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ARTICLE

Parasitoid avoidance of intraguild predation drives enemy complementarity in a multi-trophic ecological network

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Abstract

How consumer diversity determines consumption efficiency is a central issue in ecology. In the context of predation and biological control, this relationship concerns predator diversity and predation efficiency. Reduced predation efficiency can result from different predator taxa eating each other in addition to their common prey (interference due to intraguild predation). By contrast, multiple predator taxa with overlapping but complementary feeding niches can generate increased predation efficiency on their common prey (enemy complementarity). When viewed strictly from an ecological perspective, intraguild predation and enemy complementarity are opposing forces. However, from an evolutionary ecology perspective, predators facing strong intraguild predation may evolve traits that reduce their predation risk, possibly leading to niche complementarity between enemies; thus, selection from intraguild predation may lead to enemy complementarity rather than opposing it. As specialized predators that live in or on their hosts, parasitoids are subjected to intraguild predation from generalist predators that consume the parasitoids' hosts. The degree to which parasitoid–predator interactions are ruled by interference versus enemy complementarity has been debated. Here, we address this issue with field experiments in a forest community consisting of multiple species of trees, herbivorous caterpillars, parasitoids, ants, and birds. Our experiments and analyses found no interference effects, but revealed clear evidence for complementarity between parasitoids and birds (not ants). Parasitism rates by hymenopterans and dipterans were negatively associated with bird predation risk, and the variation in the strength of this negative association suggests that this enemy complementarity was due to parasitoid avoidance of intraguild predation. We further argue that avoidance of intraguild predation by parasitoids and other arthropod predators may explain enigmatic patterns in vertebrate–arthropod–plant food webs in a variety of terrestrial ecosystems.

Andrew B. Hennessy and Riley M. Anderson contributed equally to this study.

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KEYWORDS
caterpillars, Diptera, enemy-free space, forests, host–parasite interactions, Hymenoptera, Lepidoptera, plant–herbivore interactions, Tachinidae, trees, tri-trophic interactions

INTRODUCTION

Elucidating relationships between consumer diversity and consumption efficiency is a central issue in ecology (Duffy et al., 2007). In the context of predation and biological control, this relationship revolves around theory of multiple predator effects on prey (Letourneau et al., 2009; Sih et al., 1998; Straub et al., 2008). The net effects of multiple predators (i.e., enemies) on the consumption rate of herbivores are expected to hinge on the roles of intraguild predation (Polis et al., 1989) versus predator complementarity (Ives et al., 2005). When multiple predators that consume the same prey also eat each other (i.e., intraguild predation), this predator–predator antagonism can reduce the net consumption rate of prey (i.e., interference) (e.g., Bosc et al., 2018; Finke & Denno, 2005; Martin et al., 2013; Vance-Chalcraft et al., 2007). When multiple predators are functionally complementary—foraging on their common prey in distinct ways, times, or places—their net predation effect on prey can be additive or synergistic (e.g., Casula et al., 2006; Finke & Snyder, 2008; Northfield et al., 2014; Schmitz, 2007). For example, Gontijo et al. (2015) found stronger suppression of woolly apple aphids when the third trophic level consisted of parasitoids and generalist arthropod predators compared with parasitoids alone. In this case, the functional complementarity between parasitoids and generalist predators resulted at least partly from temporal partitioning of the common aphid prey. Other studies show complementarity between enemies owing to behavioral differences and spatial partitioning (e.g., Cardinale et al., 2003). Explaining and predicting how multiple enemies affect predation efficiency is an active area of research (e.g., Chang & Cardinale, 2020; Snyder, 2019), representing an important facet of research on the relationship between biodiversity and ecosystem function (Ives et al., 2005; Letourneau et al., 2009).

The evolutionary ecology concept of enemy-free space—ways of living that reduce mortality from enemies due to anti-predator defenses or use of refugia (Jeffries & Lawton, 1984)—offers an alternative perspective on multiple enemy effects. Rather than a strictly ecological view pitting intraguild predation against enemy complementarity, this perspective predicts that intraguild predation can cause enemy complementarity, perhaps yielding unexpected food web structure and dynamics. The rationale is that enemies subjected to intraguild predation (e.g., parasitoids) are hypothesized to evolve anti-predator traits in response to selection from predation (e.g., predators of the parasitoids' hosts) (Fritz, 1982). The avoidance of host environments with high intraguild predation risk could provide parasitoids with enemy-reduced space (Murphy et al., 2014). As such, we hypothesize that the acquisition of enemy-reduced space by parasitoids will promote functional complementarity between parasitoids and their potential intraguild predators. A few studies have addressed the possibility that enemies of herbivores might have evolved traits in response to the risk of intraguild predation (reviewed in Frago, 2016; Murphy et al., 2014). However, this possibility requires further study, especially at a community level (Frago, 2016).

To address this gap, this study investigates the roles of predator–parasitoid interference and enemy complementarity in consumption of herbivorous caterpillars by parasitoids and generalist predators in a temperate forest community (Figure 1). As specialized predators, parasitoids are major enemies of caterpillars (e.g., Greeney et al., 2012; Hawkins et al., 1997; Stireman & Shaw, 2022), while generalist predators, such as birds and ants (e.g., Remmel et al., 2011; Roslin et al., 2017; Singer et al., 2014), are potential intraguild predators of immature parasitoids living in or on caterpillars. Many studies show that immature parasitoids are subjected to intraguild predation via predation of the parasitoids' hosts (Frago, 2016). Intraguild predation would especially interfere with predation of herbivores if predation were biased toward parasitized hosts (e.g., Ferguson & Stiling, 1996; Jones, 1987; Tscharntke, 1992). Here, we test this possibility (interference hypothesis) by comparing parasitism rates of caterpillars in predator-exclusion versus predator-access environments. Reduced parasitism rates of caterpillars exposed to predation would be evidence of intraguild predation biased toward parasitized hosts. The reasoning is that preferential predation of parasitized hosts will reduce the percentage of parasitized caterpillars in the exposed treatment relative to that in the predator-exclusion treatment (Jones, 1987).

