

Drivers of winter population cycles in the Varied Thrush (*Ixoreus naevius*)

Walter D. Koenig ^{a,b} and Johannes M.H. Knops ^c

^aHastings Reserve, University of California, Berkeley, 38601 E. Carmel Valley Road, Carmel Valley, CA 93924, USA; ^bCornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA; ^cDepartment of Health and Environmental Sciences, Xi'an Jiaotong-Liverpool University, Suzhou 215123, Jiangsu Province, People's Republic of China

Corresponding author: **Walter D. Koenig** (email: wdkoenig@berkeley.edu)

Abstract

The drivers of year-to-year difference in winter abundance patterns, particularly dramatic in the “eruptions” of many boreal seed-eating birds, are poorly understood. Varied Thrush (*Ixoreus naevius* (Gmelin, 1789)), endemic to the Pacific Northwest of North America, is a boreal species that exhibits pronounced, often biennially cyclic, changes in winter abundance within most of its normal wintering range. Although the drivers of this variability have not previously been explored, it has been suggested that differences in acorn abundance, a key winter food resource, might be important. Here, we examine three hypotheses for the drivers of this pattern: the acorn crop within the bird's normal winter range, weather within the bird's winter range, and weather during the previous breeding season within the bird's breeding range. Analyses supported the importance of breeding season conditions, particularly breeding season rainfall, with more birds wintering following wetter years. No support was found for the hypotheses that winter conditions, neither the acorn crop nor winter weather, correlate with winter abundance patterns. For this forest species, year-to-year differences in winter abundance patterns are apparently not driven by the “pull” of winter food supply or winter conditions, but by environmental factors during the prior breeding season that presumably affect reproductive success and subsequent population size.

Key words: acorn crop, *Ixoreus naevius*, population eruptions, population variability, Varied Thrush

Résumé

Les facteurs à l'origine des variations interannuelles des motifs d'abondance hivernale, dont les « éruptions » de nombreux oiseaux granivores boréaux constituent des exemples particulièrement frappants, ne sont pas bien compris. La grive à collier (*Ixoreus naevius* (Gmelin, 1789)), endémique à la région de la côte nord-ouest du Pacifique d'Amérique du Nord, est une espèce boréale qui présente des variations prononcées, suivant souvent un cycle de deux ans, d'abondance hivernale dans la majeure partie de son aire d'hivernage normale. Bien que les facteurs à l'origine de cette variabilité n'aient pas été explorés par le passé, il a été proposé que des variations de l'abondance de glands, une ressource alimentaire hivernale clé, pourraient être importantes. Nous examinons trois facteurs qui pourraient être à l'origine de ce motif, à savoir : la production de glands dans l'aire d'hivernage normale de l'oiseau, la météo dans l'aire d'hivernage de l'oiseau et la météo durant la saison de reproduction précédente dans l'aire de reproduction de l'oiseau. Des analyses appuient l'importance des conditions durant la saison de reproduction, en particulier la pluviométrie, un plus grand nombre d'oiseaux hivernant après des années plus humides. Aucun résultat n'appuie les hypothèses voulant que les conditions hivernales, qu'il s'agisse de la production de glands ou de la météo hivernale, soient corrélées aux motifs d'abondance hivernale. Pour cette espèce forestière, les variations interannuelles des motifs d'abondance hivernale ne semblent pas mues par l'attrait de ressources alimentaires hivernales ni pas les conditions hivernales, mais plutôt par des facteurs environnementaux durant la saison de reproduction précédente, qui ont présument un effet sur le succès de reproduction et la taille subséquente de la population. [Traduit par la Rédaction]

Mots-clés : production de glands, *Ixoreus naevius*, éruptions démographiques, variabilité démographique, grive à collier

Introduction

Dramatic year-to-year variability in wintering abundance and distribution patterns, particularly among boreal seed-eating birds, has often been associated with cycles in food

availability (Lack 1954; Bock and Lepthien 1976; Koenig and Knops 2001). However, environmental factors — mainly weather — have been found to correlate with winter abundance patterns as well (Koenig 2001; Koenig and Knops 2001;

Strong et al. 2015). There have been few tests of alternative hypotheses for the drivers of such year-to-year variability, however.

