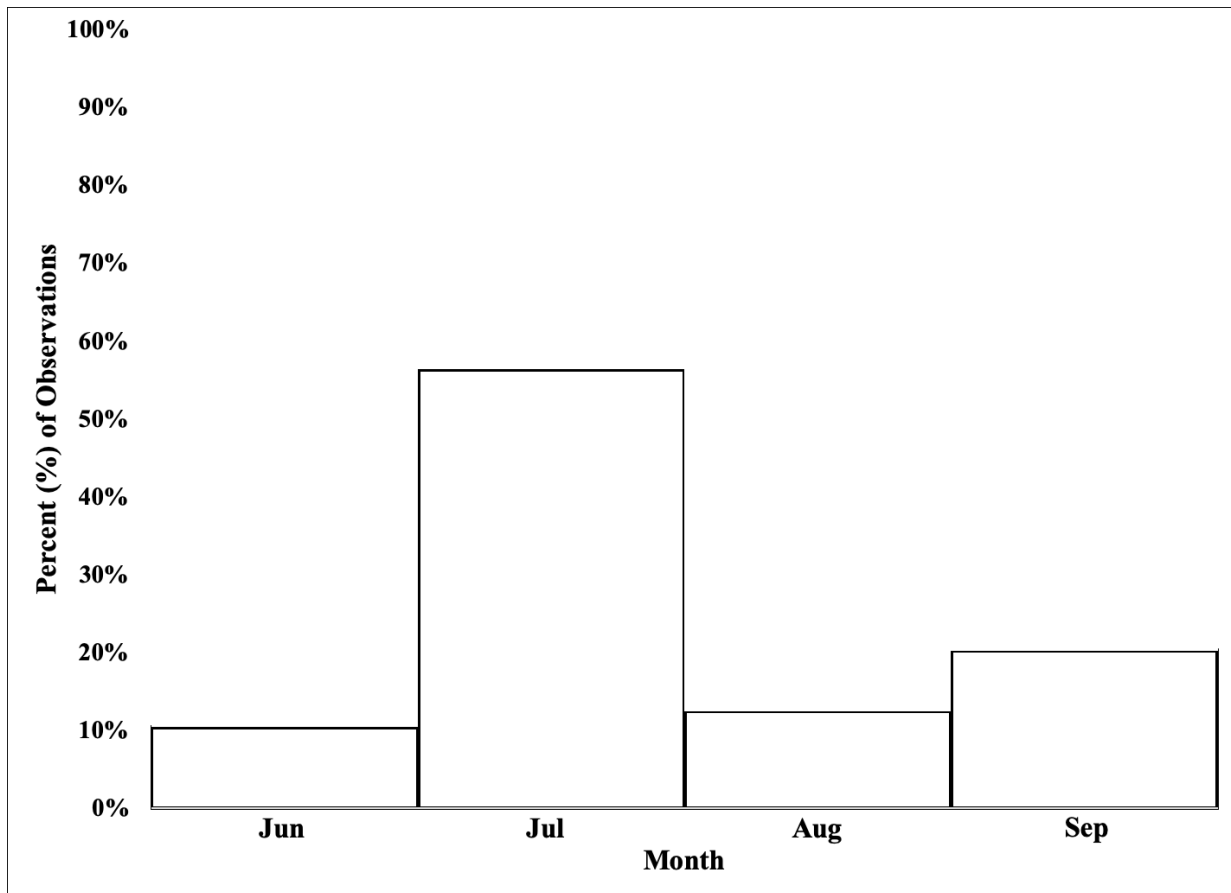


**Figure 2.** Examining the state of all 10 AHY Flammulated Owl primary feathers on the left wing under an ultraviolet light. Enumerations on feathers indicate order of the primaries. The first four primaries are the brightest – and the newest – feathers, whereas the last two primaries are the dimmest – and thus oldest – feathers.