On the other hand, prior work in a variety of ecosystems suggests that parasitoids may have acquired enemy-reduced space from predators of their hosts (e.g., Baer & Marquis, 2020; Frago, 2016; Fritz, 1982; Gentry & Dyer, 2002; Murphy et al., 2014; Stireman & Singer, 2003). For example, caterpillar species with

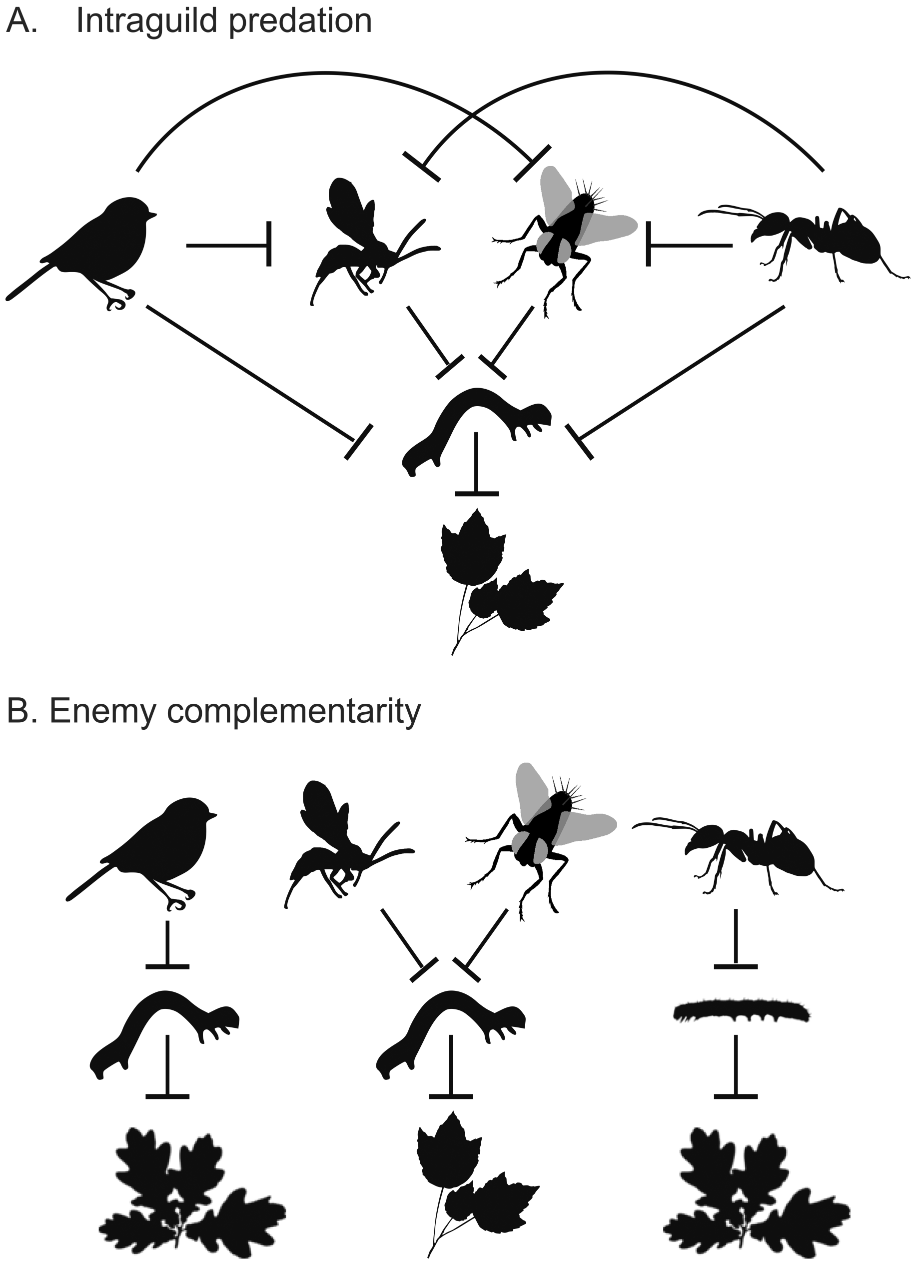

FIGURE 1 Conceptual illustrations of the interference hypothesis (A) and the enemy complementarity hypothesis (B). Different icons represent different taxa. Dashed lines and flat tips represent antagonistic species interactions. All icons are from PhyloPic and are in the public domain.

strong anti-predator defenses (Gentry & Dyer, 2002; Murphy et al., 2014) and those that apparently suffer reduced predation (Baer & Marquis, 2020) experience increased mortality from parasitoids. These observations are consistent with the hypothesis that host use by parasitoids is under selection from intraguild predation, but inferences have been inconclusive because variation in parasitism rates among caterpillar species is potentially confounded with direct and indirect interactions between parasitoids, caterpillars, and host plants. To more rigorously evaluate the hypothesis that parasitoids avoid intraguild predation, we test three corollary predictions in a community we have studied extensively. First, parasitism rates of caterpillars will be negatively associated with predation risk per se across various combinations of caterpillar species and host–plant species. Second, this negative relationship will be stronger for bird predation risk versus ant predation risk because, on average, bird predation has been stronger than ant predation on caterpillars in this community (Singer et al., 2017). Third, this negative relationship will be stronger for parasitism by dipteran versus hymenopteran parasitoids (Murphy et al., 2014).

While most of the hymenopteran parasitoids (i.e., microgastrine braconids) in this community attack early instar caterpillars and exit their hosts by the middle instars, most of the dipteran parasitoids (i.e., tachinids) do not emerge from their hosts until the final instar, pre-pupal, or pupal stage of their hosts (Stireman & Shaw, 2022). Considering this difference and evidence that bird predation is biased toward larger (i.e., later instar) caterpillars in this community (Singer et al., 2017), the dipteran parasitoids are, on average, expected to face a greater bird predation risk than their hymenopteran counterparts.

METHODS

Overview of study

We analyzed the probability of mortality due to parasitoids (parasitism rate) across an assemblage of caterpillars sampled from eight tree species over multiple years and sites. To assess interference effects between parasitoids and predators of caterpillars, we compared the parasitism rate of caterpillars in predator-exclusion treatments versus predator-access treatments of multi-year field experiments. Evidence of predator–parasitoid interference would be manifested as reduced parasitism rates of caterpillars exposed to predation compared with those in predator-exclusion treatments. To assess parasitoid and predator complementarity and the possible acquisition of enemy-reduced space by parasitoids, we analyzed the relationship between parasitism rate and predation effect sizes (predation risk) across caterpillar–plant species combinations by collating data from observational studies of parasitism and from the predation experiments mentioned above. Strong evidence of enemy complementarity would be manifested as a negative association between parasitism rate and predation risk even when caterpillar species and host–plant species are each included in the same statistical models as independent predictors of parasitism rate.

