

# Latitudinal decrease in acorn size in bur oak (*Quercus macrocarpa*) is due to environmental constraints, not avian dispersal

Walter D. Koenig, Johannes M.H. Knops, Janis L. Dickinson, and Benjamin Zuckerberg

**Abstract:** The size of acorns produced by several species of eastern North American oaks decreases with latitude. We investigated three hypotheses for this pattern in the bur oak (*Quercus macrocarpa* Michx.) using samples collected over 2 years throughout the species' range. We found strong support for the hypothesis that abiotic factors, including both temperature and rainfall, constrain acorn size. There was also a smaller but important difference in acorn size related to whether sites were glaciated or not, providing support for the hypothesis that some factor associated with the history of glaciation affects acorn mass. In contrast, although blue jays (*Cyanocitta cristata* L.) prefer smaller acorns and are an important dispersal agent, the latitudinal patterns of acorn size and variability were not consistent with predictions of the hypothesis that they are the product of blue jay dispersal during bur oak's postglacial Holocene expansion. Assuming that there is a lower limit to the size that acorns can be and still be successful, the strong role of environmental constraints on acorn size may be important in explaining the apparently contradictory interspecific pattern that North American oaks successfully colonizing areas further north during the Holocene are those that produce relatively larger acorns.

**Key words:** blue jay, differential dispersal, life-history trade-offs, latitudinal gradient, seed dispersal, seed size.

**Résumé :** La dimension des glands produits par plusieurs espèces de chênes nord-américains diminue avec la latitude. Les auteurs ont étudié trois hypothèses pour expliquer ce patron chez le chêne à gros fruits (*Quercus macrocarpa* Michx.), en utilisant des échantillons récoltés sur deux années dans l'ensemble de l'aire de distribution de cette espèce. Les auteurs ont trouvé un support important pour l'hypothèse basée sur des facteurs abiotiques restreignant la dimension des glands, incluant la température et les précipitations. On observe également une différence plus petite, mais significative dans la dimension des glands selon que les sites forment de la glace ou non, supportant l'hypothèse que certains facteurs associés à l'histoire de la glaciation affectent la dimension des glands. Au contraire, bien que le geai bleu (*Cyanocitta cristata* L.) préfère les glands plus petits et en constitue un agent de dispersion important, la distribution latitudinale de la dimension des glands et de sa variabilité ne concorde pas avec les prédictions de l'hypothèse qu'elles proviendraient de la dispersion par les geais bleus au cours de l'expansion postglaciaire de l'Éocène, du chêne à gros fruits. En assumant qu'il y a une limite à la dimension des glands pour demeurer fonctionnels, le rôle considérable des contraintes environnementales sur la dimension des glands pourrait être important pour expliquer le patron interspécifique apparemment contradictoire que les chênes de l'Amérique du Nord colonisant avec succès les aires plus nordiques au cours de l'Holocène, sont ceux qui produisent des glands relativement plus gros.

**Mots-clés :** geai bleu, dispersion différentielle, contre parties de l'histoire de vie, gradient latitudinal, dispersion des graines, dimension des graines.

[Traduit par la Rédaction]

## Introduction

Offspring size is generally believed to be under strong selection to optimize fitness through balancing trade-offs between current and future reproduction, quantity and quality of offspring, and investment in one versus many offspring (Smith and Fretwell 1974). In plants there is particularly

good evidence for selection favoring large seed size, with numerous studies demonstrating that larger seeds do better in the face of seedling competition for nutrients and light, herbivory, and nutrient limitation (Leishman and Westoby 1994; Hewitt 1998; Seiwa 2000; Gómez 2004). On the other hand, since seed number limits annual reproductive potential, there is always selection for producing more seeds

Received 2 May 2008. Published on the NRC Research Press Web site at botany.nrc.ca on 25 March 2009.

