Received: 22 May 2023 | Revised: 8 November 2023 | Accepted: 9 November 2023

DOI: 10.1002/ecs2.4790

ARTICLE

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

Decomposing an elevational gradient in predation by insectivorous birds

Lydia S. Dean[1,2] | **Carla Vázquez-González**[1,3] | **Sierra Hellwitz**[1] | **Luis Abdala-Roberts**[4] | **Kailen A. Mooney**[1,2]

[1]Department of Ecology and Evolutionary Biology, University of California-Irvine, Irvine, California, USA

[2]Rocky Mountain Biological Laboratory, Crested Butte, Colorado, USA

[3]Misión Biológica de Galicia (MBG-CSIC), Pontevedra, Spain

[4]Departamento de Ecología Tropical, Campus de Ciencias Biológicas y Agropecuarias, Universidad Autónoma de Yucatán, Mérida, Mexico

Correspondence
Lydia S. Dean
Email: lsdean@uci.edu

Funding information
National Science Foundation, Grant/Award Numbers: DEB-2032435, IOS-1951244

Handling Editor: Robert R. Parmenter

Abstract

Insectivorous birds have ecologically important effects on prey abundance, behavior, and evolution, and through top-down control, birds indirectly reduce herbivory and promote plant growth. While several studies sought to characterize biogeographic patterns in top-down control by birds, variation in bird predation along elevational gradients is not well characterized in terms of both its commonness and the mechanisms underlying such variation. Here, we characterized variation in bird predation along a 700-m montane elevation gradient using artificial clay caterpillars, assessing the roles of variation in aridity, other elevational effects not associated with aridity (e.g., most notably growing season length), and bird abundance and diversity. Multivariate models revealed increasing attack rates with aridity (when controlling for the effects of elevation) and elevation (when controlling for aridity). Because aridity declines with elevation, elevational patterns were not detectable in a univariate analysis. Bird abundance (but not diversity) decreased with elevation (but not aridity) and did not provide an explanation for our results, suggesting that the underlying mechanisms were behaviorally based. We speculate that the declining abundance of insect prey with elevation and aridity leads to increased bird foraging efforts and thus the likelihood of attacking clay caterpillars. If widespread, these dynamics have important consequences for both the interpretation of predation bioassays generally and our understanding of the multivariate drivers of variation in top-down control by predators and predation risks experienced by prey.

KEYWORDS
biotic interactions, bird predation, climate gradients, natural enemies, *Populus tremuloides*, predator–prey interactions

INTRODUCTION

Predators exert strong top-down control of insect prey and through this contribute to increased plant growth and fitness (Bael et al., 2008; Hairston et al., 1960; Mooney, Gruner, et al., 2010; Paine, 1980; Vidal & Murphy, 2018). In addition, predation is fundamental to structuring community dynamics through shaping prey behavior and life histories (Camacho & Avilés, 2019; Holt & Lawton, 1994; Jeffries & Lawton, 1984; Lima & Dill, 1990; Schemske et al., 2009). Previous synthetic work has shown that the strength of top-down control of insect herbivores by predators is highly variable (Mooney, Gruner, et al., 2010; Vidal & Murphy, 2018). For instance, biotic factors such as primary productivity (Oksanen et al., 1981) and herbivore diversity and behavior (Wilby & Orwin, 2013) can determine the strength of top-down control by influencing predator abundance and community composition. Similarly, abiotic factors such as temperature, precipitation, and nutrient availability (Camacho & Avilés, 2019; Galmán et al., 2018; Mooney, Gruner, et al., 2010; Moreira et al., 2018) can drive variation in top-down control through effects on predator resource limitation, metabolism, and energetic needs (Del Grosso et al., 2008). Yet while some important factors driving top-down control have been identified, it is unclear whether and how these mechanisms work collectively to generate predictable patterns of spatial variation in trophic structure (Moreira et al., 2018).

A long-standing paradigm in ecology is that the strength of biotic interactions increases toward lower latitudes and elevations due to warmer and more stable climates (Fischer, 1960; Hillebrand, 2004; Roslin et al., 2017; Schemske et al., 2009). Biogeographic gradients, such as those associated with latitude or elevation, covary with abiotic factors, such as temperature and precipitation, making them powerful tools for understanding how climate is linked to ecological and evolutionary processes that produce spatial variation (Descombes et al., 2020; Fischer, 1960; Moreira et al., 2018; Pellissier et al., 2018; Schemske et al., 2009; Schluter & Pennell, 2017; Willig et al., 2003). This has mostly been assessed in plant–herbivore interactions, whereby herbivore pressure is predicted to be stronger at lower elevations and latitudes (Connell, 1971; Dobzhansky, 1950; Janzen, 1970). However, empirical studies testing this prediction yielded contrasting results, with some studies showing positive (Matías & Jump, 2015; Moreira et al., 2014; Zhang et al., 2015), negative (Hülber et al., 2015; Metcalfe et al., 2014), or no linear association with elevation or latitude (Hódar & Zamora, 2004; Lay et al., 2013; Loughnan & Williams, 2019; Sam et al., 2020). Gradients in predation rates remain largely untested, limiting our knowledge not only of the sources of variation in predator–herbivore interactions and intraguild predation dynamics but also of how such variation may ultimately modulate herbivory and affect plant fitness (Moles & Ollerton, 2016; Moreira et al., 2018; Zhang et al., 2015).