Study system

Sites

All field sites were forest patches located in central and eastern Connecticut, USA. The sites varied among years of the study, in total consisting of 23 deciduous or mixed-deciduous upland forest patches with oak–hickory and maple–beech-dominated canopies, typical of the Northeastern Coastal Forest ecoregion (Olson et al., 2001).

Plants

The eight host–plant taxa include *Acer rubrum* (red maple, Sapindaceae), *Betula lenta* (black birch, Betulaceae), *Carya* spp. (hickories, Juglandaceae), *Hamamelis virginiana* (witch hazel, Hamamelidaceae), *Prunus serotina* (black cherry, Rosaceae), *Quercus rubra* (red oak, Fagaceae), *Quercus alba* (white oak, Fagaceae), and *Fagus grandifolia* (American beech, Fagaceae). Hickories (*Carya* spp.) include the closely related *Carya ovata* (shagbark hickory), *Carya tomentosa* (mockernut hickory), and *Carya glabra* (pignut hickory) (Singer et al., 2012). *Q. rubra* includes phenotypically variable individuals within the hybridizing red oak group (Singer et al., 2012). These tree species represent 52% of trees in the upland temperate forest (unpublished data) and vary in the strength of parasitism (Farkas & Singer, 2013) and bird predation (Singer et al., 2012) of caterpillars.

Parasitoids

The insect parasitoids sampled from caterpillars in this community include tachinid flies (Diptera) and wasps (Hymenoptera) from several families, mainly Braconidae (mostly Microgastrinae) and Ichneumonidae. All tachinids and the majority of wasps are endoparasitoids, with larvae developing and feeding from within the caterpillar, while some wasps feed and develop as ectoparasitoids (Stireman & Shaw, 2022). Any adult parasitoids that emerged from a collected caterpillar were identified as hymenopteran, tachinid, or unknown. We were unable to identify the parasitoids at the species level (see Farkas & Singer, 2013).

Caterpillars

The caterpillar assemblage was sampled from the low canopy and understory (1–3 m above ground) of these tree taxa and consisted of 125 species from 10 families and ranged from dietary specialists that feed on a single host–plant species to dietary generalists that feed on all eight plant taxa (Singer et al., 2014, 2017). Most caterpillars could be identified at the time of collection or during the rearing process (using Wagner, 2005; Wagner et al., 2001, 2011), but occasionally, species identification required pupation and emergence as an adult.

Predators

We studied bird predation of caterpillars during the breeding season for many songbirds (late May–early July), a period of high bird density as both resident and migratory birds search for mates, nest sites, and prey (for details, see Anderson et al., 2019; Lichter-Marck et al., 2015; Singer et al., 2017). We studied ant predation of caterpillars during the same season (for details, see Clark et al., 2016; Clark & Singer, 2018; Singer et al., 2017, 2019).

Experimental design

From 2007 to 2019, predator-exclusion experiments were conducted for 10 nonconsecutive field seasons over 23 field sites (forest patches 3–1000 ha in size) across central and eastern Connecticut to test effects of predators on the caterpillar assemblage. The experiments were designed as a single or factorial exclusion of birds and ants (i.e., bird exclusion, ant exclusion, dual exclusion, and control), with each experimental unit being a low branch of a tall tree or the terminal section of a sapling (hereafter “branch”), typically 1–3 m above ground (see Appendix S1: Table S1 for detailed differences among experimental designs). In each field experiment, the design included spatial blocks with multiple branches of each tree species represented in the experimental replicate (see Singer et al., 2012 for further details).

Bird exclusion branches were bagged with nylon mesh (13 or 20 mm size) secured around the branch (Singer et al., 2012). This mesh size excludes birds while allowing most moths to pass through or (for the very largest moths, which are rare) at least access the foliage in contact with the mesh. Bird-access control branches lacked these bags. Ant exclusion branches were treated with sticky resin (Tanglefoot, Contech Enterprises) (see Singer et al., 2017, 2019 for details). Experimental branches in the same replicate (representing all treatments and controls) were selected to be closely situated (typically 1–10 m apart), either on the same individual tree or nearby trees matched for similar light exposure as well as tree and branch size.

The predator exclosures were established in May of each year, and branches were sampled either once or twice (June–early July), with 3 weeks between the setup and sampling as well as between first and second sampling events (Singer et al., 2012, 2017). Branches were inspected and beat-sampled (Wagner, 2005) during setup to dislodge any ants before treatments were applied. Collected caterpillars were reared until pupation or the emergence of a parasitoid (immature or adult) and fed wild-collected leaves from the host–plant species they were found on. Caterpillar counts were summed over the multiple sampling events per season, caterpillar species, plant species, and field site. The number of leaves on each experimental branch was recorded at the last sampling event to estimate the leaf area per branch, which was used to estimate caterpillar density per branch (Appendix S1: Section S1).

Additional parasitism data came from a field study (2004–2007) conducted prior to the predator-exclusion experiments. Caterpillars were systematically sampled from haphazardly chosen branches of each of the eight tree species used in the predator-exclusion experiments. One branch of each tree species was sampled around the same time and location, as a complete spatio-temporal block, to minimize confounding environmental effects (Farkas & Singer, 2013). As previous analyses found no bias in parasitism due to the sampling method (Farkas & Singer, 2013), one of the parasitism datasets analyzed here included parasitoids reared from the systematically sampled caterpillars (described above) along with caterpillars opportunistically found on additional branches of the same eight tree species.

The general methods as described above remained consistent across years, but the specific sites, host–plant species, number of replicates, number of blocks, and levels of predator exclusion varied across years (Appendix S1: Section S1, Table S1).

Data analysis

Interference hypothesis

To test whether parasitized caterpillars were subjected to more predation than unparasitized caterpillars, we analyzed parasitism rate as a function of predator-exclusion treatments, thus assessing predator–parasitoid interference. The number of caterpillar–plant species combinations included in each analysis was limited by our chosen cutoff of at least five replications per caterpillar species, plant species, and predator treatment. These minimum sample size requirements restricted our dataset to 21 caterpillar–plant species combinations in the models of ant exclusion effects and 35 such combinations in the models of bird exclusion effects (Appendix S1: Table S2). To estimate the probability of parasitism for each caterpillar–plant species combination, we used rearing records from bird exclusion experiments in 2007–2009, 2011; and ant exclusion experiments in 2011–2012. We summed the total number of parasitized caterpillars, the number parasitized by each of the two major parasitoid taxa, and the number of unparasitized caterpillars for each caterpillar–plant species combination to create the parasitism dataset we analyzed.