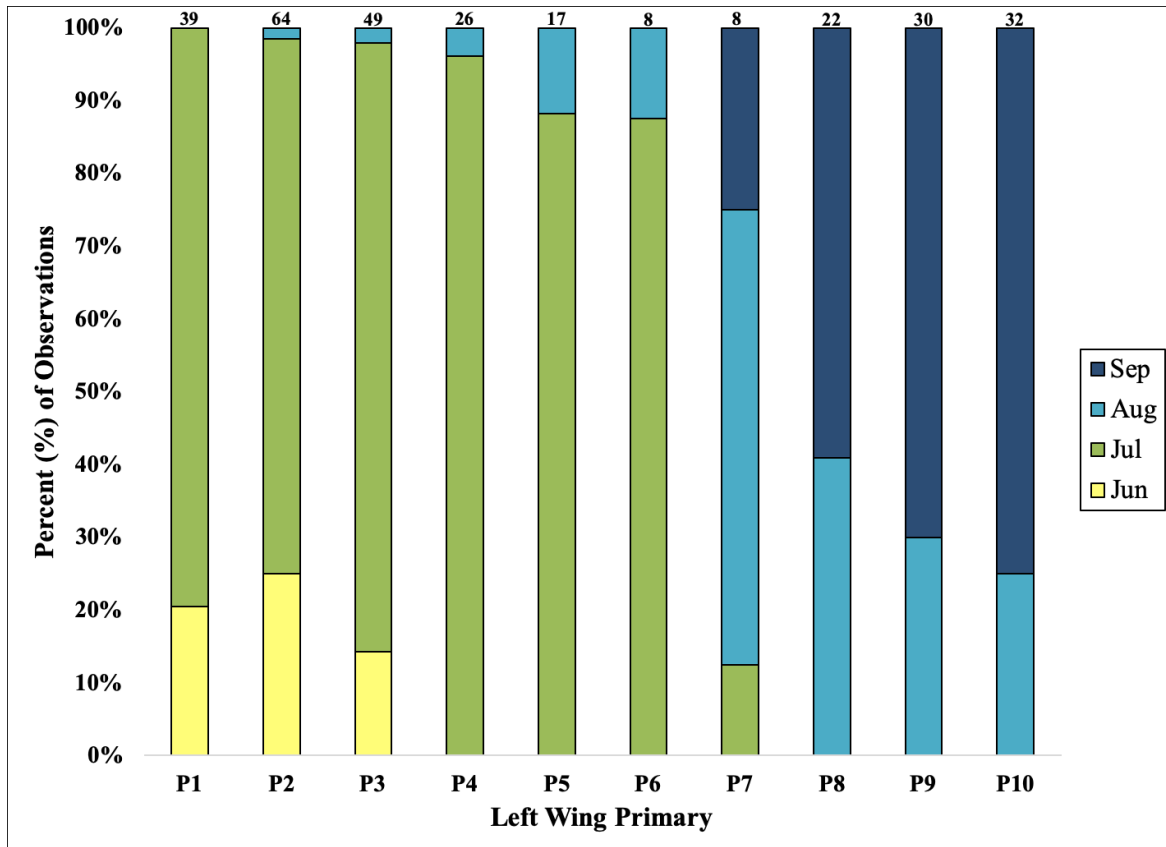


**Figure 3.** Examining the state of all 10 AHY Flammulated Owl primary feathers on the left wing in terms of visible wear. The first four primaries represent the least worn – and thus newest – feathers, while the subsequent primaries are more visibly worn as exhibited in the increased frays and abrasions (particularly the last three primaries).

