Ornithology

Timing and duration of molt in temperate-zone passerines is shaped by frequency of double brooding, migration distance, and wing length

--Manuscript Draft--

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Abstract:	Previous studies have shown that duration of the post-breeding molt in temperate-zone passerines is inversely related to migration distance. However, it is unclear whether this relationship arises directly—because long-distance migration selects for more rapid molt, or indirectly—because long-distance migration precludes double brooding and allows molt to begin earlier under more favorable environmental conditions. We investigated this issue by examining the effects of migration distance, frequency of double brooding, and wing length on the timing and duration of the post-breeding molt for 33 passerine species captured during banding operations at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Consistent with predictions of the indirect pathway hypothesis, we found that long-distance migration is strongly associated with single brooding, and single-brooded species initiate flight-feather molt about one month earlier than double-brooded species. However, contrary to the predictions of the indirect pathway hypothesis, frequency of double brooding has no effect on molt duration; instead, molt duration increases with increasing wing length and decreases with increasing migration distance. The strong negative relationship between migration distance and molt duration is consistent with the direct pathway hypothesis and suggests that the time constraints imposed by long-distance migration lead directly to natural selection for rapid post-breeding molt. Our results also indicate that the rapid molt of long-distance migrants is achieved by an increase in the number of remiges being replaced simultaneously (molt intensity), and apparently also by an increase in the rate at which remiges grow. Unexpectedly, our estimates of molt duration were bimodally distributed, with 25 species showing rapid molt (40–65 d) and 8 showing slow molt (82–103 d). Overall, our findings clarify the effects of migration distance, double brooding, and wing length on phenology of passerine post-breeding molt, and highlight opportunities to expand avian life-history theory to incorporate interspecific variation in molt strategies.
Response to Reviewers:	

Additional Information:	
Question	**Response**
Have you submitted this article to this journal previously?	Yes
All accepted Research Articles, Perspectives, Commentaries, and Reviews are published with a foreign language abstract (in addition to the English abstract). Which language would you prefer your abstract be translated into? If there is another language you would prefer for your abstract, choose "Other" and provide that foreign language abstract with your submission.	Spanish
Enter the manuscript number if you have it, otherwsie enter "n/a". as follow-up to "Have you submitted this article to this journal previously?"	ORNITH-25-182

Ms. No. ORNITH-25-182
Response to Comments from the Associate Editor and Reviewers
27 March 2026

Editorial and reviewer comments are shown in black plain text. Responses are shown in blue text. Line numbers in the responses refer to the track-changes version of the revision.

Associate Editor and Reviewer comments:

Two reviewers both see a lot of merit in this work and have provided substantial comments to help improve the manuscript. The comments are relatively minor and I think the authors should be able to address everything.

Reviewer #1: This manuscript leverages a long-term banding dataset to examine relationships between the timing/duration of molt and the breeding and migratory life history stages. In particular the authors test hypotheses for direct and indirect pathways by which the time constraints associated with a migratory life history may drive the onset and duration of molt, with the indirect pathway being driven by associated limits migration places on breeding (as measured by propensity for double brooding). I found the manuscript to be generally well written, the analysis to be appropriate, and the results novel. I feel that the study makes important advances in a portion of the annual cycle that is chronically understudied and it provides some compelling results for drivers of its' organization at the population level.

Overall, I only have two somewhat major concerns about the manuscript, both of which should be fairly straight forward to address in revision. Firstly, I found the results section quite verbose and a bit of a slog to get through, which is surprising given the analysis is relatively straight forward and examining a small number of variables. I feel much of the issue arises from the discussion of post hoc analyses that were done on reduced versions of the dataset. Thus, I would suggest summarizing the post hoc modifications that were made in the Methods section and sticking purely to the results in that section. This is particularly true of explanations for why and how different sets were analyzed. I do very much appreciate the summary of the outcomes towards the end of the section, so I would still keep that, given the dataset was analyzed in various ways.
We agree, and have followed this recommendation in the revision (lines 220-238). The main problem we face is that the completely unexpected bimodal distribution of the molt duration data creates analytical problems that simply could not have been anticipated *a priori*. The only solutions, therefore, are either to defer justification of some analytical decisions until after the relevant findings have been presented in the Results—the course we pursued in the original submission—or to foreshadow the relevant findings in the Methods section—the course we now pursue in the revision. We have, however, limited the foreshadowing to the essential statistical details necessary to justify the inclusion of duration models 2 and 3 (Table 2B) in our analysis. Nonetheless, in our revision you will now find references to Tables 1-2 and Figures 2-3 in the Methods section, and some purists may find that objectionable.

My second major concern is that I found the Discussion section short and somewhat lacking in applying the findings here to broader implications, as well as more discussion of the limitations of both examining these relationships at the population scale and the variables utilized. I point out additional specifics below, but two particular things I would like to see addressed are 1) the limitations of utilizing double brooding as the only metric of breeding effort, and 2) how within populations these patterns can be variable at the individual level (and implications therein). For

the former, we know from many studies of passerines that, while double brooding is possible within a particular population, it is not ubiquitous and in some years can be entirely absent, due to annual variations in breeding conditions (e.g., Nagy and Holmes 2005). Furthermore, even in the absence of double brooding, species can vary considerably in propensity for renesting after predation, further causing variation in the timing of the cessation of breeding. Somewhat related to this is the 2nd concern about individual variation. The results are discussed as if patterns are consistent across species, but I find more treatment is necessary around the variation that can occur within a population and how this could impact the relationships between breeding, molt, and migration. Hypotheses for how individuals may balance the costs and benefits of adjusting schedules were presented in the recent perspective piece, which the authors cite in the Introduction (Tsuru and Tonra 2026). While I am not suggesting an extensive review of how those hypotheses apply to the present study, I do think the authors should make clear that the patterns they observe are generalized across a population of each species that is made up of individual responses to environmental conditions, breeding outcomes, and associated downstream effects on molt and, for some species, migration. In particular, they may want to explore how individuals may alter their responses due to annual variation in conditions and, in turn, how that may alter patterns observed in the broader population.
We agree, and have added four paragraphs to the discussion, including paragraphs on (1) the limitations of using qualitative frequency of double brooding as our metric of late-season breeding effort (lines 427-443) and (2) within-population heterogeneity in molt schedules, including individual and annual variation (lines 444-453); however, the main focus of our study is an interspecific comparative analysis that inevitably must largely ignore interesting annual and individual variation in molt schedules within species.

In addition to these overall concerns, below I list some more specific edits/comments.

Line 70 - Perhaps worth noting the exception of a large number of western NA species that exhibit molt-migration
In the revised manuscript we have added a paragraph to the Discussion about molt-migration (lines 409-415). For the Introduction, however, we thought it best not to get into the details of possible exceptions and maintain sharp focus on the two potential explanations for why the duration of post-breeding molt is inversely related to migration distance (Figure 1).

Line 86 - I was expecting it may come up later, but I do not believe it did: What about the implications for plumage quality? Are there potential adaptations to this in some species (e.g. - feather composition)?
There are indeed potential implications of rapid molt for plumage quality, and these are mentioned at several points in the manuscript, including the Introduction (line 59, lines 116-117) and Discussion (lines 359-363).

Line 103 - This pertains to my 2nd major concern above, but we know many individuals in some species will overlap molt with final breeding attempts, including second broods. I believe this should be discussed, given it could be a means by which birds respond to time constraints.
We agree, and we have added a paragraph to the Discussion about how our interspecific comparative analysis inevitably masks interesting within-population variation in molt phenology, and how molting individuals may variably manage potential conflicts and trade-offs with breeding and migration (lines 444-453). As noted above, however, we want the Introduction to be focused on developing the two hypotheses shown in Figure 1, and have limited mention of trade-offs and conflicts to the last sentence of the first paragraph (lines 57-63).

Line 210 - Here is somewhere you could move a lot of the description of responses to patterns found in the dataset from the Results to the Methods. I would note the bimodality here. You don't have to completely exclude this as a finding in the Results, but feel you need to justify this categorization here, as there is no information on the criteria for sorting them.
As noted above, we have followed this recommendation and now foreshadow the bimodality of the molt duration data in the Methods section (lines 220-238.

Line 273 - would add a "respectively" here
Actually the “respectively” was already present (now on line 300), although perhaps not at the location the reviewer was expecting to see it.

Line 288 - I find "linked" to be too strong here, and would keep it to related or correlated.
We agree, and have changed it to “correlated with” (now line 316).

Line 300-308 - run-on sentence, please edit.
We agree, and have split the sentence into two separate sentences (now lines 332-337).

Line 324 - Should ptilochronology be specifically mentioned here?
We appreciate the point, but given that there are multiple ways to study how variation in feather growth rates affects plumage quality, we do not think it is necessary to single out ptilochronology.

Line 345 - Are there any life history similarities within these groups that are worth exploring?
Not that we have been able to discern. However, we have added text to this paragraph highlighting that small, long-distance migrants are more likely to be classified as “fast” molters (lines 366-369).

Line 353 - please elaborate on how there is potential linkage with cavity nesting, as I do not find this intuitive.
We agree that our original phrasing was non-intuitive and confusing. We have revised this section to emphasize that the unusually early molt of the Black-capped Chickadee is likely related to its unique status as the only resident or partial migrant in our dataset that is single-brooded, and perhaps secondarily to the fact that it is also the only cavity-nesting species in our dataset (now lines 391-398).

Line 366 - I feel there needs to be more discussion of molt-migration more broadly, especially since you included a species that exhibits it. How are your results here relevant to hypotheses on the adoption of such a strategy?
We agree, and in the revised manuscript we have added a short paragraph to the Discussion about molt-migration (lines 409-415).

Reviewer #2: The manuscript entitled "Timing and duration of molt in temperate-zone passerines is shaped by frequency of double brooding, migration distance, and wing length" advances our understanding of how migration distance, body size, and brood number affect molt schedules. In particular, it disentangles the effects of migration distance and double brooding to explicitly test two hypotheses on how migration distance may influence molt phenology.

Molt is an important annual cycle stage with important consequences for other life-history stages and overall fitness. Accordingly, the findings presented here are highly relevant for understanding, and potentially conserving, migratory passerines. Through a clear and hypothesis-driven analytical framework, the manuscript addresses knowledge gaps that have remained unresolved in previous research on the factors shaping molt phenology.

Major comments:
The manuscript would benefit from improved consistency in the use of molt terminology. In several places (e.g. line 130), two terms with the same meaning are combined (e.g. "post-breeding prebasic molt"). As this may confuse readers, I recommend consistently using either post-breeding or prebasic throughout the manuscript. In addition, a short but explicit explanation of the chosen term should be provided at its first occurrence, as different terminologies are used in molt research and may not be familiar to all readers (see Kiat 2023, Ibis 165(2)).
We agree, and because our manuscript is really focused on the complete molt that occurs after breeding, and not prebasic molts that occur after migration to the nonbreeding range, in the revised manuscript we consistently use “post-breeding” molt and cite Kiat 2023 in the first paragraph of the Methods section (line 136).

Although the statistical analyses are hypothesis-driven, this is not consistently reflected throughout the manuscript, particularly in the Introduction and Abstract. Only in the Discussion do the authors explicitly frame the direct and indirect pathways as two competing "hypotheses". I recommend introducing these two pathways clearly as hypotheses in the Introduction and using this formulation consistently throughout the manuscript. This would substantially improve conceptual clarity and help guide the reader through the analyses and results.
We agree with this excellent suggestion, and we have revised the Abstract, Introduction, and Figure 1 to clarify that the two pathways are competing hypotheses.

The selection of focal species is clearly described in the Methods. However, I strongly recommend excluding Swainson's Thrush from the main analyses. The results highlight that this species differs markedly from the others in both molt duration and strategy. The distinct biology of molt-migrants makes direct comparisons with the other species questionable. Excluding this species would, in my opinion, substantially improve the generalizability of the findings.
The recommendations of the two reviewers are in direct conflict on this issue, as Reviewer 1 requested greater emphasis and discussion of how our findings relate to molt-migration. We have elected to follow Reviewer 1; although the molt of Swainson’s Thrush is clearly unusual, including the species in our comparative analysis is both illustrative and informative (lines 398-415).

Molt duration is treated both as a categorical and a continuous variable, resulting in two separate PLGS models. How to define molt duration is a conceptual decision, and I recommend choosing a single definition, either categorical or continuous. Presenting both approaches may complicate the interpretation. In general, treating molt duration as a continuous variable may better reflect biological complexity; however, the authors show that molt intensity differs distinctly between the two groups, which could justify a categorical treatment. This decision ultimately lies with the authors, but it should be clearly justified and transparently communicated, rather than explored through parallel models.
The reviewer’s concerns here are related to the unexpected bimodality of the molt duration data, and the statistical problems that such bimodality creates. As noted above, we have tried to clarify the nature of these problems in the revised Methods section, and explain why multiple statistical models for molt duration are useful in this case (lines 220-233). We note here,

however, that molt duration is consistently considered to be continuous dependent variable in all analyses; in molt duration model 2 (Table 2B), the bimodality of the duration data is acknowledged by including the slow/fast dichotomy as a categorical explanatory variable, not as a dependent variable.

Please expand the Discussion to address limitations associated with the estimation of migration distance. Breeding and non-breeding ranges can be extensive, as illustrated by Swainson's Thrush, which may overwinter anywhere from Mexico to Argentina, but also by other species (e.g. Black-and-white Warbler or Gray Catbird) with broad non-breeding distributions around the Gulf of Mexico and the Caribbean. Alternative approaches, such as using morphometric proxies known to correlate with migration distance (e.g. wing formula; Mönkkönen 1995, Evol. Ecol. 9), might yield clearer patterns. In addition, are there local tracking studies that better define the non-breeding ranges of the focal populations? While I fully understand that using the centroid of the potential non-breeding range may be the only feasible approach here, its limitations should be discussed explicitly.
We agree, and we have added a paragraph to the Discussion noting the limitations of our estimates of migration distance and frequency of double brooding, and that our estimates are necessarily rough proxies for more nuanced reality (lines 427-443) Nonetheless, these rough proxies succeed in helping to explain a significant fraction of the interspecific variation in molt schedules.

The results of the Parulidae-specific model should be discussed in more detail. The rationale for analyzing this group separately to compare it with the overall pattern is statistically sound. However, while the results are reported, the Discussion currently lacks interpretation of these findings. Expanding on how these results align with, or differ from, the broader patterns would strengthen the manuscript.
We agree, and we have added a paragraph to the Discussion discussing the Parulid-specific analyses (lines 340-349).

Minor comments:
Overall, the manuscript is well written. However, several long sentences (e.g. lines 5-9, 51-55, 56-61) could be broken down into shorter sentences to improve clarity. In addition, some formulations are repetitive, such as "Unexpectedly, however," which would read more smoothly if only one of these words were used. More generally, I recommend avoiding the use of multiple hyphenated compound terms together (e.g. lines 23, 67, 87). For example, "shorter post-breeding molt" would be easier to read than "short-duration post-breeding molt."
We have shortened two of the noted sentences as requested (now lines 5-9 and 51-57), eliminated the repetitive formulation (line 23), and eliminated the adjacent compound adjectives (now lines 69 and 89).

In a few places, the findings are phrased in very strong or absolute terms (e.g. line 125 "clarifies the role" or line 378 "has clarified"). Given that the authors correctly acknowledge the importance of other, unmeasured factors, I suggest moderating these formulations accordingly.
We have not followed this recommendation, as the OED definition of *clarify*—"make (a statement or situation) less confused and more clearly comprehensible"—indicates that our usage is appropriate and does not imply absolute clarity.

Line 5: I recommend starting the Abstract with a brief introduction to molt and its importance for the annual cycle and birds' fitness. This context is provided in the Introduction and Lay Summary but is currently missing from the Abstract.

While we enthusiastically agree in principle, at 297 words we are up against the 300-word limit for the Abstract, and adding introductory material about molt would require elimination of text that describes some of our key findings. We do not believe that this trade-off is worth it, especially because, as the Reviewer notes, some of this context is provided in the Lay Summary.

The authors mention in the Methods (line 142) that the study focuses on species with a complete post-breeding molt. This should already be stated in the Introduction. Similarly, the focus on the molt of remiges should be mentioned earlier in the Introduction, rather than only in the Methods (line 134).
We agree, and we have revised the final paragraph of the Introduction to incorporate both points (lines 125-132).

Lines 107-114 may be overly detailed for the Introduction and might fit better in the Discussion. In my view, it would be sufficient to introduce the two pathway hypotheses, briefly refer to the supporting evidence, and then focus on the study's predictions, leaving more detailed discussion for later.
We appreciate and understand this concern. However, the indirect pathway hypothesis is novel, and in our view requires full context, development, and supporting evidence to convince readers that it is a viable alternative explanation for the strong negative association between migration distance and molt duration. We have therefore made no changes to the text here (now lines 106-117).

In line 124, the study site is briefly mentioned. The Introduction would benefit from a slightly more detailed description of the study system, including a clear statement that most species breed at the study site and some information on where focal species spend the non-breeding period.
We have not followed this suggestion, for two reasons: (1) in our view the goals and objectives outlined in the Introduction are intelligible without the requested details about the study system, and (2) the requested details emerge in the first subsection of the Methods section; it would be redundant to touch upon them in both places. We have, however, provided additional details about the Powdermill study site and netting effort in lines 136-141 of the Methods (see comment below).

Line 131: Please provide a few additional details on the banding effort. For example, is this a constant-effort scheme? Are birds trapped daily? What trapping methods were used?
We agree that more detail about the mist-netting effort at Powdermill would be helpful to readers, and we now provide this context on lines 136-141.

The statistical approach using PGLS models and controlling for normality represents good practice. However, I did not find information on whether collinearity among predictors was assessed and, if so, how it was handled. In addition, model performance should be reported in the main text (not only in Tables 2 and 3), and the R^2 values should be interpreted in the Discussion.
In the revision, we have added a new paragraph at the end of the Methods section that focuses on PGLS model validation, and it includes information about predictor collinearity, residuals, and overall model performance as indicated by adjusted R^2 values (lines 234-238). However, we have not otherwise followed the suggestion to report all R^2 values in the text, as AOS publication guidelines imply that information reported in tables and figures should not be repeated in the text, and vice versa. We have also not interpreted R^2 values in the Discussion,

as we think it unnecessary and redundant given the new Methods paragraph on model validation.

Line 204: Please clarify whether the predictor variables are treated as categorical or continuous.
We have added these clarifications, now lines 213-215.

Line 204: Wing length and migration distance are measured on different scales. Were the variables standardised to allow comparison of effect sizes?
We did not think it necessary to calculate effect sizes, which primarily protect against finding statistically significant but trivial effects in large samples, for two reasons: (1) Our comparative analysis is based on a small sample of species (33) that vary considerably in both timing and duration of molt (Figure 2), reducing the probability of finding statistically significant effects that are biologically trivial. (2) The figures generally provide clear visual indications of the relative magnitude of the effects we report.

Lines 233-241: The reported differences in molt intensity between slow and fast molting groups, as well as the effect of double brooding on migration distance and molt onset, remain largely descriptive. Including simple statistical tests (e.g. t-tests) could strengthen the support for these patterns.
We now report the PGLS t-test and *P*-value for the difference in molt intensity between slow and fast molters (lines 261-262). However, the statistical details for the effects of double brooding on migration distance and molt onset are noted in the legend for Figure 4, and following AOS guidelines are not repeated in the text.

Generally, effect sizes and p-values are often missing from the Result section text and are only presented in tables or figures. I recommend reporting these values also in the main text.
Again, we are following AOS guidelines to avoid this kind of repetition.

Lines 277-283: I suggest deleting this summary within the Results section, as it is repetitive of the preceding text and not strictly necessary.
Here is another situation where the recommendations of the two reviewers are in conflict, as Reviewer 1 explicitly noted that “I do very much appreciate the summary of the outcomes towards the end of the section.” We have elected to retain it (now lines 305-311), as the bimodality of the molt duration data makes straightforward statistical interpretation challenging and the summary useful.

The bimodal distribution of molt duration is described as "surprising" (line 325) and "unexpected" (line 327). If this result was indeed unexpected, the corresponding prediction and supporting references should be made explicit. Otherwise, a more neutral formulation may be more appropriate.
We have changed “surprising” to “unexpected” (line 364); we think this word choice is appropriate because there is simply no *a priori* reason to expect that interspecific variation in molt duration would show a bimodal distribution.

Lines 333-345: The critical discussion of previous studies (Morrison et al. 2015; de la Hera et al. 2009) is important and well argued in terms of methodological differences. However, I miss a discussion of the biological interpretation of the patterns observed in the present study. Speculating on possible biological mechanisms could help guide future research by formulating clear, testable predictions and would strengthen the conclusions.
This comment is similar to one made by Reviewer 1, and we have added text to this paragraph noting that migration distance and wing length appear to be important contributors to the

slow/fast molt dichotomy, and that long-winged residents and short-distance migrants are more likely to be slow molters (lines 366-368). However, we are reluctant to propose any hypotheses for why the dichotomy exists until convincing evidence becomes available that the bimodality is not simply an artifact of non-random species sampling in our dataset.