Enemy complementarity hypothesis

To test for negative associations between parasitism rate and predation risk across caterpillar–plant species combinations as evidence of enemy complementarity, we used additional data to analyze parasitism rate as a function of predation risk. Caterpillar–plant species combinations with sparse replicates had high leverage in preliminary models; thus, we restricted combinations to those with at least 10 replicates of each caterpillar species per plant species for bird and ant predation effect sizes and 15 replicates of each caterpillar species per plant species for parasitism. These minimum sample size requirements excluded all samples from *B. lenta* plants and restricted the number of caterpillar–plant species combinations to 39–59, depending on the analysis (Appendix S1: Table S2). For each caterpillar–plant species combination, the rearing records from the 2004–2007 observational study, unbagged experimental branches from the 2008–2019 predator exclusion experiments, and caterpillars opportunistically collected from nonexperimental branches were combined. The parasitism dataset we analyzed was summed in the same manner as described in the previous section.

Estimating predation risk

We used the log response ratio (LRR; Hedges et al., 1999) to calculate effect sizes of predation (predation risk) because this method is especially useful for comparing and combining datasets using similar treatments or projects spanning multiple years with changes in design (Lajeunesse, 2015). We calculated LRR as the log of the ratio of caterpillar density in predator-exclusion treatments relative to controls across experimental branches for each caterpillar–plant species combination (Appendix S1: Section S1). We calculated LRR variance as the SD of the predation effect for each caterpillar–plant species combination in each experimental treatment. The inverse of the variance was used as a weight in most of our models so that caterpillar and host–plant species combinations with high variance (either due to low sample sizes or large SDs) received lower weights in the model. We also employed a bias correction of LRRs and variance described in Lajeunesse (2015) to further account for low sample sizes. These bias-corrected LRRs were calculated for both bird and ant predation and used as continuous predictor variables in generalized linear models.

Statistical models

Interference hypothesis

All analyses were performed in R, version 4.0.2 (R Core Team, 2020). To test the interference hypothesis, we modeled the probability of parasitism (ratio of parasitized to unparasitized caterpillars) as a function of predator-exclusion treatment along with the independent variables of caterpillar species and host–plant species as fixed effects using generalized linear models in the *stats* package using a logit link function and assuming a quasibinomial error distribution. We included the fixed effects of caterpillar species and host–plant species to account for known sources of variation in the probability of parasitism (Farkas & Singer, 2013) and reduce noise in the model fitting process. All fixed effects were deemed necessary for addressing our hypotheses and predictions as specifically as possible. Models with additional terms (e.g., interaction term between treatment and host–plant species) were not selected because they represent exploratory departures from our inferential goal (sensu Tredennick et al., 2021). In addition, singularities in the data precluded some interaction terms (e.g., treatment × caterpillar species × host–plant species). Because taxonomic variation in caterpillar and plant species was limited in this dataset (e.g., few taxonomic families), we chose not to include higher taxonomic variation as additional terms in the models. We used separate models to test for effects of bird and ant exclusion because predator-exclusion experiments were not consistently fully factorial. We also used separate models for total parasitism, hymenopteran parasitism, and tachinid parasitism, giving a total of six models (Table 1).

Enemy complementarity hypothesis

All analyses were performed in R, version 4.1.3 (R Core Team, 2022). To test the predictions of the enemy complementarity hypothesis, we used the same model structure as described above, with predation risk (LRR) replacing predator-exclusion treatment as the fixed effect of interest for hypothesis testing. We used nine models with different permutations of parasitoid and predator type(s) (Table 2; Appendix S1: Section S1, Figure S1). The three additional Models 7–9 in these analyses included two LRR terms (bird predation risk, ant predation risk). Models containing both bird and ant predation risks were included to see whether accounting for predation effects of both predator taxa mattered. Models 1–6 were weighted by the inverse variance for the given risk of predation included as a predictor variable. The models with both bird and ant predation risks as predictor variables (Models 7–9) were weighted by the inverse of the sum of variance for both bird and ant predation risks. Additional predictor terms included fixed effects of caterpillar species and host–plant species, which

TABLE 1 Regression results for models that follow the general equation of: Probability of parasitism ~ Exclusion_treatment + fixed effects.

Predictor	Response	*N*	Adj-R^2	Odds ratio (95% CI)	*p*-value
Bird exclusion	All	33	0.679	0.945 (0.702–1.277)	0.714
	Tachinid	33	0.652	1.094 (0.761–1.583)	0.632
	Hymenopteran	33	0.689	0.819 (0.551–1.224)	0.331
Ant exclusion	All	21	0.686	0.422 (0.221–0.762)	0.012
	Tachinid	21	0.630	0.761 (0.429–1.301)	0.347
	Hymenopteran	21	0.802	0.123 (0.019–0.454)	0.015

Abbreviations: Adj-R^2, adjusted-R^2 values; *N*, sample size of caterpillar–plant species combinations.

TABLE 2 Regression results for models 1–9 that follow the general equation of: Probability of parasitism ~ $\text{LRR}_{\text{birds}}$ + LRR_{ants} + fixed effects.

Predator	Model	Response	*N*	Adj-R^2	Predictor	Odds ratio (95% CI)	*p*-value
Birds	1	All	52	0.970	$\text{LRR}_{\text{birds}}$	0.794 (0.570–1.117)	0.190
	2	Tachinid	52	0.962	$\text{LRR}_{\text{birds}}$	0.487 (0.209–1.129)	0.101
	3	Hymenopteran	52	0.910	$\text{LRR}_{\text{birds}}$	0.666 (0.463–0.972)	0.042
Ants	4	All	46	0.974	LRR_{ants}	1.275 (0.576–2.931)	0.564
	5	Tachinid	46	0.971	LRR_{ants}	3.588 (0.713–19.461)	0.145
	6	Hymenopteran	46	0.923	LRR_{ants}	0.849 (0.384–1.941)	0.696
Both	7	All	39	0.985	$\text{LRR}_{\text{birds}}$	0.645 (0.380–1.108)	0.130
					LRR_{ants}	1.530 (0.742–3.225)	0.274
	8	Tachinid	39	0.987	$\text{LRR}_{\text{birds}}$	0.213 (0.114–0.396)	0.000
					LRR_{ants}	3.664 (1.604–8.678)	0.009
	9	Hymenopteran	39	0.940	$\text{LRR}_{\text{birds}}$	0.752 (0.446–1.281)	0.307
					LRR_{ants}	1.008 (0.489–2.107)	0.982

