

SPECIES-SPECIFIC DIFFERENCES IN BUMBLEBEE WORKER BODY SIZE BETWEEN ELEVATIONS: IMPLICATIONS FOR POLLINATOR COMMUNITY STRUCTURE UNDER CLIMATE CHANGE

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Abstract—Pollinator populations face growing threats from global climate change, particularly in alpine environments with rapidly rising temperatures. Understanding how bumblebees, critical alpine pollinators, respond to these temperature changes is therefore an important goal. Predicting species' responses to climate change requires several different approaches, one of which is to compare processes at different elevations, which experience different temperature regimes. Bumblebee body size is linked to fitness through its influence on nutritional requirements and foraging capacity. It is also a highly plastic trait that depends on ecological factors such as temperature. Thus, understanding how body size varies at different elevations may help predict bumblebee fitness under climate change. We collected bumblebee workers from five species in a single growing season, at two distinct elevations in the Swiss Alps. Our study aimed to examine whether body size responses differed among species and across functional traits related to foraging and nesting. Larger body size is thought to confer an advantage under cold conditions; we therefore expected greater body size with elevation, but with species-specific relationships. Contrary to our expectation, not all species were larger at high elevations. Specifically, while two species were significantly larger at high elevation, one (*Bombus terrestris*) was significantly smaller at high elevation, and two showed no size differences with elevation. Additionally, interspecific variation in body size was greater at low elevations. This suggests a divergence of body size with warming, although local factors may also play a role in shaping functional traits.

Keywords—*Bombus*, body size, climate change, elevation, functional traits, rising temperatures

INTRODUCTION

Climate change poses unprecedented challenges to plant-pollinator interactions (Memmott et al. 2007; Hegland et al. 2009). In addition to documented shifts in species' abundances, distributions, and phenology (Bartomeus et al. 2011; CaraDonna et al. 2017), evolutionary and plastic responses to climate change by plants and pollinators can also alter species interaction outcomes. For example, phenotypically plastic floral attraction traits in high-altitude *Aquilegia coerulea* plants readily respond to increases in temperature and drought levels (Brunet & Van Etten 2019), and a study revealed an increase in relative hair length in wild

bees across an elevation gradient, which may affect pollen carriage (Osorio-Canadas et al. 2022). Indeed, plant and pollinator functional traits are known to vary broadly along climate gradients (Aguirre-Gutiérrez et al. 2016). The complex suite of responses to climate change, including plastic and adaptive responses, raises questions about the fate of plant-pollinator interactions in a warming world. Empirical approaches to answering these questions include observing and measuring functional trait variation linked to performance across climate gradients.

Rising temperatures directly affect pollinator physiology, metabolism, and movement (Scaven & Rafferty 2013). Pollinators must also contend with

the indirect effects of climate via alteration of the floral resource landscape, which can reshape dietary options and preferences (Aldridge et al. 2011; Ogilvie et al. 2017). Both of these factors can drive plastic and adaptive changes in functional traits to buffer against warming. Physiological adaptations, such as alterations in metabolism and thermal tolerance, play a crucial role in enabling insects to cope with the changing environmental conditions in alpine regions (González-Tokman et al. 2020). One important aspect of insect responses to climate change in alpine ecosystems is body size, as shifts in size can have significant implications for their resource utilization, ecological interactions, and overall fitness (Rubalcaba & Olalla-Tárraga 2020).

Bumblebees (*Bombus spp.*), common and highly effective pollinators in alpine environments, are specialized to colder environments and have specific climate tolerances (Totland 1993). Bumblebee body size is determined by several different factors, including larval nutrition, floral resource availability, and temperature (Fitzgerald et al. 2022). There is high variation among and within bumblebee species, and different species exhibit different degrees of size variation (Peat et al. 2005; Austin & Dunlap 2019). Relatively large or small body size can have different benefits or costs. For example, small body size can have the advantage of protection from overheating during flight (Rubalcaba & Olalla-Tárraga 2020) and from starvation, as smaller bumblebee workers live longer when food is scarce (Couvillon & Dornhaus 2010). However, small workers may decrease colony success over time, as they return to the nest with lower foraging loads and colony growth decreases (Herrmann et al. 2018). At higher elevations, large body size may buffer insects against cold temperatures, but require greater caloric intake to maintain bodily function (Rasmont et al. 2021). Thus, body size can influence colony success, pollination efficiency, population dynamics, and ecosystem functioning, underscoring the need to investigate the potential consequences of changing body size in response to mountain elevation. Recent studies examining bumblebee (and other bee species) body size in mountain habitats report larger bees with increasing elevation (McCabe et al. 2019; Maihoff et al. 2023). However, in these studies differences

in overall body size within the genus are attributed at least partially to changes in species composition.