Varied Thrush (*Ixoreus naevius* (Gmelin, 1789)) of Pacific Northwestern North America is notable for exhibiting large fluctuations in abundance within their winter range and showing up as vagrants as far away as the Atlantic coast and Britain (Grinnell and Miller 1944; Bent 1949; Keith 1968; Wilson 2003). A previous analysis by Wells et al. (1996) documented a biennial cyclic pattern of winter abundance throughout most of this species' normal winter range using data from Audubon Christmas Bird Counts (CBCs) and Project FeederWatch, two large-scale community science projects (Sauer and Link 2002; Bonter and Greig 2021). This pattern was uncorrelated with the incidence of vagrant records, except for birds detected on CBC in southern California (USA) at the southern edge of their winter range. Wells et al. (1996) speculated that the observed year-to-year variability might be driven by acorn abundance, an important food resource for this species during the winter (Bent 1949; Martin et al. 1951) and one that varies greatly from year to year (Koenig et al. 1994a; Koenig and Knops 2005).

Here, we test three hypotheses for the drivers of winter numbers of Varied Thrush, focusing on the coastal subspecies *Ixoreus naevius naevius* (Gmelin, 1789). The first is that numbers are driven by acorn abundance, as proposed by Wells et al. (1996); we refer to this as the “acorn” hypothesis. The second is that winter numbers are dependent on winter environmental conditions (the “winter conditions” hypothesis), and the third is that winter numbers are driven by environmental conditions during the prior breeding season (the “prior breeding conditions” hypothesis).

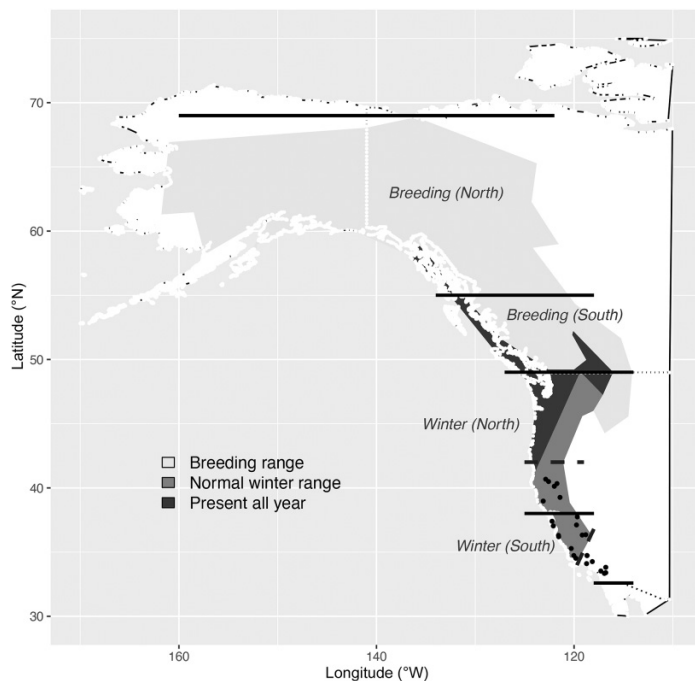
The first two hypotheses are similar in that both assume that birds are attracted or “pulled” into wintering areas exhibiting favorable conditions. The third postulates that favorable conditions during the prior breeding season result in relatively high reproductive success or survivorship that subsequently “pushes” large numbers of birds onto their wintering grounds (Byrne et al. 2019). All three are potentially dependent on food availability driving the observed year-to-year variability. Only the acorn hypothesis makes this connection explicit, whereas the other two hypotheses assume that environmental conditions, either during the winter or during prior breeding season, drive winter numbers of birds without specifying the mechanism or resource involved.

Materials and methods

Bird data

Winter bird abundance was estimated from Audubon CBCs, one-day surveys conducted within a two-week period around the end of December limited to a 24 km diameter circle (Sauer and Link 2002). Values were standardized for effort by dividing the number of birds counted by the number of independent groups of individuals reported for each survey (“party hours”; standardized values are referred to as “birds per party hour” or BPPH). For illustrating annual variation, we further standardized BPPH within sites to a mean

of 0 and standard deviation of 1. Counts used were those conducted throughout the normal winter range of Varied Thrush (George 2020) except for sites in coastal British Columbia (Canada) and Southeast Alaska (USA) (Fig. 1). When analyses involved multiple sites, BPPH values were averaged across sites. Tests directly comparing the three hypotheses were conducted using linear mixed-effects models, as the mean BPPH (the dependent variable) was normally distributed (Shapiro test, $W = 0.93$, $P = 0.15$). CBC data are reported for the year during which results are published; thus, one year was subtracted from published results to match data with the prior year's acorn crop and environmental conditions. Only CBC sites with data for at least 10 years were used in the analyses.



of 0 and standard deviation of 1. Counts used were those conducted throughout the normal winter range of Varied Thrush (George 2020) except for sites in coastal British Columbia (Canada) and Southeast Alaska (USA) (Fig. 1). When analyses involved multiple sites, BPPH values were averaged across sites. Tests directly comparing the three hypotheses were conducted using linear mixed-effects models, as the mean BPPH (the dependent variable) was normally distributed (Shapiro test, $W = 0.93$, $P = 0.15$). CBC data are reported for the year during which results are published; thus, one year was subtracted from published results to match data with the prior year's acorn crop and environmental conditions. Only CBC sites with data for at least 10 years were used in the analyses.