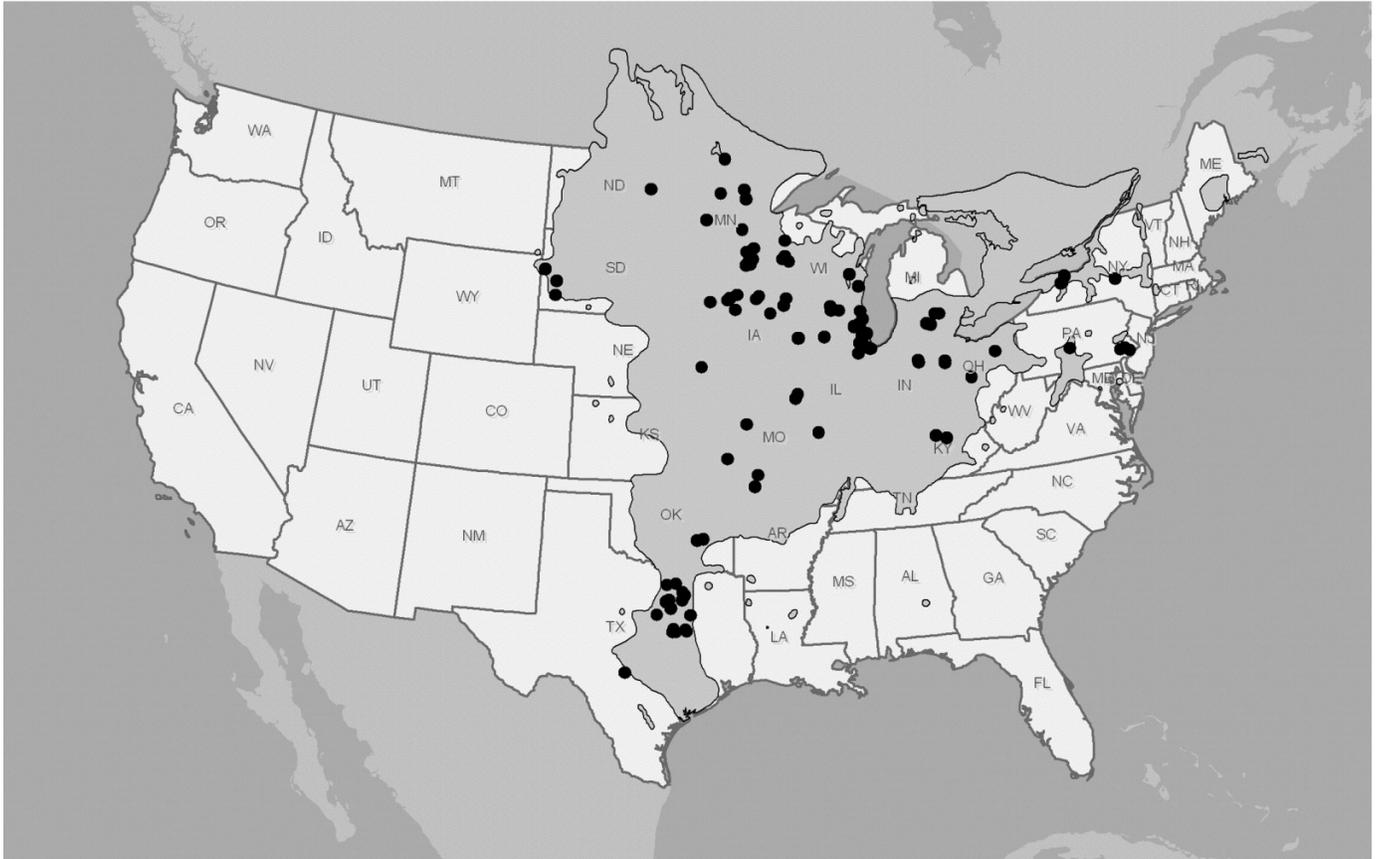
**W.D. Koenig**<sup>1</sup> Cornell Laboratory of Ornithology and Department of Neurobiology and Behavior, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.

**J.M.H. Knops**, Department of Biological Sciences, 348 Manter Hall, University of Nebraska, Lincoln, NE 68588, USA.

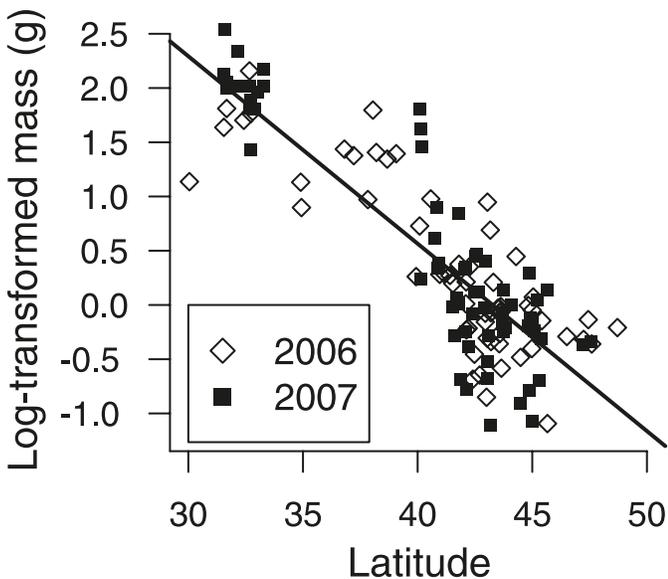
**J.L. Dickinson and B. Zuckerberg**, Cornell Laboratory of Ornithology and Department of Natural Resources, Cornell University, 159 Sapsucker Woods Road, Ithaca, NY 14850, USA.

<sup>1</sup>Corresponding author (e-mail: wdk4@cornell.edu).

**Fig. 1.** Geographic distribution of bur oak (USGS 2008). Sites from which samples of acorns were obtained are marked.



**Fig. 2.** Scattergram of log-transformed mean acorn mass vs. latitude for the 2 years of the study combined. Line is the linear regression. Spearman rank correlation  $r_s = -0.77$ ,  $P < 0.001$ .



which, because of the evolutionary size–number trade-off in these key life-history traits, may lead to smaller seed size (Westoby et al. 1992; Leishman 2001). Selection for smaller seeds can also come from either a preference for large seeds by predators (Gómez 2004) or for small seeds by dispersers

(Darley-Hill and Johnson 1981; Scarlett and Smith 1991; Moore and Swihard 2006). Abiotic factors may also influence seed size. For example, if size is limited by the growing season, seeds would be expected to decrease in size with increasing latitude (Aizen and Woodcock 1992; Moles and Westoby 2003; Moles et al. 2007). Given this complexity, it is not surprising that the evolutionary ecology of seed size is an active area of research (Baker 1972; Aizen and Patterson 1990; Westoby et al. 1992; Leishman 2001; Moles et al. 2007).