Lines 385-388: In the final sentence of the Conclusion, the authors state that migration distance is a key factor. Linking this result more explicitly to potential fitness consequences and conservation implications, such as potential effects of time pressure during molt on flight performance or predator avoidance, could further strengthen the manuscript, particularly in the context of declining long-distance migrants.
This is an excellent suggestion, and we have revised the last two sentences of the concluding paragraph accordingly (lines 467-472).

The authors used molt data collected over approximately two decades. Did the authors test for temporal trends across years? Given expected effects of climate change on molt and migration, exploring temporal patterns and potentially incorporating environmental variables (e.g. temperature) could be informative.
This is an excellent suggestion for future work, but really beyond the scope of the current manuscript, which is focused on an interspecific variation only. However, one of the new paragraphs added to the discussion now raises the possibility of long-term changes in molt schedules driven by climate change (lines 444-453).

Several references are missing DOIs and should be completed.
We followed AOS reference guidelines, which do not include DOIs for standard journal articles.

I suggest moving Table 1 to the supplementary material, as it is very detailed and not essential for the main text. In addition, Table 3 (warbler-specific results) could also be considered for the supplementary material, as it represents a complementary analysis rather than a core result.
We appreciate the concern and suggestion, but in our view Table 1 is the heart and soul of the paper, as it provides the essential molt parameter estimates for the comparative analyses that follow. We therefore feel strongly that it should be included in the main manuscript. Regarding Table 3, the suggestion to move it to the Supplemental Material is somewhat in conflict with the suggestion above that more discussion of the warbler results was needed, so we have elected to retain Table 3.

Finally, I encourage the authors to share both data and code on a publicly available repository to facilitate transparency and advance research based on these novel and valuable findings.
Following AOS guidelines, we will share the data on Dryad.

Timing and duration of molt in temperate-zone passerines is shaped by frequency of double brooding, migration distance, and wing length

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Ethics statement

Molt data were collected during routine bird-banding operations and associated field research at Powdermill Avian Research Center, and authorized under a series of banding permits from the U. S. Bird Banding Laboratory and the Pennsylvania Game Commission.

Conflict of interest statement

The authors declare that they have no conflict of interest.

Author contributions

R.S.M. and D.N. collected, curated, maintained, and provisionally analyzed the Powdermill molt data. All three authors conceived and initiated the project. R.L.M fully analyzed the data and prepared an initial draft of the manuscript, and all three authors contributed to editing and revising the manuscript.

Data availability

If the manuscript is accepted for publication, data will be archived at the data depository Dryad.

Timing and duration of molt in temperate-zone passerines is shaped by frequency of double brooding, migration distance, and wing length

ABSTRACT

Previous studies have shown that duration of the post-breeding molt in temperate-zone passerines is inversely related to migration distance. However, it is unclear whether this relationship arises directly—because long-distance migration selects for more rapid molt, or indirectly—because long-distance migration precludes double brooding and allows molt to begin earlier under more favorable environmental conditions. We investigated this issue by examining the effects of migration distance, frequency of double brooding, and wing length on the timing and duration of the post-breeding molt for 33 passerine species captured during banding operations at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Consistent with predictions of the indirect pathway hypothesis, we found that long-distance migration is strongly associated with single brooding, and single-brooded species initiate flight-feather molt about one month earlier than double-brooded species. However, contrary to the predictions of the indirect pathway hypothesis, frequency of double brooding has no effect on molt duration; instead, molt duration increases with increasing wing length and decreases with increasing migration distance. The strong negative relationship between migration distance and molt duration is consistent with the direct pathway hypothesis and suggests that the time constraints imposed by long-distance migration lead directly to natural selection for rapid post-breeding molt. Our results also indicate that the rapid molt of long-distance migrants is achieved by an increase in the number of remiges being replaced simultaneously (molt intensity), and apparently also by an increase in the rate at which remiges grow. Unexpectedly, our estimates of molt

duration were bimodally distributed, with 25 species showing rapid molt (40–65 d) and 8 showing slow molt (82–103 d). Overall, our findings clarify the effects of migration distance, double brooding, and wing length on phenology of passerine post-breeding molt, and highlight opportunities to expand avian life-history theory to incorporate interspecific variation in molt strategies.

Keywords: body size, double brooding, migration distance, molt, passerines, phenology, post-breeding molt, songbirds, wing length

LAY SUMMARY

- Adults of most songbird species in the northern temperate zone completely replace the feathers in their plumage during an annual post-breeding molt.
- Because it is energetically and nutritionally demanding, molt is usually scheduled to avoid overlap with two other demanding phases of the songbird annual cycle, breeding and migration.
- We investigated how migration distance, the frequency of double brooding, and wing length influence the timing and duration of post-breeding molt in 33 songbird species captured during banding operations at Powdermill Avian Research Center in southwest Pennsylvania, USA.
- Our results indicate that long-distance migrants are usually single-brooded, and single-brooded species initiate molt about one month earlier than double-brooded species that typically continue nesting through late summer.

- Although larger birds have longer molt durations, molt duration nonetheless decreases with increasing migration distance, suggesting that the time constraints imposed by long-distance migration lead directly to natural selection for rapid post-breeding molt.

INTRODUCTION

Molt is one of the most challenging phases of the avian annual cycle, as the replacement of feathers in the plumage is energetically and nutritionally demanding (Murphy and King 1992, Murphy 1996, Jenni and Winkler 2020). Molt can also produce temporary but significant deficits in flight performance (Swaddle and Witter 1997, Hedenström 2023) and thermoregulatory efficiency (Dolnik and Gavrilov 1979, Schieltz and Murphy 1997), compounding the difficulties molting birds face in safely acquiring the calories and protein required to renew their plumage. Because of these challenges, molt is usually temporally segregated from two other demanding phases of the avian annual cycle, reproduction and migration, as overlap can be costly and lead to conflicts and trade-offs affecting plumage quality, parental care, foraging behavior, offspring recruitment, migratory behavior, survival, and other traits (Hemborg and Lundberg 1998, Hemborg 1999, Stutchbury et al. 2011, Echeverry-Galvis and Hau 2012, 2013; Kiat et al. 2019, Mumme 2018, Jenni and Winkler 2020, Tsuru and Tonra 2025).

The timing and duration of molt are therefore crucial components of avian life history, especially for small passerines that typically undergo a complete annual molt that must be scheduled in a way that minimizes its potential negative impact on reproduction and survival (Holmgren and Hedenström 1995, Barta et al. 2007, Kiat et al. 2019, Jenni and Winkler 2020). Molt phenology is particularly important for migratory temperate-zone passerines with a complete post-breeding molt; in these species, molt has the potential to conflict with late-season

reproduction and parental care on the front end (Hemborg 1999, Mumme 2018), and with timely migratory preparation and departure on the back end (Stutchbury et al. 2011, Tsuru and Tonra 2025).

Two factors known to influence the duration of post-breeding molt in passerines are body size and migration distance (de la Hera et al. 2009, Kiat et al. 2019, Jenni et al. 2020, Jenni and Winkler 2020). Larger birds with longer flight feathers require disproportionately more time to complete molt because of allometric relationships among body size, lengths of the flight feathers, and feather growth rates (Rohwer et al. 2009, Jenni et al. 2020). In passerines, sexual dimorphism in body size and wing length is likely to contribute to the widespread observation that the duration of flight-feather molt is typically longer for males than females (Mumme et al. 2025b). Migration distance has also long been recognized as an important determinant of molt speed, as populations and species that are either non-migratory or short-distance migrants typically have a slower pace of molt and longer molt durations than those with greater migration distances (Lundberg and Eriksson 1984, Kjellén 1994, Voelker and Rohwer 1998, de la Hera et al. 2009, Kiat et al. 2019, Jenni and Winkler 2020). For passerines, the most comprehensive analysis of the effects of body size and migration distance on post-breeding molt duration is that of de la Hera et al. (2009); based on molt data for 48 species of European passerines drawn from Ginn and Melville (1983), larger and more sedentary species have molt durations that are greater than those of smaller and more migratory species (de la Hera et al. 2009).

Long-distance migration can lead to a shorter post-breeding molt via two different hypothetical pathways. In the direct pathway hypothesis (Figure 1A), the time constraints imposed by long-distance migration lead directly to natural selection for a rapid post-breeding molt, as shortening the period of molt frees additional time for successful completion of

migration (e.g., Lundberg and Eriksson 1984, Voelker and Rohwer 1998, de la Hera et al. 2009, Kiat et al. 2019) and reduces the potential for conflicts and trade-offs between molt and migration (e.g., Stutchbury et al. 2011, Tsuru and Tonra 2025). However, a second pathway, one that is indirect and based on the effects of migration distance on the frequency of double brooding, can also produce the observed association between migration distance and molt duration. In this indirect, reproduction-mediated hypothesis (Figure 1B), the time constraints imposed by long-distance migration lead first to a low frequency of double brooding, a relationship that is well documented in temperate-zone passerines (Martin 1995, Böhning-Gaese et al. 2000, Bruderer and Salewski 2008, Winger and Pegan 2021). The early cessation of reproduction by long-distance migrants may then facilitate an early onset of molt (e.g., Mulvihill et al. 2009), which occurs under favorable mid-summer conditions and may proceed more rapidly than in double-brooded species molting later under shorter days and potentially less favorable late-summer conditions (Figure 1B).

Some evidence suggests that the indirect, reproduction-mediated pathway is plausible. For example, double-brooded species of migratory New World warblers (family Parulidae) breeding in eastern North America initiate molt later than single-brooded species (Mumme et al. 2021), a result that is expected given the general temporal segregation of reproduction and molt. Surprisingly, however, late-molting warblers also molt at a slower pace, a result contrary to the expectation that late-molting species would be under strong migratory time constraints and would have an accelerated pace of molt. One possible explanation for the slow molt of late-molting warblers is that unfavorable environmental conditions in late summer select for longer molt durations (Mumme et al. 2021); shorter days, less time for foraging, and perhaps reduced food availability may make rapid late-summer molt prohibitively costly in terms of energetics,

and perhaps also in terms of resulting plumage quality (Dawson et al. 2000, de la Hera et al. 2010, Vágási et al. 2012).

The relative contributions of the direct and indirect pathways in producing the strong negative association between migration distance and molt duration are unknown. Thus, the inverse relationship between the two variables could arise because: (1) long-distance migrants are under direct selection to molt rapidly, (2) the frequent double brooding and delayed molt of residents and short-distance migrants select for a slow pace of molt, or (3) both processes are important (Figure 1). Here, our objective is to address this issue and to tease apart the interacting effects of migration distance, double brooding, and body size on interspecific variation in the timing and duration of the post-breeding molt in temperate-zone passerines. Drawing on molt data collected at a single banding station in eastern North America, we analyze estimates of the onset and duration of flight-feather molt for 33 species of passerines that undergo a complete post-breeding molt at our study site. Our comparative analysis extends earlier groundbreaking work on the determinants of molt duration in European passerines (de la Hera et al. 2009) and clarifies the roles that migration distance and double brooding have on interspecific variation in molt phenology.

METHODS

Collection of Molt Data

Data on passerine post-breeding molt (Kiat 2023) were collected 1986–2004 in association with year-round netting and banding operations at Powdermill Avian Research Center (40.164°N, 79.267°W) in southwestern Pennsylvania, USA (Mumme et al. 2025a,b). Mist nets were located in a 10-ha area of shrubby second growth adjacent to deciduous forest, ponds, and agricultural

land. Weather permitting, netting and banding occurred 5–6 days per week, beginning 1 h before sunrise and ending mid-afternoon. Each banded bird was assigned a total remex molt score (0–90), primarily by one individual (RSM), based on the molt status of the 18 remiges (9 primaries and 9 secondaries) on the right wing, using the 0–5 molt scoring system of Ginn and Melville (1983): 0 = old feather, 1 = old feather missing or new pin feather, 2 = new feather emerging from sheath up to one-third grown, 3 = new feather between one-third and two-thirds grown, 4 = new feather more than two-thirds grown but still sheathed at base, and 5 = fully grown new feather with no trace of the sheath. In a subset of captured individuals, scores were also recorded for each of the 18 remiges, allowing calculation of molt intensity, which for this analysis we defined as the number of remiges being actively replaced (i.e., with molt score 1–4) during mid-molt, when molt was 20–80% completed (total molt score 18–72).

Our analysis focused on species that undergo a complete post-breeding molt at our study site, and we excluded species or individuals having partial or suspended molts. Additional criteria for species inclusion were either: (1) at least 20 records of birds in active molt, i.e., with remex molt score 1–89, or (2) at least 15 records of birds in active molt with some data from individuals recaptured during the same molt cycle, as recapture data substantially improve estimation of molt parameters (Boersch-Supan et al. 2024, Mumme et al. 2025a). A total of 33 species from 11 passerine families, with a combined 3,324 records of birds in active molt, including 2,068 records of molt intensity, are included in the final dataset (Table 1).

All but 1 of the 33 species examined breed locally in the Powdermill area; the exception is the molt-migrant *Catharus ustulatus* (Swainson’s Thrush; Cherry 1985), which we included because individuals of this species regularly initiate and complete molt during their migratory stopover at Powdermill before continuing south to their nonbreeding range in Central and South

America. Of the remaining 32 species, 24 are completely migratory at Powdermill and 5 are partial migrants, i.e., migratory species whose nonbreeding range includes the Powdermill region; for these species, the local breeding population may comprise a mix of individuals that migrate after completing molt and others that remain resident through the winter (Table 1). We classified 3 species—*Poecile atricapillus* (Black-capped Chickadee), *Haemorhous mexicanus* (House Finch), and *Cardinalis cardinalis* (Northern Cardinal)—as nonmigratory permanent residents; although some individuals in northeastern *H. mexicanus* populations may migrate short distances, the great majority appear to be nonmigratory (Badyaev et al. 2020, Fink et al. 2025).

Estimation of Molt Parameters

We estimated molt start date and molt duration for the 33 species using methods developed and described previously (Mumme et al. 2025a,b). In brief, individual molt scores of birds in active molt were expressed as the proportion of remex molt completed and then arcsine-transformed to linearize the molt process and account for its slow progression at the earliest and latest stages of molt, when few remiges are being actively replaced. Transformed molt scores were then rescaled as a proportion, allowing mean ± SE molt start date and molt duration to be taken directly from estimates of the intercept and slope of regression equations obtained via either Pimm mixed-model regression (Mumme et al. 2025a), for 29 species where data were available for individuals recaptured during the same molt cycle, or standard Pimm regression (Pimm 1976), for 4 species where recapture data were lacking. These methods produce accurate and unbiased estimates of molt phenology whenever molt data are collected across a broad range of dates, and are unaffected by molt-dependent sampling bias, which is widespread in the Powdermill data

(Mumme et al. 2025a). Tabular and graphical presentations of the molt data for the 33 species are provided in Table 1 and Supplementary Material Figure S1.

Ecological and Morphological Explanatory Variables

We examined how interspecific variation in molt phenology is influenced by two ecological and one morphological explanatory variables: estimated migration distance, frequency of double brooding, and wing length. To estimate migration distance for the 25 completely migratory species, we used the range maps available at Birds of the World (Billerman et al. 2025) and the polygon tool of the image analysis program Fiji (Schindelin et al. 2012) to estimate the centroid of the stationary nonbreeding range; we then calculated the distance between the centroid and Powdermill. For the 5 species of partial migrants (Table 1), we used the centroid of the portion of the nonbreeding range located to the south of Powdermill. The 3 species considered to be permanent residents were assigned a migration distance of 0. For frequency of double brooding, we used the 33 species accounts at Birds of the World (Billerman et al. 2025) to qualitatively determine if double brooding was described as occasional, regular, or frequent (scored as 1 or "Yes"; 19 species) vs. absent or rare (scored as 0 or "No"; 14 species) for breeding populations in the Powdermill region. Data on wing length, a strong indicator of overall body size and one that is particularly relevant to remex molt, were obtained from birds measured during banding at Powdermill (Mulvihill et al. 2004).

Statistical Analysis

In most analyses we controlled for the non-independence resulting from shared evolutionary histories via Phylogenetic Generalized Least Squares (PGLS) regression. PGLS regressions were

run with the R package *caper* version 1.04 (Orme et al. 2025) under R version 4.5.1 (R Core Team 2025) based on a phylogeny (Supplementary Material Figure S2) of the 33 species in our dataset drawn from McTavish et al. (2025) using the R package *clootl* version 0.1.2 (Cornell Lab of Ornithology Open Tree of Life, Aves tree 1.5, 2023 taxonomy; Miller et al. 2025).

Our general approach was to build PGLS regression models for molt start date and molt duration that included all 3 explanatory variables: estimated migration distance (continuous), wing length (continuous), and frequency of double brooding (categorical). Initial models included interaction terms, but non-significant interactions were excluded from final models (Table 2). To determine if similar statistical patterns were evident within the single family best represented in the dataset, we also built comparable PGLS models restricted to the 13 species of New World warblers (Parulidae).

Because of unexpected strong bimodality in the molt duration data (Figure 2), our initial PGLS model for all 33 species (duration model 1) explained a relatively small proportion of the interspecific variation in molt duration (adjusted $R^2 = 0.29$, Table 2B). We therefore built two additional PGLS models of molt duration to account for and incorporate this unanticipated bimodality; for these analyses we excluded frequency of double brooding as an explanatory variable, as duration model 1 (Table 2B) showed that it has virtually no effect on molt duration. In molt duration model 2, we included the slow/fast molt duration dichotomy (Figure 2) as a categorical explanatory variable along with migration distance and wing length (Table 2B). In duration model 3, we included molt intensity (Figure 3) as a continuous explanatory variable along with migration distance and wing length (Table 2B). Duration models 2 and 3 explained a substantially higher proportion of the total interspecific variation in molt duration, with adjusted R^2 values of 0.84 and 0.79, respectively (Table 2B).

Across all PGLS models, predictor variables showed weak collinearity (correlation coefficients < 0.6 and variance inflation factors < 2.0), and all residuals approximated a normal distribution (Supplementary Material Figure S3). With the exception of molt duration model 1 (discussed above), PGLS model performance was generally good, with adjusted R^2 values of 0.55–0.92.

RESULTS

Variation in Molt Phenology, Migration Distance, and Double Brooding

The 33 passerine species included in the analysis vary considerably in both timing and duration of the post-breeding molt (Table 1, Supplementary Material Figure S1). Estimates of molt start date encompass a range of 101 days, from ordinal day 148 (28 May) for *Poecile atricapillus* (Black-capped Chickadee) to ordinal day 249 (6 Sep) for *Spinus tristis* (American Goldfinch). Interspecific variation in molt duration was also substantial, from 40 days in the molt-migrant *Catharus ustulatus* (Swainson's Thrush) to 103 days in *Bombycilla cedrorum* (Cedar Waxwing; Table 1).

Although the data for molt start date closely approximate a normal distribution, data for molt duration do not (Figure 2); molt duration shows a pronounced bimodal distribution, with 25 species of "fast" molters (molt duration 40–65 days) and 8 species of "slow" molters (molt duration 82–103 days). The 8 slow-molting species include all 3 (100%) of the nonmigratory resident species included in the dataset (*P. atricapillus, Haemorhous mexicanus* [House Finch], and *Cardinalis cardinalis* [Northern Cardinal]), 2 (40%) of the 5 species that are partial migrants (*B. cedrorum* and *Haemorhous purpureus* [Purple Finch]), and 3 (12%) of the 25 completely migratory species, *Sayornis phoebe* (Eastern Phoebe) and two members of the family

Cardinalidae (*Pheucticus ludovicianus* [Rose-breasted Grosbeak] and *Piranga olivacea* [Scarlet Tanager]; Figure 2).

The bimodal interspecific variation in molt duration is strongly reflected by variation in molt intensity, the number of remiges on the right wing being replaced simultaneously during mid-molt (Figure 3). Mean ± SD molt intensity is 4.4 ± 0.5 for the 8 slow-molting species, but 6.8 ± 0.8 for the 25 fast-molting species (PGLS t = -3.83, $P < 0.001$).

Interspecific variation in estimated migration distance and molt start date is closely associated with the frequency of double brooding (Figure 4). The 14 species where double brooding is absent or rare have a longer mean ± SD migration distance (3174 ± 1455 km) and an earlier onset of molt (2 Jul, ordinal day 183 ± 16 d) in comparison to the 19 species with regular or frequent double brooding (1668 ± 949 km and 1 Aug, ordinal day 213 ± 17 d; Figure 4).

Factors Affecting Molt Start Date

PGLS regression indicates that the frequency of double brooding has a strong positive effect on the estimated date of molt onset, even after controlling for the effects of migration distance and wing length (Table 2A). The PGLS regression coefficients relating molt start date to estimated migration distance and wing length are negative, suggesting an earlier molt onset as migration distance and body size increase, but neither effect was statistically significant (Table 2A).