Acorn data

Acorn data came from the California Acorn Survey, a survey of acorn production conducted annually since 1994 (Koenig and Knops 2005, 2013). Data were available for approximately 1100 trees of nine species of acorn-producing trees (eight species of *Quercus* and tanbark oak (*Notholithocarpus densiflorus* (Hook. & Arn.) Manos, Cannon & S. Oh)) growing at 23 sites across the state (Fig. 1). Surveys consisted of two observers with binoculars, each counting as many acorns as they could for 15 s on marked trees (Koenig et al. 1994b). Values were summed (N30) and averaged across all individuals

of each species sampled at each site. N individuals per site ranged between 10 and 86.

Weather data

Mean temperature and total rainfall during the winter (September through December, covering the season prior to CBC surveys around the end of December) were obtained from PRISM climate group gridded data (Oregon State University, Corvallis, Oregon, USA). Sites were restricted to those within the normal US winter range of Varied Thrush (Fig. 1), excluding coastal British Columbia and Southeast Alaska, where birds are present all year. Annual values were estimated by averaging data for all sites located within the relevant winter range. Mean temperature and rainfall for the Canadian breeding range during the prior breeding season (March–August) were estimated similarly using gridded data (anomalies from 30-year means) from CANGRD (<https://open.canada.ca/data/en/dataset/3d4b68a5-13bc-48bb-ad10-801128aa6604>). Weather data for the Alaskan breeding range were not included in the analyses.

Analyses

For testing the effect of the acorn crop on winter abundance of Varied Thrush, the following analyses were conducted: (1) N30 values were averaged across all sites and acorn-producing species for each year of the California Acorn Survey and tested against mean winter abundance of Varied Thrush from all California CBC sites, including those in southern California outside the normal winter range (i.e., acorn survey sites south of the lower green line in Fig. 1); (2) N30 values were averaged across California Acorn Survey sites within the normal winter range of Varied Thrush and tested against mean winter abundance of Varied Thrush across CBC sites within their normal California winter range (sites within the green lines in Fig. 1); and (3) in four cases, mean N30 values for a site were matched with the local nearby CBC and analyzed individually. The four sites used in this last analysis included (from north to south) the following: Hopland Research and Extension Center (39.00°N, 123.08°W; acorn species *Quercus lobata* Née, *Quercus douglasii* Hook. & Arn., *Quercus kelloggii* Newberry, *Quercus chrysolepis* Liebm., and *Quercus wislizeni* A. DC.; years surveyed 1994–2018; matched with the Ukiah CBC); Jasper Ridge Biological Station (37.40°N, 122.24°W; acorn species *Q. lobata*, *Q. douglasii*, and *Quercus agrifolia* Née; years surveyed 1989–2018; matched with the Palo Alto CBC); Hastings Reserve (36.38°N, 121.56°W; acorn species *Q. lobata*, *Q. douglasii*, *Q. chrysolepis*, *Q. agrifolia*, and *Q. kelloggii*; years surveyed 1980–2018; matched with the Monterey CBC); and Sedgwick Reserve (34.69°N, 120.04°W; acorn species *Q. lobata*, *Q. douglasii*, and *Q. agrifolia*; years surveyed 1994–2018; matched with the Santa Barbara CBC). Spearman rank correlations were used in all analyses to determine the relationship between winter abundance of Varied Thrush and the prior autumn's acorn crop.

We used linear mixed-effects models to compare the success of the three hypotheses as explanations for the mean BPPH counted within the Varied Thrush's normal winter

range (Table 1). Comparisons were made using Akaike's information criterion corrected for sample size (ΔAIC_c) (Burnham and Anderson 2002; Anderson 2008). Given the large latitudinal range of Varied Thrush, and that the population breeding at higher latitudes (consisting primarily of *I. n. meruloides*) tends to migrate to more interior sites (Grinnell 1901; George 2020), breeding and winter ranges were divided into two latitudinal sections (for breeding range: 40°N–55°N and 55°N–70°N latitude; for winter range: 32.5°N–38°N and 38°N–49°N latitude). In all models, the divided breeding and winter ranges were included as a random factor with four values corresponding to the four combinations of breeding and winter latitudinal ranges. Analyses were conducted using R 4.0.2 (R Core Team 2020) and packages “nlme” (Pinheiro et al. 2022) and “bblme” (Bolker et al. 2022).