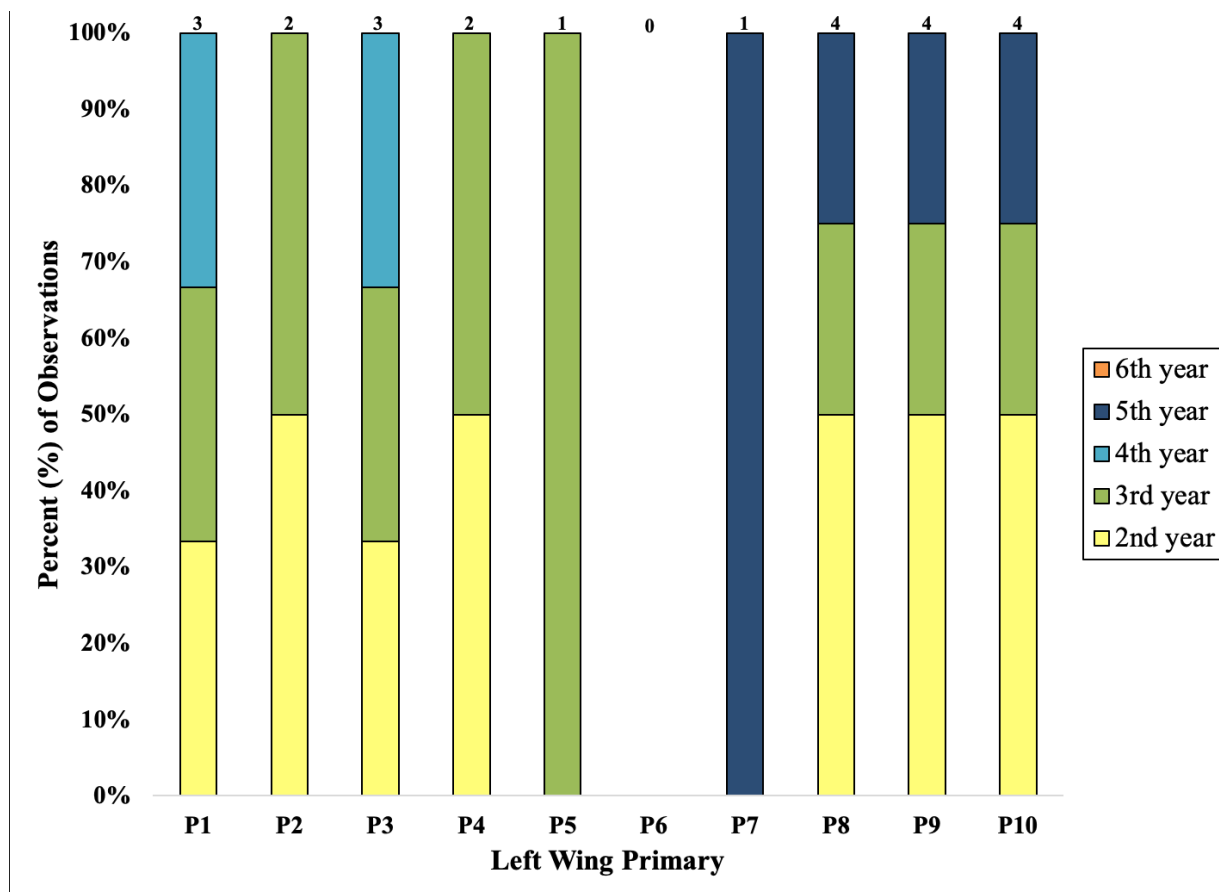




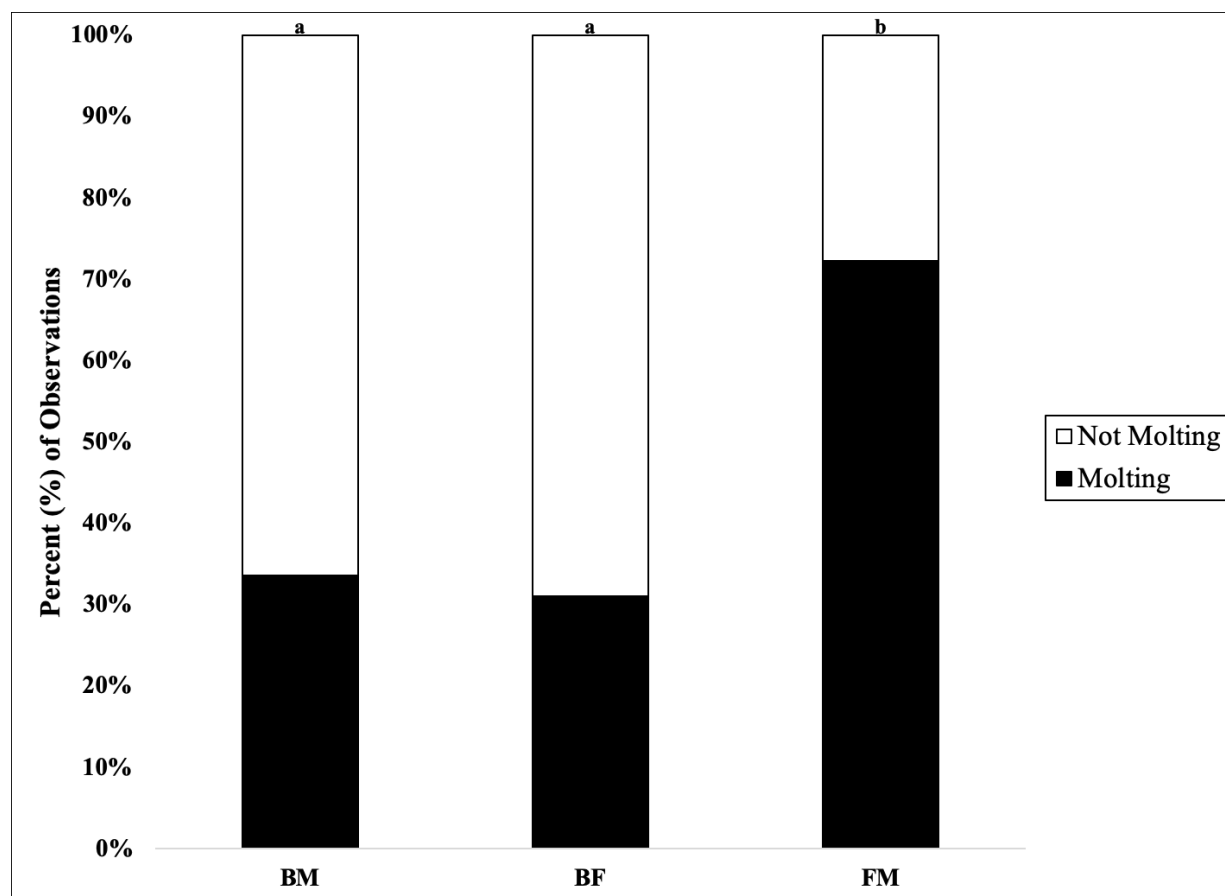
**Figure 4.** The general timing of primary feather molt in all Flammulated Owls indicated that the molting process began in the late nestling/early fledgling period and continued just prior to fall migration. This figure is based off high sampling effort for June and July, however, the lack of sampling data in August and September skewed the results for these two months. The actual percentage of molt observations was likely much higher for the months of August and September.