Past works exploring elevational and latitudinal gradients in herbivore natural enemies have found contradicting patterns both within and between taxa. While there is strong support for decreasing predation and parasitism by invertebrates with elevation (Camacho & Avilés, 2019; Hodkinson, 2005; Roslin et al., 2017; Tiede et al., 2017; Zvereva et al., 2019), gradients in predation by vertebrates (e.g., birds) have been found to be positive (Tvardikova & Novotny, 2012), neutral (Roslin et al., 2017; Schwenk et al., 2010), or nonlinear (Sam et al., 2015, 2023) with elevation. Additionally, Sam et al. (2015) suggest that with the elevational decrease in ant predation, the relative importance of bird predation increases, further highlighting the importance of taxonomic groups when assessing predation (Roslin et al., 2017; Sam et al., 2015; Tvardikova & Novotny, 2012; Zvereva et al., 2019). Inconsistent outcomes could be driven by varying study locations, gradient lengths, and methods, but a global study of predation across latitude and elevation conducted by Roslin et al. (2017) found neither a latitudinal nor an elevational gradient in predation with birds. This is striking, as it is well known that birds are a key natural enemy exerting strong predation effects on insect herbivores (Bael et al., 2008; Maas et al., 2016; Van Bael et al., 2003), and while intraguild predation should be expected to dampen top-down control by birds, past meta-analyses have failed to detect such effects (Mooney, Gruner, et al., 2010). The known differences in arthropod consumption based on biome type (increased consumption in tropical forests compared with temperate forests; Nyffeler et al., 2018) and plant community composition (increased plant diversity drives increased attack rates; Nell, 2018) indicate that there are other biotic and abiotic sources driving variation in bird predation.

Elevational gradients are particularly relevant because they reduce the confounding effects of historical and biogeographical differences that occur in latitudinal gradients (Hodkinson, 2005; Rasmann et al., 2014). Several factors that may underlie elevational variation in bird predation, and drive this variation in findings among past studies, are climate, predator abundance and composition, and predator foraging behavior. First, temperature and precipitation can differentially constrain the physiology of endotherms versus ectotherms (e.g., birds vs. arthropods), directly affecting predator activity rates, as well as indirectly via changes in primary productivity and prey abundance (Avery & Krebs, 1984; Mazía et al., 2004; Van Bael & Brawn, 2005). Second, bird abundance and diversity has been found to decline overall with elevation, but expresses a nonlinear pattern with diversity and abundance, peaking at mid-elevation, driven by insectivorous birds (Blake & Loiselle, 2000; Ding et al., 2021; Herzog et al., 2005; Pan et al., 2016; Sam et al., 2015, 2023). Variation in predator diversity and density could increase the suppression of arthropods via species differences in predator niche, and foraging behaviors could drive the magnitude of effect on arthropods (Bael et al., 2008; Griffin et al., 2013; Maas et al., 2016; Nell, 2018). Third, decreased herbivore abundance at higher elevations could drive increased predator activity with limited prey availability (Camacho & Avilés, 2019). In contrast, positive density-dependent foraging in birds could drive higher attack rates at lower elevations (Singer et al., 2012). Variation in the range of elevational gradients and environmental conditions used across different studies makes it difficult to generalize trends, and thus warrants further research aiming to test for elevational gradients in birds and the underlying mechanisms that could explain variation in these patterns.

Here, we explored patterns of predation by insectivorous birds along an elevational gradient in the Rocky Mountains (Gothic, Colorado, USA), and whether such patterns were mediated by climate and/or predator abundance and diversity. To do so, we deployed model clay caterpillars (Low et al., 2014) in aspen trees across sites spanning a 700-m elevational gradient (2450–3150 m) and estimated attack rates by birds during peak bird activity over a 14-day period in summer 2020. We then obtained data on temperature, precipitation, and insectivorous bird diversity and abundance along this same gradient in order to explore the mechanistic basis of any observed patterns in bird predation. By reporting patterns of bird predation along elevational gradients and testing for the potential underlying mechanisms, this study contributes to understanding the evolutionary and ecological processes responsible for patterns of elevational variation in prey–predator interactions.

METHODS

Study area

We conducted this study in Gunnison County near the Rocky Mountain Biological Laboratory (RMBL) in Gothic, CO (38.96° N, −106.99° W), in August 2020. In the Rocky Mountain region, *Populus tremuloides* grows from 2100 to 3350 m, a 1250-m gradient (DeByle & Winokur, 1985). Our study sites span a 700-m elevational gradient from 2453 to 3154 m, which represents nearly all of the aspen elevational distribution within Gunnison County. Abundant insectivorous birds in this region are mountain chickadees, mountain bluebirds, and orange-crowned warblers, and, during this time of year, are postfledging. This elevation gradient encompasses variation in numerous abiotic factors, most notably temperature, growing season length (declining with elevation), and precipitation (increasing with elevation), with the tight covariation in temperature and precipitation being best characterized as a gradient in aridity that declines with elevation (Nelson, Pratt, et al., 2019; Nelson, Symanski, et al., 2019; Petry et al., 2016).