Abbreviations: Adj-R^2, adjusted-R^2 values; LRR, log response ratio; *N*, sample size of caterpillar–plant species combinations.

accounted for known sources of variation in the probability of parasitism (Farkas & Singer, 2013) and reduced noise in the model fitting process. To build models that specifically addressed our hypotheses and predictions, we elected not to include additional terms (e.g., year, site), interaction terms, or higher taxonomic variation (limited in this dataset), and not to use hierarchical models. An analysis of deviance was performed on all models to show the reduction in residual deviance provided by each predictor term in the model. This method compares the contribution of each predictor variable to the model fit by comparing the reduction in residual deviance provided by each predictor term (Nelder & Wedderburn, 1972) and has been used in prior multi-factor analyses of parasitism (e.g., Hawkins et al., 1997). Reduction in residual deviance values is reported instead of model coefficients for the fixed effects of caterpillar species and host–plant species (Appendix S1: Table S3).

RESULTS

Interference hypothesis

In our interference dataset consisting of 2825 reared caterpillars, 11% were parasitized (4.7% by tachinids, 5.8% by hymenopterans, and 0.57% by unidentified parasitoids). Bird exclusion had negligible effects on parasitism rates from all parasitoids combined (odds ratio $\beta = 0.945$, 95% CI $= 0.702$–1.277, $p = 0.714$), hymenopterans only (*odds ratio* $\beta = 0.819$, 95% CI $= 0.551$–1.224, $p = 0.331$), or tachinids only (odds ratio $\beta = 1.094$, 95% CI $= 0.761$–1.583, $p = 0.631$) (Figure 2, Table 1). In contrast, excluding ants reduced the odds of parasitism by all parasitoids by 58% (odds ratio $\beta = 0.422$, 95% CI $= 0.221$–0.762, $p = 0.012$) and by hymenopterans specifically by 88% (odds ratio $\beta = 0.123$, 95% CI $= 0.019$–0.454, $p = 0.015$), but did not affect the odds of parasitism by tachinids (odds ratio

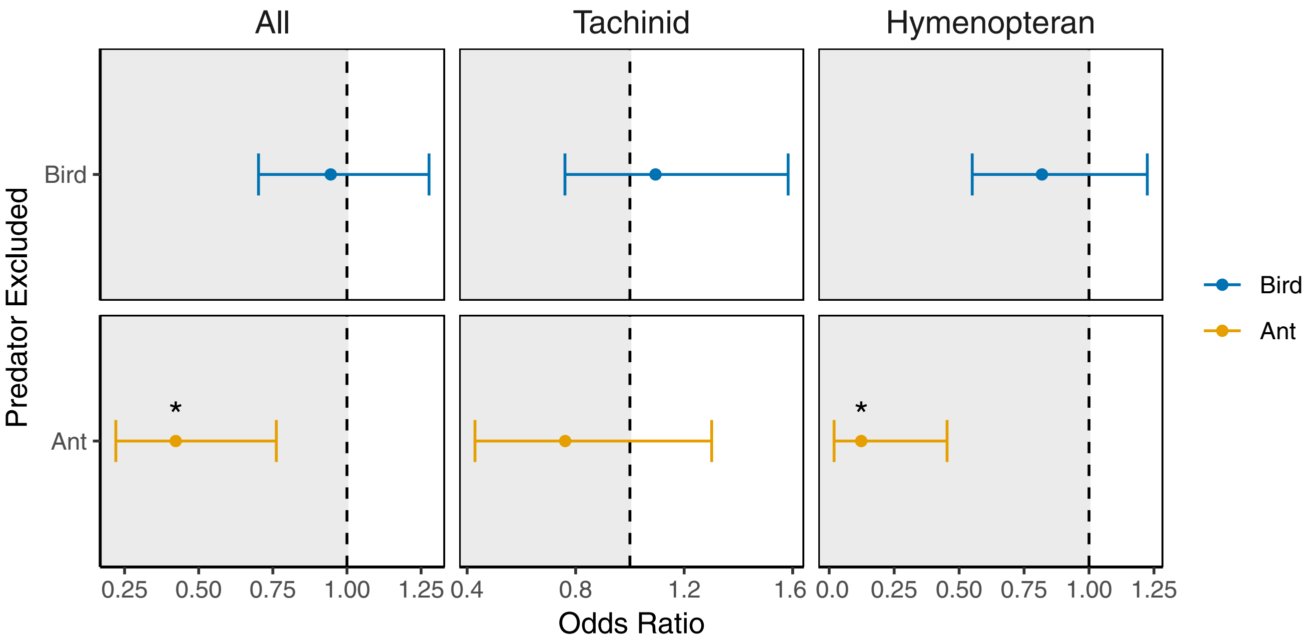

FIGURE 2 Regression results testing the interference hypothesis. Models follow the general equation of: Probability of parasitism ~ predator exclusion treatment + fixed effects. In headings, All, Tachinid, and Hymenopteran refer to the likelihood of parasitism by all parasitoids, tachinid flies, and hymenopterans parasitoids, respectively. Values less than an odds ratio of 1 (to the left of the dashed lines, with gray background) indicate that the probability of parasitism is reduced when predators are excluded, while values greater than 1 (to the right of the dashed lines, with white background) indicate that the probability of parasitism is increased when predators are excluded. Points correspond to the odds ratios estimated from the models, and error bars correspond to the 95% CIs. Blue, ant exclusion; orange, bird exclusion. Asterisks indicate significance: $^*p < 0.05$.

$\beta = 0.761$, 95% CI = −0.429 to 1.301, $p = 0.347$) (Figure 2, Table 1). Interestingly, the reduction in parasitism rates of caterpillars in the ant exclusion treatment contradicts the pattern predicted by the interference hypothesis.

