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Authors: Walker, Brett L., and Schroeder, Michael A.

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Atypical primary molt patterns in greater sage-grouse: implications for age classification

Brett L. Walker and Michael A. Schroeder

B. L. Walker (https://orcid.org/0000-0003-1183-3449) ✉ (brett.walker@state.co.us), Colorado Parks and Wildlife, Grand Junction, CO, USA. – M. A. Schroeder (https://orcid.org/0000-0002-7246-5603), Washington Dept of Fish and Wildlife, Bridgeport, WA, USA.

Age-specific patterns of primary molt facilitate age classification of native North American upland gamebirds, a critical step in understanding their ecology, behavior, life history, population dynamics and harvest. However, deviations from typical molt patterns can create confusing plumages that complicate age classification. We examined data from live-captured greater sage-grouse *Centrocercus urophasianus* across seven studies in five U.S. states and wings from harvested birds in Oregon and Colorado for evidence of atypical primary molt. We documented atypical replacement through primary nine during preformative molt, atypical retention of juvenile primary 10 during second prebasic molt, and atypical retention of basic outer primaries during definitive prebasic molt. Atypical primary molts were observed more often in live-captured females (3.2%, n = 561) than males (0.8%, n = 494). Many individuals with atypical primary patterns, especially females, are difficult or impossible to reliably age by plumage or morphology and may bias research and harvest data.

Keywords: atypical molt, *Centrocercus urophasianus*, flight feathers, Galliformes, molt, prebasic molt, preformative molt, remiges, Tetraonidae

Understanding age-related molt cycles and resulting plumage patterns is an essential part of upland gamebird conservation, management and research. Accurate age classification is essential for understanding gamebird life histories and population dynamics (Bergerud and Gratson 1988), generating age-specific vital rate estimates from marked bird populations (Connelly et al. 2011), modeling population demography and viability (Johnson and Braun 1999, Taylor et al. 2012, McCaffery and Lukacs 2016) and estimating productivity from harvest data (Hagen and Loughin 2008, Hansen et al. 2012, Braun et al. 2015). Accurate age classification is also essential for understanding age-specific behavioral and ecological phenomena in gamebirds, such as lek attendance, dispersal, site fidelity and migration (Schroeder et al. 2020).

Native North American upland gamebirds (including turkey, grouse, ptarmigan and quail) all show a similar sequence of annual molt cycles that facilitates age determination (Johnsgard 2008, Lyons et al. 2020; Supporting information). As in other species, greater sage-grouse *Centrocercus urophasianus* have a distinct first molt cycle and all subsequent cycles are usually considered definitive (Pyle 2008). Birds in their first molt cycle grow all juvenile primaries during a complete prejuvenile molt (also known as the first prebasic molt; Howell et al. 2003) at hatch. Within the first month, birds then begin an incomplete preformative molt into formative plumage. During preformative molt, birds replace juvenile primaries with formative primaries in sequence from P1 through P8, but typically retain the two outermost juvenile primaries, P9 and P10. Birds undergo second prebasic molt (and therefore, start their second molt cycle) in summer and fall of their second calendar year. Birds typically have a complete, second prebasic molt and complete, definitive prebasic molts in summer and fall in all subsequent definitive cycles, in which they replace all 10 primaries in sequence from P1 to P10.

Birds in their first molt cycle in formative plumage therefore normally show contrast in wear, color, markings and tip shape between newer, replaced, formative inner primaries (P1–P8) and older, retained, juvenile outer primaries (P9 and P10). This contrast, along with the age of retained juvenile primaries P9 and P10, allows biologists to distinguish birds in formative plumage from those in basic plumage. Age-related primary patterns are one of the main criteria used to classify the age of both harvested birds in fall and live birds captured year-round (Braun and Schroeder 2015). State wildlife agencies in the U.S. classify age and sex of thousands of wings collected from hunters in early fall each year to generate indices of annual productivity, age ratios and sex ratios for harvest management (Hagen and Loughin

2008, Braun et al. 2015, Wann et al. 2020). Research and management studies also capture, classify age and sex, and mark thousands of live greater sage-grouse throughout the species' range each year.

Atypical primary replacement or retention, defined as any deviation from the typical primary molt patterns described above (excluding adventitious molt), can create confusing and sometimes contradictory plumages that lead to uncertainty or errors in age classification. Three previous studies have suggested that atypical primary molt occurs in greater sage-grouse (Pyle 2008, Braun and Schroeder 2015, Braun et al. 2020). However, evidence presented for atypical primary retention during definitive prebasic molt in those studies could instead be explained by other phenomena, such as temporary suspension of prebasic molt or atypical replacement through P10 during preformative molt (Braun et al. 2020). Evidence for both atypical primary retention during second prebasic molt and atypical primary replacement during preformative molt is also lacking. It is also unclear how commonly atypical molt occurs in greater sage-grouse (Braun and Schroeder 2015) and whether it occurs more often in males than females as suggested by Pyle (2008).