Factors Affecting Molt Duration

PGLS duration model 1 indicates that estimated migration distance and wing length are both significant predictors of molt duration (Table 2B); molt duration decreases with increasing migration distance, but increases with increasing wing length. The frequency of double brooding,

in contrast, has no significant effect on molt duration once the effects of migration distance and wing length are statistically controlled.

In duration model 2 (Table 2B), which includes the slow/fast molt dichotomy (Figure 2) as a categorical explanatory variable, migration distance is a strong negative predictor of molt duration, indicating that long migration routes are associated with a shorter duration of molt even after controlling for the slow/fast dichotomy (Figure 5A). Wing length, in contrast, has no overall or consistent effect on molt duration after controlling for the slow/fast dichotomy (Figure 5B; Table 2B). However, a weak but significant interaction between migration distance and wing length (Table 2B, duration model 2) suggests that while wing length has little or no effect on molt duration for short-distance migrants, it has a more pronounced positive effect for long-distance migrants.

In duration model 3 (Table 2B), migration distance and wing length respectively have strong negative and positive effects on molt duration even after controlling for variation in molt intensity (Figure 6). In addition, we found a strong significant interaction between molt intensity and wing length, suggesting that variation in intensity has a more pronounced effect on molt duration for large birds than for small birds (Table 2B, duration model 3; Figure 6).

In summary: (1) Migration distance has a strong and consistent negative effect on molt duration, even after controlling for variation in molt intensity and the slow/fast bimodality of the observed molt duration data. (2) Wing length is an important predictor of the slow/fast dichotomy in molt duration, and has generally positive effects on molt duration through its interactions with migration distance and molt intensity. (3) Frequency of double brooding has no effect on molt duration once the effects of migration distance and wing length are controlled statistically.

Factors Affecting Molt Phenology in the Parulidae

Estimated migration distance is a significant negative predictor of both the timing and duration of molt for the 13 species of New World warblers included in the dataset (Table 3, Figure 7A, B). Frequency of double brooding is positively correlated with molt start date (Figure 7C), but wing length is not a significant predictor of either timing or duration of molt in warblers (Table 3).

DISCUSSION

The goals of our study were: (1) to clarify the roles that migration distance, frequency of double brooding, and wing length (body size) play in shaping interspecific variation in the phenology of post-breeding molt in temperate-zone passerines, and (2) to assess the relative importance of the direct and indirect (reproduction-mediated) pathways (Figure 1) in contributing to the inverse relationship between migration distance and molt duration. Consistent with the indirect pathway hypothesis (Figure 1B), we found strong evidence that the frequency of double brooding in 33 North American temperate-zone passerines is associated with both shorter migration distances (Figure 4A) and later molt initiation dates (Figures 4B, 7C), and that frequency of double brooding is the primary factor that determines the timing of post-breeding molt (Tables 2A, 3A). However, contrary to the prediction of the indirect pathway hypothesis, we found that the frequency of double brooding has no effect on molt duration once the effects of migration distance and wing length are statistically controlled. Instead, molt duration increases with increasing wing length and decreases with increasing migration distance (Tables 2B, 3B), a result consistent with previous studies (Rohwer et al. 2009, de la Hera et al. 2009, Kiat et al.

2019, Jenni et al. 2020). It is also consistent with the direct pathway hypothesis (Figure 1A), suggesting that the time constraints imposed by long-distance migration lead directly to natural selection for rapid post-breeding molt. Thus, while frequency of double brooding is more important than migration distance in determining the timing of post-breeding molt, migration distance is more important than frequency of double brooding in determining its duration.

Separate analyses restricted to the 13 species of parulid warblers corroborate these conclusions; warbler species with regular or frequent double brooding initiate molt significantly later than single-brooded species, and long-distance migration is significantly associated with a shorter molt duration (Table 3, Figure 7). Our analysis of the warblers, however, produced two findings that differ from those obtained for the entire dataset: (1) Migration distance has a significant negative effect on the date of molt onset in warblers (Table 3A, Figure 7), a relationship that was negative but not statistically significant in the entire dataset (Table 2A). (2) Wing length has no significant positive effect on molt duration in warblers (Table 3B), a finding that may be related to the relatively limited range of wing lengths present within the Parulidae (Figure 5).

Rapid flight-feather molt in birds is usually achieved by increasing molt intensity—the number of remiges being replaced simultaneously—rather than by increasing the rate at which individual remiges grow (de la Hera et al. 2011, Rohwer and Rohwer 2013). Our results, however, suggest that both processes may be important in explaining the rapid molts of long-distance migrant passerines. As other studies have also shown (de la Hera et al. 2011, Rohwer and Rohwer 2013), we found that molt duration decreases with increasing molt intensity (Figure 3). But when molt intensity is included as an explanatory variable in a phylogenetically-controlled statistical model (Table 2B, duration model 3), molt intensity and migration distance

both have significant negative effects on molt duration (Figure 6), suggesting that long-distance migrants increase molt speed via a mechanism separate from an increase in molt intensity. This evidence, however, is indirect, and studies that directly measure feather growth rates are needed to determine if long-distance migrants grow feathers more rapidly during molt, and if more rapid feather growth compromises plumage quality (Dawson et al. 2000, de la Hera et al. 2010, 2011; Vágási et al. 2012, Rohwer and Rohwer 2013).

One of the unexpected results of our study is that estimates of molt duration for the 33 focal passerine species show a bimodal distribution (Figure 2), with 25 species having rapid molt (duration 40–65 d) and 8 having slow molt (duration 82–103 d). Migration distance and wing length both appear to be important predictors of the bimodality, with small, long-distance migrants disproportionately represented in the "fast" group (Figure 5). Although this bimodality could be simply an artifact of non-random species sampling in our dataset, it is also possible that the bimodality reflects fundamentally different strategies of post-breeding molt employed by temperate-zone passerines. For example, Morrison et al. (2015) detected a similar bimodality in duration of the post-breeding molt for 15 species of passerines from the United Kingdom, with 5 species of fast molters (duration 67–80 d) and 10 species of slow molters (duration 94–111 d). However, the results of Morrison et al. (2015) should be viewed with some caution, for two reasons. First, their estimates of molt duration were based on methods (Underhill and Zucchini 1988, Erni et al. 2013) that can produce inaccurate estimates of molt phenology under molt-dependent sampling bias, which appears to be common in temperate-zone passerines (Boersch-Supan et al. 2024, Mumme et al. 2025a); indeed, the estimates of molt duration reported by Morrison et al. (2015) average 50% greater than comparable estimates reported for the same species by Ginn and Melville (1983; figure 1 in de la Hera et al. 2009), and many of the

367 estimates for long-distance migrants appear to be unrealistically large. Second, de la Hera et al.
368 (2009, figure 2) found no evidence of bimodality in estimates of molt duration in a larger sample
369 (48 species) of passerines drawn from Ginn and Melville (1983). Thus, it remains uncertain
370 whether the bimodality we observed in molt duration (Figure 2) is biologically meaningful or
371 artifactual; additional studies of post-breeding molt in temperate-zone passerines are needed to
372 answer this question.

373 Two species in our comparative analysis are notable for the exceptional timing or
374 duration of their post-breeding molt. First, *Poecile atricapillus* (Black-capped Chickadee) has an
375 extraordinarily early mean molt start date (28 May; Table 1, Figure 2) and a prolonged, low-
376 intensity molt (97 d) that is unexpected for a bird of its relatively small size (Table 1, Figures 3,
377 5B). These unusual molt characteristics are undoubtedly related to its breeding biology; *P.*
378 *atricapillus* is the only single-brooded species among the 8 species in our dataset that are either
379 non-migratory or partially migratory (Table 1, Figure 4A). In addition, it is the only cavity-
380 nesting species in our dataset, and cavity-nesting passerines often have unusual constellations of
381 life-history traits that differ from those of open-cup nesters (Martin and Li 1992, Martin 1995,
382 Winger and Pagan 2021). Second, the molt-migrant *Catharus ustulatus* (Swainson's Thrush) has
383 an extraordinarily rapid (40 d), high-intensity molt (Table 1, Figures 2, 3), a finding that is
384 consistent with previous work (Cherry 1985) but surprising given the species' relatively large
385 size (Figure 5B). Because molting individuals at our study site in southwestern Pennsylvania had
386 already migrated from breeding areas in boreal forests to the north, in comparison to other
387 single-brooded species *C. ustulatus* initiates molt exceptionally late as well (Figure 4B), with a
388 mean start date of 8 Aug (Table 1). How *C. ustulatus* supports its rapid, high-intensity molt
389 under relatively short late-summer days is an intriguing question for future research; for

example, actively molting individuals of this species may eat proportionately more insects and less fruit than purely migratory individuals (Blanc-Benigeri et al. 2024), a finding consistent with the high protein demands of rapid molt.

Our findings for *Catharus ustulatus* also provide indirect support for the leading hypothesis for the evolution of molt-migration: that poor late-summer resource availability on the breeding grounds selects for migration to more resource-rich areas that can better support the energetic and nutritional demands of molt (Rohwer et al. 2005, Pageau et al. 2020). Although we do not have data on late-summer resource availability in their boreal forest breeding areas, the extraordinarily rapid, high-intensity molt of *C. ustulatus* at Powdermill (Figures 2, 3) would clearly not be possible without the availability of rich food resources to support it.

Our study has focused on how interspecific variation in post-breeding molt phenology is affected by the frequency of double brooding, migration distance, and wing length; other factors, however, may also contribute to interspecific variation in the timing and duration of molt in passerines. For example, species that regularly fly long distances as part of routine foraging flights appear to have slow, low-intensity molts, presumably because they can ill afford the aerodynamic costs associated with rapid, high-intensity molt (Kiat et al. 2016). Although we did not explicitly investigate this possibility, variation in foraging flight behavior could explain some of the interspecific variation in molt duration we observed in our dataset. *Bombycilla cedrorum* (Cedar Waxwing), for example, is nomadic and wanders widely in search of fruit during its post-breeding molt (Witmer et al. 2020), and this almost certainly is a contributing factor to its unusually slow, low-intensity molt (Table 1, Figure 3).

One of the limitations of our study is that our estimates of two key explanatory variables, migration distance and frequency of double brooding, are less than ideal. We estimated

migration distance for the 30 migratory species in our dataset as the distance between Powdermill and the approximate centroid of the nonbreeding range, which provides at best only a rough approximation of true migration distance. Ideally, we would have data derived from modern avian tracking technologies (Torstenson et al. 2024) showing nonbreeding home range and migration routes for a large sample of individuals from each species, allowing precise estimation of both mean and variation in true migration distance. Frequency of double brooding in our analyses was summarized as a qualitative (categorical) predictor variable, with 19 species where double brooding was considered to be occasional, regular, or frequent, and 14 species where it was considered to be absent or rare. Ideally, for each of the 33 species in our analysis we would have accurate quantitative estimates of the frequency of double brooding, and also complete information on the timing and duration of nesting and post-fledging parental care. Despite these deficiencies, our rough approximations of migration distance and frequency of double brooding performed well, and in conjunction with other predictor variables helped to explain a significant fraction of the interspecific variation in the onset and duration of post-breeding molt (Tables 2, 3).

A general feature of interspecific comparative analyses such as ours is that important intraspecific and within-population variation is lost when variables of interest are condensed to species-typical values. It is therefore important to acknowledge that the estimates of molt onset and duration for our 33 focal species (Table 1) are multi-year population averages that mask important within-species heterogeneity in molt schedules, including heterogeneity due to sex- and age-based variation (Mumme et al. 2025b), annual variation (Tattoni et al. 2025), long-term responses to climate change (Tomotani et al. 2018), and other factors. Within-population variation in reproduction and molt schedules can also lead to individual differences in how

molting birds manage conflicts and potential trade-offs with parental care and migration (Hemborg 1999, Mulvihill et al. 2009, Stutchbury et al. 2011, Mumme 2018, Tsuru and Tonra 2025).

In conclusion, our study has clarified how interspecific variation in the phenology of post-breeding molt in temperate-zone passerines is shaped by migration distance, the frequency of double brooding, and wing length. While the frequency of double brooding is the most important variable contributing to interspecific variation in the timing of molt, migration distance and wing length are the most important variables contributing to interspecific variation in its duration, with longer migration distances and shorter wings leading to more rapid, short-duration molt. Our study contributes to the growing body of evidence that migration distance is a key factor in the evolution of passerine life history strategies (Martin 1995, Böhning-Gaese et al. 2000, Bruderer and Salewski 2008, de la Hera et al. 2009, Winger and Pagan 2021), and highlights the opportunity to explicitly incorporate data on the timing and duration of molt into avian life history theory (Martin 2004). Our findings also underscore the tight time limitations that long-distance migration places on temperate songbirds, in many cases constraining their options to single brooding and reduced annual fecundity (Bruderer and Salewski 2008, Winger and Pagan 2021), a high-intensity molt that compromises flight performance (Mumme et al. 2021, Hedenström 2023), or both. These constraints are likely to exacerbate the daunting conservation challenges facing migratory songbirds (Rosenberg et al. 2019).

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Table 1. Estimates of mean ± standard error (SE) ordinal start date and duration of post-breeding molt for 33 species of passerines captured during banding operations at Powdermill Avian Research Center in southwestern, Pennsylvania, USA. Molt parameters were estimated with either Pimm mixed model regression, for 29 species with data from individuals recaptured during the same molt cycle, or standard Pimm regression, for 4 species without recapture data. Four-letter species codes used in the figures and migratory status at Powdermill (CM = completely migratory, PM = partially migratory, R = resident) are also shown for each species.

Species	Family	*n*	Ordinal molt start date ± SE	Molt duration (d) ± SE
Sayornis phoebe (Eastern Phoebe, EAPH), CM	Tyrannidae	23	186.7 ± 3.5	96.2 ± 4.9
Vireo griseus (White-eyed Vireo, WEVI), CM	Vireonidae	74	203.1 ± 1.5	61.5 ± 1.8
Poecile atricapillus (Black-capped Chickadee, BCCH), R	Paridae	24	147.9 ± 4.6	97.4 ± 7.6
Bombycilla cedrorum (Cedar Waxwing, CEDW), PM	Bombycillidae	79	234.0 ± 2.4	102.9 ± 4.8
Dumetella carolinensis (Gray Catbird, GRCA), CM	Mimidae	148	210.8 ± 1.2	51.2 ± 2.1
Hylocichla mustelina (Wood Thrush, WOTH), CM	Turdidae	31	203.9 ± 2.8	65.2 ± 4.6
Catharus ustulatus (Swainson's Thrush, SWTH), CM	Turdidae	37	220.2 ± 2.1	39.8 ± 0.6
Catharus fuscescens (Veery, VEER), CM	Turdidae	115	192.4 ± 1.1	47.7 ± 1.8
Haemorhous mexicanus (House Finch, HOFI), R	Fringillidae	33	196.6 ± 3.3	96.8 ± 3.6
Haemorhous purpureus (Purple Finch, PUFI), PM	Fringillidae	68	205.0 ± 2.7	89.0 ± 4.0
Spinus tristis (American Goldfinch, AMGO), PM	Fringillidae	523	249.3 ± 0.7	61.9 ± 1.6
Spizella passerina (Chipping Sparrow, CHSP), CM	Passerellidae	24	226.2 ± 4.7	50.5 ± 7.9
Spizella pusilla (Field Sparrow, FISP), PM	Passerellidae	32	230.2 ± 2.5	55.1 ± 3.9
Melospiza melodia (Song Sparrow, SOSP), PM	Passerellidae	48	223.7 ± 1.8	61.9 ± 2.3
Pipilo erythrophthalmus (Eastern Towhee, EATO), CM	Passerellidae	23	218.0 ± 1.8	60.3 ± 1.3
Icteria virens (Yellow-breasted Chat, YBCH), CM	Icteriidae	17	189.1 ± 3.5	51.1 ± 1.6
Seiurus aurocapilla (Ovenbird, OVEN), CM	Parulidae	125	186.1 ± 1.1	55.7 ± 1.4
Parkesia motacilla (Louisiana Waterthrush, LOWA), CM	Parulidae	51	170.2 ± 1.5	51.4 ± 2.1
Vermivora chrysoptera (Golden-winged Warbler, GWWA), CM	Parulidae	33	173.3 ± 1.9	52.6 ± 2.4
Geothlypis formosa (Kentucky Warbler, KEWA), CM	Parulidae	69	191.3 ± 1.8	53.9 ± 2.5

Geothlypis trichas (Common Yellowthroat, COYE), CM	Parulidae	285	209.6 ± 0.8	55.8 ± 0.8
Mniotilta varia (Black-and-white Warbler, BAWW), CM	Parulidae	120	180.6 ± 1.4	56.2 ± 1.1
Setophaga ruticilla (American Redstart, AMRE), CM	Parulidae	576	177.3 ± 0.6	51.2 ± 0.8
Setophaga citrina (Hooded Warbler, HOWA), CM	Parulidae	157	201.3 ± 1.3	56.0 ± 1.1
Setophaga americana (Northern Parula, NOPA), CM	Parulidae	20	191.9 ± 7.1	54.2 ± 13.7
Setophaga magnolia (Magnolia Warbler, MAWA), CM	Parulidae	33	202.0 ± 2.4	57.9 ± 1.4
Setophaga petechia (Yellow Warbler, YEWA), CM	Parulidae	71	174.1 ± 1.2	43.7 ± 1.1
Setophaga pensylvanica (Chestnut-sided Warbler, CSWA), CM	Parulidae	33	199.9 ± 2.5	50.9 ± 1.2
Setophaga virens (Black-throated-Green Warbler, BGGN), CM	Parulidae	60	193.5 ± 3.0	53.6 ± 4.8
Pheucticus ludovicianus (Rose-breasted Grosbeak, RBGR), CM	Cardinalidae	125	184.7 ± 0.7	82.6 ± 1.8
Passerina cyanea (Indigo Bunting, INBU), CM	Cardinalidae	181	225.0 ± 1.1	51.8 ± 1.1
Cardinalis cardinalis (Northern Cardinal, NOCA), R	Cardinalidae	25	235.4 ± 6.4	84.5 ± 12.6
Piranga olivacea (Scarlet Tanager, SCTA), CM	Cardinalidae	61	184.4 ± 1.9	81.6 ± 4.5

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Table 2. Phylogenetic Generalized Least Squares (PGLS) regression models examining the effects of migration distance, wing length, and frequency of double brooding on molt start date (A) and molt duration (B) in 33 species of temperate-zone passerines sampled at Powdermill Avian Research Center in southwestern Pennsylvania, USA. For molt duration, two additional PGLS models that include either the dichotomy between slow and fast molters (Figure 2) or molt intensity (Figure 3) as explanatory variables are also shown. Normal quantile-quantile plots of the residuals for all four models are provided in Supplementary Material Figure S3.

A. Molt start date				
Start date model 1: Molt start date ~ Migration distance + Wing length + Double brooding (adjusted R^2 = 0.55)				
Term	Estimate	SE	*t*	*P*
Intercept	193.5	28.0	6.91	< 0.001 *
Migration distance	-0.00384	0.00255	-1.50	0.14
Wing length	-0.0975	0.258	-0.38	0.71
Double brooding (Yes)	20.7	4.43	4.66	< 0.001 *
B. Molt duration				
Duration model 1: Molt duration ~ Migration distance + Wing length + Double brooding (adjusted R^2 = 0.29)				
Term	Estimate	SE	*t*	*P*
Intercept	49.2	19.3	2.55	0.016 *
Migration distance	-0.00514	0.00176	-2.92	0.007 *
Wing length	0.511	0.177	2.88	0.007 *
Double brooding (Yes)	-0.302	3.05	-0.10	0.92
Duration model 2: Molt duration ~ Migration distance × Wing length + Slow/fast molt (adjusted R^2 = 0.84)				
Term	Estimate	SE	*t*	*P*
Intercept	86.5	12.3	7.03	< 0.001 *
Migration distance	-0.0138	0.00402	-3.47	0.002 *

Wing length	-0.239	0.142	-1.68	0.10
Slow/fast molt (Slow)	30.8	3.25	9.48	< 0.001 *
Migration distance × wing length	0.000129	0.0000469	2.76	0.01 *
Duration model 3: Molt duration ~ Migration distance + Wing length × Molt intensity (adjusted R^2 = 0.79)				
Term	Estimate	SE	*t*	*P*
Intercept	-28.5	26.2	-1.09	0.29
Migration distance	-0.00451	0.000855	-5.27	< 0.001 *
Wing length	1.99	0.339	5.87	< 0.001 *
Molt intensity	14.3	4.03	3.54	0.001 *
Wing length × Molt intensity	-0.276	0.0547	-5.05	< 0.001 *

629 * indicates a statistically significant effect

Table 3. Phylogenetic Generalized Least Squares (PGLS) regression models examining the effects of migration distance, wing length, and frequency of double brooding on molt start date (A) and molt duration (B) in 13 species of migratory New World warblers (family Parulidae) sampled at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Normal quantile-quantile plots of the residuals for both models are provided in Supplementary Material Figure S3.