Approach overview

Our approach was to first test for elevational gradients in bird attack in parallel with past studies in other regions (Sam et al., 2015, 2023; Tvardikova & Novotny, 2012). We then sought to explore the underlying dynamics with two approaches. First, we decomposed the effect of elevation in a multivariate model that tested for the effects of aridity and—having controlled for aridity—the residual effects of elevation, most notably growing season length. We then explored whether elevation and aridity were associated with variation in the abundance and diversity of insectivorous birds.

Bird predation

Within the study area, we selected five valleys (East River, Washington Gulch, Taylor River Lower, Tayler River Upper, Spring Creek), and within each valley, we chose four separate locations (sites hereafter) within the aspen groves (Figure 1). There are two high-elevation valleys and three low-elevation valleys, with elevational variation within and among (Appendix S1: Table S1). Valleys, and sites within valleys, were separated by at least 2.5 km and 213 m, respectively. In each site, we selected 10, 2–3-m tall quaking aspen saplings (Salicaceae: *P. tremuloides*) separated by at least 1 m. We estimated attack rates by birds by attaching two 50-mm long and 5-mm wide model clay caterpillars made of green nontoxic modeling clay (Sargent Art) using a clay extruder (Walnut Hollow) to tree branches with super glue (Loctite) (Low et al., 2014), with the size, shape, and color imitating Lepidopteran larvae (Roels et al., 2018; Roslin et al., 2017; Sam et al., 2015; Tvardikova & Novotny, 2012). We selected branches located 1–2.5 m from the ground and placed two caterpillars on the surface of the branches, 10–30 cm away from the branch tip. The nonhardening clay allows an accurate assessment of attack and some precision in distinguishing the identity of the attacker (e.g., avian, arthropod, reptile, and mammal). Where necessary, we pruned leaves around the caterpillars to prevent contact with the clay and replaced caterpillars in the same location following any predator attack. The month of August at our field sites is generally postfledging time for bird communities, which in turn may drive higher rates of predation as