Other bumblebee functional traits may interact with body size and play a role in species' susceptibility to climate change. Glossa (tongue) length is another trait with strong implications for bumblebee performance. Access to floral nectar varies depending on the match between floral morphology and tongue length, and longer-tongued species tend to specialize on flowers with longer corollas (Miller-Struttman et al. 2015). Climate change affects plant species assemblages, including the diversity and abundance of species with long-tubed flowers, with potential feedback effects on pollinator populations (Miller-Struttman et al. 2015). In addition, bumblebees exhibit two main strategies for provisioning pollen to developing larvae: They either deposit pollen into centralized hoppers near brood cells, feeding all larvae at once (pocket-makers), or they store pollen in former brood cells and feed larvae individually (pollen-storers, Sladen 1912). Populations of pollen-storer species tend to be more robust due to equal distribution of pollen across larvae (Hagen & Dupont 2013).

Here, we ask to what extent body sizes of species that exist along an elevation gradient exhibit similar patterns of change between high and low elevations. Given previous work reporting overall larger body size with increasing elevation, we expected the same pattern in all species we collected; however, we hypothesized there would be some variation among species. We also asked whether species functional traits can predict whether individuals are, on average, smaller or larger at high elevation compared to low. Specifically, we examine the influence of tongue length and nesting ecology. Because adult and larval diet plays such an important role in determining body size, we chose these traits due to their association with these factors (Goulson & Sparrow 2009). Tongue length determines the suite of floral species bees can visit; it is believed that longer-tongued species tend to be more specialized, while shorter-tongued species are more generalized (Miller-Struttman et al. 2015). Since floral resource availability can change with elevation, it stands to reason that generalist bee species should be better equipped for foraging at different elevations. As nutrition is less limiting for

growth in this case, we predicted less pronounced differences in body size across elevations in short-tongued species. Similarly to tongue length, we expect nutrition to be less limiting for the growth of pollen-storer species and hypothesize these species would have less pronounced differences in body size across elevations. To test our hypotheses, we measured body sizes from five bumblebee species collected at two elevations in the Swiss Alps.

By comparing these two habitats, it is possible to generate predictions about pollinator functional trait assemblages in the future. However, it is important to note that our study was restricted to a single site at each elevation, so it is necessary to be conservative about drawing direct inference between current observations and future predictions. Understanding the specific impacts of climate change on pollinator communities in alpine environments, which comprise 15% of the world's surface, is nevertheless of particular importance due to animals' perceived vulnerability to rising temperatures (Inouye 2020). Furthermore, these environments are home to high

levels of biodiversity and endemism, and many alpine populations are under threat due to rapid warming (Noroozi et al. 2018).

MATERIALS AND METHODS

FIELD SAMPLING

The study was carried out on Calanda Mountain, in Canton Graubünden in the Swiss Alps. We worked at two distinct sites: Nesselboden (NBO; 46.869208, 9.490178), at 1400 m asl, which is characterized by a pasture within a forest; and Calanda (CAL; 46.887778, 9.489398) at 2000 m asl, which is located above the treeline and is comprised of open grassland. The distance between the two sites is approximately 2 km (Fig. 1).

We spent 2 person-hours collecting worker bumblebees directly from flowers once per week between 18 May and 13 September 2022. We collected between the hours of 10:00–16:00 and in good weather conditions (avoiding rain). We alternated the order of site visits each week to avoid sampling bias. We collected bees following a circular transect at the middle of the site, walking



Figure 1. Location of the two study sites, coordinates: NBO, 1400 m: 46.869208, 9.490178; CAL, 2000 m: 46.887778, 9.489398. NBO is a meadow habitat located within a forest matrix; CAL is located just above the timberline. Map generated by Google Maps.

anti-clockwise until reaching a distance of 50 m from the centre, at which point we would start back in the centre and walk the transect again until the time was up.