Previous work examining acorn size in eastern North American oaks (*Quercus*) using forestry handbooks (Schopmeyer 1974) and museum material has found two seemingly contradictory patterns: species with larger acorns tend to be those whose ranges extend into higher latitudes (Aizen and Patterson 1990, 1992) while at the same time the overall tendency within species is toward smaller acorns with increasing latitude (Aizen and Woodcock 1992). This indicates that species with larger acorns have been superior dispersers and (or) competitors during the postglacial Holocene expansion of this taxon, but that within species, acorns have become smaller as they colonized more northern areas. The potential cause of these patterns has not been previously examined.

Here we focus on geographic variation in seed size of bur oak (*Quercus macrocarpa* Michx.), a species widespread in midwestern North America (Fig. 1) and one of the species exhibiting a strong cline of decreasing acorn size with increasing latitude (Aizen and Woodcock 1992). We tested

**Table 1.** Candidate models for explaining variation in mean (log-transformed) acorn mass ( $N = 126$  sites) compared using bias-adjusted  $AIC_c$  values derived from general linear models ranked from best to worst.

Model	Variables	$K$	$AIC_c$	All models	
				$\Delta AIC_c$	$w$
1	Environmental variables	9	154.1	0.0	0.49
2 (global)	Glaciation	10	154.5	0.4	0.41
	Latitude				
3	Environmental variables	4	158.6	4.5	0.05
	Glaciation				
4	Latitude	9	160.0	5.9	0.03
	Environmental variables				
5	Latitude	3	162.1	8.0	0.01
6	Environmental variables	8	162.7	8.6	0.01
7	Annual environmental variables only	5	163.8	9.7	0.00
8	Seasonal environmental variables only	5	182.0	27.9	0.00
9	Glaciation	3	289.4	135.3	0.00

**Note:**  $K$ , number of parameters in the model;  $AIC_c$ , bias-adjusted Akaike's information criteria;  $\Delta AIC_c$ , difference from minimum  $AIC_c$  value;  $w$ , relative Akaike weights for each model. Proportion of variance explained by the global model  $R^2 = 0.77$ . Environmental variables include seasonal rainfall, seasonal mean maximum and mean minimum temperatures, annual rainfall and annual mean temperature, and NPP; the first three are the seasonal environmental variables, while the latter three are the annual environmental variables.

three hypotheses for the geographic pattern of seed size variation found in this species.

## Hypotheses

**ABIOTIC CONSTRAINTS HYPOTHESIS:** Acorn size is constrained by rainfall, temperature, primary productivity, or some other environmental factor that decreases with increasing latitude (Moles et al. 2007). The prediction of this hypothesis is that there should be a strong relationship between the environmental factor and acorn size independent of latitude, and that the relationship should be in the direction of smaller acorns going along with more constrained conditions such as lower rainfall or primary productivity.

**VICARIANCE HYPOTHESIS:** Acorn size is related to soils, nutrients, or some other abiotic factor associated with glaciation independent of latitude per se. This hypothesis predicts that the apparent latitudinal gradient is attributable to whether sites were glaciated or not during the most recent Wisconsin ice age and that the latitudinal gradient is a by-product of glaciation having primarily been a more northern phenomenon.

**DIFFERENTIAL DISPERSAL HYPOTHESIS:** This hypothesis postulates that acorn size is smaller in higher latitudes owing to differential seed dispersal by animals, specifically the blue jay (*Cyanocitta cristata* L.), which is the primary dispersal vector of acorns in the bur oak's range (Darley-Hill and Johnson 1981; Johnson and Webb 1989) and is known to prefer smaller acorns (Scarlett and Smith 1991; Moore and Swihard 2006). This hypothesis predicts two patterns: first, the size distribution of acorns further north should essentially be drawn from the smaller acorns present in more southern areas, and thus, although the maximum size of acorns should decrease latitudinally, the minimum should remain more or less the same. As a corollary, the variability of acorn size should decrease as one moves north and larger