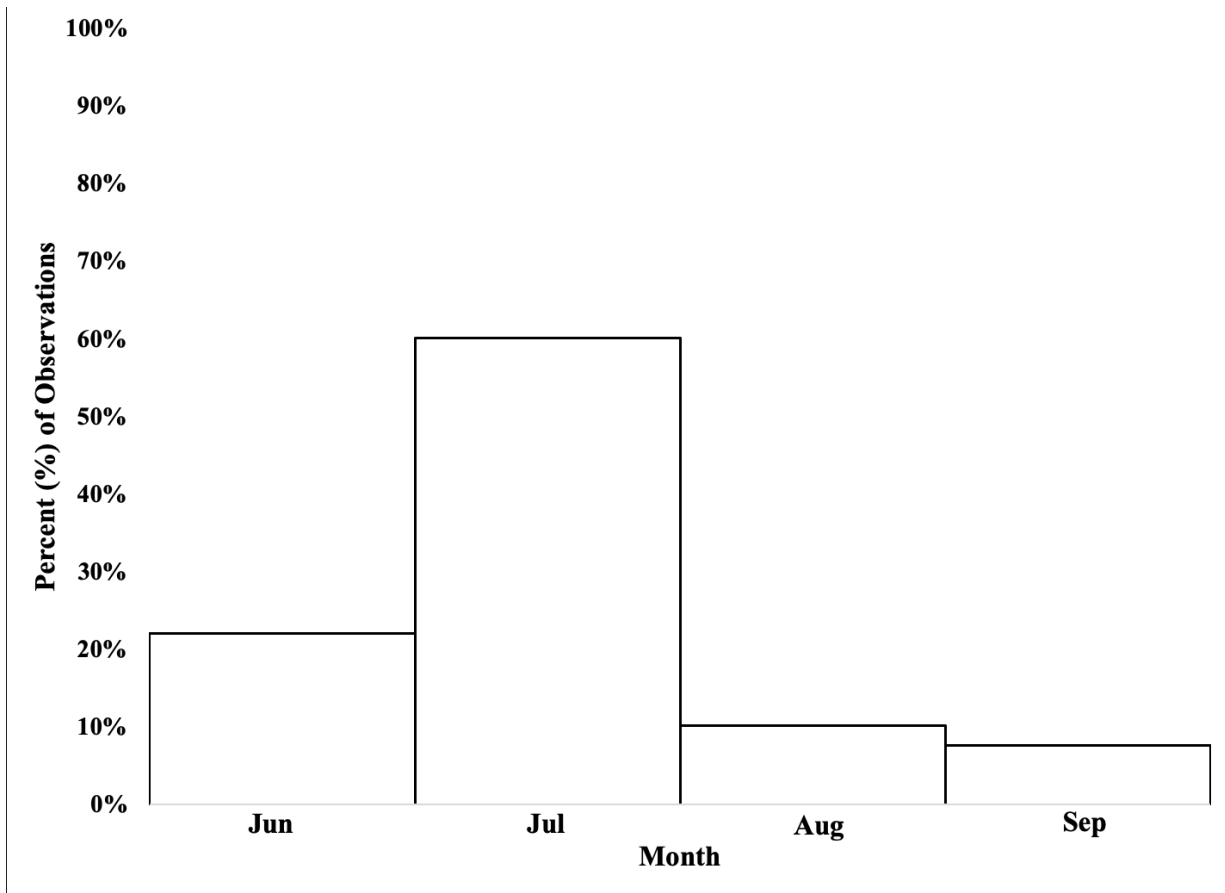
**Figure 5.** Data analysis indicating a timeline of the months in which Flammulated Owls typically molted each primary feather. Numbers on top of the bars indicate sample size.



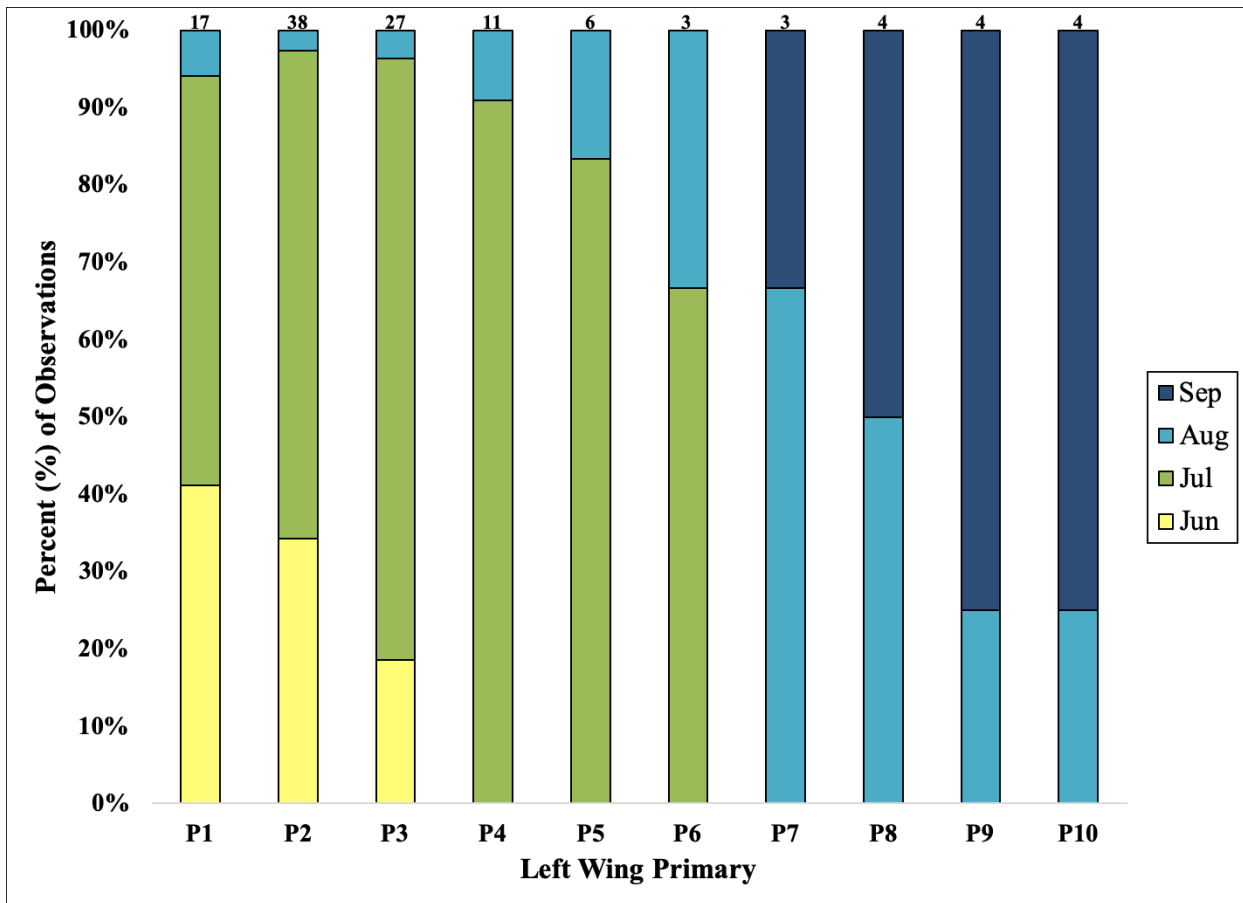
**Figure 6.** Graph depicts the proportion of primary molt observations of known age owls as broken down by age. Numbers on top of the bars indicate cumulative sample size of all ages for each primary. Data stem from a total of eight individuals observed in molt. No sixth-year owls were observed in molt.