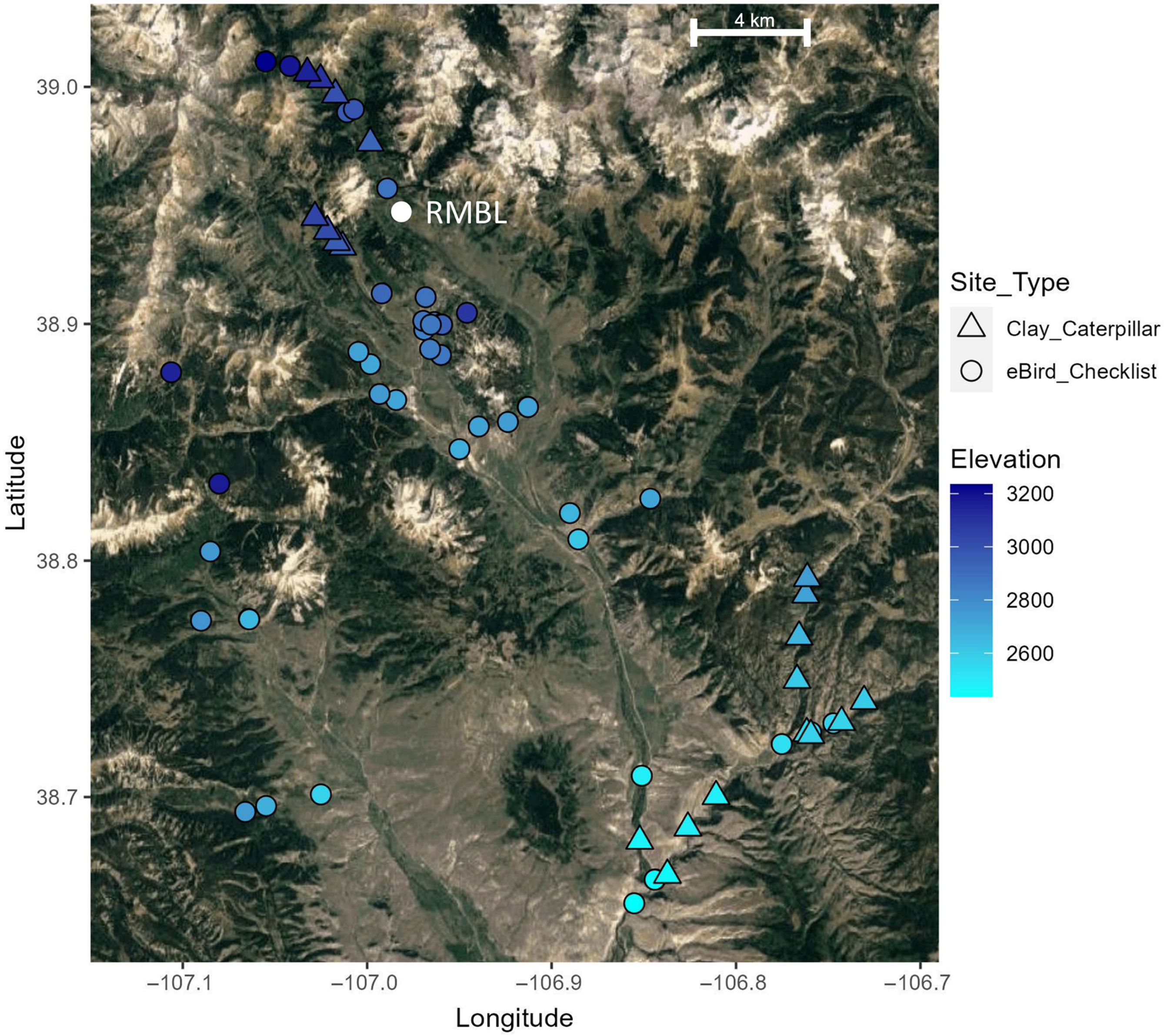

FIGURE 1 Map of study region showing sites used for predation bioassay on aspen trees (Clay_caterpillar) and from which bird data were collected (ebird_checklist). The Rocky Mountain Biological Laboratory (RMBL) location is indicated on the map.

naive birds have been shown to increase attack rates due to higher risk taking and unlearned behaviors (Zvereva & Kozlov, 2021, 2023), although this is true for all our field sites and is therefore unbiased. We recorded models attacked by birds four separate times from July 31 to August 13, on day 3 (3 days of deployment), day 5 (2 days of deployment), day 7 (2 days of deployment), and day 14 (7 days of deployment), with the exception of one valley (Taylor River Lower) which was initiated on day 3 and subsequently checked three times. When checking for attack, caterpillars that were missing (0.003% across deployed caterpillars and between checks) were replaced and not recorded as an attack.

Bird abundance and diversity data

To characterize the insectivorous bird community, we obtained citizen science data on bird abundance and diversity from our study area using eBird, the largest biological citizen science reporting program (Sullivan et al., 2009, 2014). In the absence of field data on the bird community, these data allowed us to characterize elevational gradients in bird abundance and diversity within the same region (Figure 1). However, given the substantial biotic and abiotic variation encompassed by this gradient, strong patterns of variation in bird abundance or community composition should be detectable. We used the "Best practices for Using eBird Data" guide to extract data from the eBird Basic Data (Version EBD_relMay-2022) and process the data to account for challenges in using citizen science datasets (Strimas-Mackey et al., 2023). Following this guide, we restricted our data to use checklists less than 5 h in duration, less than 5 km in length, and fewer than 10 observers, reducing variation in the data. We filtered the checklists to August 2020 and within the same region (portions of Gunnison County) and elevational gradient of the sites used to obtain attack rates with clay caterpillars. We removed checklists classified as stationary, incidental, or historical observations to further reduce variation in our data. Our use of these checklists to test for an elevational gradient, in insectivorous birds, presented three challenges. First, because observers travel during data collection, the spatial data for a checklist may not be precise. However, this error is unbiased and small, given the large scale of the elevational gradient being assessed among checklists. Second, at popular locations, checklists are assigned to "hotspots" (common or shared locations) that do not necessarily reflect the exact location of the checklist. To account for this, we averaged data at hotspot locations to constitute a single checklist. Third, the checklists can vary in time (searching effort) and the total distance covered. To account for this, we included the checklist duration as a covariate in statistical models. Lastly, there are taxonomic biases in reporting bird species, in which certain species are erroneously favored, resulting in other species going unreported. This was mitigated by only using complete checklists, where the observer claimed to have identified and reported all encountered species. Other common issues such as temporal or spatial biases driven by increases in observations due to popularity, availability, and accessibility (Strimas-Mackey et al., 2023) are not likely a concern in our analysis as the studied locations are similar in these regards.

A value for elevation was assigned to each checklist using the R package Elevatr (Hollister et al., 2021), which uses the coordinates to extract elevation from the USGS Elevation Point Query Service (https://nationalmap.gov/epqs/). With elevation for the checklists, we were able to create an elevational gradient for the insectivorous bird community. We used Elton Traits v1.0 (Wilman et al., 2014) to obtain the feeding guilds of each bird observed. The Elton Traits database characterizes global species attributes, such as diet and foraging strategies, for mammals and birds, based on literature sources. We removed from our analyses any bird that did not have a diet of at least 50% invertebrates to include omnivores in our analyses.

Climate data

We used the PRISM (Parameter-elevation Regressions on Independent Slopes Model) Climate Group Model to interpolate, within 4-km grids, the average daily temperature and total precipitation at each site for the month of August 2020 when the study was conducted (Daly, 2006). This source of climate data has been used in many studies conducted in the same region (Nelson, Pratt, et al., 2019; Nelson, Symanski, et al., 2019; Petry et al., 2016) and is an unbiased source of data as it takes into account variation in terrain. Across sites, precipitation ranged from 14.55 to 47.938 mm, and the average daily temperature ranged from 16.6 to 13.3°C. We summarized precipitation and temperature data using principal components analysis (PCA). The first principal component (PC1) explained 83.6% of the multivariate covariation between the climate variables and was positively associated with temperature and negatively associated with precipitation, thus being an effective proxy of aridity. Given that these are the two climatic variables that drive the aridity of the environment experienced by birds, we hereafter refer to PC1 as representing an aridity gradient. Importantly, elevation was negatively associated with aridity. The PCA was calculated separately based on data from the clay caterpillar sites (Appendix S1: Figure S1) and the locations of the bird checklists (Appendix S1: Figure S2), with the resulting PC1 (explaining 71.7% of the multivariate covariation between the climate variables) being similar in both cases.