We collected a total of 584 bumblebees, which were stored in individual vials and subsequently euthanized by freezing at -20°C . We identified the caste of each collected bumblebee and restricted our analysis to workers. We preserved bees by pinning and used the pinned specimens to take measurements and identify bees to species. We measured worker inter-tegular distance (ITD), the distance between the two insertion points of the wing. The ITD is measured on the thorax which contains flight muscles and is also strongly correlated with other size parameters like dry body mass and wing size (Cane 1987). All the specimens were measured with digital calipers. We identified all specimens to the species level and collected a total of 16 species. However, we restricted our analyses to the five most common species in our collection. Using published literature, we classified them either as long-tongued or short-tongued species. We also determined their nesting ecology from the literature, *i.e.*, whether they are pocket-makers (pollen delivered to larvae from hoppers built near the brood cells) or pollen-storers (pollen stored in former pupal cells and delivered to larvae individually, Sladen 1912). We were explicitly interested in these life history traits because of their connection to diet and colony fitness. Tongue length can provide an indication of degree of floral specialization (Stang *et al.*, 2009), and nesting biology plays a role in larval nutrition outcomes, as it determines how much food each larvae could receive from the workers (Rasmont *et al.* 2021).

STATISTICAL ANALYSES

All analyses were performed using R version 4.3.0 (R Core Team 2023). We tested whether average worker body size differed between elevations (site), among species, and in response to life history traits. We performed several linear mixed models (LMM) each with worker inter-tegular distance (ITD) as the response variable. First, site and species were used as crossed fixed effects and week of year was included as a random effect to account for repeated measures and control for differences in between-site phenology. We performed additional, individual species models

(LMM) to test whether body size differed between sites, using ITD as a response variable, site as a fixed effect, and week of year as a random effect. Finally, we performed models using tongue length (short or long) and nesting ecology (pocket-maker or pollen-storer) classification as fixed effects, each interacting with site. Week of year and species were included as random effects. We tested for an overall effect of fixed effects using likelihood ratio tests. To further address the question of community homogenization, we performed Chi-square analyses (with Yates' continuity correction) asking if the proportion of long- versus short-tongued, and pocket-making versus pollen-storing individuals shifted in response to elevation.

RESULTS

We found that, contrary to our expectation, not all species were larger at higher elevations with body size neither uniformly increasing or decreasing with elevation for most species. Rather, there were species-specific differences in whether workers were larger or smaller at high elevation compared to low elevations (Fig. 2a). The significant interaction between site and species further reveals how different species' body sizes responded differently between elevations (Table 1). This effect was driven by increases in average body size for two species (*Bombus humilis* and *B. wurflenii*, 10% and 5% larger at high elevation, respectively) and, notably, a decrease in average body size in *B. terrestris* (9% smaller at high elevation). We also found that long-tongued species tended to be smaller than short-tongued species at low elevations; but did not vary in size at high elevations (Fig. 2b, Table 1). Similarly, pocket-making species tended to be smaller than pollen-storing species at low elevation but the difference at high elevation was not detected. However, results of the likelihood ratio test revealed the interaction between nesting ecology and site to be marginally statistically significant (Fig. 2c, Table 1). There was a relatively similar proportion of long- and short-tongued bees at high elevations, while long-tongued bees were more abundant at low elevation ($X^2_1 = 25.126$, $P < 0.001$, Fig. 3a). Pollen-storers were approximately twice as abundant at high elevation, while the proportions at low elevation were reversed ($X^2_1 = 19.251$, $P < 0.001$, Fig. 3b).