Results

Winter abundance of birds

Plots of the mean abundance of Varied Thrush within their normal winter range for years 1980–2018 are presented in Fig. 2. As reported earlier by Wells et al. (1996), winter abundance varies considerably from year to year (Fig. 2a), typically exhibiting a biennially cyclic pattern (Fig. 2b).

Winter abundance and the acorn crop

There were no significant correlations between the overall winter abundance of Varied Thrush in California and the overall mean size of the statewide acorn crop; between the winter abundance of Varied Thrush and the acorn crop at California Acorn Survey sites within the bird's normal winter range; or between annual acorn counts at any of the four individual survey sites and winter numbers of Varied Thrush from the corresponding nearby CBC (Table 2).

Winter abundance: comparison of models

Models comparing the three hypotheses yielded strong support for the prior breeding season hypothesis (Table 3). Not only were the only two models receiving support ($\Delta AIC_c < 2.0$; Anderson 2008) those involving prior breeding season weather conditions (rainfall or both rainfall and mean temperature), but the three top models (all of which involved only breeding season variables and were the only ones with more support than the null model) achieved an aggregated likelihood of 0.99 (Table 3). None of the models involving winter weather conditions or the acorn crop received support, nor did any outperform the null model. The relationship between breeding season rainfall and winter Varied Thrush abundance is illustrated in Fig. 3.

Discussion

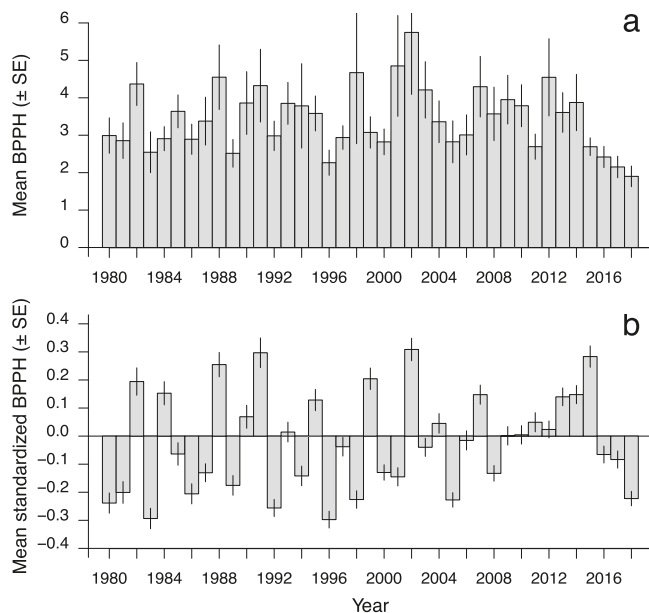
A considerable number of boreal bird species are known to undergo cyclic or quasi-cyclic patterns of winter abundance. For many of these, variability in annual food abundance during the breeding season, usually small mammalian prey or seeds from masting trees, is thought to be the main driver of

Table 1. Independent variables used in the linear mixed-effects models.

Model	Variables in the model	Source	Notes
1	Breeding season rainfall	CANGRD	March–August
2	Breeding season mean temperature	CANGRD	March–August
3	Breeding season mean temperature Breeding season rainfall	CANGRD	March–August
4	Winter rainfall	PRISM	October–December
5	Winter mean temperature	PRISM	October–December
6	Winter mean temperature Winter rainfall	PRISM	October–December
7	Breeding season rainfall Breeding season rainfall	CANGRD PRISM	March–August October–December
8	Mean acorn crop	California Acorn Survey	September (fall survey)
9	Breeding season rainfall Winter rainfall Mean acorn crop	CANGRD PRISM California Acorn Survey	March–August October–December September (fall survey)
10	Null model	—	—

Note: In all cases, standardized “birds per party hour” (BPPH) was the response variable, and the four combinations of northern and southern summer and winter ranges were included as a random variable. “Source” refers to the source of the data; “Notes” specify the months included in seasonal independent variables. See text for more details.

Fig. 2. (a) Mean (\pm SE) abundance of Varied Thrush (*Ixorius naevius*) (mean birds per party hour (BPPH)) on Christmas Bird Count sites in their normal winter range (California (USA), Oregon (USA), Washington (USA), and British Columbia (Canada)), 1980–2018. (b) The same values as in panel a standardized within sites to a mean of 0 and standard deviation of 1.



these cycles, with eruptions of birds well beyond their normal winter range occurring when relatively large populations following a successful breeding season face a subsequent year of low food availability (Svärdson 1957; Bock and Lepthien 1976; Koenig and Knops 2001; Newton 2006). Less well known is the role winter conditions play in attracting eruptive species, often to areas far beyond their normal winter range. Winter factors have recently been inferred to play a role in eruptions

of Pine Siskins (*Spinus pinus* (A. Wilson, 1810)), where west to east movements within North America were correlated with climatic dipoles suggesting that low food availability pushes birds from one side of the continent toward areas likely to have high food availability on the other side (Strong et al. 2015; Zuckerberg et al. 2020).