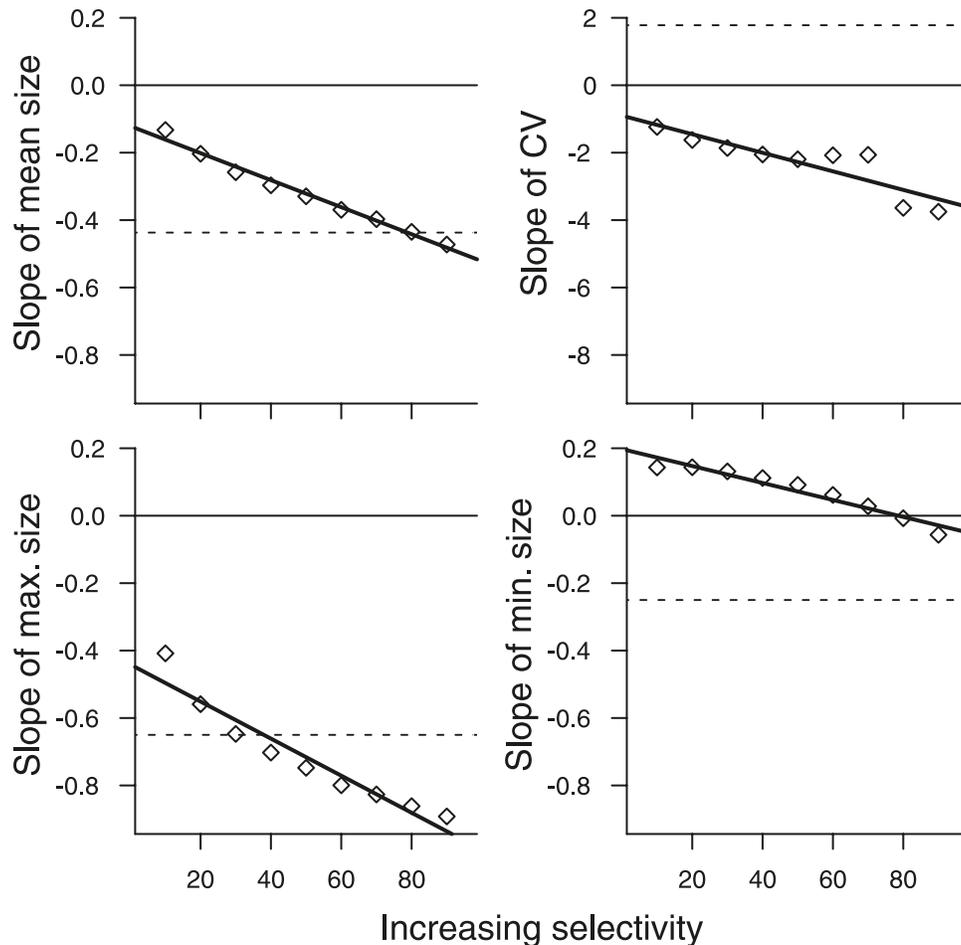
acorns are progressively lost. These predictions are discussed in more detail below.

## Methods

Our data consisted of acorns collected by Citizen Science volunteers (CitizenScience.ca) from trees located throughout the range of bur oaks (Fig. 1) during fall and winter of 2006 and 2007. Volunteers were given directions and photos for identifying bur oaks and bur oak acorns, which have a distinctive spiny cap, and were asked to collect up to five acorns from each of five different trees located within the same local area either directly off the tree or from the ground below the tree in cases where there was no ambiguity as to which tree the acorn originally came from. We asked that people keep acorns from the same tree together, collect only mature acorns, and that they not select acorns based on size, excluding acorns only if they were malformed, parasitized, or otherwise clearly abnormal. Small envelopes, each containing acorns from a single tree and marked with the date and collection locality, were then put together in a package and sent to the senior author, where they were inspected for potential misidentification and then frozen until processing.

Processing consisted of drying acorns at 50 °C to constant weight, shelling each acorn to remove the endosperm from the husk, and then weighing the endosperm to the nearest 0.01 g. Seeds that were insect damaged or otherwise malformed were excluded from the analyses. In all, we measured a total of 1467 acorns (699 in 2006; 768 in 2007) from 420 trees (217 in 2006; 203 in 2007) and 126 localities (61 in 2006; 65 in 2007; Fig. 1), the latter encompassing trees within the same local area collected by the same person in the same year. Although in some cases individuals collected acorns in both years, trees were not individually identified and no attempt was made to match sites from one year to the next. For each site, we averaged dry acorn mass

**Fig. 3.** Results of the simulation model. Values shown are the mean ( $N = 500$  trials) slope of regression coefficients for mean, CV, maximum, and minimum acorn size on latitude for each of nine values of increasing selectivity for smaller acorns by the hypothetical dispersal agent. In each panel, a solid line is drawn at slope = 0 and a broken line is drawn at the value corresponding to that of the observed data (Fig. 4).



within individual trees and then averaged the tree means within the site to yield site means.

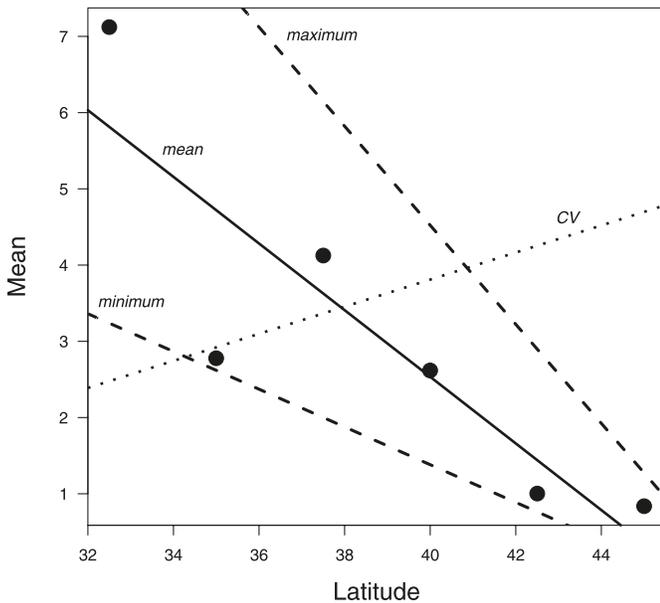
Latitude, longitude, and elevation of each site were determined from the Geographical Names Information System web site (United States Geological Survey (USGS) 2007). Sites (Fig. 1) were distributed throughout the distributional range, except for Canada. Elevation varied little in the dataset (95% of the sites were between 119 and 499 m.a.s.l. in elevation, a range of only 380 m) and was thus not analyzed further.