A. Molt start date				
Warbler start model 1: Molt start date ~ Migration distance + Wing length + Double brooding (adjusted R^2 = 0.92)				
Term	Estimate	SE	*t*	*P*
Intercept	243.1	17.6	13.81	< 0.001 *
Migration distance	-0.0138	0.00288	-4.79	< 0.001 *
Wing length	-0.332	0.216	-1.54	0.56
Double brooding (Yes)	13.3	2.49	5.37	< 0.001 *
B. Molt duration				
Warbler duration model 1: Molt duration ~ Migration distance + Wing length + Double brooding (adjusted R^2 = 0.64)				
Term	Estimate	SE	*t*	*P*
Intercept	69.7	10.6	6.55	< 0.001 *
Migration distance	-0.00602	0.00174	-3.45	0.007 *
Wing length	0.00735	0.130	0.06	0.96
Double brooding (Yes)	1.13	1.50	0.75	0.47

* indicates a statistically significant effect

Figure 1. Two hypothetical pathways by which long-distance migration can lead to short-duration post-breeding molt in temperate-zone passerines. In the direct pathway hypothesis (A), the strong time constraints imposed by long-distance migration lead directly to selection for more rapid molt. In the indirect (reproduction-mediated) pathway hypothesis (B), the time constraints imposed by long-distance migration result in a low incidence of double brooding and an earlier onset of molt under more favorable environmental conditions. In contrast, regular or frequent double-brooding by short-distance migrants and residents leads to a delayed molt under less favorable conditions—e.g., short late-summer days and declining food availability—that may prohibit rapid molt and select for slow, long-duration molt.

Figure 2. Frequency distributions and the relationship between molt duration and ordinal molt start date for 33 species of temperate-zone passerines sampled at Powdermill Avian Research Center in southwest Pennsylvania, USA. While molt start date closely fits a normal distribution (Anderson-Darling $A^2 = 0.24$, $P = 0.77$), molt duration does not ($A^2 = 2.66$, $P < 0.001$); it is bimodally distributed in the Powdermill sample, with 25 species showing rapid molt (duration 40–65 days) and 8 showing slow molt (duration 82–103 days). A bimodal normal 2-mixture distribution is a more appropriate fit to the duration data than is a unimodal skewed SHASH (sinh-arcsinh) distribution for both the raw data (AICc = 261.6 vs. 269.1, respectively) and $\log_{10}$-transformed data (AICc = -63.8 vs. -55.5, respectively). After controlling for the dichotomy between slow and fast molters, molt start date has a weak but significant positive effect on molt duration (Phylogenetic Generalized Least Squares regression coefficient = 0.114 ± 0.048, t = 2.37, $P = 0.02$). Plotted lines portray standard linear regression equations for slow and fast molters. Individual species are identified by the four-letter codes shown in Table 1.

Figure 3. Bimodal interspecific variation in molt duration is in large part reflected by variation in molt intensity, the number of remiges on the right wing being simultaneously replaced during the middle stages of molt. The Phylogenetic Generalized Least Squares regression equation is $y = -6.78x + 116.9$ ($t = -5.19$, $P < 0.001$, adjusted $R^2 = 0.45$). Individual species are identified by the four-letter codes shown in Table 1.

Figure 4. Box plots showing that regular or frequent double brooding is strongly associated with both shorter migration distances (A) and later molt start dates (B) in the 33 species of temperate-zone passerines included in our analysis. Phylogenetic Generalized Least Squares (PGLS) models indicate that species with regular or frequent double brooding have significantly shorter migration distances ($t = -3.19$, $P = 0.003$) and significantly later molt initiation dates ($t = 6.24$, $P < 0.001$) than those for species where double brooding is absent or rare. Individual species are identified by the four-letter codes shown in Table 1.

Figure 5. Effects of estimated migration distance (A) and wing length (B) on molt duration for 33 species of slow- and fast-molting temperate-zone passerines. Note in panel (A) that long-distance migration is associated with both a higher probability of categorization as a fast molter and a shorter duration of molt within each category. In contrast, short-winged birds are more likely to be categorized as fast molters, but wing length has no consistent effect on molt duration within categories (B). Plotted lines portray standard linear regression equations for slow and fast molters. Individual species are identified by the four-letter codes shown in Table 1.

Figure 6. Predictions of a Phylogenetic Generalized Least Squares (PGLS) regression model examining the effects of migration distance, wing length, and molt intensity on molt duration in

33 species of temperate-zone passerines (Table 2B, duration model 3). Note that: (1) Even after controlling for variation in molt intensity, migration distance has a strong and consistent negative effect on molt duration. (2) Long-winged species generally have longer molt durations than short-winged species. (3) Wing length and molt intensity interact such that molt intensity has a proportionally greater negative effect on molt duration for long-winged species.

Figure 7. Migration distance and frequency of double brooding have strong effects on the timing and duration of molt in 13 species of migratory warblers (family Parulidae) sampled at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Warbler species with longer migrations initiate molt earlier (A) and complete it more rapidly (B) than those with shorter migrations, and single-brooded species initiate molt earlier than species that are frequently double-brooded (C). Plotted lines portray standard linear regression equations, but coefficients of the complete Phylogenetic Generalized Least Squares (PGLS) regression models are provided in Table 3. Individual species are identified by the four-letter codes shown in Table 1.

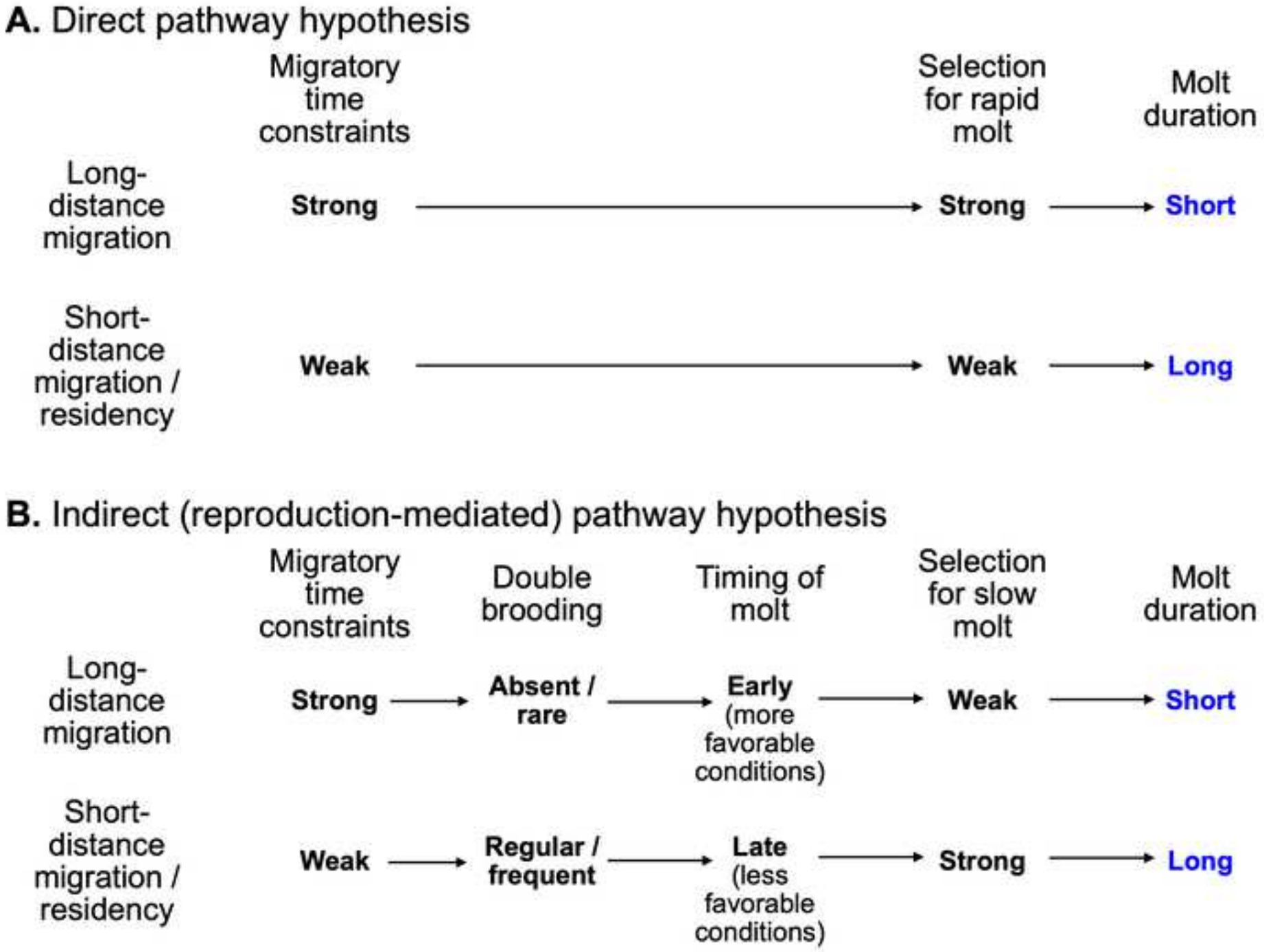

Figure 2

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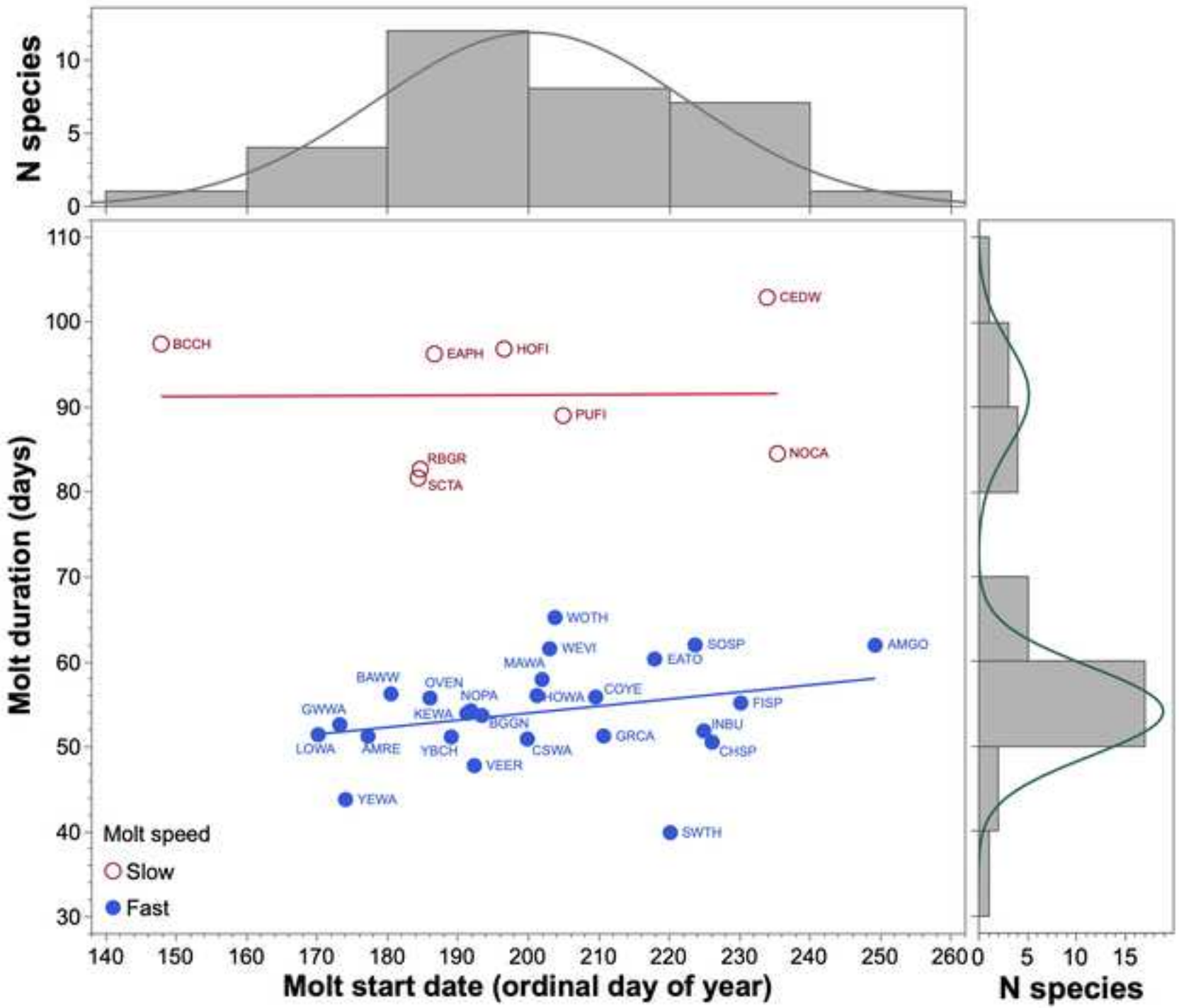

Figure 3

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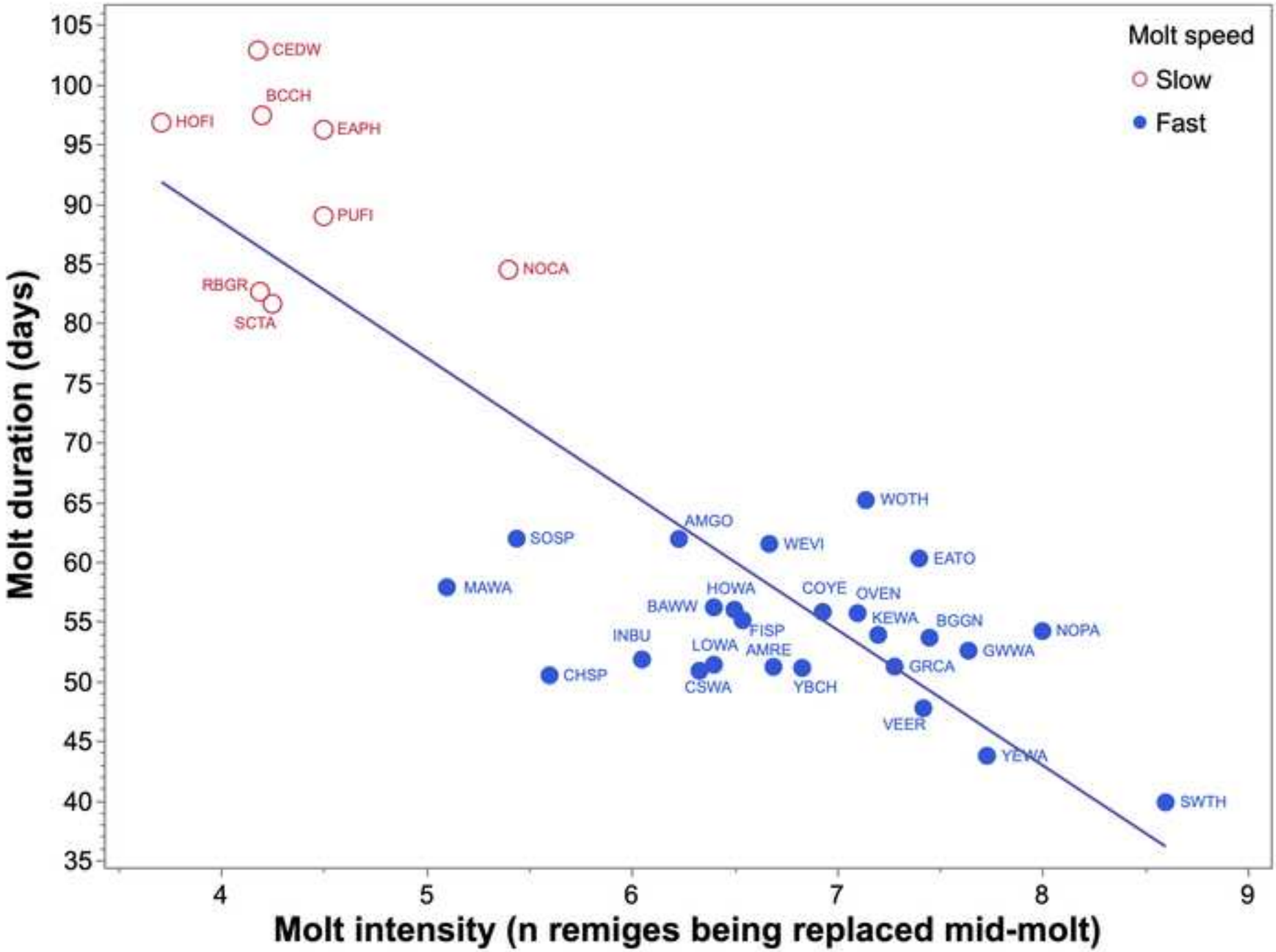