Varied Thrush is a boreal forest species that undergoes considerable variability in winter abundance but is neither a small mammal specialist nor a typical boreal seed-eating species. Instead, its main diet during the breeding season consists of ground-dwelling arthropods (Beck and George 2000), switching to fruits, berries, and nuts, including acorns, in the winter (Beal 1915; Hagar 1960; George 2020). Consequently, the factors affecting winter abundance are not obvious. Given their cyclic variability peaking every 2–5 years, Wells et al. (1996) speculated that variability in the acorn crop might be the key factor driving these cycles.

Oaks (*Quercus* spp.), the most common acorn-bearing tree throughout a good proportion of the winter range of Varied Thrush, are “masting” species, producing highly variable and geographically synchronized acorn crops, cycling at roughly similar length as Varied Thrush (Koenig et al. 1994a; Koenig and Knops 2002). We tested the hypothesis that acorn abundance drives winter Varied Thrush abundance using data from the California Acorn Survey, an annual statewide survey of acorn production. Although encompassing a tiny fraction of the estimated 5.3×10^6 ha of oak forest and oak woodland in California (Gaman and Firman 2006), acorn production is typically highly spatially synchronous within, and in some cases between, species over scales of hundreds of kilometres (Koenig and Knops 2005, 2013). Thus, the California Acorn Survey provides a reasonable estimate of overall acorn abundance across the state (Koenig et al. 2009).

Tests of the acorn hypothesis were conducted at both large (statewide) and local (individual site) geographic scales, and in models comparing support for the acorn hypothesis and

Table 2. Correlations between winter abundance of Varied Thrush (VATH; *Ixorius naevius*) as estimated by the mean standardized birds per party hour (BPPH) and the overall size of the prior autumn's acorn crop, including all California Christmas Bird Count (CBC) sites, California CBC sites within VATH's normal winter range, and at four localities in the California coast ranges.

Bird data	Acorn crop data	<i>r</i> value	<i>P</i> value	<i>N</i> years
All California CBC sites	California Acorn Survey, all sites	0.27	0.21	24
California CBC sites within VATH's normal winter range	California Acorn Survey, sites within VATH's normal winter range	0.13	0.56	24
Ukiah CBC	Hopland Research and Extension Center	0.01	0.97	24
Palo Alto CBC	Jasper Ridge Biological Station	-0.01	0.97	29
Monterey CBC	Hastings Reserve	-0.17	0.32	34
Santa Barbara CBC	Sedgwick Reserve	-0.05	0.78	24

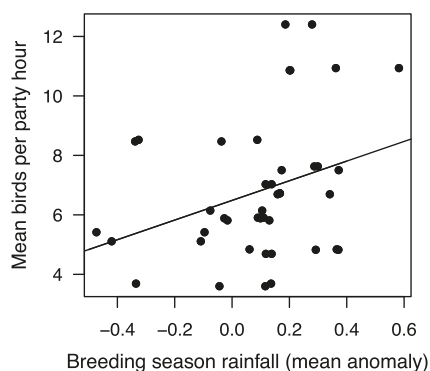
Note: Analyses by Spearman rank correlation. See text for details.

Table 3. Results of models testing factors driving winter abundance of Varied Thrush (*Ixorius naevius*).

Model	Fixed factors	Estimate \pm SE	Δ AIC _c	df	Model weight
1	Breeding season rainfall	3.305 \pm 1.076	0.0	4	0.51
3	Breeding season rainfall Breeding season mean temperature	2.395 \pm 1.176 -0.563 \pm 0.314	0.5	7	0.39
2	Breeding season mean temperature	-0.839 \pm 0.289	3.5	4	0.09
10	Null model	—	8.1	3	0.01
7	Breeding season rainfall Winter rainfall	3.229 \pm 1.081 -0.002 \pm 0.002	13.3	5	<0.001
8	Mean acorn crop	0.050 \pm 0.037	14.0	4	<0.001
5	Winter mean temperature	-0.018 \pm 0.066	14.5	4	<0.001
9	Breeding season rainfall Winter rainfall Mean acorn crop	3.167 \pm 1.080 -0.001 \pm 0.002 0.042 \pm 0.035	20.3	6	<0.001
4	Winter rainfall	-0.002 \pm 0.002	20.6	4	<0.001
6	Winter mean temperature Winter rainfall	-0.290 \pm 0.124 -0.009 \pm 0.004	20.8	5	<0.001