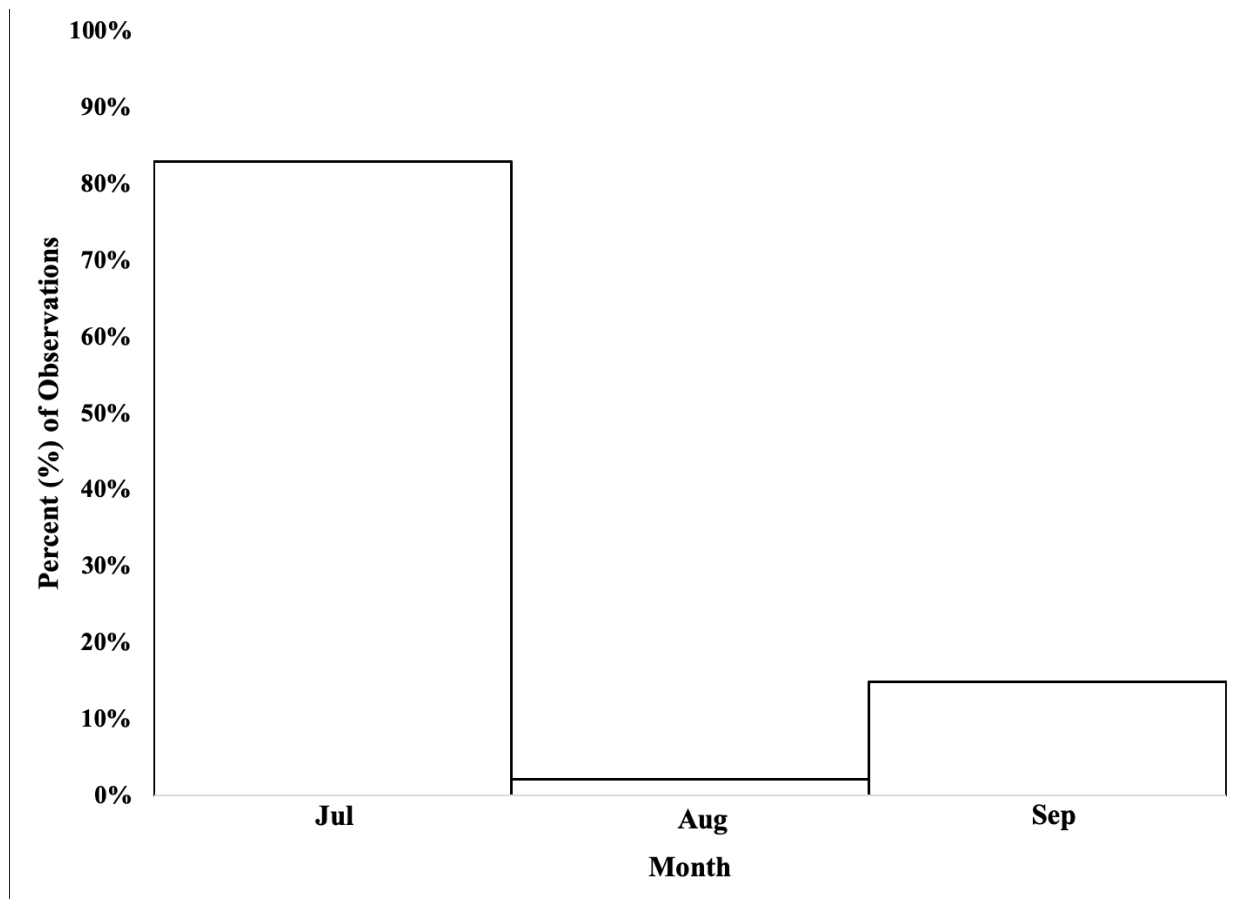
**Figure 7.** Graph depicts the percentage of molt observations indicating at least one primary feather was in molt in three groups of Flammulated Owls: breeding males (BM), breeding females (BF), and floater males (FM). All observations took place between June 21, which was the first day of the season in which observations of feathers in molt had been recorded, and just prior to fall migration in late August and September. Groups that do not share a letter are statistically significant. Total sample sizes were as follows: 152 observations of breeding males, 71 observations of breeding females, and 31 observations of male floaters.