For these reasons, a comprehensive review of the occurrence of atypical primary molt patterns in greater sage-grouse is warranted. In this study, our objectives were to identify atypical primary molt patterns in harvested and live-captured birds, estimate the percent of live-captured birds of each sex with atypical primary patterns, and identify other possible atypical primary patterns that require further investigation. We also discuss implications of atypical primary patterns for age classification (and misclassification) of harvested wings and live-captured birds.

Methods

Starting in 2003, we collected data on, and in many cases, photos of, atypical primary patterns on wings of live-captured greater sage-grouse that we marked during the course of other research in Colorado (Walker et al. 2016, 2020), Montana (Walker 2008), Wyoming (Doherty 2008), Oregon and Washington (Sage-Grouse Conservation Partnership 2015, Schroeder et al. 2019), as well as on wings of harvested greater sage-grouse collected by state wildlife agencies from parts of Colorado (2019–2020) and Oregon (2004 and 2012) for evidence of atypical molt. For detailed descriptions of Montana and Wyoming study areas, see Walker (2008) and Doherty (2008); for Colorado study areas, see Walker et al. (2016, 2020); and for Washington and Oregon study areas, see Sage-Grouse Conservation Partnership (2015) and Schroeder et al. (2019).

We defined the age of atypical birds by their calendar age and molt cycle at the time of harvest or capture. We used calendar-based age classes recognized by the U.S. Bird Banding Laboratory (BBL): HY = hatch year, SY = second year, TY = third year, AHY = after hatch year, ASY = after second year and ATY = after third year. But using only calendar-based age classes is problematic because they do not convey which molt cycle and plumage a bird is in (Howell et al. 2003). Birds were therefore also classified as being in their first cycle, second cycle or definitive cycle. Although the second molt cycle in sage-grouse is usually considered definitive, birds that have an atypical, incomplete, second prebasic molt would retain juvenile (or possibly formative) outer primaries, whereas birds that had an atypical, incomplete, definitive prebasic molt would retain basic outer primaries. Therefore, we consider second and definitive cycles separately.

Under this definition, the first molt cycle in sage-grouse includes HY birds and SY birds through the start of their second prebasic molt, the second cycle includes SY and TY birds from the start of their second prebasic molt though the start of their third prebasic molt, and definitive cycles include TY and older birds (including ASYs, ATYs, etc.) from the start of their third prebasic molt onward. Because each molt cycle spans two calendar years, we list two BBL age classes and specify either which plumage or which molt cycle they are in when referring to all birds within one molt cycle. We encourage readers unfamiliar with age class terminologies based on molt cycles and plumages to review molt cycles, molts and plumages of greater sage-grouse in relation to BBL age classes and age classes commonly used in the gamebird literature (juvenile, yearling, adult and breeding age; Braun and Schroeder 2015) before proceeding (Supporting information). We also cross reference these with age codes based on molt cycle, plumage and molt status for readers that use Wolfe–Ryder–Pyle terminology (Wolfe et al. 2010, Johnson et al. 2011) (Supporting information).

We calculated occurrence as the percent of individuals with atypical primary molt in samples of live-captured birds. We did not attempt to quantify the percent of harvested birds with atypical molt because the presence of active primary molt in early fall often makes it difficult or impossible to reliably identify individuals with atypical primary patterns, especially among birds in their first cycle that have not yet completed preformative molt.

Because morphometric data is often informative regarding age in grouse (Pyle 2008, Braun and Schroeder 2015), we measured primary lengths, tail length and mass of live-captured females in Lake and Harney counties, Oregon and Douglas Co., Washington and fully-grown primaries of harvested females in Oregon. Primaries were measured to the nearest mm from the proximal side of a feather's insertion point to the tip of the straightened feather. Tail length was measured to the nearest mm from the insertion point to the tip of the center of the tail (longest feathers). This allowed comparison of measurements from females with atypical molt against measurements from females with typical primary patterns in each age class.

Results

We documented 31 cases of atypical primary molt, 23 cases among 1055 live-captured greater sage-grouse and 8 cases among 1327 harvested birds (Supporting information). We documented 10 cases of atypical primary retention. We confirmed atypical retention of two basic outer primaries (and corresponding primary coverts) following definitive prebasic molt in one marked female known to be > 3.5 years old (F1505 in the Supporting information; Fig. 1A). This female was banded in November 2009 as an AHY and recaptured and recorded as an ASY in April 2012. Based on her age in 2009,

this female was in at least her fourth molt cycle (and therefore in a definitive cycle). This female represents the first confirmed evidence of atypical retention of basic primaries during definitive prebasic molt in greater sage-grouse. We also documented seven other females presumed to be ASY or ATY birds that appeared to have retained from two to five outermost basic primaries following a definitive prebasic molt (Supporting information; Fig. 1B, C; but see Discussion). We also identified two atypical males that had retained juvenile P10 during second prebasic molt. One TY male in spring (2140 in Supporting information) had a retained juvenile P10, but it was in definitive basic plumage and all of the bird's measurements unambiguously matched those of typical ASY males captured in spring, including mass (2880 g). Another male (M3536 in Supporting information) was captured and color-banded in March 2013 with juvenile P10 on both wings (Fig. 1D). It was described as 'adult-looking with 10th primary juvenile' and had a long, pointed tail typical of an ASY male (Fig. 1E). Its mass (~2450 g) was intermediate between SY and ASY males captured in spring. This male was also recorded as an ASY when resighted on four occasions by three observers that spring. We therefore classified M3536 as a TY male that had retained juvenile P10 during its second prebasic molt.