Note: Tests by linear mixed-effects models; model numbers as in Table 1. In all cases, the dependent variable was the mean number of Varied Thrushes counted per party hour (BPPH). Analyses included the breeding and normal winter ranges divided into north (N) and south (S) sections (N breeding area 55°N–70°N; S breeding area 55°N–40°N; N wintering area 38°N–49°N; S wintering area 32°N–38°N) as a random factor (see text). Analysis includes the 21 years for which both data on the acorn crop and weather were available, 1994–2014. Δ AIC_c, comparison made using Akaike's information criterion corrected for small sample size.

Fig. 3. Scattergram of winter Varied Thrush (*Ixorius naevius*) numbers from Christmas Bird Count (CBC) sites versus breeding season rainfall (measured as anomalies from 30-year mean values). Line is the linear regression.



hypotheses involving environmental conditions during the breeding season and winter. None of the analyses supported the proposal that the acorn crop plays a role in driving winter abundance patterns, nor was there support for the “winter

conditions” hypothesis — either rainfall or mean temperature — affecting winter abundance. Apparently, winter environmental conditions play little or no role in driving annual differences in winter abundance of the coastal subspecies of Varied Thrush, at least within their normal winter range. Factors influencing annual variability in *I. n. meruloides*, the interior subspecies, as well as other weakly differentiated forms (George 2020), remain to be investigated.

In contrast, we found strong support for conditions during the breeding season (the “prior breeding conditions” hypothesis) driving winter abundance patterns, most strongly rainfall. This finding corresponds to prior work by Root (1988), who found annual rainfall to be the environmental factor most strongly associated with overall (i.e., not year-to-year) abundance of Varied Thrush in their winter range. Given this predilection for wet habitats, it is reasonable to assume that Varied Thrush breed more successfully during wetter years. Thus, these analyses support the hypothesis that varying numbers of wintering Varied Thrush are driven primarily by density-independent favorable conditions during breeding that subsequently result in relatively large numbers of wintering birds.

Although acorns appear to have little, if any, influence on winter abundance of Varied Thrush, it is possible that abundance of other winter foods may be important. The dense, humid forests, where wintering Varied Thrush are most common, often contain oaks (or tanbark oak), but such acorn-producing trees are often not the dominant members of the forest community. Their winter diet primarily consists of vegetable matter, including wild fruit, seeds, and berries, in addition to acorns (Bent 1949; Martin et al. 1951). How these other winter food resources vary from year to year, and thus whether they may affect winter numbers of Varied Thrush, remains to be determined. Another factor potentially affecting winter abundance is mortality during migration, as recent work has found that Varied Thrushes are disproportionately vulnerable to bird–window collisions, particularly during the fall (De Groot et al. 2021).

Although these analyses indicate that winter abundance patterns are affected by environmental conditions during the breeding season, the demographic effects of breeding season conditions on the demography of the birds are not known. Rainfall can have a variety of potential effects on breeding success and survivorship of fledglings via both food-resource-related and predator-mediated processes (Morrison and Bolger 2002; Styrsky and Brawn 2011; Öberg et al. 2015).

These are only a few of the many questions about Varied Thrush that remain to be investigated. In addition to the varying winter abundance patterns analyzed here, periodic, extralimital eruptions of this species take place, with birds wintering far beyond their normal winter range and appearing as far away as the east coast of North America and Britain. Wells et al. (1996) suggested that such apparent vagrants involved the relatively poorly known *I. n. meruloides* rather than the better known, more coastal *I. n. naevius*, and might involve a widespread but sparse winter distribution rather than birds wandering outside their normal range. Much remains to be discovered about the geographical ecology of this intriguing species.

Acknowledgements

We thank the reviewers and all those who have contributed to the California Acorn Survey over the years. We especially thank the people and organizations in charge of California Acorn Survey field sites, including the University of California (UC) Natural Reserve System, UC Division of Agriculture and Natural Resources, Stanford University, the Nature Conservancy, Sequoia Riverlands Trust, USDA Forest Service, the California State Parks, and the National Park Service.

Article information

History dates

Received: 18 February 2022

Accepted: 21 May 2022

Accepted manuscript online: 9 June 2022

Version of record online: 9 August 2022

Copyright

© 2022 The Author(s). This work is licensed under a [Creative Commons Attribution 4.0 International License](https://creativecommons.org/licenses/by/4.0/) (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

Data availability

The data generated and analyzed during this study are available from the corresponding author upon reasonable request.