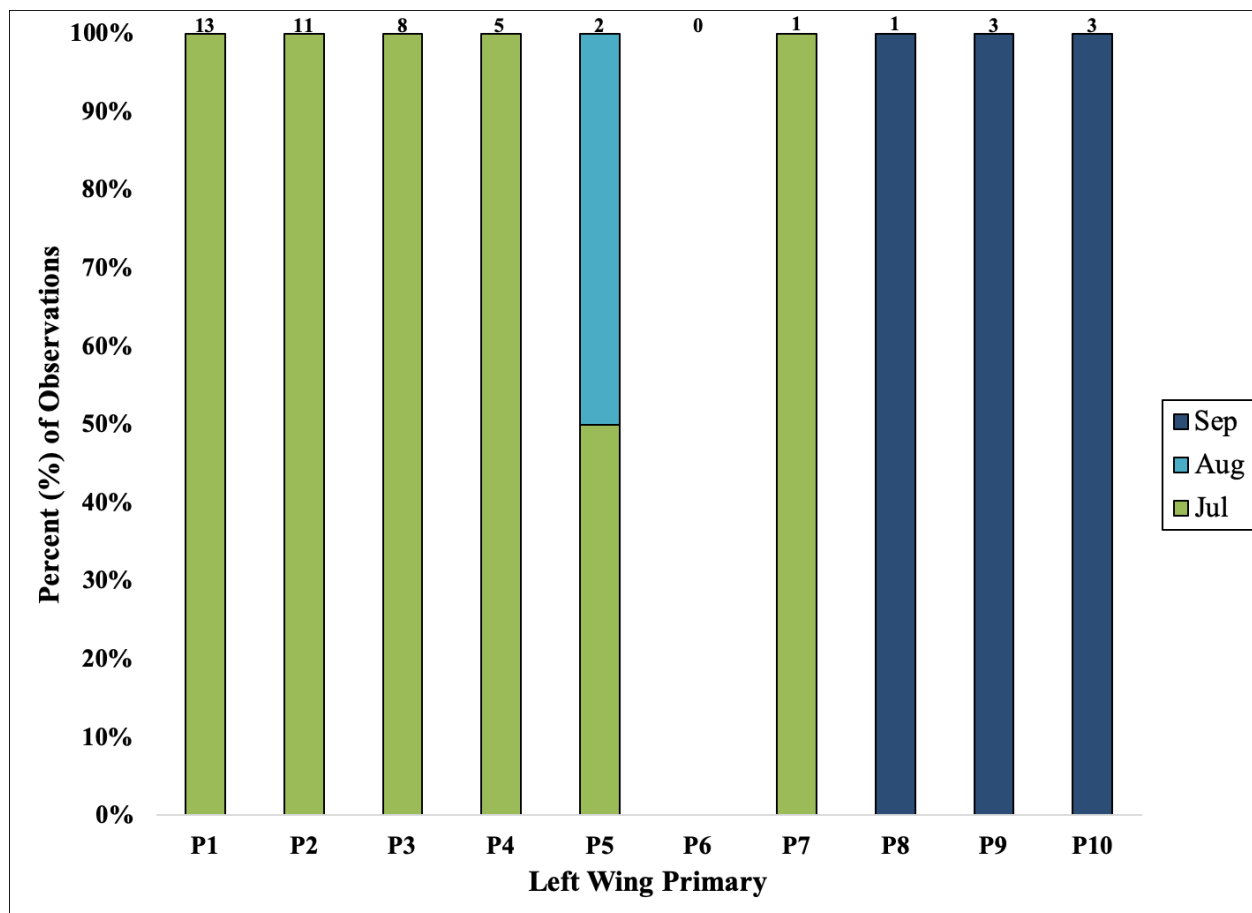
**Figure 8.** The general timing of primary feather molt in breeding male Flammulated Owls indicated that the molting process began in the late breeding season and continued just prior to fall migration. Data were comprised of 53 molt observations. This figure is based off high sampling effort for June and July, however, the lack of sampling data in August and September skewed the results for these two months. The actual percentage of molt observations was likely much higher for the months of August and September; however, data were severely lacking for this time.



**Figure 9.** Data analysis indicating a timeline of the months in which breeding male Flammulated Owls typically molted each primary feather. Numbers on top of the bars indicate sample size.