We observed atypical primary replacement during preformative molt (i.e. replacement through P9 rather than P8) in two SY males captured in spring in formative plumage with retained juvenile P10 (2107 and M3125 in the Supporting information; Fig. 1F). Measurements for male 2107 clearly matched those of SY males captured in spring. Male M3125 had asymmetric primary molt, with juvenile P10 on one wing and juvenile P9 and P10 on the other, and mass (2500 g) that was intermediate between SY and ASY males captured in spring.

We were unable to reliably age the remaining 19 atypical birds with retained juvenile P10 only (Supporting information) because we were unable to determine if they were HY or SY birds in formative plumage that had replaced through P9 during preformative molt or SY or TY birds in second basic plumage that had retained juvenile P10 during second prebasic molt (Fig. 1G, H). Of those 19, two females (P95/1104 and 1006) were asymmetrical, with a juvenile P10 on one wing and an adult P10 on the other wing (Supporting information).

Females with atypical primary molt could not be assigned to age based on morphological criteria alone. Our analysis of measurements from sage-grouse in Oregon showed distinctly different distributions for mass, tail length and lengths of P1 and P2 between typical HY and SY females in formative plumage and typical SY or ASY females in second or definitive basic plumage (Fig. 2). However, two of three presumed ASY and ATY females in definitive basic plumage with retained old, rounded outer primaries (MAS0400 and 1114; Supporting information) also had extremely small measurements that would normally suggest a HY or SY female in formative plumage, despite having unambiguous older and adult-like (i.e. basic or formative) outermost primaries with rounded tips (Fig. 2). In contrast, four females captured in spring that retained only juvenile P10 (951, 1016, 1017 and 1131 in the Supporting information) had relatively large measurements that would normally suggest an ASY female in second or definitive basic plumage (Fig. 2).

Atypical primary molt was less common in our sample of live-captured males than females (Table 1). Across studies, the percent of birds with atypical primary molt varied by sex from a low of 0.8% of 254 males to a high of 9.5% of 74 females across seven studies (Table 1). Separating capture records by sex and including only studies with $\geq$ 30 individuals per sex (to exclude estimates based on small sample size), occurrence rates varied from 1.0 to 9.5% across studies in females and 0.0–3.1% across studies in males (Table 1). Based on a total of 1055 live-captured birds, the percent of individuals with atypical primary molt was four times higher in females (3.2%, n = 561) than males (0.8%, n = 494) ($t_{1053} = 2.832$; $p = 0.0047$).

Discussion

Greater sage-grouse are often presumed to be easy to classify by age based on published criteria. This is probably the case for live-captured males, in which differences in mass and in formative and basic plumage facilitate ageing. However, atypical molt patterns can produce contradictory plumage features that lead to confusion and age misclassification of harvested wings and live-captured birds of both sexes, but especially females. Our data suggest that atypical birds may represent, in some cases, up to 9.5% of live-captured females and 3.1% of males, with most being problematic for age classification. Error rates that high for females could substantially bias demographic studies of marked greater sage-grouse.

The inability to differentiate atypical HY or SY females that replaced through P9 (rather than P8) during preformative molt from atypical SY or TY females that retained juvenile P10 (rather than replace all primaries) during second prebasic molt reveals some of the complexities of age classification caused by atypical molt. We attempted to understand this complexity by examining morphological measurements that show the least overlap between known age classes. However, despite differences in average morphological measurements between typical HY and SY females in formative plumage and typical SY and ASY females in second or definitive basic plumage, overlap in distributions prevented atypical females from being reliably aged by morphology alone. This problem is exacerbated by the fact that, if there are no differences in primary patterns, HY and SY females in formative plumage are often indistinguishable from SY and ASY females in basic plumage.

In spring, misclassification of live-captured, atypical, TY females that retained juvenile P10 during second prebasic molt as atypical SY females that replaced through P9 during preformative molt, and vice versa, may bias estimates of age-specific female survival and reproductive success in research studies. However, misclassification of birds with atypical molt in fall should have little influence on harvest data. First, HY females in formative plumage with retained juvenile P10 are probably rarely harvested due to the timing of preformative molt (Braun and Schroeder 2015). Harvest in most states typically occurs in September, and preformative molt typically finishes in late September through October (Pyle 2008, Braun et al. 2020). Second, wings of atypical TY females with retained juvenile P10 harvested in fall would