Author information

Author ORCIDs

Walter D. Koenig <https://orcid.org/0000-0001-6207-1427>

Johannes M.H. Knops <https://orcid.org/0000-0002-9647-9209>

Competing interests

The authors declare no competing interests.

Funding information

The California Acorn Survey was funded by National Science Foundation grants DEB-0816691 and DEB-1256394.

References

- Anderson, D.R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, NY.
- Beal, F.E.L. 1915. Food of the robins and bluebirds of the United States. US Dept. Agric. Bull. **171**.
- Beck, M.J., and George, T.L. 2000. Song post and foraging site characteristics of breeding varied thrushes in northwestern California. *Condor*, **102**: 93–103. doi:10.1093/condor/102.1.93.
- Bent, A.C. 1949. Life histories of North American thrushes, kinglets, and their allies. US Nat. Mus. Bull. **196**.
- Bock, C.E., and Lepthien, L.W. 1976. Synchronous eruptions of boreal seed-eating birds. *Am. Nat.* **110**: 559–571. doi:10.1086/283091.
- Bolker, B., Team R Core, and Giné-Vázquez, I. 2022. bblme: tools for general maximum likelihood estimation. R package version 1.0.25. Available from <https://CRAN.R-project.org/package=bblme>.
- Bonter, D.N., and Greig, E.I. 2021. Over 30 years of standardized bird counts at supplementary feeding stations in North America: a citizen science data report for project feederwatch. *Front. Ecol. Evol.* **9**: 619682. doi:10.3389/fevo.2021.619682.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multi-model inference: a practical information-theoretic approach. 2nd ed. Springer, New York, NY.
- Byrne, A.W., O’Keeffe, J., Buesching, C.D., and Newman, C. 2019. Push and pull factors driving movement in a social mammal: context dependent behavioral plasticity at the landscape scale. *Curr. Zool.* **65**: 517–525. doi:10.1093/cz/zoy081. PMID: 31616482.
- De Groot, K.L., Porter, A.N., Norris, A.R., Huang, A.C., and Joy, R. 2021. Year-round monitoring at a pacific coastal campus reveals similar winter and spring collision mortality and high vulnerability of the varied thrush. *Ornithol. Appl.* **123**: duab027.
- Gaman, T., and Firman, J. 2006. Oaks 2040: the status and future of oaks in California. California Oak Foundation, Oakland. Available from https://www.sierraforestlegacy.org/Resources/Conservation/FireForestEcology/ThreatenedHabitats/OakWoodland/OakWoodlands-Gama_n06.pdf.
- George, T.L. 2020. Varied Thrush *Ixoreus naevius*, version 1.0. In *Birds of the World*. Edited by A.F. Poole and F.B. Gill. Cornell Lab of Ornithology, Ithaca, NY.
- Grinnell, J. 1901. Two races of the Varied Thrush. *Auk*, **18**: 142–145. doi:10.2307/4069497.