Enemy complementarity hypothesis

In our enemy complementarity dataset, there were 4629 reared caterpillars with 15.5% of these caterpillars being parasitized (5.62% by tachinids, 8.19% by hymenopterans, 1.69% by unidentified parasitoids). There was evidence for enemy complementarity between parasitoids and birds. Bird predation risk alone predicted reduced probability of parasitism in Models 1–3 (Figure 3, Table 2). The negative effect of bird predation risk on total parasitism was weak (Model 1: odds ratio $\beta = 0.794$, 95% CI = 0.570–1.117, $p = 0.190$) relative to models in which hymenopteran and tachinid parasitoids were considered separately. For each unit increase in LRR birds, the odds of parasitism by hymenopterans decreased by 34% (Model 3: odds ratio $\beta = 0.666$, 95% CI = 0.463–0.972, $p = 0.042$). This effect was even stronger for tachinid parasitism: For each unit increase in LRR birds, the odds of parasitism by tachinids decreased by 51% (Model 2: odds ratio $\beta = 0.487$, 95% CI = 0.209–1.129, $p = 0.101$). For all three models, bird predation risk reduced residual deviance, indicating a meaningful biological effect (Appendix S1: Table S3). The fixed effects of host–plant species and caterpillar species reduced deviance by roughly 10–20 times as much (Appendix S1: Table S3).

In contrast to bird predation, there was no evidence for enemy complementarity between parasitoids and ants in these models (Figure 3, Table 2). In Models 4 and 6, ant predation risk did not predict total parasitism (Model 4: odds ratio $\beta = 1.275$, 95% CI = 0.576–2.931, $p = 0.564$) or hymenopteran parasitism (Model 6: odds ratio $\beta = 0.849$, 95% CI = 0.384–1.941, $p = 0.696$). In Model 5, ant predation risk was positively associated with tachinid parasitism (Model 5: odds ratio $\beta = 3.588$, 95% CI = 0.713–19.461, $p = 0.145$). In all three models, the risk of ant predation reduced deviance slightly with the most, albeit marginal, explanatory power when total parasitism was the response variable (Model 4; Appendix S1: Table S3). By contrast, caterpillar species and host–plant species strongly reduced residual deviance in these three models (Appendix S1: Table S3).

The models using both bird predation risk and ant predation risk as independent predictors (Models 7–9; Figure 3, Table 2) showed the strongest evidence of

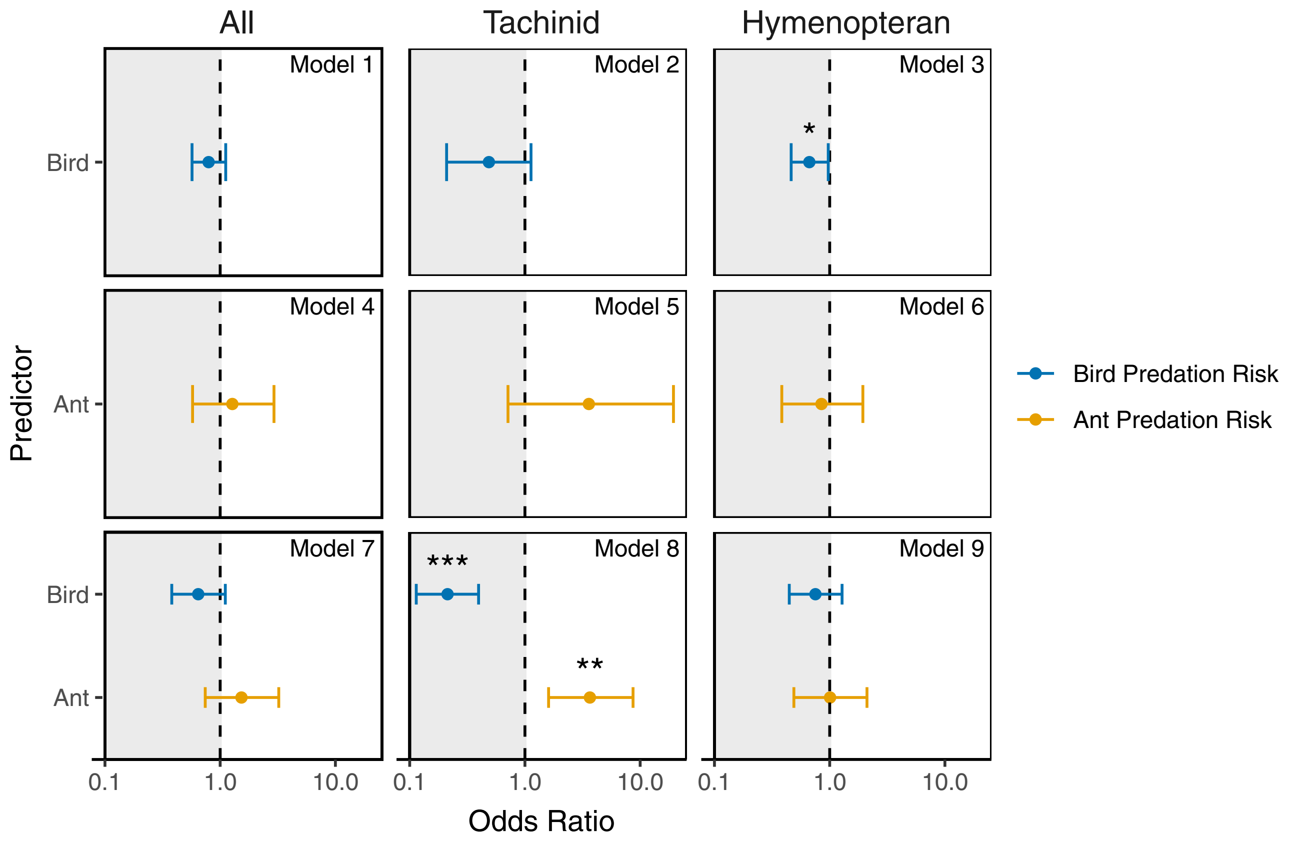

FIGURE 3 Regression results testing the enemy complementarity hypothesis. Models 1–9 follow the general equation of: Probability of parasitism ~ $\mathrm{LRR}_{\mathrm{birds}} + \mathrm{LRR}_{\mathrm{ants}}$ + fixed effects. In Models 1, 4, and 7, the response is probability of parasitism by all parasitoids; in Models 2, 5, and 8, the response is probability of parasitism by tachinid flies; and in Models 3, 6, and 9, the response is probability of parasitism by hymenopterans. Models 1–3 have only $\mathrm{LRR}_{\mathrm{birds}}$ + fixed effects, Models 4–6 have only $\mathrm{LRR}_{\mathrm{ants}}$, and Models 7–9 include $\mathrm{LRR}_{\mathrm{birds}} + \mathrm{LRR}_{\mathrm{ants}}$. Points correspond to the odds ratios estimated from the models, and error bars correspond to the 95% CIs. Values less than odds ratio of 1 (to the left of the dashed lines, with gray background) indicate that parasitism decreases with increased predation risk, while values greater than 1 (to the right of the dashed lines, with white background) indicate that parasitism increases with increased predation risk. Note the x-axis is on a log scale for clearer data visibility. Blue, bird predation risk; orange, ant predation risk. LRR, log response ratio. Asterisks indicate significance: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