We gathered environmental data including monthly rainfall, mean monthly maximum temperatures, and mean monthly minimum temperatures for each locality from September 2005 through August 2007 using the PRISM database (PRISM 2008). From these data we determined the following six environmental variables for 2006 and 2007: (i) rainfall, (ii) mean maximum temperature, and (iii) mean minimum temperature during the main growing season from March through August (when acorns generally mature); (iv) annual rainfall and (v) mean annual temperature, measured from September the prior year through August; and (vi) net primary productivity (NPP), estimated using the Miami model (Adams et al. 2004) from annual rainfall and mean

annual temperature, determined from September the prior year through August. Finally, we divided sites into those that were covered by glaciers during the most recent ice age and those that were not based on maps of the maximum extent of the Wisconsin ice sheet in North America approximately 18 000 years ago (Isachsen et al. 1990; Pielou 1991; Fischer 2008).

Analyses were performed on both raw individual acorn mass and on log-transformed mean acorn mass. Results were similar and, with the exception of the analyses involving the dispersal simulation model, only results based on the log-transformed values are discussed. Spearman rank correlations and Mann–Whitney  $U$  tests were performed to confirm the direction and correlation of the relationships between predictor variables. However, to test the performance of different sets of variables, candidate explanatory models were compared using a model selection process of calculating bias-adjusted  $AIC_c$  values,  $AIC_c$  differences from the best-performing model, and model probabilities [ $w = \text{Prob}(H | \text{data})$ ] (Burnham and Anderson 2002; Anderson 2008). Candidate models included various combinations of latitude, the environmental variables, and history of glaciation (whether sites were glaciated or not during the last ice

**Fig. 4.** The four variables calculated in the randomization model using the observed data. Filled circles are the mean acorn mass of acorns collected at sites binned into the six 2.5° latitudinal blocks used in the model (32°30'N to 45°N). Lines are the regressions of mean (solid line), maximum (upper broken line), minimum (lower broken line), and CV (dotted line; values divided by 10 to fit on the graph) on latitude. Slopes of the regressions on latitude are: -0.44 (mean), -0.65 (maximum), -0.25 (minimum), and 1.78 (CV).



age). We also contrasted the performance of the three seasonal environmental variables (seasonal rainfall, mean minimum, and mean maximum temperature) with the three annual environmental variables (annual rainfall, annual mean temperature, and NPP). All model selection metrics were calculated from general linear models assuming a Gaussian error distribution (R Development Core Team 2008).

To examine the differential dispersal hypothesis quantitatively, we designed a simulation model. The model consisted of trials starting with 100 acorns chosen from a normal distribution with a mean  $\pm$  SD of  $7.54 \pm 2.79$  g, values matching those of the acorns collected from sites located within the southernmost 2.5° latitudinal range (31°15'N to 33°45'N) of our dataset. Each trial consisted of choosing the acorns moving into the next most northern 2.5° block as follows: from the original distribution, the largest  $x$  acorns were dropped from the distribution, where  $x$  was a “selectivity coefficient” that varied between 10 (low selectivity) and 90 (high selectivity). The mean and SD of the remaining  $(100-x)$  acorns was then determined, from which a new set of 100 acorns was chosen using a normal distribution. The procedure was repeated for each more northerly 2.5° latitudinal block up to 45°N. Parallel trials were performed using log-transformed values with comparable results. However, because coefficients of variation could only be calculated consistently using the untransformed values, we present only the latter here.

For each trial we determined the mean, CV, maximum, and minimum of the 100 acorns at each of the six latitudinal blocks between 32°30'N and 45°N latitude and calculated the regression coefficients of each of the four variables on latitude. We then averaged values across 500 trials and plot-

ted the slopes vs. the various values of  $x$  and contrasted results with values from the actual data determined by binning sites into the same set of six 2.5° latitudinal blocks.

## Results

There was no significant difference in acorn mass between the 2 years of the study (general linear model controlling for latitude;  $t_{\text{year}} = 0.1$ ,  $df = 1$ ,  $P = 0.9$ ); thus, years were combined in subsequent analyses. As found in previous studies, there was a strong inverse latitudinal gradient in acorn size (Fig. 2).

### Abiotic factors hypothesis

All six environmental variables (seasonal rainfall, seasonal mean maximum and mean minimum temperature, annual rainfall, annual mean temperature, and NPP) correlated negatively with latitude ( $-0.87 < r_s < -0.43$ ) and positively with mean acorn mass ( $0.29 < r_s < 0.73$ ). Thus, as predicted by this hypothesis, acorns were smaller in drier, colder sites with lower NPP.

A comparison of models indicated that the best model for acorn mass of those considered with a relative Akaike weight ( $w$ ) of 0.49 included the environmental variables in combination with the history of glaciation (Table 1, model 1). Including latitude as well (model 2) resulted in a global model slightly less probable ( $w = 0.41$ ) than the model without latitude. By comparison, none of the other more simplified models testing the separate influence of the environmental variation, latitude, or history of glaciation was supported by the data (models 3–9). The overall fit of the models was good, as indicated by an adjusted  $R^2$  of 0.77 for the global model.