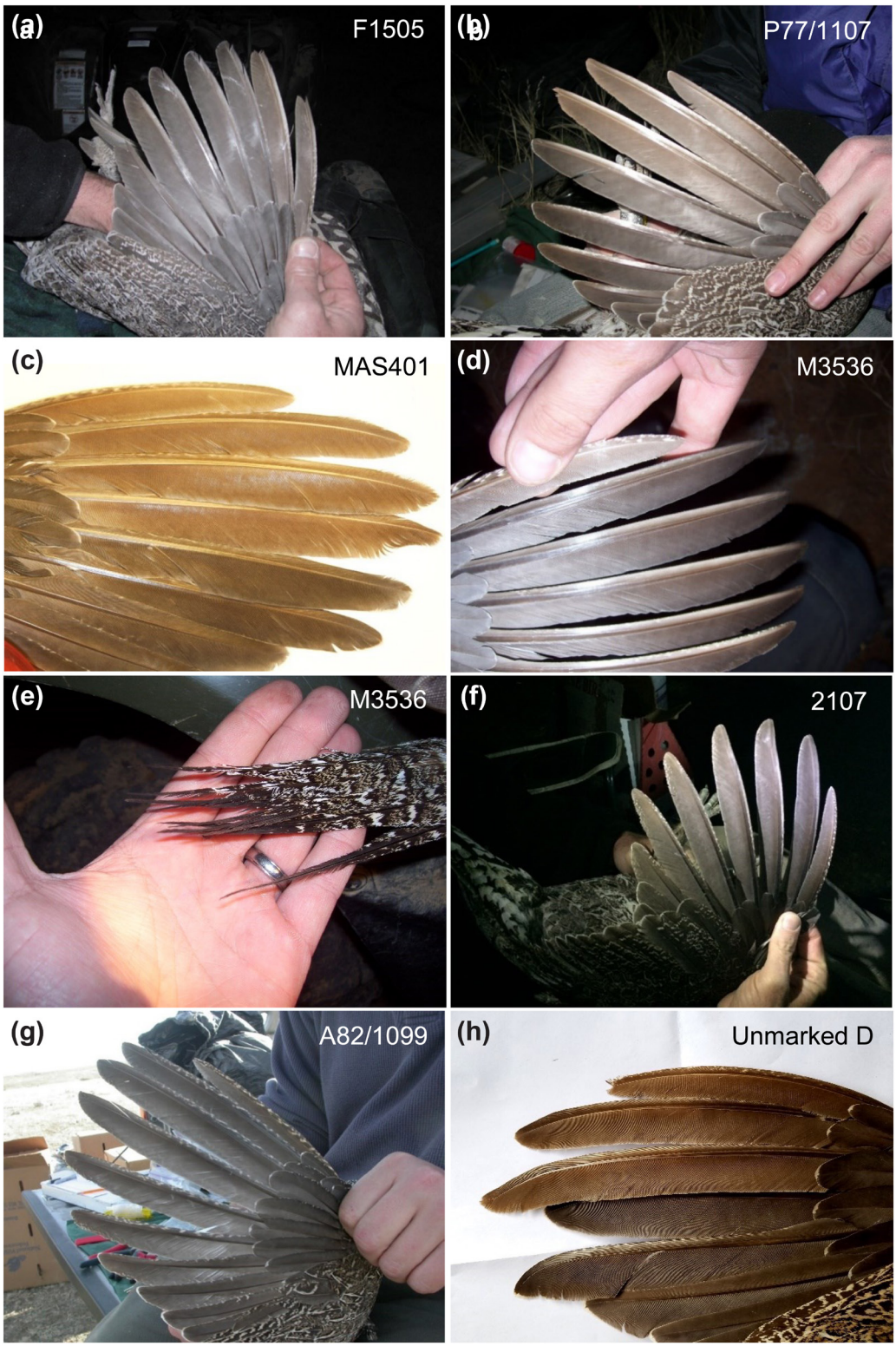

Figure 1. Examples of atypical outer primary (and primary covert) retention and replacement in greater sage-grouse: (a) F1505, a recaptured ATY female > 3.5 years old in definitive basic plumage with old, retained definitive basic primaries P9 and P10 and retained corresponding primary coverts on both wings; (b) P77/1107, a captured, presumed ATY female with three retained, old, basic primaries (P8–P10) and ≥ 2 retained basic outer primary coverts on both wings; (c) MAS0401, a harvested, presumed ATY female with no active primary molt and four old, retained, basic primaries (P7–P10); (d, e) M3536, a TY male captured in spring that retained juvenile P10 (again) on both wings following its second prebasic molt; (f) 2107, an SY male captured in spring that replaced through P9 during its preformative molt; (g) A82/1099, a female captured in spring that was either an SY bird that replaced through primary P9 during its preformative molt or a TY bird that retained juvenile P10 following its second prebasic molt; and (h) unmarked D, a female harvested in fall while undergoing prebasic molt that was either an SY bird that replaced through primary P9 during its preformative molt or a TY bird that retained juvenile P10 following its second prebasic molt. See text and Supporting information for more information about each individual.