Figure 4

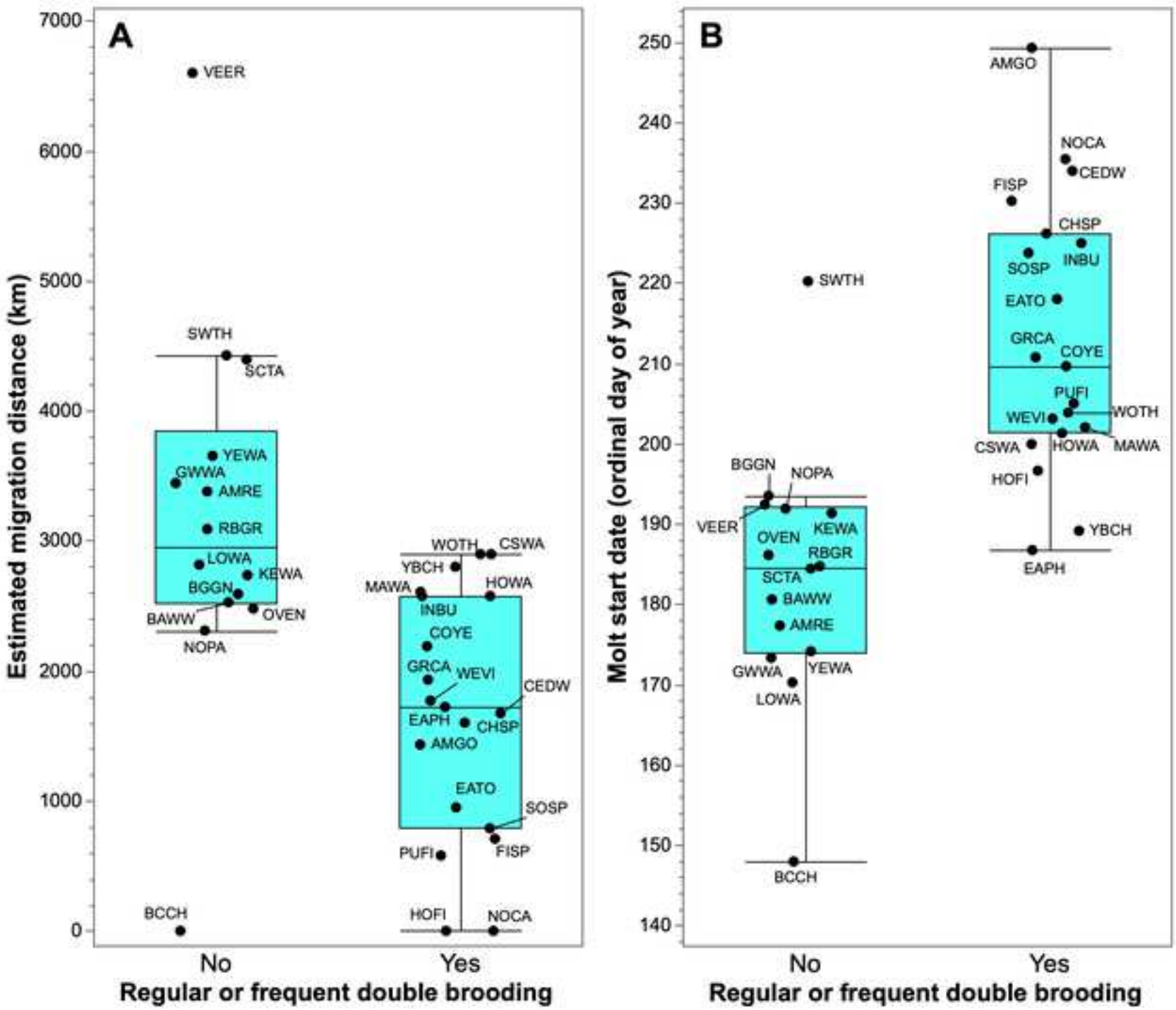


Figure 5

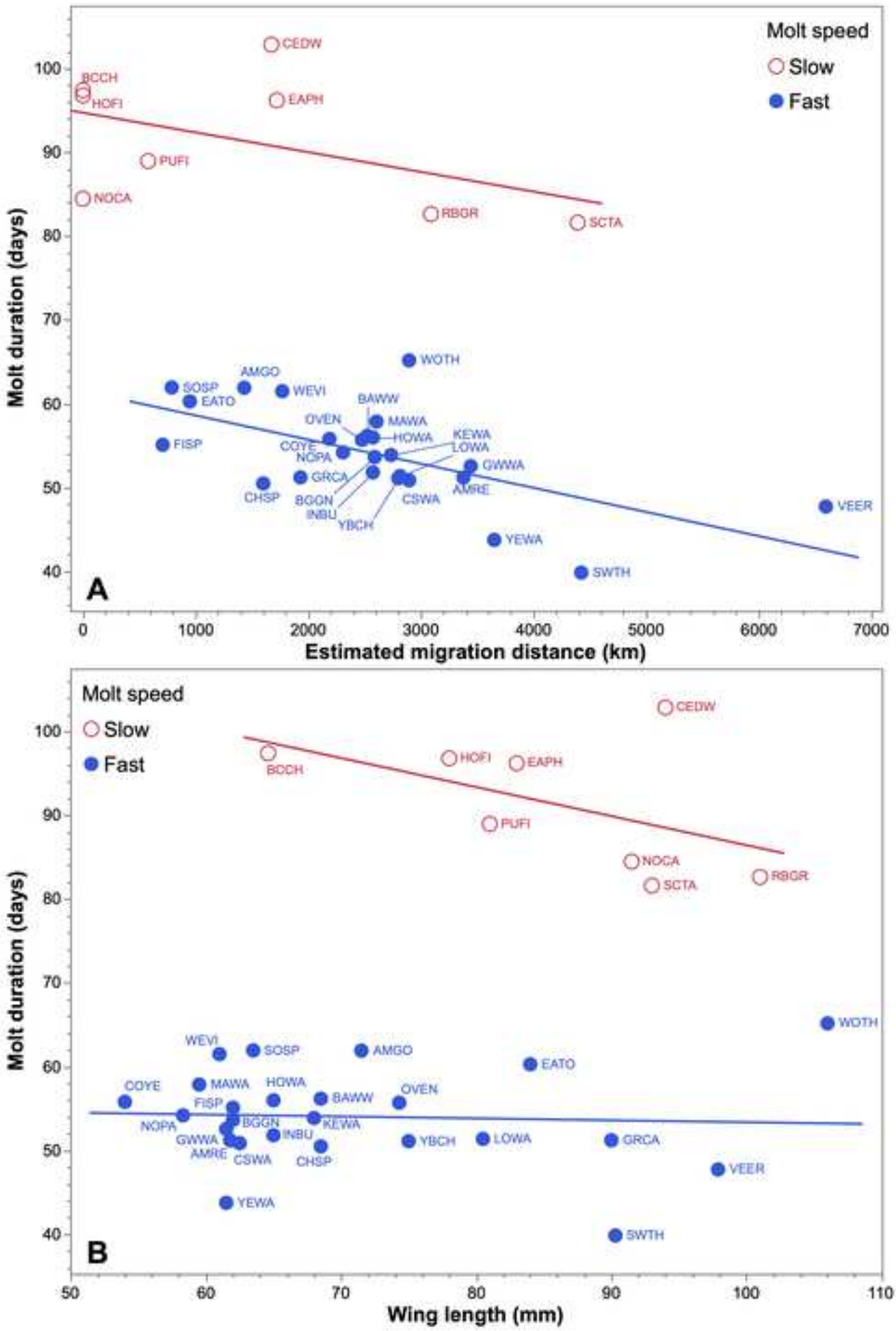


Figure 6

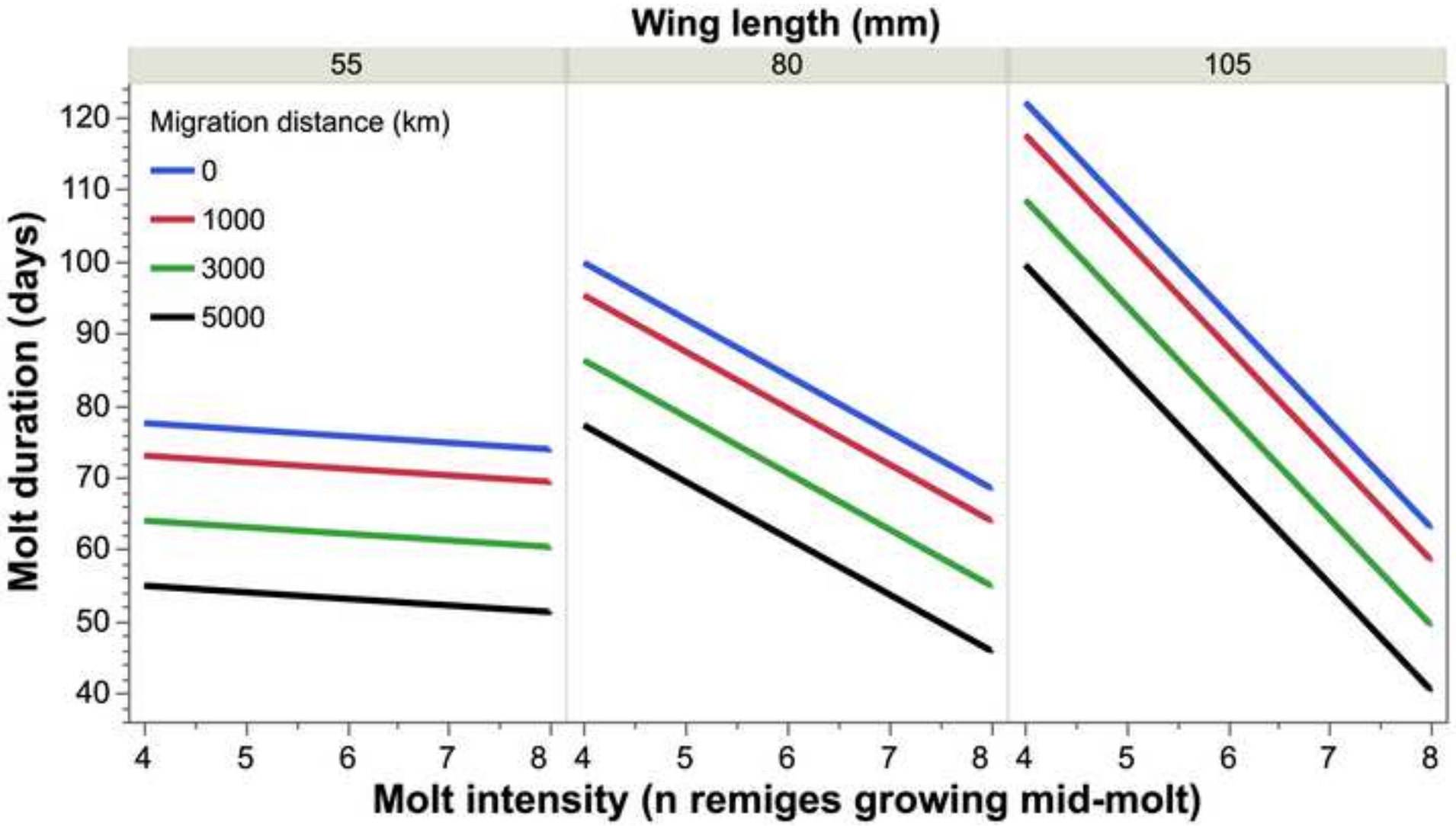
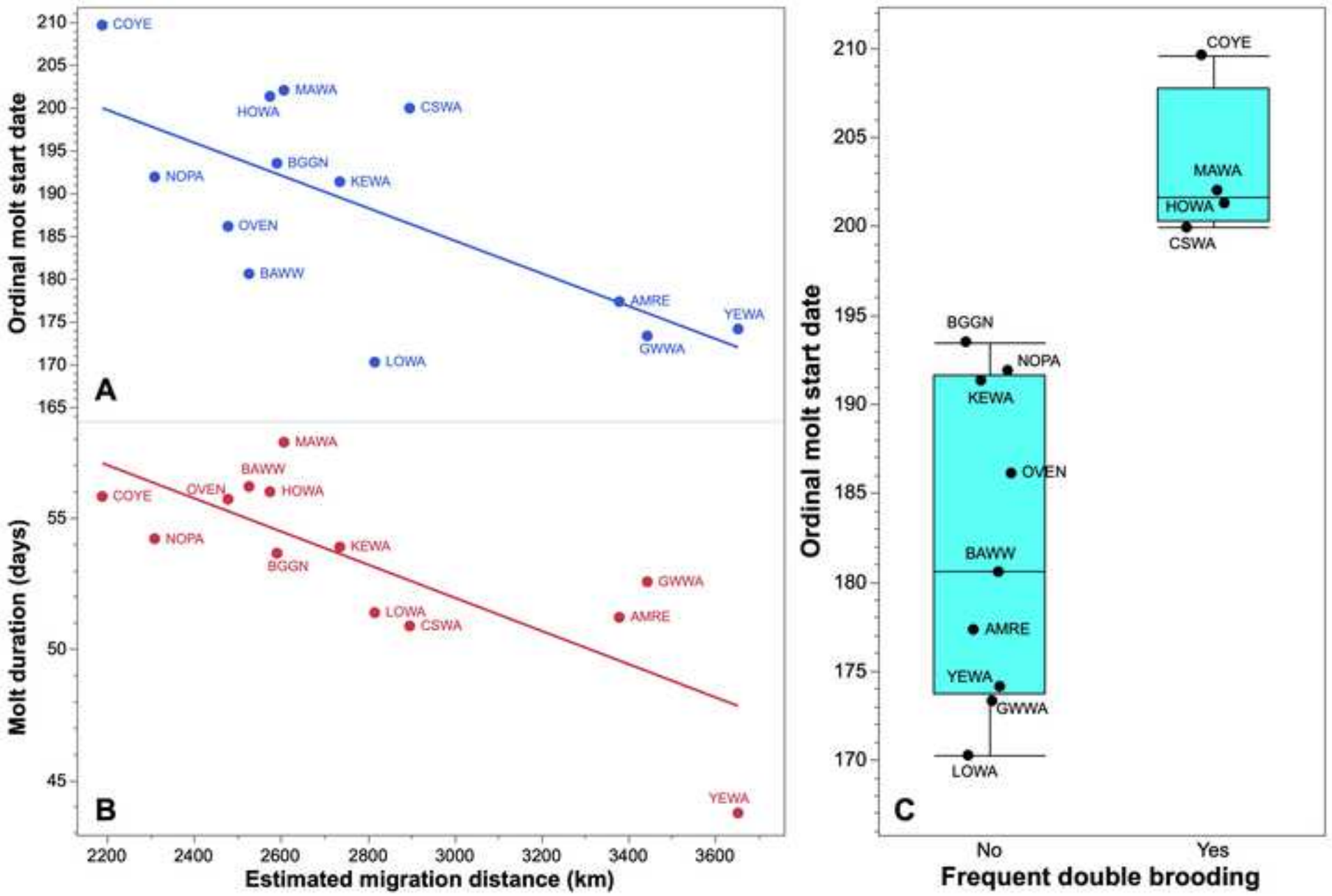


Figure 7



Timing and duration of molt in temperate-zone passerines is shaped by frequency of double brooding, migration distance, and wing length

ABSTRACT

Previous studies have shown that duration of the post-breeding molt in temperate-zone passerines is inversely related to migration distance~~;~~. However, ~~but~~ it is unclear whether this relationship arises directly—because long-distance migration selects for more rapid molt, or indirectly—because long-distance migration precludes double brooding and allows molt to begin earlier under more favorable environmental conditions. We investigated this issue by examining the effects of migration distance, frequency of double brooding, and wing length on the timing and duration of the post-breeding ~~prebasic~~ molt for 33 passerine species captured during banding operations at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Consistent with predictions of the indirect pathway hypothesis, we found that long-distance migration is strongly associated with single brooding, and single-brooded species initiate flight-feather molt about one month earlier than double-brooded species. However, contrary to the predictions of the indirect pathway hypothesis, frequency of double brooding has no effect on molt duration; instead, molt duration increases with increasing wing length and decreases with increasing migration distance. The strong negative relationship between migration distance and molt duration is consistent with the direct pathway hypothesis and suggests that the time constraints imposed by long-distance migration lead directly to natural selection for rapid post-breeding molt. Our results also indicate that the rapid molt of long-distance migrants is achieved by an increase in the number of remiges being replaced simultaneously (molt intensity), and apparently also by an increase in the rate at which remiges grow. Unexpectedly, ~~however,~~ our estimates of

molt duration were bimodally distributed, with 25 species showing rapid molt (40–65 d) and 8 showing slow molt (82–103 d). Overall, our findings clarify the effects of migration distance, double brooding, and wing length on phenology of passerine post-breeding molt, and highlight opportunities to expand avian life-history theory to incorporate interspecific variation in molt strategies.

Keywords: body size, double brooding, migration distance, molt, passerines, phenology, post-breeding molt, ~~prebasic molt,~~ songbirds, wing length

LAY SUMMARY

- Adults of most songbird species in the northern temperate zone completely replace the feathers in their plumage during an annual post-breeding molt.
- Because it is energetically and nutritionally demanding, molt is usually scheduled to avoid overlap with two other demanding phases of the songbird annual cycle, breeding and migration.
- We investigated how migration distance, the frequency of double brooding, and wing length influence the timing and duration of post-breeding molt in 33 songbird species captured during banding operations at Powdermill Avian Research Center in southwest Pennsylvania, USA.
- Our results indicate that long-distance migrants are usually single-brooded, and single-brooded species initiate molt about one month earlier than double-brooded species that typically continue nesting through late summer.

- Although larger birds have longer molt durations, molt duration nonetheless decreases with increasing migration distance, suggesting that the time constraints imposed by long-distance migration lead directly to natural selection for rapid post-breeding molt.

INTRODUCTION

Molt is one of the most challenging phases of the avian annual cycle ~~(Jenni and Winkler 2020). T~~, as the replacement of feathers in the plumage is energetically and nutritionally demanding (Murphy and King 1992, Murphy 1996, Jenni and Winkler 2020). Molt~~, and~~ can also produce temporary but significant deficits in flight performance (Swaddle and Witter 1997, Hedenström 2023) and thermoregulatory efficiency (Dolnik and Gavrilov 1979, Schieltz and Murphy 1997), compounding the difficulties molting birds face in safely acquiring the calories and protein required to renew their plumage. Because of these challenges, molt is usually temporally segregated from two other demanding phases of the avian annual cycle, reproduction and migration, as overlap can be costly and lead to conflicts and trade-offs affecting plumage quality, parental care, foraging behavior, offspring recruitment, migratory behavior, survival, and other traits (Hemborg and Lundberg 1998, Hemborg 1999, Stutchbury et al. 2011, Echeverry-Galvis and Hau 2012, 2013; Kiat et al. 2019, Mumme 2018, Jenni and Winkler 2020, Tsuru and Tonra 2025).

The timing and duration of molt are therefore crucial components of avian life history, especially for small passerines that typically undergo a complete annual molt that must be scheduled in a way that minimizes its potential negative impact on reproduction and survival (Holmgren and Hedenström 1995, Barta et al. 2007, Kiat et al. 2019, Jenni and Winkler 2020). Molt phenology is particularly important for migratory temperate-zone passerines with a

complete post-breeding ~~pre-migratory~~ molt; in these species, molt has the potential to conflict with late-season reproduction and parental care on the front end (Hemborg 1999, Mumme 2018), and with timely migratory preparation and departure on the back end (Stutchbury et al. 2011, Tsuru and Tonra 2025).

Two factors known to influence the duration of post-breeding molt in passerines are body size and migration distance (de la Hera et al. 2009, Kiat et al. 2019, Jenni et al. 2020, Jenni and Winkler 2020). Larger birds with longer flight feathers require disproportionately more time to complete molt because of allometric relationships among body size, lengths of the flight feathers, and feather growth rates (Rohwer et al. 2009, Jenni et al. 2020). In passerines, sexual dimorphism in body size and wing length is likely to contribute to the widespread observation that the duration of flight-feather molt is typically longer for males than females (Mumme et al. 2025b). Migration distance has also long been recognized as an important determinant of molt speed, as populations and species that are either non-migratory or short-distance migrants typically have a slower pace of molt and longer molt durations than those with greater migration distances (Lundberg and Eriksson 1984, Kjellén 1994, Voelker and Rohwer 1998, de la Hera et al. 2009, Kiat et al. 2019, Jenni and Winkler 2020). For passerines, the most comprehensive analysis of the effects of body size and migration distance on post-breeding molt duration is that of de la Hera et al. (2009); based on molt data for 48 species of European passerines drawn from Ginn and Melville (1983), larger and more sedentary species have molt durations that are greater than those of smaller and more migratory species (de la Hera et al. 2009).

Long-distance migration can lead to ~~short-duration~~a shorter post-breeding molt via two different hypothetical pathways. In the direct pathway hypothesis (Figure 1A), the time constraints imposed by long-distance migration lead directly to natural selection for a rapid post-

breeding molt, as shortening the period of molt frees additional time for successful completion of migration (e.g., Lundberg and Eriksson 1984, Voelker and Rohwer 1998, de la Hera et al. 2009, Kiat et al. 2019) and reduces the potential for conflicts and trade-offs between molt and migration (e.g., Stutchbury et al. 2011, Tsuru and Tonra 2025). However, a second pathway, one that is indirect and based on the effects of migration distance on the frequency of double brooding, can also produce the observed association between migration distance and molt duration. In this indirect, reproduction-mediated ~~pathway~~ hypothesis (Figure 1B), the time constraints imposed by long-distance migration lead first to a low frequency of double brooding, a relationship that is well documented in temperate-zone passerines (Martin 1995, Böhning-Gaese et al. 2000, Bruderer and Salewski 2008, Winger and Pegan 2021). The early cessation of reproduction by ~~single-brooded~~ long-distance migrants may then facilitate an early onset of molt (e.g., Mulvihill et al. 2009), which occurs under favorable mid-summer conditions and may proceed more rapidly than in double-brooded species molting later under shorter days and potentially less favorable late-summer conditions (Figure 1B).

Some evidence suggests that the indirect, reproduction-mediated pathway is plausible. For example, double-brooded species of migratory New World warblers (family Parulidae) breeding in eastern North America initiate molt later than single-brooded species (Mumme et al. 2021), a result that is expected given the general temporal segregation of reproduction and molt. Surprisingly, however, late-molting warblers also molt at a slower pace, a result contrary to the expectation that late-molting species would be under strong migratory time constraints and would have an accelerated pace of molt. One possible explanation for the slow molt of late-molting warblers is that unfavorable environmental conditions in late summer select for longer molt durations (Mumme et al. 2021); shorter days, less time for foraging, and perhaps reduced

food availability may make rapid late-summer molt prohibitively costly in terms of energetics, and perhaps also in terms of resulting plumage quality (Dawson et al. 2000, de la Hera et al. 2010, Vágási et al. 2012).

The relative contributions of the direct and indirect pathways in producing the strong negative association between migration distance and molt duration are unknown. Thus, the inverse relationship between the two variables could arise because: (1) long-distance migrants are under direct selection to molt rapidly, (2) the frequent double brooding and delayed molt of residents and short-distance migrants select for a slow pace of molt, or (3) both processes are important (Figure 1). Here, our objective is to address this issue and to tease apart the interacting effects of migration distance, double brooding, and body size on interspecific variation in the timing and duration of the post-breeding molt in temperate-zone passerines. Drawing on molt data collected at a single banding station in eastern North America, we analyze ~~Our analysis, which is based on~~ estimates of ~~molt start date~~the onset and duration of flight-feather molt for 33 species of passerines ~~sampled at a single banding station in eastern North America~~that undergo a complete post-breeding molt at our study site.~~,~~ Our comparative analysis extends earlier groundbreaking work on the determinants of molt duration in European passerines (de la Hera et al. 2009) and clarifies the roles that migration distance and double brooding have on interspecific variation in molt phenology.

METHODS

Collection of Molt Data

Data on ~~the~~passerine post-breeding ~~prebasic~~ molt (Kiat 2023) ~~of passerines~~ were collected 1986–2004 in association with year-round netting and banding operations at Powdermill Avian

Research Center (40.164°N, 79.267°W) in southwestern Pennsylvania, USA (Mumme et al. 2025a,b). Mist nets were located in a 10-ha area of shrubby second growth adjacent to deciduous forest, ponds, and agricultural land. Weather permitting, netting and banding occurred 5–6 days per week, beginning 1 h before sunrise and ending mid-afternoon. Each banded bird was assigned a total remex molt score (0–90), primarily by one individual (RSM), based on the molt status of the 18 remiges (9 primaries and 9 secondaries) on the right wing, using the 0–5 molt scoring system of Ginn and Melville (1983): 0 = old feather, 1 = old feather missing or new pin feather, 2 = new feather emerging from sheath up to one-third grown, 3 = new feather between one-third and two-thirds grown, 4 = new feather more than two-thirds grown but still sheathed at base, and 5 = fully grown new feather with no trace of the sheath. In a subset of captured individuals, scores were also recorded for each of the 18 remiges, allowing calculation of molt intensity, which for this analysis we defined as the number of remiges being actively replaced (i.e., with molt score 1–4) during mid-molt, when molt was 20–80% completed (total molt score 18–72).