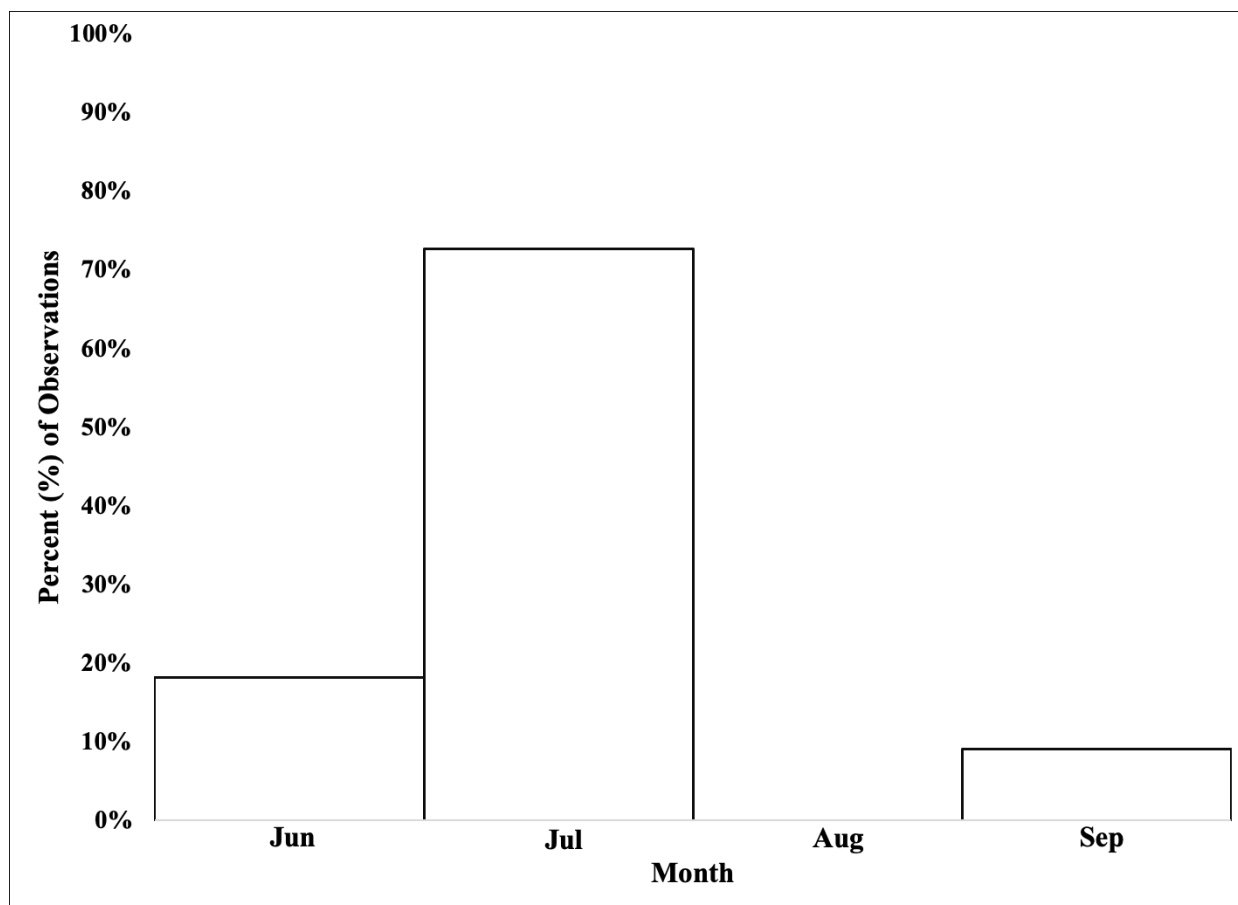


**Figure 10.** The general timing of primary feather molt in breeding female Flammulated Owls indicates that the molting process begins in the late breeding season and continues just prior to fall migration. Data are comprised of 22 molt observations. This figure is based off high sampling effort in July, however, the lack of sampling data in June, August, and September skewed the results for these months. We lack data from June because this is a very sensitive time in the breeding process when the female is incubating eggs and tending to young nestlings. The actual percentage of molt observations was likely much higher for the months of August and September; however, data were severely lacking for this time.

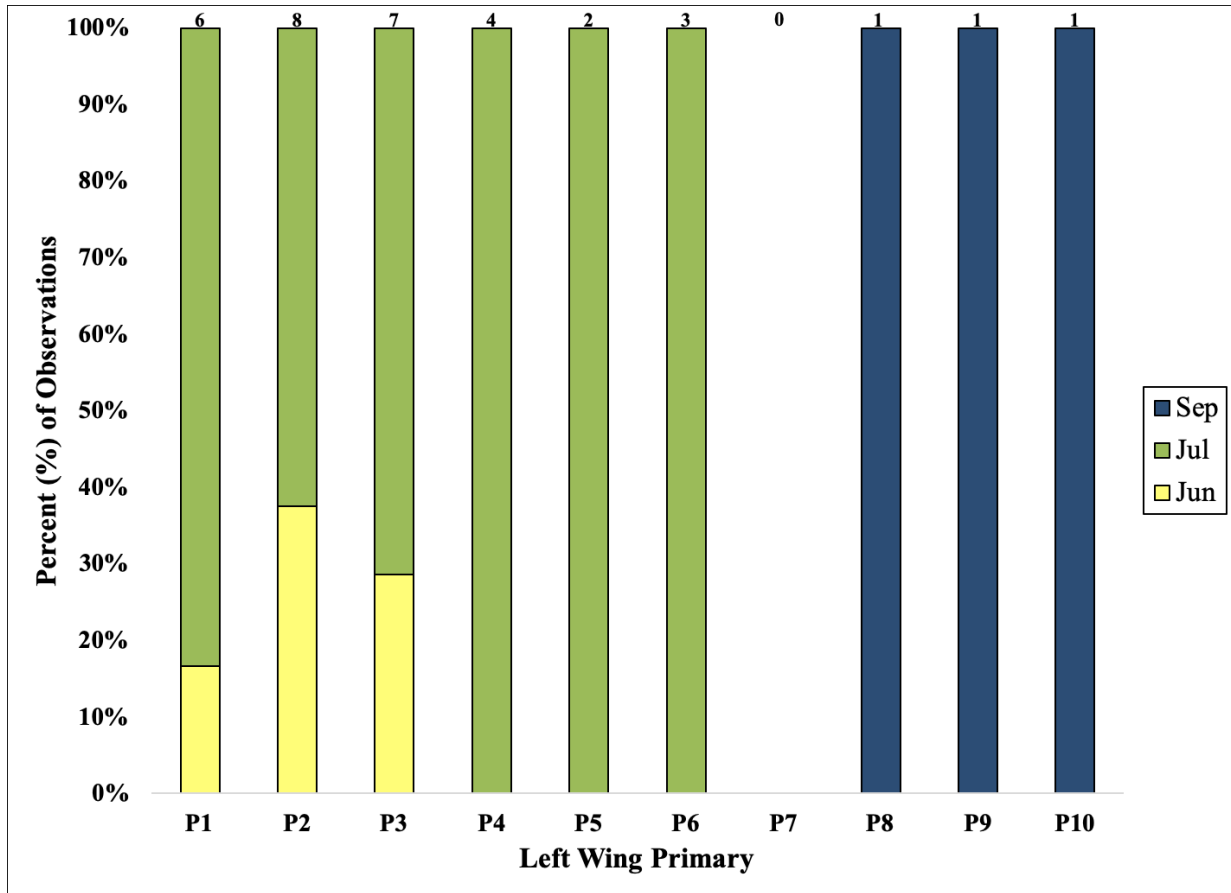


**Figure 11.** Data analysis indicating the timeline of the months in which breeding female Flammulated Owls typically molted each primary feather. Numbers on top of the bars indicate sample size. We lack data from June because this is a very sensitive time in the breeding process when the female is incubating eggs and tending to young nestlings. Additionally, given the small sample sizes, particularly for observations in August and September, this depiction should not be viewed as an accurate representation of the breeding female Flammulated Owl primary feather molt timeline. It is likely more similar to the breeding male timeline.