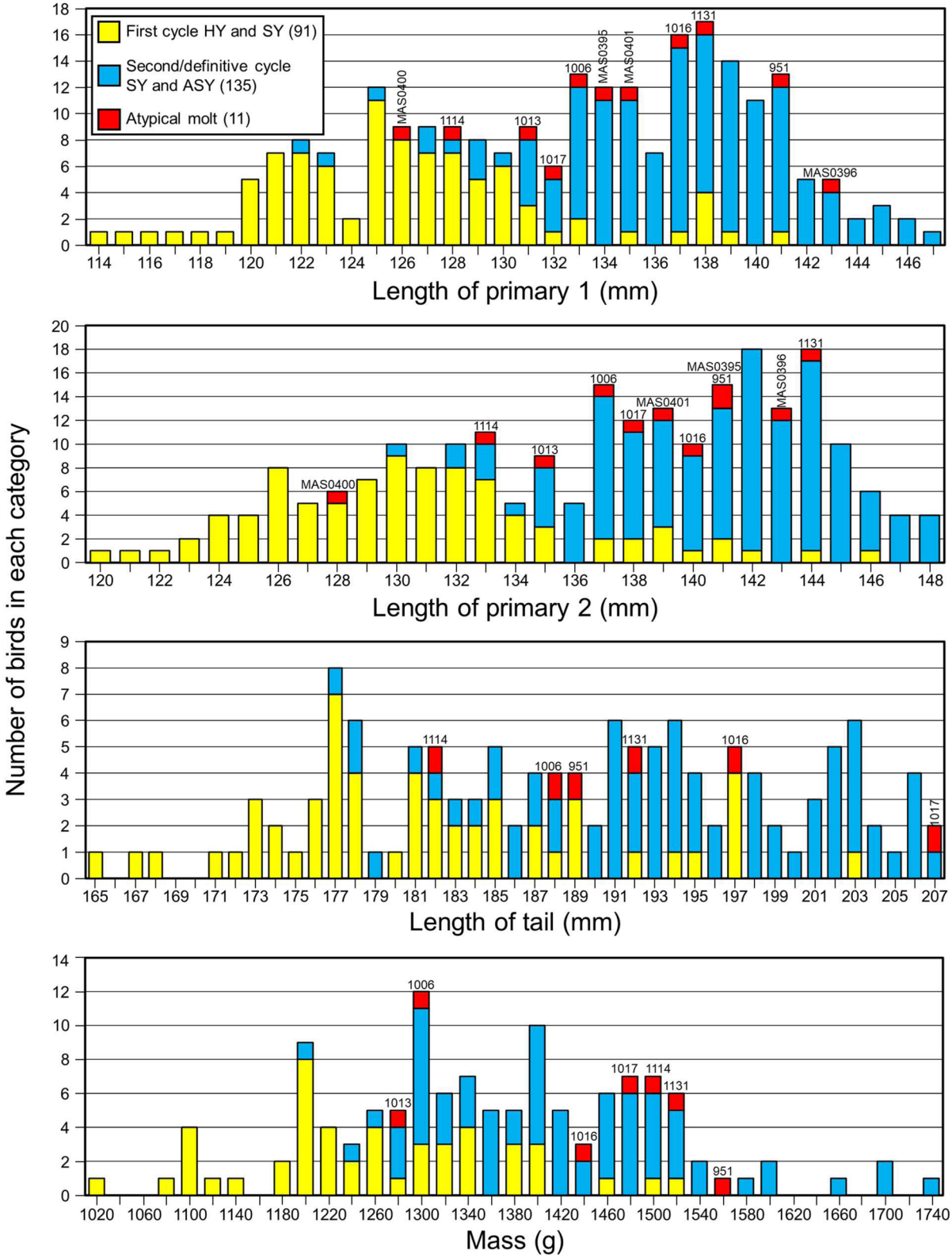

Figure 2. Lengths of primary 1 (P1) and primary 2 (P2), tail length and mass for female greater sage-grouse captured or harvested in Oregon between 2004 and 2015. 'First cycle HY and SY' includes HY and SY birds in their first molt cycle in formative plumage with typical primary patterns (i.e. formative P1–P8 and retained juvenile P9 and P10). 'Second/definitive cycle SY and ASY' includes SY and ASY birds in basic plumage in their second or definitive molt cycles, respectively, with typical primary patterns (uniform, basic P1–P10). Sample sizes for each age category are in parentheses. Atypical individuals are shown in red, and the numbers above them refer to individuals described in the text, in Supporting information or both.

Table 1. Percent of live-captured birds with atypical primary molt across seven studies of greater sage-grouse in the western U.S.

Location (County, State)	Years	No. captured			No. birds with atypical primaries		Occurrence (% atypical)		
		Total	F	M	F	M	Total	F	M
Bighorn, MT/Sheridan, WY	2003–2007	271	222	49	6	0	2.2%	2.7%	0.0%
Garfield, Rio Blanco, CO	2008–2010	48	46	2	2	0	4.2%	4.3%	–
Garfield, Rio Blanco, CO	2012–2014	76	2	74	1	0	1.3%	–	1.4%
Moffat, CO/Sweetwater, WY	2007–2009	209	209	0	2	0	1.0%	1.0%	–
Moffat, CO/Sweetwater, WY	2010–2013	254	0	254	0	2	0.8%	–	0.8%
Harney, Lake, Malheur, OR	2011–2015	124	74	50	7	0	5.6%	9.5%	0.0%
Douglas, Yakima, WA	2012–2020	73	8	65	0	2	2.7%	–	3.1%
Total		1055	561	494	18	4	2.1%	3.2%	0.8%

be misclassified as atypical SYs, but this is less consequential because both classes are considered AHY (i.e. breeding-age) birds in age ratios used as indices of productivity (Connelly et al. 2003, Hagen and Loughin 2008).