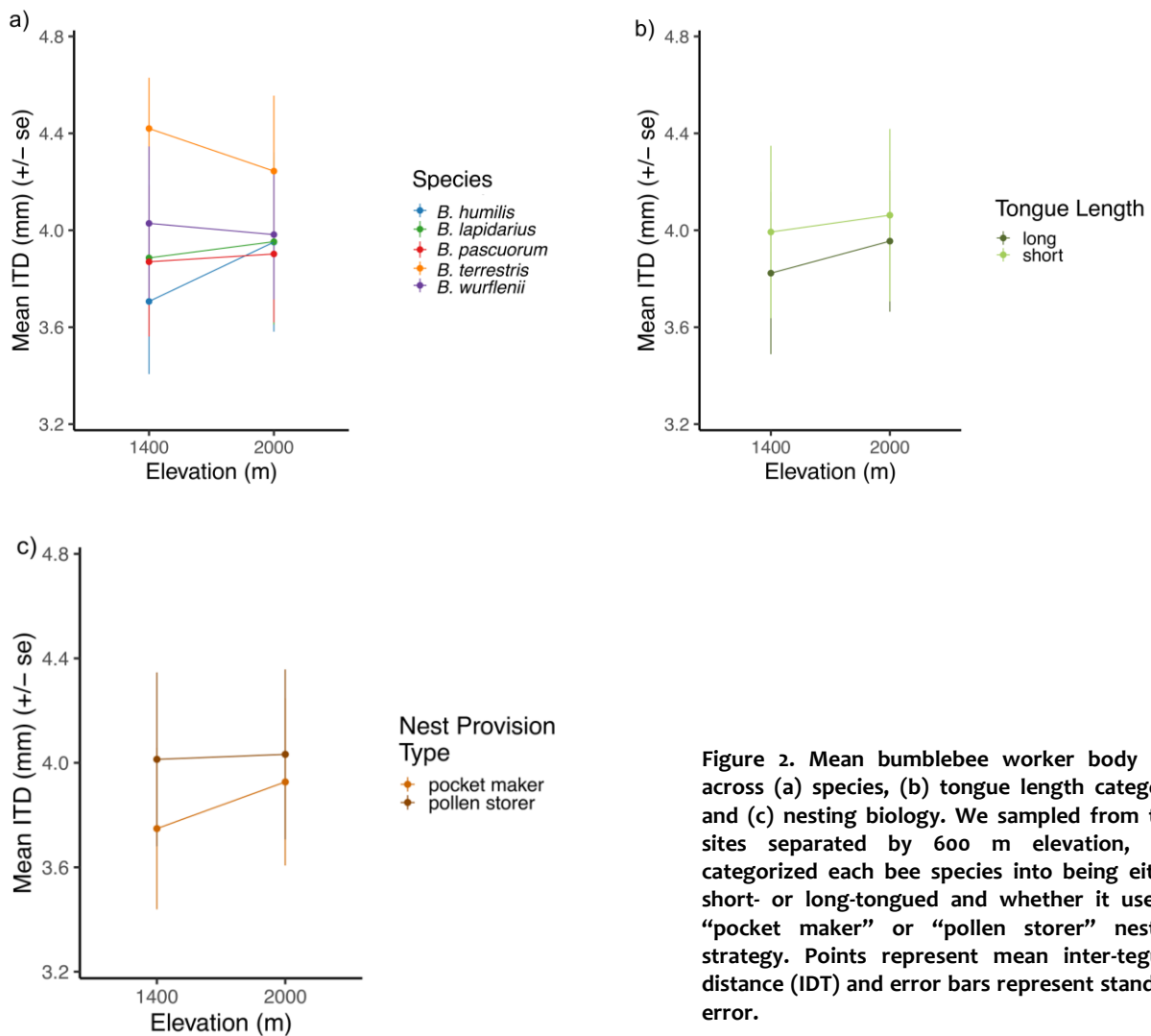


Figure 2. Mean bumblebee worker body size across (a) species, (b) tongue length category, and (c) nesting biology. We sampled from two sites separated by 600 m elevation, and categorized each bee species into being either short- or long-tongued and whether it uses a “pocket maker” or “pollen storer” nesting strategy. Points represent mean inter-tegular distance (ITD) and error bars represent standard error.

DISCUSSION

Though we expected body size to generally be larger at the high site across species, our findings revealed species-specific differences in the directionality and magnitude of differences in body size between sites (Fig. 2a). While this finding was somewhat surprising, similar responses have been seen in bumblebee species assemblages in urban environments. One study measuring body size of three of the species observed in our study (*B. lapidarius*, *B. pascuorum*, *B. terrestris*) across an urbanization gradient in Germany reported body size differences across habitat types only in *B. terrestris*, although all three species trended towards smaller body size in response to higher ambient temperature (Theodorou et al. 2021). A second study focusing on urbanization gradients in the United States found differences in the

magnitude and directionality of differences in body size in response to level of urbanization (Austin et al. 2022). Interestingly, these two studies demonstrate how urbanization, another anthropogenic threat to bumblebees and other pollinators, can impart similar effects as temperature. While temperature is an important component of urbanization, as urban areas tend to be warmer on average than rural areas, other factors, namely fragmentation of flower patches and availability of nest sites, are also at play (Tommasi et al. 2022).