Our analysis focused on species that undergo a complete post-breeding ~~prebasic~~ molt at our study site, and we excluded species or individuals having partial or suspended molts. Additional criteria for species inclusion were either: (1) at least 20 records of birds in active molt, i.e., with remex molt score 1–89, or (2) at least 15 records of birds in active molt with some data from individuals recaptured during the same molt cycle, as recapture data substantially improve estimation of molt parameters (Boersch-Supan et al. 2024, Mumme et al. 2025a). A total of 33 species from 11 passerine families, with a combined 3,324 records of birds in active molt, including 2,068 records of molt intensity, are included in the final dataset (Table 1).

All but 1 of the 33 species examined breed locally in the Powdermill area; the exception is the molt-migrant *Catharus ustulatus* (Swainson's Thrush; Cherry 1985), which we included because individuals of this species regularly initiate and complete molt during their migratory stopover at Powdermill before continuing south to their nonbreeding range in Central and South America. Of the remaining 32 species, 24 are completely migratory at Powdermill and 5 are partial migrants, i.e., migratory species whose nonbreeding range includes the Powdermill region; for these species, the local breeding population may comprise a mix of individuals that migrate after completing molt and others that remain resident through the winter (Table 1). We classified 3 species—*Poecile atricapillus* (Black-capped Chickadee), *Haemorhous mexicanus* (House Finch), and *Cardinalis cardinalis* (Northern Cardinal)—as nonmigratory permanent residents; although some individuals in northeastern *H. mexicanus* populations may migrate short distances, the great majority appear to be nonmigratory (Badyaev et al. 2020, Fink et al. 2025).

Estimation of Molt Parameters

We estimated molt start date and molt duration for the 33 species using methods developed and described previously (Mumme et al. 2025a,b). In brief, individual molt scores of birds in active molt were expressed as the proportion of remex molt completed and then arcsine-transformed to linearize the molt process and account for its slow progression at the earliest and latest stages of molt, when few remiges are being actively replaced. Transformed molt scores were then rescaled as a proportion, allowing mean ± SE molt start date and molt duration to be taken directly from estimates of the intercept and slope of regression equations obtained via either Pimm mixed-model regression (Mumme et al. 2025a), for 29 species where data were available for individuals recaptured during the same molt cycle, or standard Pimm regression (Pimm 1976), for 4 species

where recapture data were lacking. These methods produce accurate and unbiased estimates of molt phenology whenever molt data are collected across a broad range of dates, and are unaffected by molt-dependent sampling bias, which is widespread in the Powdermill data (Mumme et al. 2025a). Tabular and g~~G~~raphical presentations of the molt data for the 33 species ~~is~~are provided in Table 1 and Supplementary Material Figure S1.

Ecological and Morphological Explanatory Variables

We examined how interspecific variation in molt phenology is influenced by two ecological and one morphological explanatory variables: estimated migration distance, frequency of double brooding, and wing length. To estimate migration distance for the 25 completely migratory species, we used the range maps available at Birds of the World (Billerman et al. 2025) and the polygon tool of the image analysis program Fiji (Schindelin et al. 2012) to estimate the centroid of the stationary nonbreeding range; we then calculated the distance between the centroid and Powdermill. For the 5 species of partial migrants (Table 1), we used the centroid of the portion of the nonbreeding range located to the south of Powdermill. The 3 species considered to be permanent residents were assigned a migration distance of 0. For frequency of double brooding, we used the 33 species accounts at Birds of the World (Billerman et al. 2025) to qualitatively determine if double brooding was described as occasional, regular, or frequent (scored as 1 or "Yes"; 19 species) vs. absent or rare (scored as 0 or "No"; 14 species) for breeding populations in the Powdermill region. Data on wing length, a strong indicator of overall body size and one that is particularly relevant to remex molt, were obtained from birds measured during banding at Powdermill (Mulvihill et al. 2004).

Statistical Analysis

In most analyses we controlled for the non-independence resulting from shared evolutionary histories via Phylogenetic Generalized Least Squares (PGLS) regression. PGLS regressions were run with the R package *caper* version 1.04 (Orme et al. 2025) under R version 4.5.1 (R Core Team 2025) based on a phylogeny (Supplementary Material Figure S2) of the 33 species in our dataset drawn from McTavish et al. (2025) using the R package *clootl* version 0.1.2 (Cornell Lab of Ornithology Open Tree of Life, Aves tree 1.5, 2023 taxonomy; Miller et al. 2025).

Our general approach was to build PGLS regression models for molt start date and molt duration that included all 3 explanatory variables: estimated migration distance (continuous), wing length (continuous), and frequency of double brooding (categorical). Initial models included interaction terms, but non-significant interactions were excluded from final models (Table 2). To determine if similar statistical patterns were evident within the single family best represented in the dataset, we also built comparable PGLS models restricted to the 13 species of New World warblers (Parulidae).

Because of unexpected strong bimodality in the molt duration data ~~For analysis of molt duration across all 33 species~~(Figure 2), our initial PGLS model for all 33 species (duration model 1) explained a relatively small proportion of the interspecific variation in molt duration (adjusted $R^2 = 0.29$, Table 2B). We therefore built two additional PGLS models of molt duration to account for and incorporate this unanticipated bimodality; for these analyses we excluded frequency of double brooding as an explanatory variable, as duration model 1 (Table 2B) showed that it has virtually no effect on molt duration. In molt duration model 2, we included the slow/fast molt duration dichotomy (Figure 2) as a categorical explanatory variable along with migration distance and wing length (Table 2B). In duration model 3, we included molt intensity

(Figure 3) as a continuous explanatory variable along with migration distance and wing length (Table 2B)~~we built additional PGLS models that included either molt intensity as a continuous explanatory variable or molt speed (fast or slow; Figure 2) as a categorical explanatory variable.~~ . Duration models 2 and 3 explained a substantially higher proportion of the total interspecific variation in molt duration, with adjusted R^2 values of 0.84 and 0.79, respectively (Table 2B).

Across all PGLS models, predictor variables showed weak collinearity (correlation coefficients < 0.6 and variance inflation factors < 2.0), and all ~~R~~residuals ~~of all PGLS models~~ approximated a normal distribution (Supplementary Material Figure S3). With the exception of molt duration model 1 (discussed above), PGLS model performance was generally good, with adjusted R^2 values of 0.55–0.92.

RESULTS

Variation in Molt Phenology, Migration Distance, and Double Brooding

The 33 passerine species included in the analysis vary considerably in both timing and duration of the post-breeding ~~prebasic~~ molt (Table 1, Supplementary Material Figure S1). Estimates of molt start date encompass a range of 101 days, from ordinal day 148 (28 May) for *Poecile atricapillus* (Black-capped Chickadee) to ordinal day 249 (6 Sep) for *Spinus tristis* (American Goldfinch). Interspecific variation in molt duration was also substantial, from 40 days in the molt-migrant *Catharus ustulatus* (Swainson's Thrush) to 103 days in *Bombycilla cedrorum* (Cedar Waxwing; Table 1).

Although the data for molt start date closely approximate a normal distribution, data for molt duration do not (Figure 2); molt duration shows a pronounced bimodal distribution, with 25 species of "fast" molters (molt duration 40–65 days) and 8 species of "slow" molters (molt

duration 82–103 days). The 8 slow-molting species include all 3 (100%) of the nonmigratory resident species included in the dataset (*P. atricapillus, Haemorhous mexicanus* [House Finch], and *Cardinalis cardinalis* [Northern Cardinal]), 2 (40%) of the 5 species that are partial migrants (*B. cedrorum* and *Haemorhous purpureus* [Purple Finch]), and 3 (12%) of the 25 completely migratory species, *Sayornis phoebe* (Eastern Phoebe) and two members of the family Cardinalidae (*Pheucticus ludovicianus* [Rose-breasted Grosbeak] and *Piranga olivacea* [Scarlet Tanager]; Figure 2).

The bimodal interspecific variation in molt duration is strongly reflected by variation in molt intensity, the number of remiges on the right wing being replaced simultaneously during mid-molt (Figure 3). Mean ± SD molt intensity is 4.4 ± 0.5 for the 8 slow-molting species, but 6.8 ± 0.8 for the 25 fast-molting species (~~Figure 3~~PGLS $t = -3.83$, $P < 0.001$).

Interspecific variation in estimated migration distance and molt start date is closely associated with the frequency of double brooding (Figure 4). The 14 species where double brooding is absent or rare have a longer mean ± SD migration distance (3174 ± 1455 km) and an earlier onset of molt (2 Jul, ordinal day 183 ± 16 d) in comparison to the 19 species with regular or frequent double brooding (1668 ± 949 km and 1 Aug, ordinal day 213 ± 17 d; Figure 4).

Factors Affecting Molt Start Date

~~A phylogenetic Generalized Least Squares (~~PGLS~~)~~ regression ~~model~~ indicates that the frequency of double brooding has a strong positive effect on the estimated date of molt onset, even after controlling for the effects of migration distance and wing length (Table 2A). The PGLS regression coefficients relating molt start date to estimated migration distance and wing length

are negative, suggesting an earlier molt onset as migration distance and body size increase, but neither effect was statistically significant (Table 2A).

Factors Affecting Molt Duration

PGLS ~~regression~~duration model 1 indicates that estimated migration distance and wing length are both significant predictors of molt duration (Table ~~3~~2B); molt duration decreases with increasing migration distance, but increases with increasing wing length. The frequency of double brooding, in contrast, has no significant effect on molt duration once the effects of migration distance and wing length are statistically controlled.

~~Because of the unexpected bimodality of the molt duration data (Figure 2), we ran two additional PGLS models of molt duration; for these analyses we excluded frequency of double brooding as an explanatory variable, as our initial PGLS model (Table 2B, duration model 1) showed that it has virtually no effect on molt duration.~~ In duration model 2 (Table 2B), which includes the ~~first model, we included the~~ slow/fast molt dichotomy (Figure 2) as a categorical explanatory variable ~~along with migration distance and wing length (Table 2B, duration model 2). In this analysis~~, migration distance is a strong negative predictor of molt duration, indicating that long migration routes are associated with a shorter duration of molt even after controlling for the slow/fast ~~molt~~ dichotomy (Figure 5A). Wing length, in contrast, has no overall or consistent effect on molt duration after controlling for the slow/fast dichotomy (Figure 5B; Table 2B~~, duration model 2~~). However, a weak but significant interaction between migration distance and wing length (Table 2B, duration model 2) suggests that while wing length has little or no effect on molt duration for short-distance migrants, it has a more pronounced positive effect for long-distance migrants.

~~Second, we constructed a PGLS model in which molt intensity (Figure 3) was included as a continuous explanatory variable along with migration distance and wing length. In this analysis (Table 2B, duration model 3)~~In duration model 3 (Table 2B), migration distance and wing length respectively have strong negative and positive effects on molt duration even after controlling for variation in molt intensity (Figure 6). In addition, we found a strong significant interaction between molt intensity and wing length, suggesting that variation in intensity has a more pronounced effect on molt duration for large birds than for small birds (Table 2B, duration model 3; Figure 6).

In summary: (1) Migration distance has a strong and consistent negative effect on molt duration, even after controlling for variation in molt intensity and the slow/fast bimodality of the observed molt duration data. (2) Wing length is an important predictor of the slow/fast dichotomy in molt duration, and has generally positive effects on molt duration through its interactions with migration distance and molt intensity. (3) Frequency of double brooding has no effect on molt duration once the effects of migration distance and wing length are controlled statistically.

Factors Affecting Molt Phenology in the Parulidae

Estimated migration distance is a significant negative predictor of both the timing and duration of molt for the 13 species of New World warblers included in the dataset (Table 3, Figure 7A, B). Frequency of double brooding is positively ~~linked to~~correlated with molt start date (Figure 7C), but wing length is not a significant predictor of either timing or duration of molt in warblers (Table 3).

DISCUSSION

The goals of our study were: (1) to clarify the roles that migration distance, frequency of double brooding, and wing length (body size) play in shaping interspecific variation in the phenology of post-breeding ~~prebasic~~ molt in temperate-zone passerines, and (2) to assess the relative importance of the direct and indirect (reproduction-mediated) pathways (Figure 1) in contributing to the inverse relationship between migration distance and molt duration. Consistent with the indirect pathway hypothesis (Figure 1B), we found strong evidence that the frequency of double brooding in 33 North American temperate-zone passerines is associated with both shorter migration distances (Figure 4A) and later molt initiation dates (Figures 4B, 7C), and that frequency of double brooding is the primary factor that determines the timing of post-breeding molt (Tables 2A, 3A). However, contrary to the prediction of the indirect pathway hypothesis, we found that the frequency of double brooding has no effect on molt duration once the effects of migration distance and wing length are statistically controlled. Instead, molt duration increases with increasing wing length and decreases with increasing migration distance (Tables 2B, 3B), a result consistent with ~~other~~previous studies (Rohwer et al. 2009, de la Hera et al. 2009, Kiat et al. 2019, Jenni et al. 2020) ~~and~~. It is also consistent with the direct pathway hypothesis (Figure 1A), suggesting that the time constraints imposed by long-distance migration lead directly to natural selection for rapid post-breeding molt. Thus, while frequency of double brooding is more important than migration distance in determining the timing of post-breeding molt, migration distance is more important than frequency of double brooding in determining its duration.

Separate analyses restricted to the 13 species of parulid warblers corroborate these conclusions; warbler species with regular or frequent double brooding initiate molt significantly later than single-brooded species, and long-distance migration is significantly associated with a

shorter molt duration (Table 3, Figure 7). Our analysis of the warblers, however, produced two findings that differ from those obtained for the entire dataset: (1) Migration distance has a significant negative effect on the date of molt onset in warblers (Table 3A, Figure 7), a relationship that was negative but not statistically significant in the entire dataset (Table 2A). (2) Wing length has no significant positive effect on molt duration in warblers (Table 3B), a finding that may be related to the relatively limited range of wing lengths present within the Parulidae (Figure 5).

Rapid flight-feather molt in birds is usually achieved by increasing molt intensity—the number of remiges being replaced simultaneously—rather than by increasing the rate at which individual remiges grow (de la Hera et al. 2011, Rohwer and Rohwer 2013). Our results, however, suggest that both processes may be important in explaining the rapid molts of long-distance migrant passerines. As other studies have also shown (de la Hera et al. 2011, Rohwer and Rohwer 2013), we found that molt duration decreases with increasing molt intensity (Figure 3). But when molt intensity is included as an explanatory variable in a phylogenetically-controlled statistical model (Table 2B, duration model 3), molt intensity and migration distance both have significant negative effects on molt duration (Figure 6), suggesting that long-distance migrants increase molt speed via a mechanism separate from an increase in molt intensity. This evidence, however, is indirect, and studies that directly measure feather growth rates are needed to determine if long-distance migrants grow feathers more rapidly during molt, and if more rapid feather growth compromises plumage quality (Dawson et al. 2000, de la Hera et al. 2010, 2011; Vágási et al. 2012, Rohwer and Rohwer 2013).

One of the ~~surprising~~unexpected results of our study is that estimates of molt duration for the 33 focal passerine species show a bimodal distribution (Figure 2), with 25 species having

rapid molt (duration 40–65 d) and 8 having slow molt (duration 82–103 d). Migration distance and wing length both appear to be important predictors of the bimodality, with small, long-distance migrants disproportionately represented in the "fast" group (Figure 5). Although this ~~unexpected~~ bimodality could be simply an artifact of non-random species sampling in our dataset, it is also possible that the bimodality ~~is a reflection~~reflects ~~of~~ fundamentally different strategies of post-breeding molt employed by temperate-zone passerines. For example, Morrison et al. (2015) detected a similar bimodality in duration of the post-breeding molt for 15 species of passerines from the United Kingdom, with 5 species of fast molters (duration 67–80 d) and 10 species of slow molters (duration 94–111 d). However, the results of Morrison et al. (2015) should be viewed with some caution, for two reasons. First, their estimates of molt duration were based on methods (Underhill and Zucchini 1988, Erni et al. 2013) that can produce inaccurate estimates of molt phenology under molt-dependent sampling bias, which appears to be common in temperate-zone passerines (Boersch-Supan et al. 2024, Mumme et al. 2025a); indeed, the estimates of molt duration reported by Morrison et al. (2015) average 50% greater than comparable estimates reported for the same species by Ginn and Melville (1983; figure 1 in de la Hera et al. 2009), and many of the estimates for long-distance migrants appear to be unrealistically large. Second, de la Hera et al. (2009, figure 2) found no evidence of bimodality in estimates of molt duration in a larger sample (48 species) of passerines drawn from Ginn and Melville (1983). Thus, it remains uncertain whether the bimodality we observed in molt duration (Figure 2) is biologically meaningful or artifactual; additional studies of post-breeding molt in temperate-zone passerines are needed to answer this question.

Two species in our comparative analysis are notable for the exceptional timing or duration of their post-breeding molt. First, *Poecile atricapillus* (Black-capped Chickadee) has an

extraordinarily early mean molt start date (28 May; Table 1, Figure 2) and a prolonged, low-intensity molt (97 d) that is unexpected for a bird of its relatively small size (Table 1, Figures 3, 5B). These unusual molt characteristics are undoubtedly related to its breeding biology; *P. atricapillus* is the only single-brooded species among the 8 species in our dataset that are either non-migratory or partially migratory (Table 1, Figure 4A). In addition, it is the only cavity-nesting species in our dataset, and ~~also the only single-brooded species of the eight resident or partially migratory species in our dataset (Figure 4A). C~~cavity-nesting passerines ~~are known to~~often have unusual constellations of life-history traits that differ from those of open-cup nesters (Martin and Li 1992, Martin 1995, Winger and Pagan 2021)._ ~~, and our analysis suggests that their molt phenology may be fundamentally different as well.~~ Second, the molt-migrant *Catharus ustulatus* (Swainson's Thrush) has an extraordinarily rapid (40 d), high-intensity molt (Table 1, Figures 2, 3), a finding that is consistent with previous work (Cherry 1985) but surprising given the species' relatively large size (Figure 5B). Because molting individuals at our study site in southwestern Pennsylvania had already migrated from breeding areas in boreal forests to the north, in comparison to other single-brooded species *C. ustulatus* initiates molt exceptionally late as well (Figure 4B), with a mean start date of 8 Aug (Table 1). How *C. ustulatus* supports its rapid, high-intensity molt under relatively short late-summer days is an intriguing question for future research; for example, actively molting individuals of this species may eat proportionately more insects and less fruit than purely migratory individuals (Blanc-Benigeri et al. 2024), a finding consistent with the high protein demands of rapid molt.

Our findings for *Catharus ustulatus* also provide indirect support for the leading hypothesis for the evolution of molt-migration: that poor late-summer resource availability on the breeding grounds selects for migration to more resource-rich areas that can better support the

energetic and nutritional demands of molt (Rohwer et al. 2005, Pageau et al. 2020). Although we do not have data on late-summer resource availability in their boreal forest breeding areas, the extraordinarily rapid, high-intensity molt of *C. ustulatus* at Powdermill (Figures 2, 3) would clearly not be possible without the availability of rich food resources to support it.

Our study has focused on how interspecific variation in post-breeding molt phenology is affected by the frequency of double brooding, migration distance, and wing length; other factors, however, may also contribute to interspecific variation in the timing and duration of molt in passerines. For example, species that regularly fly long distances as part of routine foraging flights appear to have slow, low-intensity molts, presumably because they can ill afford the aerodynamic costs associated with rapid, high-intensity molt (Kiat et al. 2016). Although we did not explicitly investigate this possibility, variation in foraging flight behavior could explain some of the interspecific variation in molt duration we observed in our dataset. *Bombycilla cedrorum* (Cedar Waxwing), for example, is nomadic and wanders widely in search of fruit during its post-breeding molt (Witmer et al. 2020), and this ~~may be~~almost certainly is a contributing factor to its unusually slow, low-intensity molt (Table 1, Figure 3).