Statistical analysis

We first tested for the effects of elevation and aridity alone in univariate models in order to explicitly compare our findings with past studies that have focused exclusively on elevation. We then performed a multivariate analysis, testing for the simultaneous effects of elevation and aridity. Because these tests for the effect of elevation controlled for the influence of aridity, they identified other aspects of elevation within our study region, most notably growing season length (Nelson, Pratt, et al., 2019; Nelson, Symanski, et al., 2019; Petry et al., 2016). Our analyses of bird attack were based on the proportion of caterpillars (20 per sites; 2 on each of 10 trees) attacked at each site per sampling date (out of 20 caterpillars; 10 trees × 2 caterpillars per tree), totaling 76 attack rates (4 valleys × 4 sites × 4 deployments = 64; 1 valley × 4 sites × 3 deployments = 12). We used a linear mixed model (LMM) to test for the independent effects of elevation and aridity (both fixed effects coded as continuous variables), including the number of days caterpillars were exposed and site as a random factor. We used a similar LMM to test for gradients in bird abundance and diversity, including the duration of each checklist as a covariate. The residuals of the models appeared normal after inspecting the Q–Q plots. Results based on the binary response of attacked versus not attacked for each individual caterpillar produced qualitatively similar results but are more difficult to interpret and visualize. In this multiple regression analysis, there is a potential concern for multiple collinearity between the two independent variables, elevation and aridity. Correlated independent variables can result in increased error of parameter estimates and reduced statistical power but do not bias parameter estimates (Lindner et al., 2020). To assess this, we inspected the variance inflation factor (VIF). In addition, because of concerns over reduced power and misestimation of p values, we also inspected Akaike information criterion (AIC) values among potential models (null model; each variable alone; both variables together) to determine whether the inclusion of both correlated variables improved fit (delta AIC > 2) as compared with the univariate models. Additionally, we tested for elevational gradients in bird abundance and diversity in a multiple regression analysis with elevation and aridity. We ran all statistical analyses in R software version R 4.2.0 (R Core Team, 2016). Specifically, we ran LMMs using the *lmer* function from the lmerTest package (Kuznetsova et al., 2017).

RESULTS

Models testing for the independent effects of elevation and aridity on attack rates by birds revealed a significant effect of both factors. In univariate models, there was no effect of elevation ($F_{1,19.077} = 1.94$, $p = 0.18$) or aridity ($F_{1,18.333} = 0.22$, $p = 0.643$). Importantly, in multivariate models, bird attack rates increased with elevation ($F_{1,18.134} = 7.24$, $p = 0.015$; Figure 2) and aridity ($F_{1,17.393} = 5.14$, $p = 0.036$; Figure 2), reflecting the fact that these two effects occur in such a way that they mask each other. Specifically, aridity and elevation are correlated, with aridity decreasing with elevation ($F_{1,18} = 100.79$, $p \leq 0.001$; Figure 3). Accordingly, the effects of elevation not associated with aridity work (e.g., growing season length) cross-purposes to aridity itself, resulting in a now-detectable overall effect of elevation in the univariate model. In this analysis, the VIF for the two correlated independent variables (elevation, aridity) was 6.6, a value that reflects the strong association between these variables but is unlikely to lead to bias in parameter estimation (Lindner et al., 2020). The AIC model comparison showed that the bivariate model (AIC = −55.203) was a superior fit as compared with the univariate models with elevation (AIC = −52.172) and aridity (AIC = −50.455) and the null model (AIC = −52.226). In multivariate models, bird abundance was associated with elevation ($F_{1,41} = 4.83$, $p = 0.034$;