The morphological analysis revealed an unexpected pattern. Two atypical females presumed to be ASY or ATY birds in definitive basic plumage had the shortest P1 and P2 lengths among all atypical females we measured, and several atypical females with retained juvenile P10 (that would most likely be classified as SY birds in spring) had measurements near the top of the range for SY and ASY females in second or definitive basic plumage. This phenomenon may be related to the amount of energy, nutritional resources or time breeding birds have available to complete prebasic molt in fall. One hypothesis is that an energy or nutritional deficiency sufficient to cause an incomplete second or definitive prebasic molt also results in slower feather growth (i.e. protein deposition) and therefore, shorter primary and tail lengths (Murphy et al. 1988, Grubb 1989, Møller and De Lope 1999). In contrast, birds with an energy or nutritional surplus sufficient to allow replacement of additional primaries during preformative molt may be more likely to grow longer feathers. Regardless, our findings suggest that measurements of P1, P2 and tail may sometimes be misleading indicators of age in females with atypical primary patterns.

Atypical primary retention (i.e. incomplete prebasic molt) is most commonly attributed to higher reproductive effort that delays initiation of molt or induces a molt-breeding tradeoff (Braun and Schroeder 2015). As in other grouse species (Zwickel and Dake 1977), female sage-grouse delay molt until they finish nesting (Pyle 2007, Braun et al. 2020). Some ASY females attempt three nests (Taylor et al. 2012) and therefore, may not initiate prebasic molt until the end of July. In contrast, males typically finish strutting in May, initiate prebasic molt in May or early June, and complete prebasic molt earlier than females (Pyrah 1954, Pyle 2007, Braun et al. 2020). Our results from live-captured birds are consistent with this hypothesis, with retained primaries being more common in females than males (contra Pyle 2008). This suggests that earlier timing of prebasic molt in males offsets the extra resources they need to grow larger feathers (Pyle 2008). If the extent of prebasic molt is determined by reproductive effort, atypical primary retention should be more common among females that successfully renest than among females with successful first nests or unsuccessful nests. However, it remains unclear whether atypical primary retention is more common during second prebasic molt in SY birds or during definitive prebasic molt in ASY birds because we could not reliably age most females with retained juvenile P10 only. Second-year females typically have lower reproductive effort (Connelly et al. 2011, Taylor et al. 2012) and initiate prebasic molt earlier than ASY females (Braun et al. 2020), so we suspect that atypical primary retention in females is less common during second prebasic molt than during definitive prebasic molt.

If the extent of preformative molt is regulated by energy, nutritional resources or time (e.g. before a photoperiod threshold is reached in fall), replacement through P9 (and possibly P10) during preformative molt in the first molt cycle may be more common among HY birds that hatch early (Schmutz and Hoffman 1991), are in better body condition, or are raised in more productive years or higher-quality brood-rearing habitat. Food availability is known to influence early juvenile mass gain in greater sage-grouse chicks, but not feather growth rate (Huwer et al. 2008), and no information is available regarding its effect on the extent of preformative molt.

Surprisingly, until their mention by Pyle (2008), Braun and Schroeder (2015) and Braun et al. (2020), we found no mention of atypical molt patterns in sage-grouse in 23 other studies from 1900 to 2020 that we reviewed (Supporting information). Combined with the low occurrence (< 10%) of birds with atypical primaries we documented among live-captured birds, this suggests that atypical primary molt is uncommon overall. Similarly, Pyle (2008) detected atypical primary molt in only two (6.5%) of 31 AHY museum specimens examined (P. Pyle, pers. comm.).

The percent of birds with atypical primary patterns we documented may be biased low for several reasons. First, some atypical birds may have been overlooked. Documenting atypical molt patterns was not the focus of these research studies, and capture and processing often occurs at night (with headlamps), in challenging weather conditions, and under time constraints to minimize stress on captured birds. Second, and more importantly, a difference in retention or replacement of only 1–2 additional primaries would produce at least two additional atypical patterns that would essentially be undetectable in live-captured females. For example, unless juvenile primary coverts or juvenile S1 was retained, most HY or SY females that had replaced all 10 primaries during preformative molt (as suggested by Braun et al. 2020) would be indistinguishable from, and consistently misclassified as, typical AHY or ASY females, respectively. The window of time in which to detect atypical replacement through