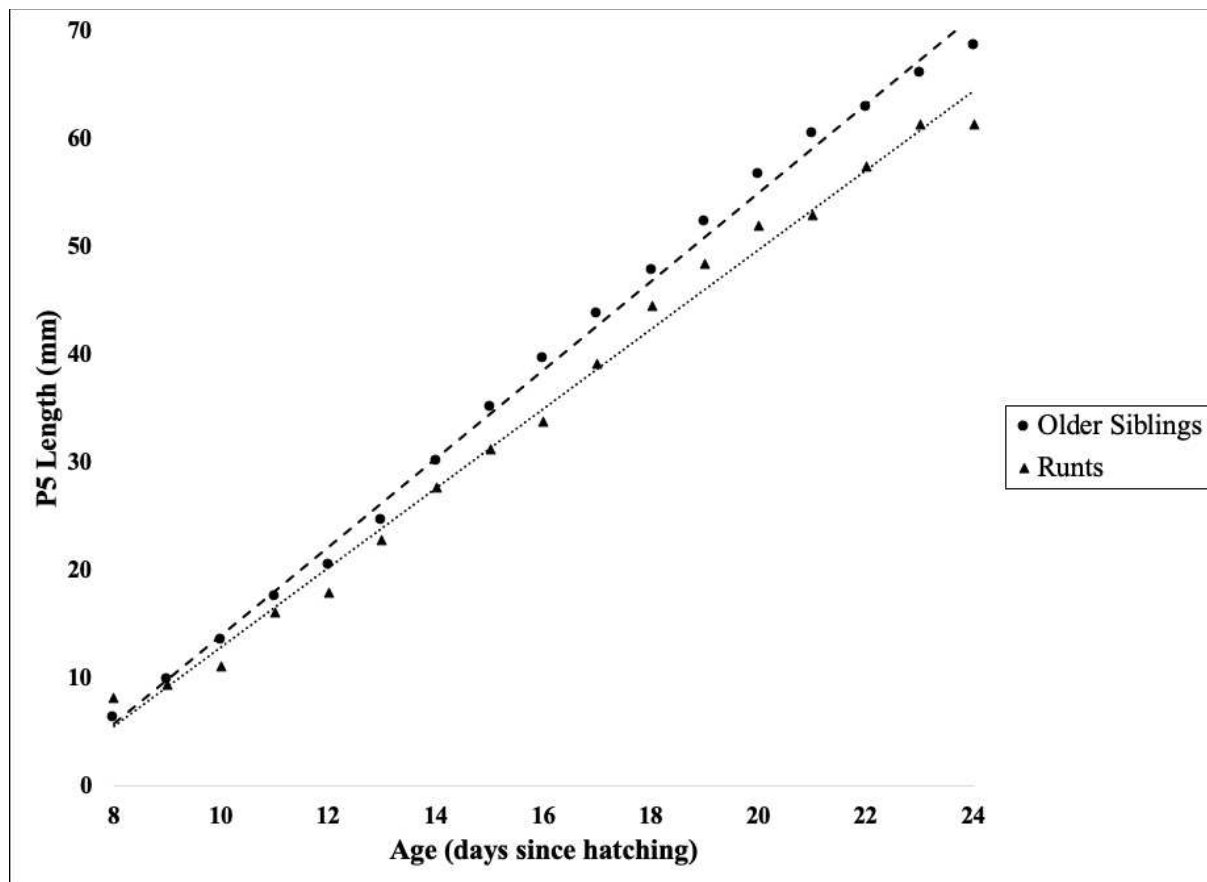




**Figure 12.** The general timing of primary feather molt in floater male Flammulated Owls indicates that the molting process begins in the late breeding season and continues just prior to fall migration. Data are comprised of 31 total observations and 13 molt observations. This figure is based off high sampling effort for June and July, however, the lack of sampling data in August and September skewed the results for these two months. The actual percentage of molt observations was likely much higher for the months of August and September; however, data were severely lacking for this time. Furthermore, after the breeding season ends in mid- to late-July, the males are no longer territorial, thus it becomes difficult to distinguish the breeding status of a male Flammulated Owl. Therefore, the only male floater observation post-breeding season is of a known age bird who was likely a floater during his second year.



**Figure 13.** Data analysis indicating a timeline of the months in which floater male Flammulated Owls typically molted each primary feather. Numbers on top of the bars indicate sample size. Data were missing for the month of August and were scarce for the month of September due to the difficulty of determining the breeding status of un-banded males after the breeding season ends.



**Figure 14.** The Flammulated Owl Nestling left fifth primary growth curve is comprised of data collected between 2003 and 2019. Data originate from a total of 80 nestlings with 64 being older siblings and 16 being runts of the broods. Observations began when the remiges first began to emerge from the shafts around Day 8 and continued until nestlings fledged, typically between Day 22 and Day 24. Dashed line indicates trendline for older siblings while dotted line indicates trendline for runts.