### Vicariance hypothesis

There was a significant difference in mean acorn mass and whether or not sites were glaciated during the most recent ice age (Mann–Whitney  $U$  test comparing glaciated and nonglaciated sites;  $z = 5.3$ ,  $P < 0.001$ ). Thus, acorns were smaller in glaciated compared with nonglaciated sites.

In the general linear models, glaciation by itself (Table 1, model 9) performed the worst of all candidate models. However, glaciation was included in the best-performing model (model 1), indicating that it contributed importantly to predicting mean acorn mass independent of latitude and the environmental variables (model 4).

### Differential dispersal hypothesis

This hypothesis postulates that differential dispersal of smaller acorns by blue jays during bur oak's postglacial range expansion is the cause of the latitudinal cline observed in acorn size of this species. Support for the prior two hypotheses counters the potential importance of this possibility. However, based on the  $R^2$  value of the global model (Table 1), 23% of the variance in acorn size remains unexplained after controlling for latitude and other known environmental gradients, suggesting that differential dispersal could still be an important contributing factor to the variation in acorn size observed in this species.

Results of the randomization trials were generally consistent with the intuitive prediction of the differential dispersal

hypothesis that there should be a negative regression of both mean and maximum acorn mass on latitude that becomes more negative with increasing selectivity (Fig. 3). In contrast, the regression of minimum acorn mass on latitude was in all cases close to zero ( $0.15 > \text{slope} > -0.06$ ) and positive except for the trials with the strongest selectivity ( $x \geq 80$ ). The slope of CV on latitude was always negative, again reflecting the fact that this hypothesis assumes that more northern acorns are a subset of acorns present further south.

Values obtained from the observed data (Fig. 4; drawn as broken lines in Fig. 3), indicate that the observed slopes of both mean and maximum acorn mass on latitude were within the range of the simulations, corresponding to values obtained when the selectivity coefficient was in the moderate ( $x \sim 30$  for maximum mass) to strong ( $x \sim 80$  for mean mass) range. However, the slope of minimum acorn mass on latitude was strongly negative ( $-0.25$ ), in contrast to the values obtained in the trials, which were generally positive and (as expected) close to zero. Finally, the slope of CV on latitude was positive using the actual data, contrasting with the negative slopes obtained in the simulations regardless of the selectivity coefficient. Thus, neither of the key patterns predicted by the differential dispersal hypothesis was supported.

## Discussion

As found previously by Aizen and Woodcock (1992), bur oaks exhibit a highly significant negative latitudinal gradient in acorn size. From the samples collected in this study, mean  $\pm$  SD for dry mass of bur oak acorns collected from sites in Texas was  $7.5 \pm 2.0$  g ( $N = 20$  trees), over eight times the size ( $0.9 \pm 0.2$  g,  $N = 25$  trees) of acorns collected at sites in Minnesota (Mann–Whitney  $U$  test,  $z = 5.7$ ,  $P < 0.001$ ). Geographic variation in acorn mass correlated strongly and positively with all environmental variables considered.

In a comparison of candidate models, the model best predicting acorn mass included the six environmental variables and the history of glaciation. This provides strong support for both the abiotic constraints and the vicariance hypotheses, although the superior performance of the environmental variables (model 6) compared with glaciation (model 9) indicates that of the two, abiotic constraints are the more important.

Although the precise mechanisms were not examined, our results are consistent with the possibility that differences in temperature and rainfall act as constraints on seed growth leading to the observed inverse latitudinal gradient in acorn size. It is possible that a history of glaciation acts as a constraint limiting acorn size over and beyond that imposed by the environmental factors as well, but exactly why this might be true remains to be investigated.

These results are generally in agreement with the taxonomically comprehensive studies of seed size variation performed by Moles and colleagues (Moles and Westoby 2003; Moles et al. 2007), who found a general pattern of declining seed mass with latitude. Much of the variation was accounted for by growth form, vegetation type, dispersal syndrome, and net primary productivity; once these factors were included latitude explained virtually no residual varia-

tion in the data. A similar pattern was seen within species, leading these authors to conclude, as we do here, that environmental factors constrain seed size in a given environment.

Within bur oaks, growth form varies little throughout their geographic range. Furthermore, bur oaks, like other *Quercus*, are wind pollinated and the main dispersal agent of seeds throughout their range is the blue jay. In contrast, vegetation type varies considerably among sites and could be an important factor influencing acorn size. For example, Laing (1966) reported that bur oaks growing in closed stands on floodplains in east central Nebraska produced seeds that were 2.5 times as large as oaks growing in nearby savannahs. Although this degree of variation was not unusual in our data [for example, among six sites between  $31^\circ\text{N}$  and  $32^\circ\text{N}$  latitude the largest tree produced acorns 2.4 times as large as the smallest tree (range 5.3 – 12.7 g), while among 24 sites between  $43^\circ\text{N}$  and  $44^\circ\text{N}$  latitude the largest tree produced acorns 8.3 times as large as the smallest tree (range 0.3 – 2.7 g)], the overall latitudinal range in acorn mass we found cannot be accounted for by vegetation differences alone (cf. the range in size between  $31^\circ\text{N}$ – $32^\circ\text{N}$  vs.  $43^\circ\text{N}$ – $44^\circ\text{N}$  latitude).