P10 in HY birds, which is after P10 has started growing but before the bird has replaced all diagnostic juvenile wing coverts, is probably extremely short. Birds that had an atypical, complete, preformative molt during their first cycle followed by an atypical, incomplete, second prebasic molt would also show a primary pattern identical to that of atypical ASY or ATY birds that retained basic primaries during an incomplete definitive prebasic molt. In fact, seven atypical females in our study (M94/1047, P77/1107, 1167, 1180, 1114, MAS0400, MAS0401 in the Supporting information, including the female shown in Figure 4 in Braun and Schroeder 2015), as well as the two atypical males reported by Pyle (2008), could actually be SY or TY birds in second basic plumage with retained formative primaries rather than ASY or ATY birds in definitive basic plumage with retained basic primaries. Similarly, SY or TY birds that retained both juvenile P9 and P10 following an atypical second prebasic molt could be challenging or impossible to distinguish from typical HY and SY females with juvenile P9 and P10 in formative plumage. For these reasons, we suspect that the occurrence of atypical primary patterns is higher, and presents a larger problem for age classification, than indicated by our data from live-captured birds. These issues could also cause age misclassification of harvested wings of both sexes.

These atypical primary patterns should be looked for in other gallinaceous species with similar molt sequences. Atypical primary molt has been reported in wild turkeys (Williams and Austin 1970, Schmutz and Hoffman 1991), white-tailed ptarmigan *Lagopus leucura* (Braun and Martin 2001), dusky grouse *Dendragapus obscurus* (Zwickel and Bendell 2020), sooty grouse *Dendragapus fuliginosus* (Bendell 1955), and chukar *Alectoris chukar* (Johnsgard 2017), but to our knowledge, have not been documented in other native North American grouse, prairie-chicken or quail species (Pyle 2008) or in gray partridge *Perdix perdix*. Notably, in some species (e.g. ruffed grouse, *Bonasa umbellus*), juvenile primaries (particularly P9) are not as distinct as in greater sage-grouse, so atypical primary molts in other species may have been overlooked.

Conclusions and recommendations

Due to the potential for misclassification of greater sage-grouse with atypical primary patterns, we encourage capture crews and inexperienced observers to review the most recent key for classifying age (Braun and Schroeder 2015), annual molt cycles, plumages and timing (Pyle 2007, 2008; Supporting information), and atypical primary patterns likely to be encountered (Supporting information, Fig. 1). We reiterate the importance of reviewing multiple criteria to accurately classify age, not just contrast between inner and outer primaries, and not just typical primary molt progression (Beck et al. 1975, Connelly et al. 2003). Careful documentation of atypical birds and wings is needed to improve our understanding of atypical molt in greater sage-grouse. Specifically, biologists should look for HY birds that replaced through P9 or P10 but still have juvenile wing coverts in early fall, SY birds and TY birds with 1–2 retained juvenile outer primaries following second prebasic molt, and ASY or ATY birds with retained basic outer primaries following definitive prebasic molt. However, HY and SY birds in formative plumage that replaced through P10 during preformative molt and SY and TY birds that retained formative (rather than juvenile) outer primaries during second prebasic molt may not be identifiable. Examination of the primaries, primary coverts and secondaries of known-aged, marked birds most likely to exhibit atypical molt (e.g. early hatched HY birds and successful SY and ASY females with late-hatching renests) in late fall may be valuable for confirming such patterns. Research on marked females to identify diagnostic differences between formative and basic contour feathers would also help resolve problematic atypical patterns. Until then, many, if not most, greater sage-grouse with atypical primary patterns, especially females, will be difficult or impossible to reliably age and may need to be excluded from age-specific demographic or behavioral analyses.

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Author contributions – Both authors contributed equally to this study.

References

Beck, T. D. I. et al. 1975. Sex and age determination of sage grouse from wing characteristics. – Colo. Div. Wildl. Game Inf. Leafl. 49 (rev.).
Bendell, J. F. 1955. Age, molt and weight characteristics of blue grouse. – Condor 57: 354–361.
Bergerud, A. T. and Gratson, M. W. 1988. Adaptive strategies and population ecology of northern grouse, volume II: theory and synthesis. – Univ. of Minnesota Press.
Braun, C. E. and Schroeder, M. A. 2015. Age and sex identification from wings of sage-grouse. – Wildl. Soc. Bull. 39: 182–187.
Braun, C. E. and Martin, K. 2001. Unusual summer plumage of white-tailed ptarmigan. – Wilson Bull. 113: 373–377.
Braun, C. E. et al. 2015. Fall population structure of sage-grouse in Colorado and Oregon, Wildl. Tech. Rep. 005-2015. – Oregon Dept. of Fish and Wildl.
Braun, C. E. et al. 2020. Body mass and primary molt patterns of greater sage-grouse in Colorado. – W. N. Am. Nat. 80: 330–336.
Connelly, J. W. et al. 2003. Monitoring of greater sage-grouse habitats and populations. – College of Natural Resources Exp. Stn. Bull. 80. Univ. of Idaho.
Connelly, J. W. et al. 2011. Characteristics and dynamics of greater sage-grouse populations. – In: Knick, S. T. and Connelly, J. W. (eds), Greater sage-grouse: ecology and conservation of a landscape species and its habitats. Studies in Avian Biology 38: 53–67.
Doherty, K. E. 2008. Sage-grouse and energy development: integrating science with conservation planning to reduce impacts. – PhD thesis, Univ. of Montana.
Grubb Jr., T. C. 1989. Ptilochronology: feather growth bars as indicators of nutritional status. – Auk 106: 314–320.