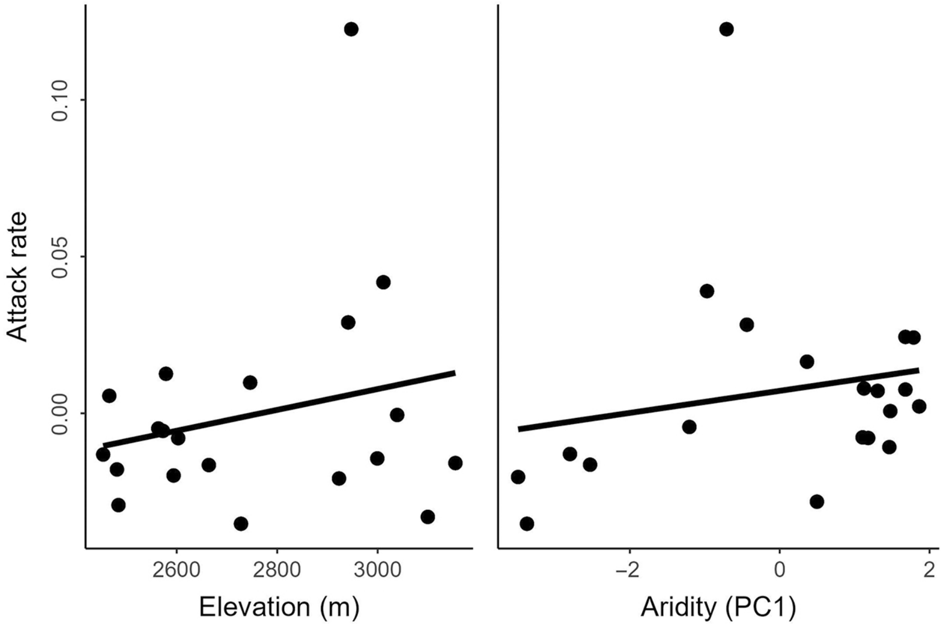

FIGURE 2 Association between elevation and aridity and proportion attack of clay caterpillars. For elevation, attack rates are residual values accounting for aridity, and for aridity, attack rates are residual values accounting for elevation. Aridity is represented as the score on the first principal component (PC1) of an ordination data on total annual precipitation and mean annual temperature from study sites. See Figure 1 for the location of the field sites. Attack rate increased significantly with both elevation and aridity.

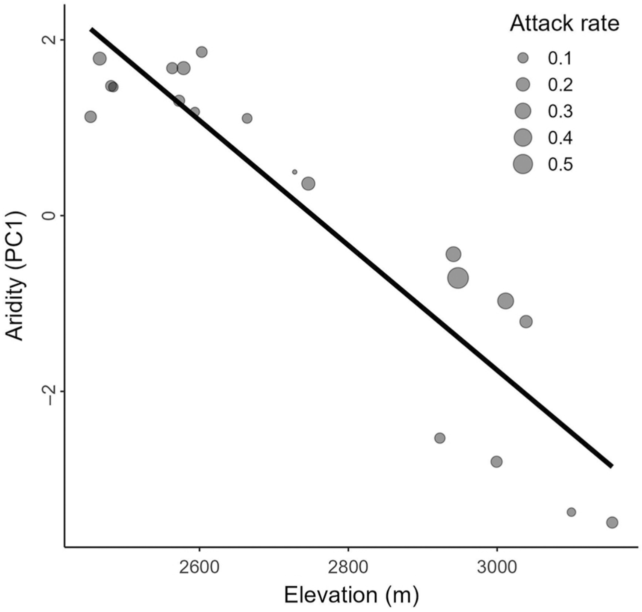

FIGURE 3 Relationship between aridity and elevation among the field sites used for the clay caterpillar bioassay ($R^2 = 0.84$). Attack rates (proportion attacked) are indicated by the marker size. Aridity is represented as the score on the first principal component (PC1) of an ordination data on total annual precipitation and mean annual temperature from study sites. See Figure 1 for the location of the field sites.

Figure 4), but not with aridity ($F_{1,41} = 0.74$, $p = 0.393$; Figure 4), whereas bird diversity was not associated with elevation ($F_{1,41} = 0.085$, $p = 0.772$; Figure 4) nor aridity ($F_{1,41} = 1.11$, $p = 0.299$; Figure 4).

DISCUSSION

Multivariate models revealed complex associations among the environmental variables driving bird attack of clay caterpillars. Increasing elevation was associated with declining aridity. Controlling for the effects of elevation, increasing aridity was associated with higher bird attack rates. Similarly, controlling for the effects of aridity, increasing elevation was associated with increased attack. Yet because aridity declines with elevation, the overall effects of elevational patterns were not detectable in a univariate analysis. Variation in the regional bird abundance and diversity did not explain variation in attack rate as abundance (but not diversity) decreased with elevation, suggesting that our findings were driven by behaviorally based mechanisms. We speculate that the positive relationships between bird attack and both elevation and aridity were driven by variation in the herbivore communities within which the caterpillars were deployed; herbivore abundance is documented to decrease with elevation and aridity (Galmán et al., 2018; Poveda et al., 2012; Suzuki et al., 2012; Zhang et al., 2015), and this may in turn increase food limitation and thus the probability of attack on clay caterpillars in a dynamic akin to apparent competition (i.e., associational susceptibility) (Holt, 1977). Such dynamics would have important consequences for both the interpretation of predation bioassays generally and for our understanding of the multivariate drivers of variation top-down control by predators and predation risks experienced by prey.