One of the limitations of our study is that our estimates of two key explanatory variables, migration distance and frequency of double brooding, are less than ideal. We estimated migration distance for the 30 migratory species in our dataset as the distance between Powdermill and the approximate centroid of the nonbreeding range, which provides at best only a rough approximation of true migration distance. Ideally, we would have data derived from modern avian tracking technologies (Torstenson et al. 2024) showing nonbreeding home range and migration routes for a large sample of individuals from each species, allowing precise estimation of both mean and variation in true migration distance. Frequency of double brooding

in our analyses was summarized as a qualitative (categorical) predictor variable, with 19 species where double brooding was considered to be occasional, regular, or frequent, and 14 species where it was considered to be absent or rare. Ideally, for each of the 33 species in our analysis we would have accurate quantitative estimates of the frequency of double brooding, and also complete information on the timing and duration of nesting and post-fledging parental care. Despite these deficiencies, our rough approximations of migration distance and frequency of double brooding performed well, and in conjunction with other predictor variables helped to explain a significant fraction of the interspecific variation in the onset and duration of post-breeding molt (Tables 2, 3).

A general feature of interspecific comparative analyses such as ours is that important intraspecific and within-population variation is lost when variables of interest are condensed to species-typical values. It is therefore important to acknowledge that the estimates of molt onset and duration for our 33 focal species (Table 1) are multi-year population averages that mask important within-species heterogeneity in molt schedules, including heterogeneity due to sex- and age-based variation (Mumme et al. 2025b), annual variation (Tattoni et al. 2025), long-term responses to climate change (Tomotani et al. 2018), and other factors. Within-population variation in reproduction and molt schedules can also lead to individual differences in how molting birds manage conflicts and potential trade-offs with parental care and migration (Hemborg 1999, Mulvihill et al. 2009, Stutchbury et al. 2011, Mumme 2018, Tsuru and Tonra 2025).

In conclusion, our study has clarified how ~~the~~interspecific variation in the phenology of post-breeding ~~prebasic~~ molt in temperate-zone passerines is shaped by migration distance, the frequency of double brooding, and wing length. While the frequency of double brooding is the

most important variable contributing to interspecific variation in the timing of molt, migration distance and wing length are the most important variables contributing to interspecific variation in its duration, with longer migration distances and shorter wings leading to more rapid, short-duration molt. Our study ~~also highlights the opportunity to explicitly incorporate data on the timing and duration of molt into avian life history theory (Martin 2004), and~~ contributes to the growing body of evidence that migration distance is a key factor in the evolution of passerine life history strategies (Martin 1995, Böhning-Gaese et al. 2000, Bruderer and Salewski 2008, de la Hera et al. 2009, Winger and Pagan 2021), and highlights the opportunity to explicitly incorporate data on the timing and duration of molt into avian life history theory (Martin 2004). Our findings also underscore the tight time limitations that long-distance migration places on temperate songbirds, in many cases constraining their options to single brooding and reduced annual fecundity (Bruderer and Salewski 2008, Winger and Pagan 2021), a high-intensity molt that compromises flight performance (Mumme et al. 2021, Hedenström 2023), or both. These constraints are likely to exacerbate the daunting conservation challenges facing migratory songbirds (Rosenberg et al. 2019).

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637 **Table 1.** Estimates of mean ± standard error (SE) ordinal start date and duration of post-breeding
638 molt for 33 species of passerines captured during banding operations at Powdermill Avian
639 Research Center in southwestern, Pennsylvania, USA. Molt parameters were estimated with
640 either Pimm mixed model regression, for 29 species with data from individuals recaptured during
641 the same molt cycle, or standard Pimm regression, for 4 species without recapture data. Four-
642 letter species codes used in the figures and migratory status at Powdermill (CM = completely
643 migratory, PM = partially migratory, R = resident) are also shown for each species.

Species	Family	*n*	Ordinal molt start date ± SE	Molt duration (d) ± SE
Sayornis phoebe (Eastern Phoebe, EAPH), CM	Tyrannidae	23	186.7 ± 3.5	96.2 ± 4.9
Vireo griseus (White-eyed Vireo, WEVI), CM	Vireonidae	74	203.1 ± 1.5	61.5 ± 1.8
Poecile atricapillus (Black-capped Chickadee, BCCH), R	Paridae	24	147.9 ± 4.6	97.4 ± 7.6
Bombycilla cedrorum (Cedar Waxwing, CEDW), PM	Bombycillidae	79	234.0 ± 2.4	102.9 ± 4.8
Dumetella carolinensis (Gray Catbird, GRCA), CM	Mimidae	148	210.8 ± 1.2	51.2 ± 2.1
Hylocichla mustelina (Wood Thrush, WOTH), CM	Turdidae	31	203.9 ± 2.8	65.2 ± 4.6
Catharus ustulatus (Swainson's Thrush, SWTH), CM	Turdidae	37	220.2 ± 2.1	39.8 ± 0.6
Catharus fuscescens (Veery, VEER), CM	Turdidae	115	192.4 ± 1.1	47.7 ± 1.8
Haemorhous mexicanus (House Finch, HOFI), R	Fringillidae	33	196.6 ± 3.3	96.8 ± 3.6
Haemorhous purpureus (Purple Finch, PUFI), PM	Fringillidae	68	205.0 ± 2.7	89.0 ± 4.0
Spinus tristis (American Goldfinch, AMGO), PM	Fringillidae	523	249.3 ± 0.7	61.9 ± 1.6
Spizella passerina (Chipping Sparrow, CHSP), CM	Passerellidae	24	226.2 ± 4.7	50.5 ± 7.9
Spizella pusilla (Field Sparrow, FISP), PM	Passerellidae	32	230.2 ± 2.5	55.1 ± 3.9
Melospiza melodia (Song Sparrow, SOSP), PM	Passerellidae	48	223.7 ± 1.8	61.9 ± 2.3
Pipilo erythrophthalmus (Eastern Towhee, EATO), CM	Passerellidae	23	218.0 ± 1.8	60.3 ± 1.3
Icteria virens (Yellow-breasted Chat, YBCH), CM	Icteriidae	17	189.1 ± 3.5	51.1 ± 1.6
Seiurus aurocapilla (Ovenbird, OVEN), CM	Parulidae	125	186.1 ± 1.1	55.7 ± 1.4
Parkesia motacilla (Louisiana Waterthrush, LOWA), CM	Parulidae	51	170.2 ± 1.5	51.4 ± 2.1
Vermivora chrysoptera (Golden-winged Warbler, GWWA), CM	Parulidae	33	173.3 ± 1.9	52.6 ± 2.4
Geothlypis formosa (Kentucky Warbler, KEWA), CM	Parulidae	69	191.3 ± 1.8	53.9 ± 2.5

Geothlypis trichas (Common Yellowthroat, COYE), CM	Parulidae	285	209.6 ± 0.8	55.8 ± 0.8
Mniotilta varia (Black-and-white Warbler, BAWW), CM	Parulidae	120	180.6 ± 1.4	56.2 ± 1.1
Setophaga ruticilla (American Redstart, AMRE), CM	Parulidae	576	177.3 ± 0.6	51.2 ± 0.8
Setophaga citrina (Hooded Warbler, HOWA), CM	Parulidae	157	201.3 ± 1.3	56.0 ± 1.1
Setophaga americana (Northern Parula, NOPA), CM	Parulidae	20	191.9 ± 7.1	54.2 ± 13.7
Setophaga magnolia (Magnolia Warbler, MAWA), CM	Parulidae	33	202.0 ± 2.4	57.9 ± 1.4
Setophaga petechia (Yellow Warbler, YEWA), CM	Parulidae	71	174.1 ± 1.2	43.7 ± 1.1
Setophaga pensylvanica (Chestnut-sided Warbler, CSWA), CM	Parulidae	33	199.9 ± 2.5	50.9 ± 1.2
Setophaga virens (Black-throated-Green Warbler, BGGN), CM	Parulidae	60	193.5 ± 3.0	53.6 ± 4.8
Pheucticus ludovicianus (Rose-breasted Grosbeak, RBGR), CM	Cardinalidae	125	184.7 ± 0.7	82.6 ± 1.8
Passerina cyanea (Indigo Bunting, INBU), CM	Cardinalidae	181	225.0 ± 1.1	51.8 ± 1.1
Cardinalis cardinalis (Northern Cardinal, NOCA), R	Cardinalidae	25	235.4 ± 6.4	84.5 ± 12.6
Piranga olivacea (Scarlet Tanager, SCTA), CM	Cardinalidae	61	184.4 ± 1.9	81.6 ± 4.5

644 **Table 2.** Phylogenetic Generalized Least Squares (PGLS) regression models examining the
645 effects of migration distance, wing length, and frequency of double brooding on molt start date
646 (A) and molt duration (B) in 33 species of temperate-zone passerines sampled at Powdermill
647 Avian Research Center in southwestern Pennsylvania, USA. For molt duration, two additional
648 PGLS models that include either the dichotomy between slow and fast molters (Figure 2) or molt
649 intensity (Figure 3) as explanatory variables are also shown. Normal quantile-quantile plots of
650 the residuals for all four models are provided in Supplementary Material Figure S3.

A. Molt start date				
Start date model 1: Molt start date ~ Migration distance + Wing length + Double brooding (adjusted R^2 = 0.55)				
Term	Estimate	SE	*t*	*P*
Intercept	193.5	28.0	6.91	< 0.001 *
Migration distance	-0.00384	0.00255	-1.50	0.14
Wing length	-0.0975	0.258	-0.38	0.71
Double brooding (Yes)	20.7	4.43	4.66	< 0.001 *
B. Molt duration				
Duration model 1: Molt duration ~ Migration distance + Wing length + Double brooding (adjusted R^2 = 0.29)				
Term	Estimate	SE	*t*	*P*
Intercept	49.2	19.3	2.55	0.016 *
Migration distance	-0.00514	0.00176	-2.92	0.007 *
Wing length	0.511	0.177	2.88	0.007 *
Double brooding (Yes)	-0.302	3.05	-0.10	0.92
Duration model 2: Molt duration ~ Migration distance × Wing length + Slow/fast molt (adjusted R^2 = 0.84)				
Term	Estimate	SE	*t*	*P*
Intercept	86.5	12.3	7.03	< 0.001 *
Migration distance	-0.0138	0.00402	-3.47	0.002 *
Wing length	-0.239	0.142	-1.68	0.10
Slow/fast molt (Slow)	30.8	3.25	9.48	< 0.001 *

Migration distance × wing length	0.000129	0.0000469	2.76	0.01 *
Duration model 3: Molt duration ~ Migration distance + Wing length × Molt intensity (adjusted R^2 = 0.79)				
Term	Estimate	SE	*t*	*P*
Intercept	-28.5	26.2	-1.09	0.29
Migration distance	-0.00451	0.000855	-5.27	< 0.001 *
Wing length	1.99	0.339	5.87	< 0.001 *
Molt intensity	14.3	4.03	3.54	0.001 *
Wing length × Molt intensity	-0.276	0.0547	-5.05	< 0.001 *

651 * indicates a statistically significant effect

Table 3. Phylogenetic Generalized Least Squares (PGLS) regression models examining the effects of migration distance, wing length, and frequency of double brooding on molt start date (A) and molt duration (B) in 13 species of migratory New World warblers (family Parulidae) sampled at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Normal quantile-quantile plots of the residuals for both models are provided in Supplementary Material Figure S3.

A. Molt start date				
Warbler start model 1: Molt start date ~ Migration distance + Wing length + Double brooding (adjusted R^2 = 0.92)				
Term	Estimate	SE	*t*	*P*
Intercept	243.1	17.6	13.81	< 0.001 *
Migration distance	-0.0138	0.00288	-4.79	< 0.001 *
Wing length	-0.332	0.216	-1.54	0.56
Double brooding (Yes)	13.3	2.49	5.37	< 0.001 *
B. Molt duration				
Warbler duration model 1: Molt duration ~ Migration distance + Wing length + Double brooding (adjusted R^2 = 0.64)				
Term	Estimate	SE	*t*	*P*
Intercept	69.7	10.6	6.55	< 0.001 *
Migration distance	-0.00602	0.00174	-3.45	0.007 *
Wing length	0.00735	0.130	0.06	0.96
Double brooding (Yes)	1.13	1.50	0.75	0.47

* indicates a statistically significant effect

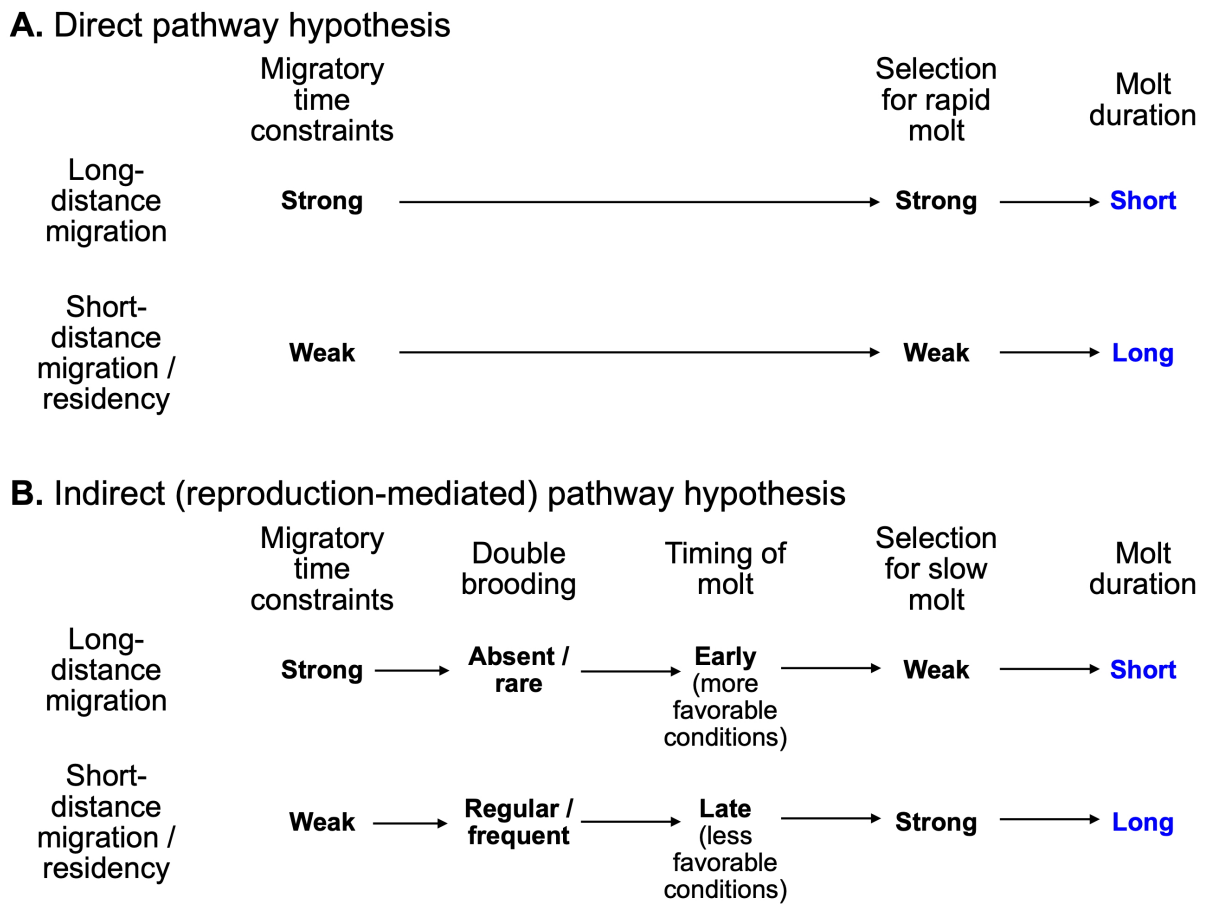
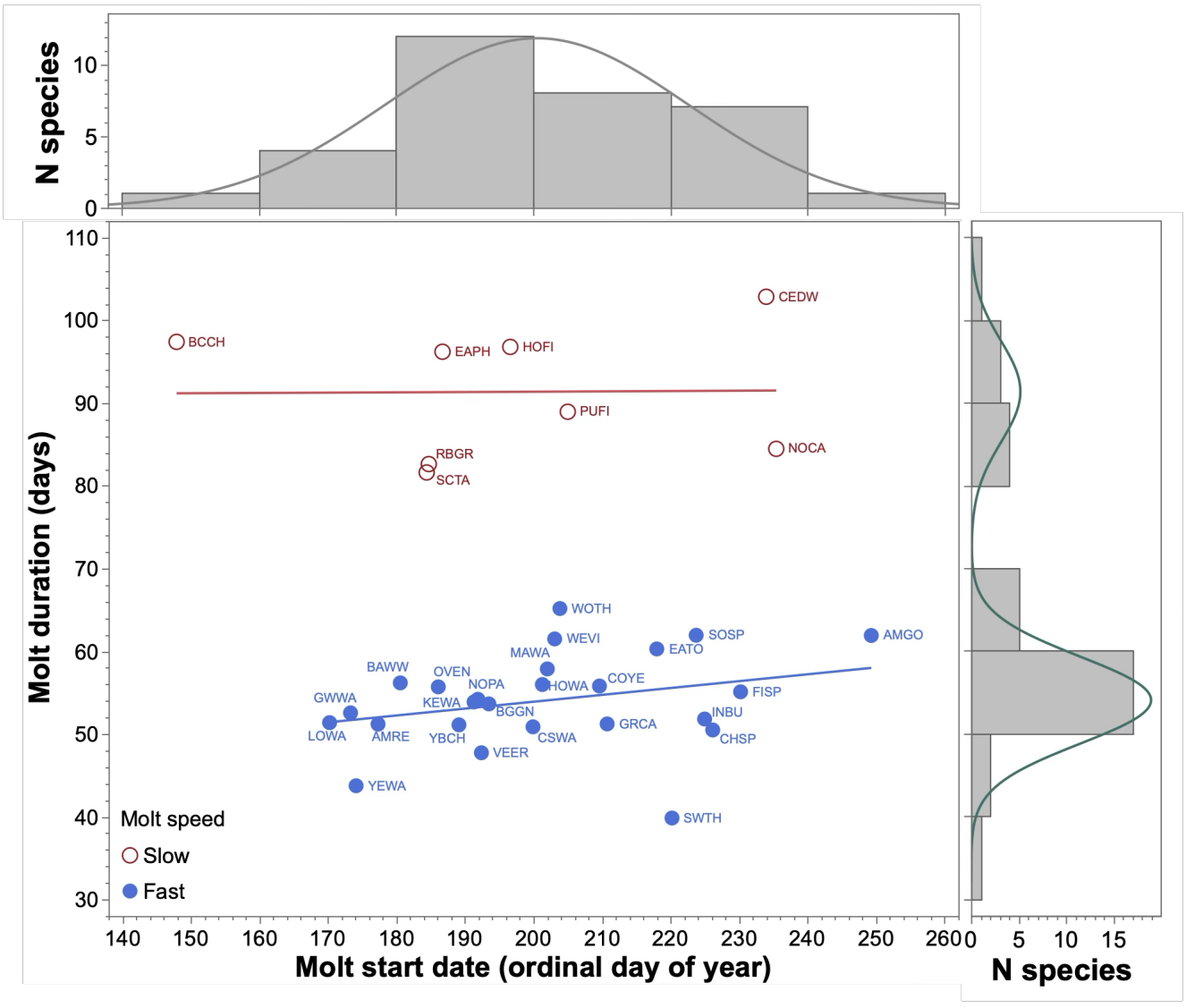


Figure 1. Two hypothetical pathways by which long-distance migration can lead to short-duration post-breeding ~~prebasic~~ molt in temperate-zone passerines. In the direct pathway hypothesis (A), the strong time constraints imposed by long-distance migration lead directly to selection for more rapid molt. In the indirect (reproduction-mediated) pathway hypothesis (B), the time constraints imposed by long-distance migration result in a low incidence of double brooding and an earlier onset of molt under more favorable environmental conditions. In contrast, regular or frequent double-brooding by short-distance migrants and residents leads to a delayed molt under less favorable conditions—e.g., short late-summer days and declining food availability—that may prohibit rapid molt and select for slow, long-duration molt.



669

670 **Figure 2.** Frequency distributions and the relationship between molt duration and ordinal molt
671 start date for 33 species of temperate-zone passerines sampled at Powdermill Avian Research
672 Center in southwest Pennsylvania, USA. While molt start date closely fits a normal distribution
673 (Anderson-Darling $A^2 = 0.24$, $P = 0.77$), molt duration does not ($A^2 = 2.66$, $P < 0.001$); it is
674 bimodally distributed in the Powdermill sample, with 25 species showing rapid molt (duration
675 40–65 days) and 8 showing slow molt (duration 82–103 days). A bimodal normal 2-mixture
676 distribution is a more appropriate fit to the duration data than is a unimodal skewed SHASH
677 (sinh-arcsinh) distribution for both the raw data (AICc = 261.6 vs. 269.1, respectively) and $\log_{10}$-
678 transformed data (AICc = -63.8 vs. -55.5, respectively). After controlling for the dichotomy
679 between slow and fast molters, molt start date has a weak but significant positive effect on molt
680 duration (Phylogenetic Generalized Least Squares regression coefficient = 0.114 ± 0.048, t =
681 2.37, $P = 0.02$). Plotted lines portray standard linear regression equations for slow and fast
682 molters. Individual species are identified by the four-letter codes shown in Table 1.