- Grinnell, J., and Miller, A.H. 1944. The distribution of the birds of California. *Pac. Coast Avifauna*, **27**: 1–607.
- Hagar, D.C. 1960. The interrelationships of logging, birds, and timber regeneration in the Douglas-fir region of northwestern California. *Ecology*, **41**: 116–125. doi:[10.2307/1931945](https://doi.org/10.2307/1931945).
- Keith, A.R. 1968. A summary of the extralimital records of the varied thrush, 1848 to 1966. *Bird-Banding*, **39**: 245–276. doi:[10.2307/4511513](https://doi.org/10.2307/4511513).
- Koenig, W.D. 2001. Synchrony and periodicity of eruptions by boreal birds. *Condor*, **103**: 725–735. doi:[10.1093/condor/103.4.725](https://doi.org/10.1093/condor/103.4.725).
- Koenig, W.D., and Knops, J.M.H. 2001. Seed-crop size and eruptions of North American boreal seed-eating birds. *J. Anim. Ecol.* **70**: 609–620. doi:[10.1046/j.1365-2656.2001.00516.x](https://doi.org/10.1046/j.1365-2656.2001.00516.x).
- Koenig, W.D., and Knops, J.M.H. 2002. The behavioral ecology of masting in oaks. In *Oak forest ecosystems*. Edited by W.J. McShea and W.M. Healy. Johns Hopkins University Press, Baltimore, MD. pp. 129–148.
- Koenig, W.D., and Knops, J.M.H. 2005. The mystery of masting in trees. *Am. Sci.* **93**: 340–347. doi:[10.1511/2005.4.340](https://doi.org/10.1511/2005.4.340).
- Koenig, W.D., and Knops, J.M.H. 2013. Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. *Ecology*, **94**: 83–93. doi:[10.1890/12-0940.1](https://doi.org/10.1890/12-0940.1). PMID: [23600243](https://pubmed.ncbi.nlm.nih.gov/23600243/).
- Koenig, W.D., Mumme, R.L., Carmen, W.J., and Stanback, M.T. 1994a. Acorn production by oaks in central coastal California: variation within and among years. *Ecology*, **75**: 99–109. doi:[10.2307/1939386](https://doi.org/10.2307/1939386).
- Koenig, W.D., Knops, J.M.H., Carmen, W.J., Stanback, M.T., and Mumme, R.L. 1994b. Estimating acorn crops using visual surveys. *Can. J. For. Res.* **24**: 2105–2112. doi:[10.1139/x94-270](https://doi.org/10.1139/x94-270).
- Koenig, W.D., Krakauer, A.H., Monahan, W.B., Haydock, J., Knops, J.M.H., and Carmen, W.J. 2009. Mast-producing trees and the geographical ecology of western scrub-jays. *Ecography*, **32**: 561–570. doi:[10.1111/j.1600-0587.2008.05617.x](https://doi.org/10.1111/j.1600-0587.2008.05617.x).
- Lack, D. 1954. *The regulation of animal numbers*. Oxford University Press, Oxford, UK.
- Martin, A.C., Zim, H.S., and Nelson, A.L. 1951. *A guide to wildlife food habits*. Dover, New York, NY.
- Morrison, S.A., and Bolger, D.T. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. *Oecologia*, **133**: 315–324. doi:[10.1007/s00442-002-1040-3](https://doi.org/10.1007/s00442-002-1040-3). PMID: [28466220](https://pubmed.ncbi.nlm.nih.gov/28466220/).
- Newton, I. 2006. *Advances in the study of irruptive migration*. Ardea, **94**: 433–460.
- Öberg, M., Arlt, D., Pärt, T., Laugen, A.T., Eggers, S., and Low, M. 2015. Rainfall during parental care reduces reproductive and survival components of fitness in a passerine bird. *Ecol. Evol.* **5**: 345–356. doi:[10.1002/ece3.1345](https://doi.org/10.1002/ece3.1345). PMID: [25691962](https://pubmed.ncbi.nlm.nih.gov/25691962/).
- Pinheiro, J.C., and Bates, D., Team R Core. 2022. nlme: linear and nonlinear mixed effects models. R package version 3.1-157. Available from <https://CRAN.R-project.org/package=nlme>.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical computing, Vienna, Austria. Available from <https://www.R-project.org/>.
- Root, T. 1988. *Atlas of wintering North American birds*. University of Chicago Press, Chicago, IL.
- Sauer, J.R., and Link, W.A. 2002. Using Christmas Bird Count data in analysis of population change. *Am. Birds*, **56**: 10–14.
- Strong, C., Zuckerberg, B., Betancourt, J.L., and Koenig, W.D. 2015. Climatic dipoles drive two principal modes of North American boreal bird irruption. *Proc. Natl. Acad. Sci. U.S.A.* **112**: E2795–E2802. doi:[10.1073/pnas.1418414112](https://doi.org/10.1073/pnas.1418414112).
- Styrsky, J.N., and Brawn, J.D. 2011. Annual fecundity of a neotropical bird during years of high and low rainfall. *Condor*, **113**: 194–199. doi:[10.1525/cond.2011.100051](https://doi.org/10.1525/cond.2011.100051).
- Svårdson, G. 1957. The “invasion” type of bird migration. *Br. Birds*, **50**: 314–343.
- Wells, J.V., Rosenberg, K.V., Tessaglia, D.L., and Dhondt, A.A. 1996. Population cycles in the varied thrush (*Ixoreus naevius*). *Can. J. Zool.* **74**: 2062–2069. doi:[10.1139/z96-234](https://doi.org/10.1139/z96-234).
- Wickham, H. 2016. *ggplot2: elegant graphics for data analysis*. Springer-Verlag, New York, NY.
- Wilson, A. 2003. Puzzling varied thrush (*Ixoreus naevius*) on long Island, New York. *Kingbird*, **53**: 105–107.
- Zuckerberg, B., Strong, C., LaMontagne, J.M., St. George, S., Betancourt, J.L., and Koenig, W.D. 2020. Climate dipoles as continental drivers of plant and animal populations. *Trends Ecol. Evol.* **35**: 440–453. doi:[10.1016/j.tree.2020.01.010](https://doi.org/10.1016/j.tree.2020.01.010). PMID: [32294425](https://pubmed.ncbi.nlm.nih.gov/32294425/).

Copyright of Canadian Journal of Zoology is the property of Canadian Science Publishing and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.