The decrease in *Bombus terrestris* body size at high elevation compared to low is notable. It is unclear as to why this species showed an opposite pattern to the others measured. It is the largest of all five species in our analysis, on average, although at high elevation its average size is comparable to *B. wurflenii* (Fig. 2a). It is possible

Table 1. Results of all statistical models. We performed an initial model testing for differences in bee body size (intertegular distance, ITD) across site and species, followed by models testing for differences in bee body size between site and morphological (tongue length) and life history (nesting biology) traits. Because the initial model showed species-specific differences, we also performed individual species models. All models are linear mixed effects models (LMM) followed by likelihood ratio tests, the results of which we show here.

Species	Model	Variable	Chisq	df	p
all	ITD ~ site * species + (1 date)	site	2.018	1	0.16
		species	78.464	4	< 0.001
		site * species	10.543	4	0.03
all	ITD ~ site * tongue length + (1 date) + (1 species)	site	10.2644	1	< 0.001
		tongue length	2.7042	1	0.1
		site * tongue length	10.6884	1	< 0.001
all	ITD ~ site * nest type + (1 date) + (1 species)	site	2.0589	1	0.15
		nest type	3.6982	1	0.05
		site * nest type	3.3352	1	0.07
<i>B. humilis</i>			3.6579	1	0.05
<i>B. lapidarius</i>			0.0901	1	0.76
<i>B. pascuorum</i>	ITD ~ site + (1 date)	site	2.3339	1	0.13
<i>B. terrestris</i>			6.2366	1	0.01
<i>B. wurflenii</i>			3.1162	1	0.08

that there are environmental stressors unique to this species that are more prevalent at high elevation, leading to the decrease in body size. In another study, heat-exposed commercial *B. terrestris* colonies in Spain produced larger workers, a pattern attributed to complex, plastic responses to stressors (Zaragoza-Trello et al. 2021). It is also possible that the other species measured are better equipped to obtain pollen at high elevation than *B. terrestris*, causing it to be the only species with smaller workers at the high site. However, *B. terrestris* is an extremely cosmopolitan species, found across a range of climates including cold-dominated high latitudes (*i.e.*, Southern Sweden, Rasmont et al. 2008), and in non-native parts of its range is considered a detriment to other, native species (Nagamitsu et al. 2007; Morales et al. 2013). Therefore, it seems more plausible that this species would fare better than others across different environments. Future studies that investigate potential drivers of smaller body size, or constraints on large body size, in this species at high elevation will be particularly illuminating.

Similar to our findings on body size across species, we only found increased body size at high elevation in one of the two larval feeding strategies present in our sample population (pocket-makers, as opposed to pollen-storers, Fig. 3). Pollen-storers show generally less intraspecific variation in body size (Fitzgerald et al. 2022), although this does not explain why they would not follow the predicted pattern of body size increasing with elevation. It is possible that pollen-storers are more likely than pocket-makers to favour worker number over worker size; that is, more workers are produced at the expense of larger workers (Cueva Del Castillo et al. 2015). Another possibility is that our sampling of pocket-makers was biased towards larger individuals due to either poor survival of small workers at high elevation, or due to division of labour within the colony, as larger workers may be more likely to function as foragers in cooler climates (Spaethe & Weidenmüller 2002).

A major caveat of our study is that we were unable to sample from more than one site per elevation, although we did sample broadly at these locations. Therefore, it is important to consider