Our results fail to support the hypothesis that the observed geographic pattern of acorn size variation is due to differential dispersal following the last ice age. Oaks are known to have moved northward at a rate of approximately  $350 \text{ m}\cdot\text{a}^{-1}$  during the late Wisconsin and early Holocene era as the continental ice sheets retreated, a rate too great to be accounted for by mammalian dispersal (Johnson and Adkisson 1986). Avian dispersal, particularly by blue jays (Johnson and Webb 1989) but also potentially by the now extinct passenger pigeon *Ectopistis migratorius* (Webb 1986), is the most likely cause of long-distance dispersal of acorns within the range of bur oaks. Unfortunately, nothing is known about the acorn preferences of passenger pigeons. However, blue jays prefer smaller acorns (Scarlett and Smith 1991; Moore and Swihard 2006), which makes them a potential cause of the inverse latitudinal gradient in intraspecific acorn size seen in bur oak and other eastern oak species (Aizen and Woodcock 1992).

Two patterns are predicted by the dispersal hypothesis. First, the maximum, but not the minimum, size of acorns should decrease with latitude, and second, the relative variability of acorn mass (CV) should decrease with latitude as larger acorns are progressively selected against by the dispersal agent. Neither of these predictions was met by our data (Fig. 4). Additional evidence against this hypothesis comes from comparing Aizen and Woodcock's (1992, Table 2) data on latitudinal trends in acorn size with data on species of acorns preferred by blue jays based on observations and preference studies (Darley-Hill and Johnson 1981; Scarlett and Smith 1991; Moore and Swihard 2006). Acorns of three species were preferred by blue jays in these studies: pin oak *Quercus palustris*, willow oak *Quercus phellos*, and black oak *Quercus velutina*, while acorns of white oak *Quercus alba* and northern red oak *Quercus rubra* were avoided. Based on Aizen and Woodcock's (1992) results, the latitudinal gradient in acorn size in all five of these species was negative, and there was no difference between the average gradient of the preferred species measured by the

slope of acorn size on latitude ( $-0.027$ ) compared with that for the two species that are avoided ( $-0.028$ ). Thus, strong negative latitudinal gradients are found in seed size of oaks regardless of whether they are preferred by blue jays or not. This does not exclude blue jays as having been important dispersers of bur oaks during the Holocene. However, it does eliminate jays as the primary cause of the inverse latitudinal gradient in acorn size observed in bur oaks and other eastern oak species. Given support for the abiotic constraints and vicariance hypotheses, these results suggest that differential dispersal by jays or other vectors has not played a significant role in producing the observed latitudinal gradient in acorn mass observed in bur oaks and probably other eastern oak species as well.

In summary, the inverse latitudinal gradient in acorn mass seen in bur oaks is explainable by constraints imposed by environmental factors in conjunction with the prior history of glaciation. In contrast, we found no evidence that selection in the form of size-dependent acorn dispersal by blue jays has played an important role in causing this pattern, despite the likely importance of avian dispersal to bur oak's postglacial northern range expansion.

It is possible that environmental constraints on acorn size are also important in the apparently contradictory findings that species of eastern North American oaks with larger acorns are those whose ranges extend into higher latitudes (Aizen and Patterson 1990, 1992), despite the intraspecific latitudinal decrease in acorn size found in many of these species. We envision that there is a limit to how small acorns can be and still be successful. If this is true, and if acorn size of all species is environmentally constrained as one goes north in a manner comparable to bur oak acorns, then as one progresses north species with initially small acorns would be expected to reach the minimum size limit and drop out, eventually leaving only those species that produce relatively larger acorns. Thus, environmental constraints may be key to understanding both intra- and interspecific geographic patterns of acorn size variation in North American oaks.

## Acknowledgments

We thank David Bonter, who advertised the project to participants of Cornell Laboratory of Ornithology's Project Feederwatch, and the many Citizen Scientists who volunteered their efforts to collect acorns. We also thank Caren Cooper, the Bird Population Studies group, and reviewers for comments and the National Science Foundation for support.