Our findings demonstrate the importance of considering and accounting for the multiple factors that can covary along environmental gradients. Specifically, elevation and aridity were highly correlated with each other in a manner that masked their individual effects; although elevation was associated with increasing attack rate in the multivariate models, in a univariate model, this effect was masked by declining aridity and associated decrease in attack. As shown by Roslin et al. (2017), there are no consistent gradients of predation by birds among sites along a 2000-m elevational gradient across the globe, indicating that there are location-dependent mechanisms driving the bird predation patterns found in single-location studies. This is likely due to the lack of gradient in elevation within each of their sites, as their gradient spanned sites from different locations. Empirical studies robustly exploring a 4000-m gradient in Papua New Guinea found a nonlinear predation gradient in birds that was associated with a similar gradient in bird abundance (Sam et al., 2015), a decrease in bird species richness with elevation and temperature (Sam et al., 2019), and a mid-elevation peak in herbivore abundance and herbivory (Sam et al., 2020). In addition Sam et al. (2023) reported the same findings, and additionally reported a decrease in arthropod densities. Lastly, along a 1700-m gradient, Tvardikova and Novotny (2012) found an increase in bird predation, consistent with our observed patterns, yet this could be expressing the beginning of the nonlinear pattern found in studies with a larger gradient. Our study encompasses the majority of the *P. tremuloides* elevation range in our study region and includes multiple high- and low-elevation valleys to rigorously test for predation gradients by accounting for between-valley variation. Future studies should expand their gradients across the entire range, including multiple transects to account for this variation. While it is convenient to focus on variation in predator abundance along elevational and latitudinal gradients, other factors that must be considered include predator diversity, temperature variation and effects on metabolism and food requirements, and variation in prey communities including prey abundance, body size, defense, and diversity.

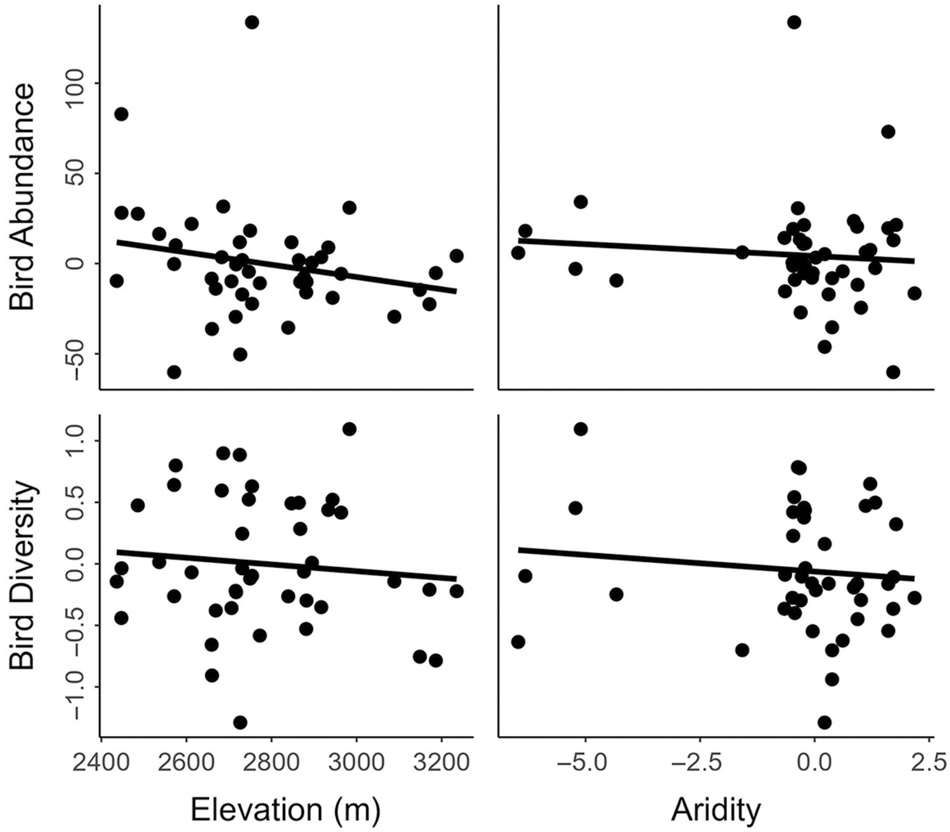

FIGURE 4 Association between elevation and aridity and bird abundance and diversity. Aridity is represented as the score on the first principal component of an ordination data on total annual precipitation and mean annual temperature from study sites. Data on bird abundance and diversity are extracted from the eBird database. See Figure 1 for the location of the field sites. Bird abundance significantly declined with elevation but did not vary with aridity, whereas bird diversity was not associated with either elevation or aridity.