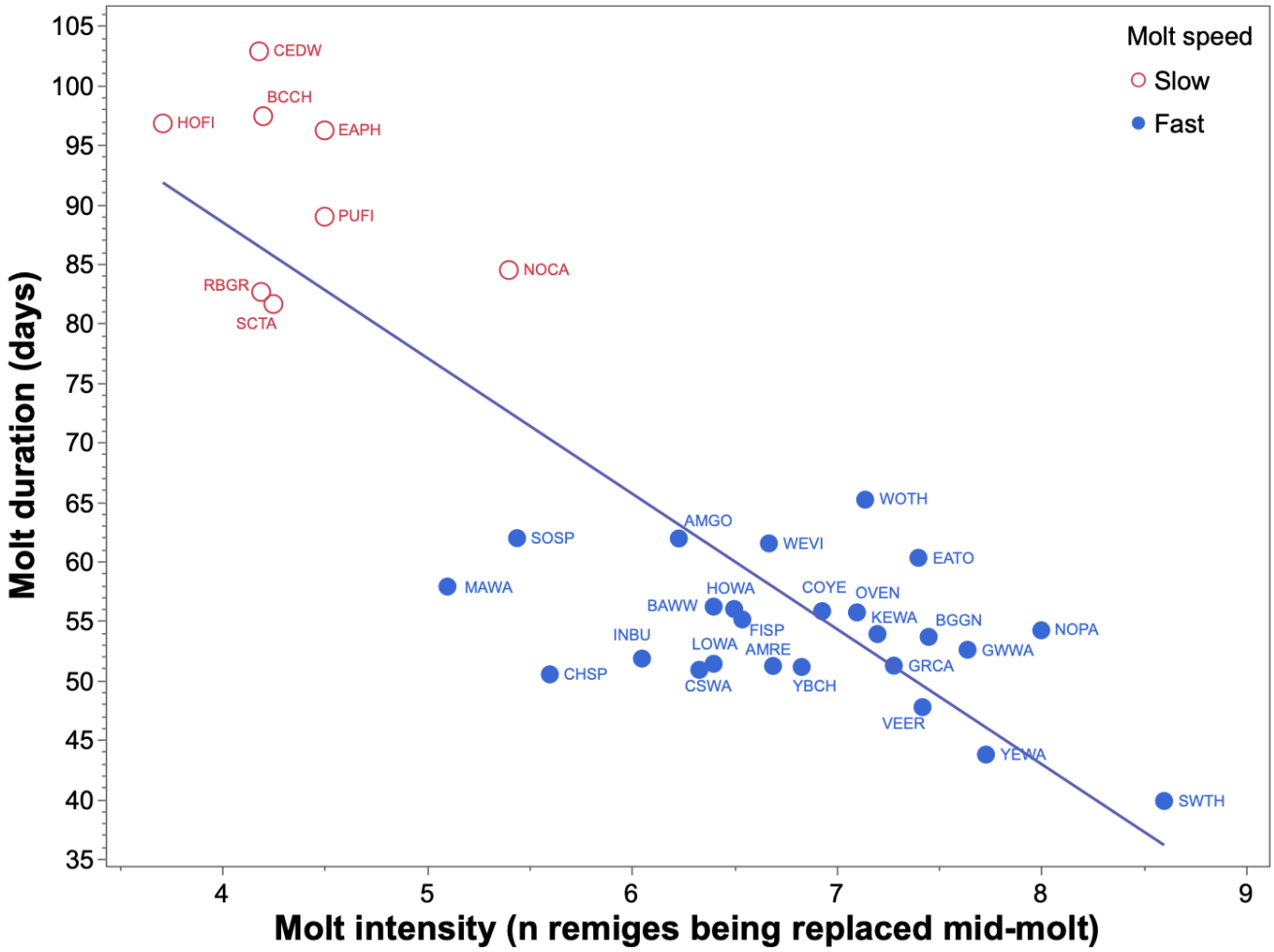


Figure 3. Bimodal interspecific variation in molt duration is in large part reflected by variation in molt intensity, the number of remiges on the right wing being simultaneously replaced during the middle stages of molt. The Phylogenetic Generalized Least Squares regression equation is $y = -6.78x + 116.9$ ($t = -5.19$, $P < 0.001$, adjusted $R^2 = 0.45$). Individual species are identified by the four-letter codes shown in Table 1.

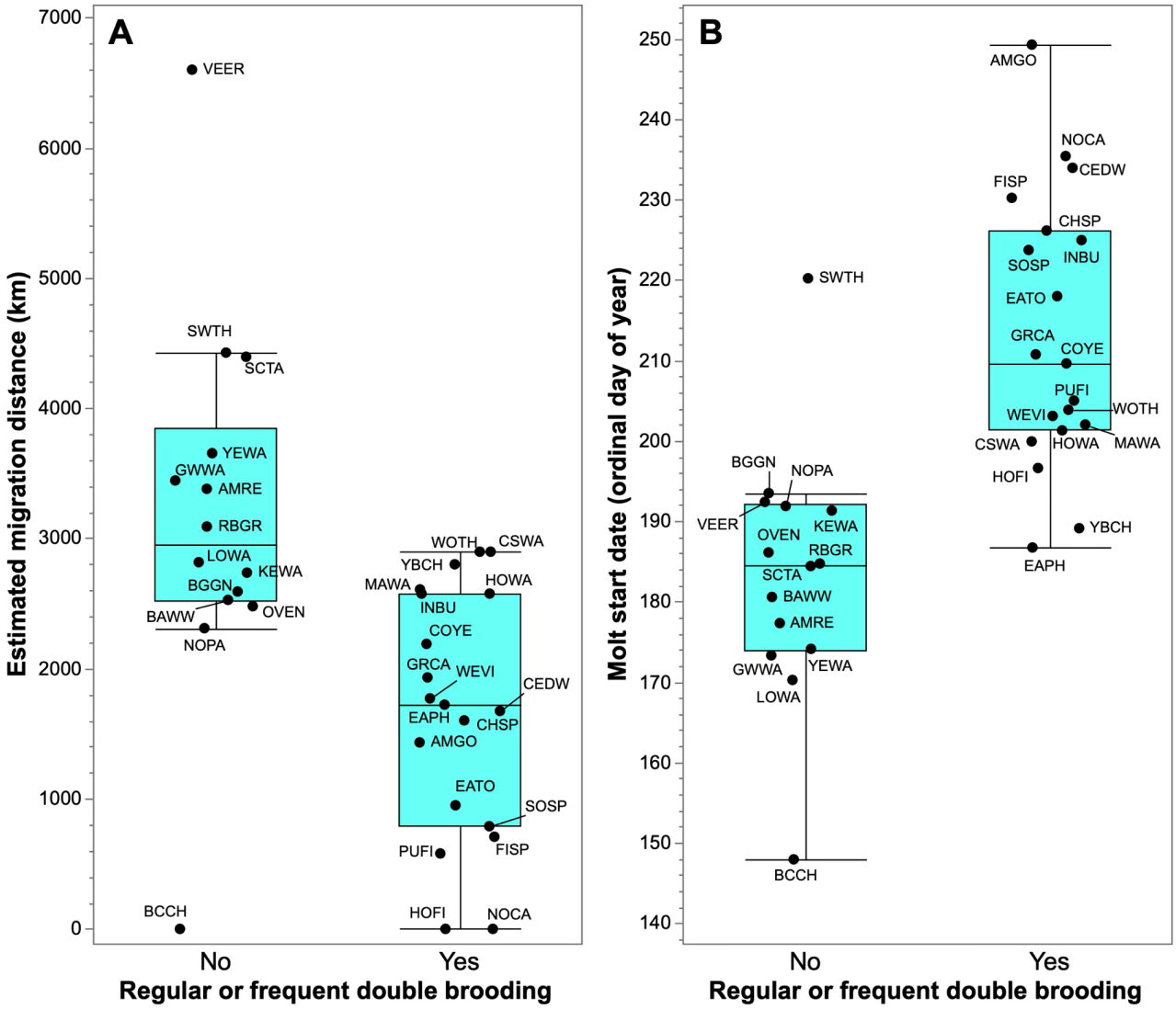


Figure 4. Box plots showing that regular or frequent double brooding is strongly associated with both shorter migration distances (A) and later molt start dates (B) in the 33 species of temperate-zone passerines included in our analysis. Phylogenetic Generalized Least Squares (PGLS) models indicate that species with regular or frequent double brooding have significantly shorter migration distances (t = -3.19, P = 0.003) and significantly later molt initiation dates (t = 6.24, P < 0.001) than those for species where double brooding is absent or rare. Individual species are identified by the four-letter codes shown in Table 1.

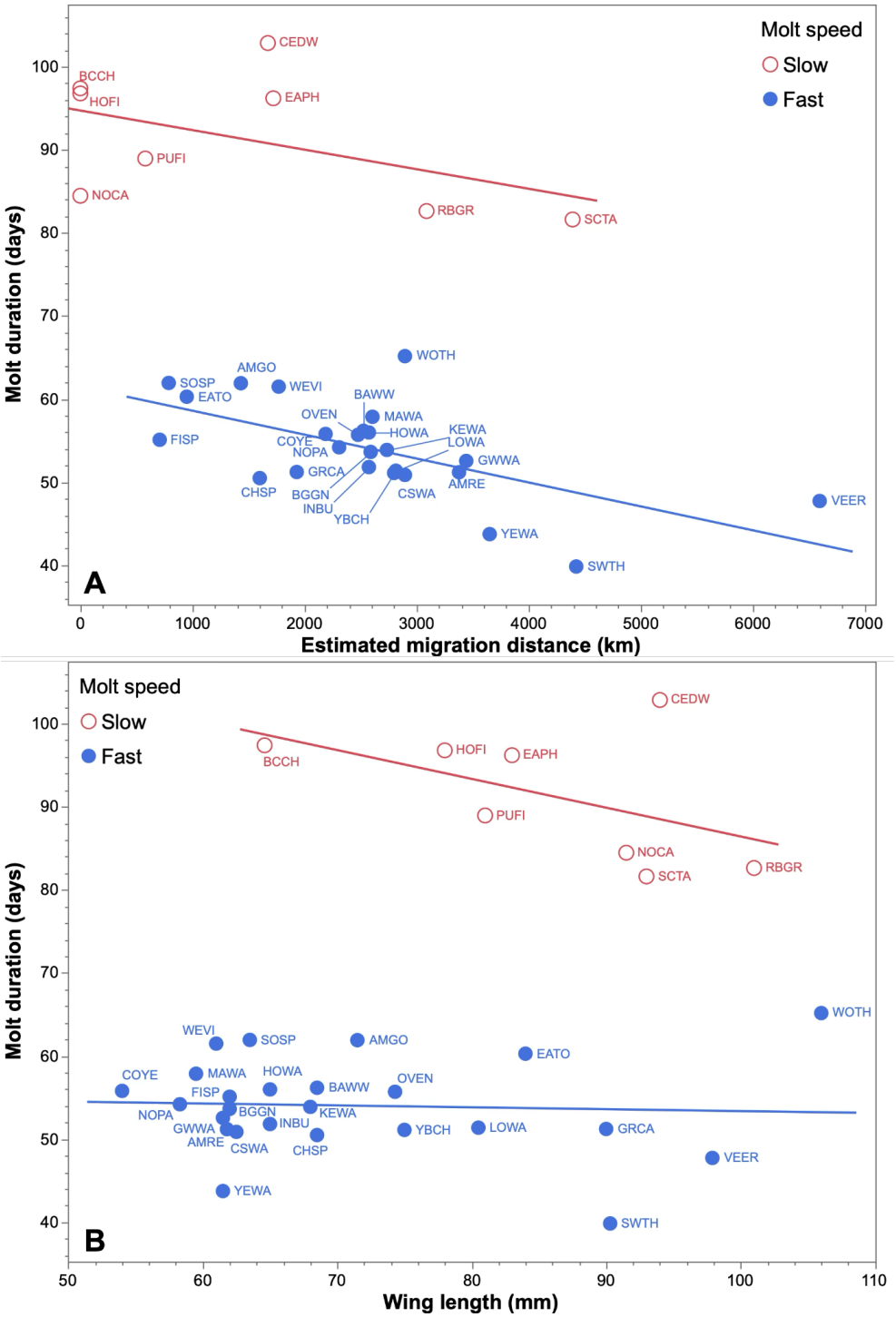


Figure 5. Effects of estimated migration distance (A) and wing length (B) on molt duration for 33 species of slow- and fast-molting temperate-zone passerines. Note in panel (A) that long-distance migration is associated with both a higher probability of categorization as a fast molter and a shorter duration of molt within each category. In contrast, short-winged birds are more likely to be categorized as fast molters, but wing length has no consistent effect on molt duration within categories (B). Plotted lines portray standard linear regression equations for slow and fast molters. Individual species are identified by the four-letter codes shown in Table 1.

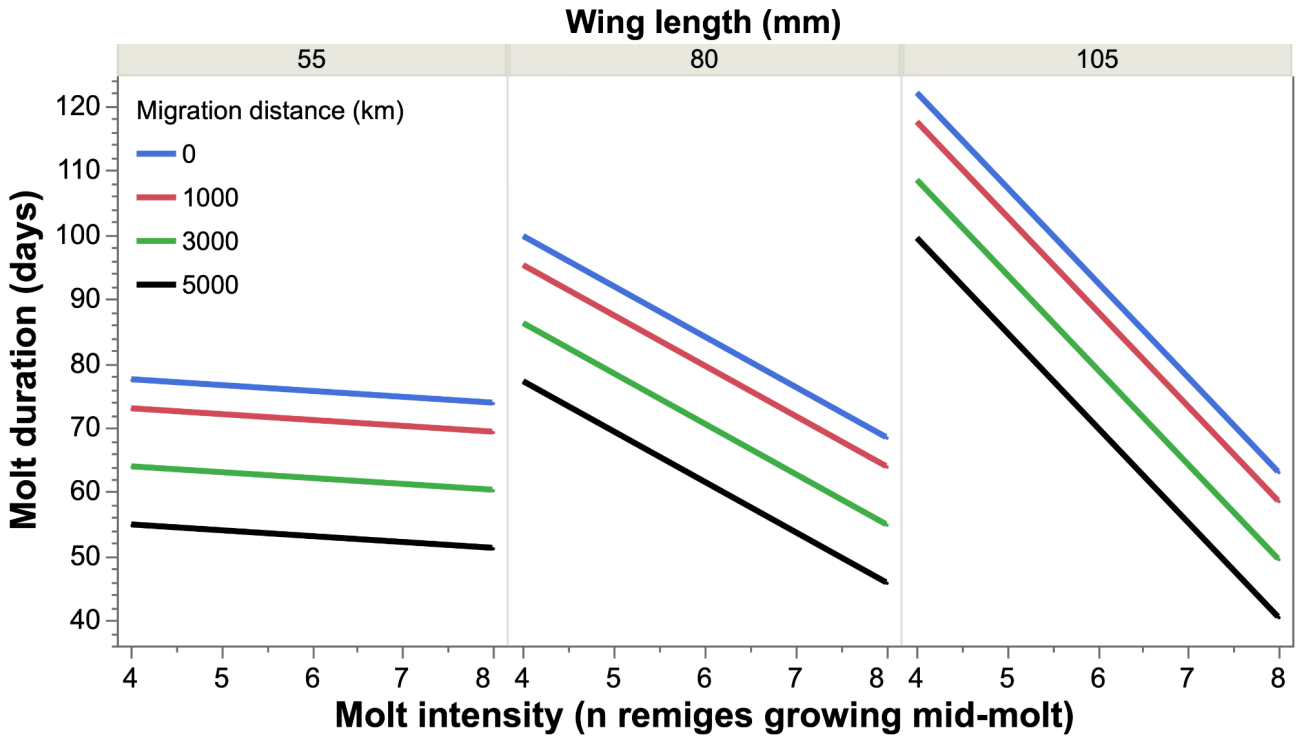


Figure 6. Predictions of a Phylogenetic Generalized Least Squares (PGLS) regression model examining the effects of migration distance, wing length, and molt intensity on molt duration in 33 species of temperate-zone passerines (Table 2B, duration model 3). Note that: (1) Even after controlling for variation in molt intensity, migration distance has a strong and consistent negative effect on molt duration. (2) Long-winged species generally have longer molt durations than short-winged species. (3) Wing length and molt intensity interact such that molt intensity has a proportionally greater negative effect on molt duration for long-winged species.

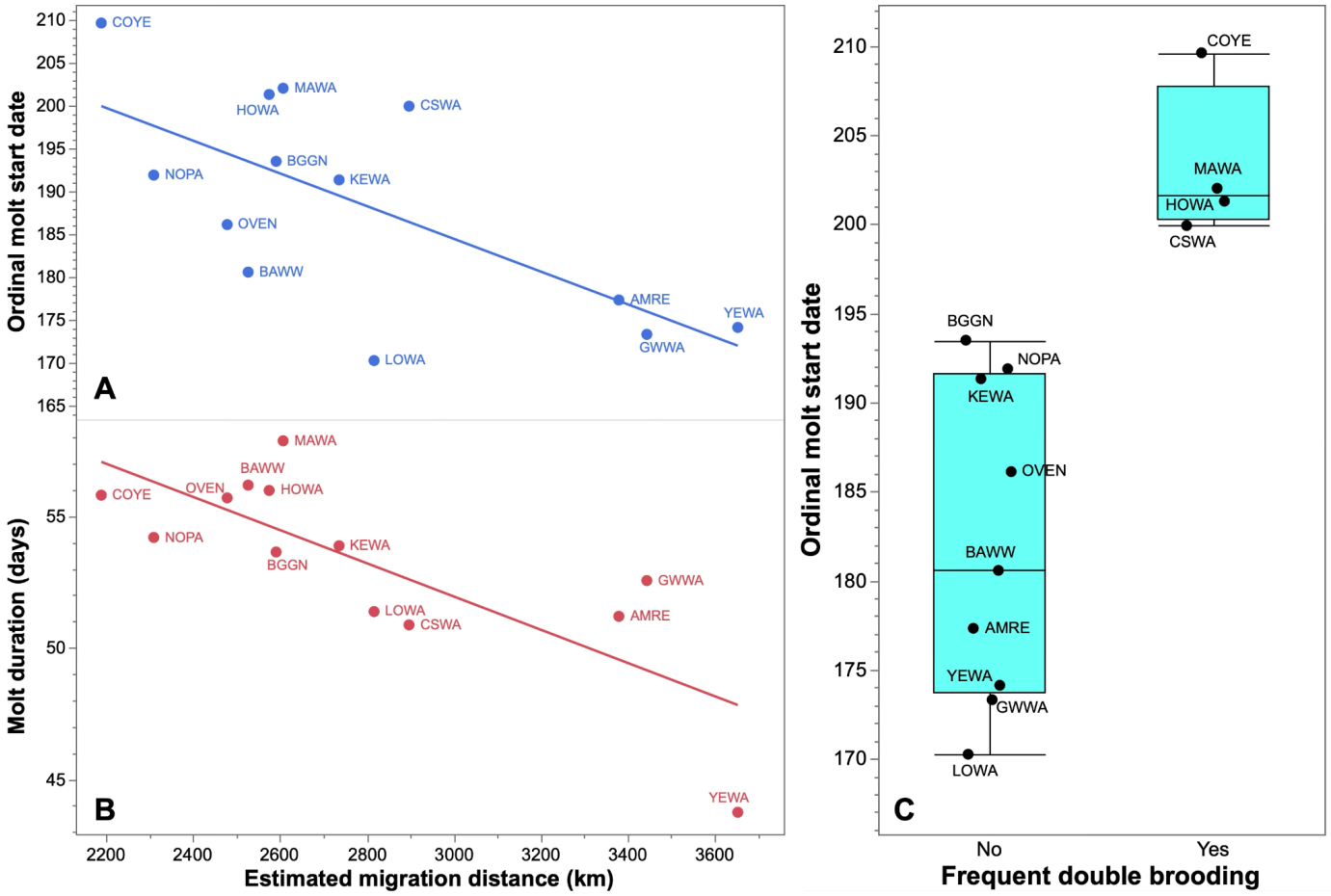


Figure 7. Migration distance and frequency of double brooding have strong effects on the timing and duration of molt in 13 species of migratory warblers (family Parulidae) sampled at Powdermill Avian Research Center in southwestern Pennsylvania, USA. Warbler species with longer migrations initiate molt earlier (A) and complete it more rapidly (B) than those with shorter migrations, and single-brooded species initiate molt earlier than species that are frequently double-brooded (C). Plotted lines portray standard linear regression equations, but coefficients of the complete Phylogenetic Generalized Least Squares (PGLS) regression models are provided in Table 3. Individual species are identified by the four-letter codes shown in Table 1.

Graphical Abstract

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