complementarity, in this case between tachinid parasitoids and birds. The probability of tachinid parasitism (Model 8) was strongly negatively associated with the risk of bird predation: A unit increase in bird predation (LRR) decreased the odds of tachinid parasitism by 77% (odds ratio $\beta = 0.213$, 95% CI = 0.114–0.396, $p < 0.001$); tachinid parasitism was also strongly positively associated with the risk of ant predation: A unit increase in ant predation (LRR) increased the odds of tachinid parasitism by 271% (odds ratio $\beta = 3.664$, 95% CI = 1.604–8.678, $p = 0.009$). Total parasitism (Model 7) showed the same trends, but these effects were weaker: risk of bird predation (odds ratio $\beta = 0.645$, 95% CI = 0.380–1.108, $p = 0.130$) and risk of ant predation (odds ratio $\beta = 1.530$, 95% CI = 0.742–3.225, $p = 0.274$). Hymenopteran parasitism (Model 9) echoed this trend for bird predation risk (odds ratio $\beta = 0.752$, 95% CI = 0.446–1.281, $p = 0.307$), but was not affected by ant predation risk (odds ratio $\beta = 1.008$, 95% CI = 0.489–2.107, $p = 0.982$). For all three models, both bird and ant predation risks reduced residual deviance, indicating meaningful biological effects (Appendix S1: Table S3). The fixed effects of host–plant and caterpillar species further reduced deviance by multiple orders of magnitude (Appendix S1: Table S3).

DISCUSSION

Enemy complementarity from a tri-trophic perspective

Our results support the enemy complementarity hypothesis because as bird predation risk increased, parasitism rates for hymenopteran and tachinid parasitoids decreased across different caterpillar–plant species combinations. This negative association indicates that birds and parasitoids primarily use different and complementary components of caterpillar niche space. By contrast, we found no interference effects of intraguild predation, as predator-exposure did not reduce parasitism rates of caterpillars relative to predator-exclusion. Some previous work identified possible cases of reduced parasitism of insects subjected to high bird predation risk, and these instances were interpreted as preferential bird predation of unparasitized prey (Otvos, 1979). However, our study discounts this interpretation, showing no avian selectivity for or against parasitized caterpillars. Interestingly, we did find possible evidence of preferential ant predation of unparasitized prey (higher parasitism rates of caterpillars exposed to ants), but there are several alternative interpretations of this result (discussed below).

Because enemy complementarity is consequential for predation efficiency (Snyder, 2019), it is important to understand its mechanisms. Prior work demonstrating complementarity by enemies of herbivores has rarely considered tri-trophic mechanisms of resource partitioning (e.g., Cardinale et al., 2003; Finke & Snyder, 2008; Gontijo et al., 2015). In the community studied here, the top-down complementarity between parasitoids and birds (this study) and between ants and birds (Singer et al., 2017) reveals the importance of tri-trophic mechanisms. That is, host–plant identity (this study) and host–plant range (Singer et al., 2017) partly predict the susceptibility of various caterpillar species to alternative enemy types. In the present study, the negative relationship between parasitism rate and bird predation risk encompasses both caterpillar species identity and plant species identity because the unit of variation in analyses is a caterpillar–plant species combination. For example, caterpillars of *Achatia distincta* experienced low parasitism in conjunction with high bird predation on the tree species *H. virginiana* (parasitism rate = 11.8%, bird LRR = 0.70) and *Q. alba* (parasitism rate = 6%, bird LRR = 1.13) and high parasitism in conjunction with low bird predation on *Carya* spp. (parasitism rate = 27.9%, bird LRR = −0.16). This tri-trophic complexity in patterns of complementarity between parasitoids and avian predators obscures the pattern from a bi-trophic perspective, highlighting the new insight offered by the tri-trophic and comparative perspective of this study. Such observations can guide additional work addressing how plant, herbivore, and predator traits mediate multiple enemy effects (Abdala-Roberts et al., 2019). The ecological consequences of this tri-trophic enemy complementarity, such as implications for herbivore population dynamics and community assembly, also merit further study.

Complementarity due to parasitoid avoidance of intraguild predation

Our results support our three corollary predictions, implicating parasitoid avoidance of intraguild predation (i.e., acquisition of enemy-reduced space) as the process responsible for the complementarity between parasitoids and avian predators. The first and most informative prediction was borne out by our finding that parasitism rates of caterpillars were negatively associated with bird predation risk across various combinations of caterpillar species and host–plant species even when caterpillar species and host–plant species were each included as independent predictors of parasitism rate. The inclusion of caterpillar species and host–plant species as fixed effects in these models accounts for traits of caterpillars and host plants known from previous work to influence parasitism rates, such as herbivore feeding niche, herbivore defensive traits, host–plant chemistry, and host–plant identity (e.g., Baer & Marquis, 2020; Farkas & Singer, 2013; Gentry & Dyer, 2002; Hawkins, 1994; Hrcek et al., 2013; Lill et al., 2002; Murphy et al., 2014; Stireman & Singer, 2003). As such, the explanatory effects of caterpillar species and plant species were understandably large in our models. Statistically accounting for these effects demonstrated that bird predation risk specifically predicts variation in parasitism rate in the direction expected if host selection by parasitoids is under selection from intraguild predation. This unique evidence enables stronger inferences than that adduced by prior community-level studies, which offered less direct evidence for parasitoid avoidance of intraguild predation (e.g., Baer & Marquis, 2020; Dyer & Gentry, 1999; Gentry & Dyer, 2002; Murphy et al., 2014; Stireman & Singer, 2003).