We speculate that the association of attack rate with elevation and aridity is driven by associational effects. It is well known that the predation risk experienced by individual prey can be influenced by neighbor effects from other members of the prey community within which it is embedded (Frank van Veen et al., 2006; Morris et al., 2005; Muller & Godfray, 1997). Associational effects are well studied in both plant–herbivore (e.g., Lau & Strauss, 2005) and herbivore–enemy interactions (e.g., Carvalheiro et al., 2008). For example, an exotic seed predator is believed to have driven an entire community of native seed predators locally extinct through the recruitment of shared natural enemies to their shared host plant (Carvalheiro et al., 2008). Two contrasting dynamics for enemy-mediated indirect interactions among prey have been examined both theoretically and empirically. With associational susceptibility (i.e., apparent competition), the abundance of one prey ("A") can negatively affect another prey ("B") by recruiting a shared predator that then preferentially attacks the latter ("B") (Connell, 1990; Holt, 1977; Holt & Bonsall, 2017; Holt & Lawton, 1994). For example, Evans and England (1996) found increased predation and rates of parasitism on the alfalfa weevil *Hypera postica* when the pea aphid *Acyrthosiphon pisum* was present. With associational resistance, one prey ("A") recruits or otherwise distracts predators away from another prey ("B"), lowering attack rates on the later ("B") (Barbosa et al., 2009; Chaneton & Bonsall, 2000). For example, Nesbit et al. (2016) found in mixed-species treatment of a chemically defended aphid *Brevicoryne brassicae* and a relatively undefended aphid *Myzus persicae*, lower rates of predation on the undefended species due to predator deterrence of poor quality prey. Accordingly, whether associational susceptibility or resistance occurs is believed to be driven by the relative value of the two prey items to their shared consumer. In the case of our predator assay, clay caterpillars are certainly of lower nutritional value to birds. Although the use of clay caterpillars is widespread, the method comes with explicit biases in that the lack of chemical and behavioral cues drives the underestimation of predation rates as compared with live sentinel prey (Nimalrathna et al., 2023; Zvereva & Kozlov, 2023). Even though the intensity of predation is likely underestimated in our study, we believe this method to be as informative of predator behavior as if using real prey, acknowledging that actual predation may be at a higher rate (Lövei & Ferrante, 2017). Furthermore, there is evidence that birds respond to response to variation in prey quality in a manner that would result in associational effects; bird attack rates of experimentally deployed blowfly puparia were 8.4-fold higher than attacks of simultaneously deployed clay models (Zvereva & Kozlov, 2023). Based upon such findings, it can be expected that estimates of predation rate with clay caterpillars are driven not only by the abundance and composition of predator communities—as is commonly assumed—but also by prey communities within which the assay is conducted.

Our speculation that associational effects underlie our results is based on the assumption that the abundance of insect prey relates to both elevation and aridity. Theory predicts that herbivore abundance will decrease with elevation due to cooler and more seasonal climates. While many studies have found support for this (Galen, 1990; Galmán et al., 2018; Poveda et al., 2012; Rasmann et al., 2014; Suzuki et al., 2012), others have found neutral (Galmán et al., 2018; Hódar & Zamora, 2004; Lay et al., 2013), or even positive (Hagen et al., 2007; Koptur, 1985; Zhang et al., 2015), relationships with elevation, further reinforcing the need to disentangle the mechanisms of this variation. Accordingly, past work exploring these dynamics across latitudinal gradients has shown that herbivore abundance declines in higher latitudes in temperate climates than in lower latitudes in tropical climates due to increased aridity and lower productivity (Anstett et al., 2016; Coley & Barone, 1996; Moreira et al., 2015; Rodríguez-Castañeda, 2013; Zhang et al., 2016). Our past work at the same field sites as in this study has documented higher abundances of several herbivorous insects (aphids; Hemiptera: Aphididae) associated with low elevation and more arid sites (Nelson, Pratt, et al., 2019; Nelson, Symanski, et al., 2019), although this work did not seek to disentangle the separate effects of aridity from other aspects of the elevational gradient. Given this, we speculate a decrease in herbivore abundance with elevation drives, increased foraging rates of birds due to lower prey availability, and increased rates of attack on clay caterpillars. Particularly because birds have been found to forage in a density-dependent manner (Singer et al., 2012). This is an important implication when assessing predation via clay caterpillars, as the risk of attack on clay caterpillars may not be as consistent across gradients as previously thought, and assessment of the biotic and abiotic factors should be included when characterizing predation rates.

We found attack rates of birds on insect prey increased with aridity and elevation after controlling for the variation of each, despite the negative correlation between aridity and elevation. This suggests that across elevational gradients, there are multiple covarying factors that may be independently driving variation in top-down control. While factors such as climate and predator community composition may drive these patterns, we suspect that these underlying mechanisms may be behaviorally based and should be fully characterized in future gradient studies. For instance, future studies should focus on experimentally investigating the independent and interactive effects of different factors covarying along latitudinal and elevational gradients of predation. Overall, our findings have important implications for interpreting predation bioassays, understanding predation risks experienced by prey, and elucidating multivariate biotic and abiotic drivers of variation in top-down control.

AUTHOR CONTRIBUTIONS

Kailen A. Mooney designed the study and collected the data. Lydia S. Dean analyzed the data and wrote the manuscript. Carla Vázquez-González, Luis Abdala-Roberts, Sierra Hellwitz, and Kailen A. Mooney contributed critically to the writing.

ACKNOWLEDGMENTS

This work was made possible by the logistical support of the Rocky Mountain Biological Laboratory and funding from National Science Foundation (NSF) grants DEB-2032435 and IOS-1951244.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Dean et al., 2024) are available from Dryad: https://doi.org/10.7280/D1CQ5V.

ORCID

Lydia S. Dean https://orcid.org/0009-0008-1760-2354
Carla Vázquez-González https://orcid.org/0000-0001-6810-164X

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Dean, Lydia S., Carla Vázquez-González, Sierra Hellwitz, Luis Abdala-Roberts, and Kailen A. Mooney. 2024. "Decomposing an Elevational Gradient in Predation by Insectivorous Birds." *Ecosphere* 15(2): e4790. https://doi.org/10.1002/ecs2.4790