Hagen, C. A. and Loughin, T. M. 2008. Productivity estimates from upland bird harvests: estimating variance and necessary sample sizes. – J. Wildl. Manage. 72: 1369–1375.
Hansen, M. et al. 2012. Temporal changes in age and sex ratios of forest grouse harvested in northeastern Oregon. – J. Wildl. Manage. 76: 356–362.
Howell, S. N. G. et al. 2003. The first basic problem: a review of molt and plumage homologies. – Condor 105: 635–653.
Huwer, S. L. et al. 2008. Using human-imprinted chicks to evaluate the importance of forbs to sage-grouse. – J. Wildl. Manage. 72: 1622–1627.
Johnsgard, P. A. 2008. Grouse and quails of North America. – Papers in the biological sciences. Univ. of Nebraska–Lincoln.
Johnsgard, P. A. 2017. The North American quails, partridges and pheasants: their biology and behavior. – Zea E-Books 58. <http://digitalcommons.unl.edu/zeabook/58>.
Johnson, E. I. et al. 2011. Modifications to a molt-based ageing system proposed by Wolfe et al. 2010. – J. Field Ornithol. 82: 422–424.
Johnson, K. H. and Braun, C. E. 1999. Viability and conservation of an exploited sage-grouse population. – Conserv. Biol. 13: 77–83.
Lyons, E. K. et al. 2020. Criteria for sex and age of birds and mammals. – In: Silvy, N. J. (ed.), The wildlife techniques manual, 8th edn. Johns Hopkins Univ. Press, 200–221.
McCaffery, R. and Lukacs, P. M. 2016. A generalized integrated population model to estimate greater sage-grouse population dynamics. – Ecosphere 7: 1–14.
Møller, A. P. and De Lope, F. 1999. Senescence in a short-lived migratory bird: age-dependent morphology, migration, reproduction and parasitism. – J. Anim. Ecol. 68: 163–171.
Murphy, M. E. et al. 1988. Malnutrition during the postnuptial molt of white-crowned sparrows: feather growth and quality. – Can. J. Zool. 66: 1403–1413.
Pyle, P. 2007. Revision of molt and plumage terminology in ptarmigan (Phasianidae: *Lagopus* spp.) based on evolutionary considerations. – Auk 124: 508–514.
Pyle, P. 2008. Identification guide to North American birds, part II. – Slate Creek Press.
Pyrah, D. B. 1954. A preliminary study toward sage grouse management in Clark and Fremont counties, Idaho, based on seasonal movements. – MSc thesis, Univ. of Idaho.
Sage-Grouse Conservation Partnership 2015. The Oregon sage-grouse action plan. – Governor's Natural Resources Office.
Schmutz, J. A. and Hoffman, R. W. 1991. Variable first prebasic primary molt in Rio Grande and Merriam's Wild Turkeys. – Wilson Bull. 103: 295–300.
Schroeder, M. A. et al. 2019. Recovery of greater sage-grouse in Washington: progress report. – Washington Dept. of Fish and Wildl.
Schroeder, M. A. et al. 2020. Greater sage-grouse *Centrocercus urophasianus*, ver. 1.0. – In: Poole, A. F. and Gill, F. B. (eds), Birds of the World. Cornell Lab of Ornithol.
Taylor, R. L. et al. 2012. Managing multiple vital rates to maximize greater sage-grouse population growth. – J. Wildl. Manage. 76: 336–347.
Walker, B. L. 2008. Greater sage-grouse response to coal-bed natural gas development and West Nile virus in the Powder River Basin, Montana and Wyoming, USA. – PhD thesis, Univ. of Montana.
Walker, B. L. et al. 2016. Mapping and prioritizing seasonal habitats for greater sage-grouse in northwestern Colorado. – J. Wildl. Manage. 80: 63–77.
Walker, B. L. et al. 2020. Quantifying habitat loss and modification from recent expansion of energy infrastructure in an isolated, peripheral greater sage-grouse population. – J. Environ. Manage. 255: 109819.
Wann, G. T. et al. 2020. Rates of ovulation and reproductive success estimated from hunter-harvested greater sage-grouse in Colorado. – J. Fish Wildl. Manage. 11: 151–163.
Williams Jr., L. E. and Austin, D. H. 1970. Complete post-juvenal (pre-basic) primary molt in Florida turkeys. – J. Wildl. Manage. 34: 231–233.
Wolfe, J. D. et al. 2010. Using molt cycles to categorize the age of tropical birds: an integrative new system. – J. Field Ornithol. 81: 186–194.
Zwickel, F. C. and Bendell, J. F. 2020. Dusky grouse *Dendragapus obscurus*, ver. 1.0. – In: Rodewald, P. G. (ed.), Birds of the World. Cornell Lab of Ornithol. Ithaca, NY, USA.
Zwickel, F. C. and Dake, J. A. 1977. Primary molt of blue grouse *Dendragapus obscurus* and its relation to reproductive activity and migration. – Can. J. Zool. 55: 1782–1787.