Our second prediction found support in the contrast between bird and ant predation risks as predictors of parasitism rates. That ant predation risk did not predict parasitism in most enemy complementarity models is consistent with previous findings of the relatively weak predatory effects of ants on caterpillars in mid- and high-latitude forests (Roslin et al., 2017) and in this community specifically (Singer et al., 2017). In short, this evidence is consistent with the expectation that host use by parasitoids is under selection from the strongest source of intraguild predation—avian predation in this case.

The stronger effect size of the negative association between bird predation and parasitism for tachinid versus hymenopteran parasitoids matched our third prediction. The timing of parasitoid wasp and fly oviposition typically differs in relation to bird predation of their caterpillar hosts. Because they tend to attack early instar caterpillars (Godfray, 1994; Shaw, 2006), parasitoid wasps are likely to oviposit before caterpillars are subjected to the strongest degree of bird predation, which targets larger, mid-, and late-instar caterpillars (Remmel et al., 2011; Singer et al., 2017). However, because tachinids frequently parasitize middle- and late-instar caterpillars (Stireman et al., 2006), tachinid larvae are subjected to increased bird predation. In addition, strong bird predation may reduce the abundance of caterpillars that are available to the adult female tachinid parasitoids prior to oviposition. If such exploitation competition from birds were selecting on tachinid host use, our evidence suggests it was acting in combination with selection imposed by intraguild predation. Alternative factors might also account for the weaker negative association between bird predation and wasp parasitism. It is possible that individual caterpillars parasitized by wasps experienced reduced bird predation risk compared with unparasitized individuals of the same caterpillar species on the same host–plant species. These individual differences could occur because some parasitoid wasp larvae reduce intraguild predation via modification of host behavior (Brodeur & Vet, 1994; Fritz, 1982; Grosman et al., 2008; Harvey et al., 2008; Murphy et al., 2014). For example, *Glyptapanteles* wasps can manipulate *Thyrinteina leucocerae* caterpillars to thrash the anterior part of their bodies when encountered by predatory stinkbugs (Grosman et al., 2008). However, parasitoid manipulation of host behavior as a defense against bird predation, while untested, seems unlikely in our system because behavioral defenses of caterpillars are ineffective against bird predation (Lichter-Marck et al., 2015).

Two unexpected results of parasitism in relation to ant predation offer more speculative support for the hypothesis that parasitoids avoid intraguild predation. First, our tests of predator–parasitoid interference showed increased wasp parasitism of caterpillars exposed to ants. This pattern might have resulted from ants selectively consuming unparasitized caterpillars, although our prior work on ant predation of caterpillars in this community suggests that ant predation on suitable caterpillar prey is more opportunistic than selective (Singer et al., 2019). Another possibility is that wasp-parasitized caterpillars avoided ant predation better than their unparasitized counterparts, perhaps through host manipulation. Alternatively, parasitoid wasps might have preferentially parasitized their caterpillar hosts in the presence of ants, as shown for *Lysiphlebus* wasps which preferentially attack ant-tended aphid hosts over untended hosts (Völkl, 1992, 1994). This behavior enables *Lysiphlebus* wasps to avoid intraguild predators, which attack their aphid hosts more frequently without ant-tending (Völkl, 1992, 1994). While the caterpillar hosts in our study are not myrmecophilous, it is possible that ants provide a net benefit to parasitoid wasps of caterpillars as follows. Ants might reduce intraguild predation by other predators (e.g., spiders, pentatomids, reduviids) to a greater degree than ants cause intraguild predation, as ant predation on caterpillars is relatively weak in this community (Singer et al., 2017). Even if adult parasitoid wasps show no preference for caterpillar hosts in the presence of ants, the reduced wasp parasitism of caterpillars in ant exclusion treatments could reflect increased intraguild predation from non-ant predators. The second unexpected result is a positive association between tachinid parasitism and ant predation risk despite a lack of interference between ants and tachinids. Tachinid parasitoids might avoid ant predation by attacking later instar hosts of caterpillar–plant species combinations most susceptible to ant predation as early instars.

Evolutionary ecology perspective on multiple enemy effects

Consideration of enemy-reduced space acquired by parasitoids, and possibly by other predators, offers an evolutionary ecology perspective often missing from analyses of the trophic dynamics predicted by multiple enemy effects (e.g., Chang & Cardinale, 2020; Letourneau et al., 2009; Schmitz, 2007; Vance-Chalcraft et al., 2007). Applying this hypothesis more broadly, we posit that avoidance of intraguild predation by small predators could explain some enigmatic top-down trophic patterns. For example, this hypothesis might explain why terrestrial food webs involving what appear to be four trophic levels (vertebrate predators, arthropod mesopredators, insect herbivores, and plants) show trophic cascades expected from tri-trophic systems (e.g., Mäntylä et al., 2011; Mooney et al., 2010) despite intraguild predation by omnivorous vertebrate predators on arthropod mesopredators (Mooney et al., 2010). Enigmatically, intraguild predation strength and trophic cascade strength were positively correlated across studies (Mooney et al., 2010). Our hypothesis explains this pattern by predicting stronger selection for small predators to avoid intraguild predation in communities with stronger vertebrate predation on arthropods. If true, the strength of top-down effects by vertebrates and the abundance of arthropod predators (relative to herbivores) would be expected to be positively correlated. This pattern was also observed by Mooney et al. (2010), who noted its inconsistency with intraguild predation theory based on the population dynamics of predation and competition alone (Holt & Polis, 1997). The acquisition of enemy-reduced space by small predators subjected to high intraguild predation risk, such as the parasitoids of caterpillars, may be an underappreciated facilitator of top-down suppression of herbivores at a community level. In essence, selection for the avoidance of intraguild predation may stabilize arthropod predator populations as well as foster complementarity by multiple enemy types despite some degree of competition and intraguild predation.

AUTHOR CONTRIBUTIONS

Michael S. Singer conceived the study. Kailen A. Mooney, and Michael S. Singer designed the experiments. Andrew B. Hennessy, Riley M. Anderson, and Michael S. Singer collected the data. Andrew B. Hennessy, Riley M. Anderson, Nora Mitchell, and Michael S. Singer analyzed the data. Andrew B. Hennessy and Michael S. Singer wrote the first draft of the manuscript. all authors contributed to editing and revising the text.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Riley Anderson, 2023) are archived in Zenodo at https://doi.org/10.5281/zenodo.8360878.

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SUPPORTING INFORMATION

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

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