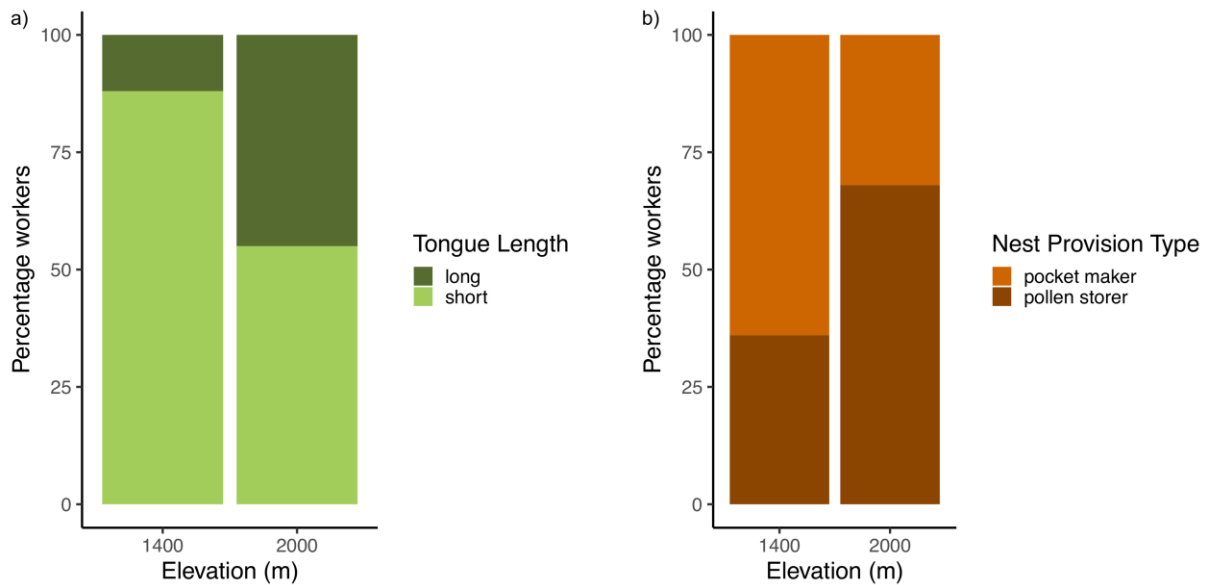


Figure 3. Proportion of all individual workers captured at each site categorized as either short- or long-tongued (a), or whether it uses a “pocket maker” or “pollen storer” nesting strategy (b).

local factors that may confound our results and preclude us from making predictions about future performance based on proxy climate scenarios. For example, it could be that resource availability or land use at our sites differs from those at the same elevation in neighbouring mountains. In Switzerland, subalpine meadows and those above, but near, treeline are consistent in that their land use history is predominantly the result of cattle grazing (Maurer et al. 2006). As is commonplace in the Swiss Alps, our site is routinely grazed by cattle every summer. While we are not aware of the full extent of grazing regimes throughout the region where our study was conducted, we do consider our sites to be exposed to relatively the same grazing history and intensity of other mountain slopes in Eastern Switzerland, based on conversations with local land managers and farmers. It is also possible that there is something unique about the floral communities at our sites that could be driving the patterns of body size we detected. Both sites we sampled from are dominated by species commonly found in (Swiss) subalpine and alpine habitats, and our field site is located close to the centre of the Alps (Fig. 1). Therefore, we do not have reason to suspect that the floral community at our sites drastically differs from others in the region. Even so, we recommend some caution in the interpretation of our results, considering the caveat of limited spatial sampling.

Between the two sites, we observed a convergence of body size, tongue length category, and nesting ecology across species at high elevation compared to low (Fig. 2). We also observed a loss of evenness between long- and short-tongued individuals at the low site compared to the high site (Fig. 3). Considering that present-day comparisons across elevations can provide insight into the effects of warming over time, this result is in contrast with prior studies suggesting climate change may lead to homogenization of functional traits within bumblebee communities (Pradervand et al. 2014). The convergence of body size and other functional traits at high elevation might lead to increased competition for resources among bumblebee species with similar size optima, potentially resulting in reduced niche differentiation and altering community dynamics (Barthell & Resasco 2023). Our results suggest that warmer climates, *i.e.*, those experienced at the low elevation site, may support a higher variation in interspecific body size and could promote a more diverse and resilient community. As mountain habitats are predicted to continue warming under climate change, the increased differentiation among species may be an important buffering factor against the negative influences of increasing temperature.

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AUTHOR CONTRIBUTION

CM and SKR designed the project, conducted fieldwork, performed analyses, and wrote the first draft of the manuscript. JHRL provided feedback on design and analyses and contributed to revisions of the manuscript.

DISCLOSURE STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code used to write this article are deposited to Zenodo, DOI: [10.5281/zenodo.11382092](https://doi.org/10.5281/zenodo.11382092).

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