## References

- Adams, B., White, A., and Lenton, T.M. 2004. An analysis of some diverse approaches to modelling terrestrial net primary productivity. *Ecol. Model.* **177**: 353–391. doi:10.1016/j.ecolmodel.2004.03.014.
- Aizen, M.A., and Patterson, W.A. 1990. Acorn size and geographical range in the North American oaks. *J. Biogeogr.* **17**: 327–332. doi:10.2307/2845128.
- Aizen, M.A., and Patterson, W.A. 1992. Do big acorns matter? — A reply to R.J. Jensen. *J. Biogeogr.* **19**: 581–582. doi:10.2307/2845777.
- Aizen, M.A., and Woodcock, H. 1992. Latitudinal trends in acorn size in eastern North American species of *Quercus*. *Can. J. Bot.* **70**: 1218–1222. doi:10.1139/b92-153.
- Anderson, D.R. 2008. Model based inference in the life sciences: a primer on evidence. Springer-Verlag, New York, N.Y.
- Baker, H.G. 1972. Seed weight in relation to environmental conditions in California. *Ecology*, **53**: 997–1010. doi:10.2307/1935413.
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, N.Y.
- Darley-Hill, S., and Johnson, W.C. 1981. Acorn dispersal by the blue jay (*Cyanocitta cristata*). *Oecologia (Berl.)*, **50**: 231–232. doi:10.1007/BF00348043.
- Fischer, M.P. 2008. Glaciers. [Online]. Available from [jove.geol.niu.edu/faculty/fischer/429\\_info/429trips/NIF/Glaciers.htm](http://jove.geol.niu.edu/faculty/fischer/429_info/429trips/NIF/Glaciers.htm) [accessed 24 March 2008].
- Gómez, J.M. 2004. Bigger is not always better: conflicting selective pressures on seed size in *Quercus ilex*. *Evolution*, **58**: 71–80. PMID:15058720.
- Hewitt, N. 1998. Seed size and shade-tolerance: a comparative analysis of North American temperate trees. *Oecologia (Berl.)*, **114**: 432–440. doi:10.1007/s004420050467.
- Isachsen, Y.W., Mock, T.D., Nyahay, R.E., and Rogers, W.B. 1990. New York state geological highway map. New York State Museum educational leaflet No. 33.
- Johnson, W.C., and Adkisson, C.S. 1986. Airlifting the oaks. *Nat. Hist.* **95**: 40–47.
- Johnson, W.C., and Webb, T. 1989. The role of blue jays (*Cyanocitta cristata* L.) in the postglacial dispersal of fagaceous trees in eastern North America. *J. Biogeogr.* **16**: 561–571. doi:10.2307/2845211.
- Laing, C.L. 1966. Bur oak seed size and shadiness of habitat in southeastern Nebraska. *Am. Midl. Nat.* **76**: 534–536. doi:10.2307/2423111.
- Leishman, M.R. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos*, **93**: 294–302. doi:10.1034/j.1600-0706.2001.930212.x.
- Leishman, M.R., and Westoby, M. 1994. The role of large seeds in seedling establishment in dry soil conditions—experimental evidence for semi-arid species. *J. Ecol.* **82**: 249–258. doi:10.2307/2261293.
- Moles, A.T., and Westoby, M. 2003. Latitude, seed predation and seed mass. *J. Biogeogr.* **30**: 105–128. doi:10.1046/j.1365-2699.2003.00781.x.
- Moles, A.T., Ackerly, D.D., Tweddle, J.C., Dickie, J.B., Smith, R., Leishman, M.R., Mayfield, M.M., Pitman, A., Wood, J.T., and Westoby, M. 2007. Global patterns in seed size. *Glob. Ecol. Biogeogr.* **16**: 109–116. doi:10.1111/j.1466-8238.2006.00259.x.
- Moore, J.E., and Swihard, R.K. 2006. Nut selection by captive blue jays: importance of availability and implications for seed dispersal. *Condor*, **108**: 377–388. doi:10.1650/0010-5422(2006)108[377:NSBCBJ]2.0.CO;2.
- Pielou, E.C. 1991. After the Ice Age. The return of life to glaciated North America. University of Chicago Press, Chicago, Ill.
- PRISM. 2008. [Online]. PRISM Group, Oregon State University, Corvallis. Available from [www.prismclimate.org](http://www.prismclimate.org) [accessed 17 October 2008].
- R Development Core Team. 2008. R: A language and environment for statistical computer, version 2.6.2. [Online]. R Foundation for Statistical Computing, Vienna, Austria. Available from [www.R-project.org](http://www.R-project.org).
- Scarlett, T.L., and Smith, K.G. 1991. Acorn preference of urban blue jays (*Cyanocitta cristata*) during fall and spring in northwestern Arkansas. *Condor*, **93**: 438–442. doi:10.2307/1368961.

- Schopmeyer, C.S. 1974. Seeds of the woody plants of the United States. USDA Agricultural Handbook No. 450.
- Seiwa, K. 2000. Effects of seed size and emergence time on tree seedling establishment: importance of developmental constraints. *Oecologia (Berl.)*, **123**: 208–215. doi:10.1007/s004420051007.
- Smith, C.C., and Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Am. Nat.* **108**: 499–506. doi:10.1086/282929.
- USGS. 2007. [Online]. US board on geographic names. Available from [geonames.usgs.gov/index.html](http://geonames.usgs.gov/index.html) [accessed 1 March 2008].
- United States Geological Survey. 2008. Digital representations of tree species range maps from Atlas of United States trees by Elbert L. Little, Jr. [Online]. Available from [esp.cr.usgs.gov/data/atlas/little](http://esp.cr.usgs.gov/data/atlas/little) [accessed 20 April 2008].
- Webb, S.L. 1986. Potential role of passenger pigeons and other vertebrates in the rapid Holocene migrations of nut trees. *Quat. Res.* **26**: 367–375. doi:10.1016/0033-5894(86)90096-7.
- Westoby, M., Jurado, E., and Leishman, M.R. 1992. Comparative evolutionary ecology of seed size. *Trends Ecol. Evol.* **7**: 368–372. doi:10.1016/0169-5347(92)90006-W.