

Trait-mediated trophic cascade creates enemy-free space for nesting hummingbirds

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The indirect effects of predators on nonadjacent trophic levels, mediated through traits of intervening species, are collectively known as trait-mediated trophic cascades. Although birds are important predators in terrestrial ecosystems, clear examples of trait-mediated indirect effects involving bird predators have almost never been documented. Such indirect effects are important for structuring ecological communities and are likely to be negatively impacted by habitat fragmentation, climate change, and other factors that reduce abundance of top predators. We demonstrate that hummingbirds in Arizona realize increased breeding success when nesting in association with hawks. An enemy-free nesting space is created when jays, an important source of mortality for hummingbird nests, alter their foraging behavior in the presence of their hawk predators.

INTRODUCTION

A “trait-mediated trophic cascade” can be triggered when apex predators cause changes in mesopredators’ behavior or other traits, with subsequent effects on lower trophic levels. The magnitude of such cascades has likely decreased in response to declines in top predator densities because of global change, yet the nature of these indirect effects has not been characterized for most terrestrial food chains (1, 2). Furthermore, rigorous empirical studies of trait-mediated cascades for any community are enhanced by life history data for the focal species involved in trophic interactions. Traits that mediate cascades should include predator avoidance or adaptations, including behavioral, physiological, and anatomical characteristics that enhance fitness (3).

The link between trait-mediated cascades and the evolution of life history parameters is not clear because of a lack of empirical data (4), and although studies have shown that nesting birds are extremely sensitive to the presence of predators (5, 6), there are few solid links between such studies and theoretical approaches to understanding trait-mediated indirect effects (1, 7, 8). Predation, however, is a major ecological force relevant to life history traits of most animals and is a principal factor limiting nesting success and shaping spatial distributions of breeding birds (9–17). The selection of safe breeding sites is an important behavioral parameter in conceptual and quantitative models of avian trophic ecology (18); breeding birds are expected to choose nest sites that reduce exposure to predators. One such strategy involves nesting in association with more aggressive or larger predatory birds (table S1) (19, 20). Black-chinned hummingbird nests (*Archilochus alexandri*, hereafter hummingbirds) in Arizona are clustered around northern goshawk and Cooper’s hawk nests (*Accipiter gentilis* and *Accipiter cooperii*, hereafter hawks), and their nests have greater success when built closer to active hawk nests (21). We explain this association by demonstrating that the presence of active hawk nests alters the foraging

behavior of a well-documented prey species for these hawks and a locally abundant nest predator (eight of eight directly observed hummingbird nest predations were by jays), the Mexican jay (*Amphelocoma wollweberi*, hereafter jays) (Fig. 1), creating enemy-free nesting habitat for hummingbirds in the vicinity of hawk nests (Fig. 2 and fig. S1).

During three nesting seasons, we documented spatial patterns of nest placement and DSRs of hummingbird nests in relation to the location and status (active/inactive) of 12 hawk nests. We also documented the three-dimensional (3D) foraging patterns of jays in relation to hawk nests. Natural interannual shifts in nest placement by hawks, as well as predator-induced failure of hawk nests, provided a mensurative experimental test of the effects of hawk nests on both the placement and success of hummingbird nests, as well as the foraging movements of jays.

HUMMINGBIRD NEST LOCATION AND SUCCESS IN RELATION TO HAWKS

Our study of 342 hummingbird nests revealed two strong patterns: hummingbirds prefer to nest in association with hawk nests and realize greater reproductive success when the associated nest is occupied by a hawk. Only 20% of hummingbird nests were built in plots without active hawk nests, and nearest-neighbor analyses indicate a clumped distribution ($R = 0.21 \pm 0.003$) of hummingbird nests with significant spatial clustering around hawk nests within uniformly acceptable nesting habitat in each plot. Hummingbird nests built anywhere within study plots with active hawk nests had higher DSRs and predicted success (PPS) than those in plots with inactive hawk nests (0.9698 versus 0.9296 DSR; 31% versus 6% PPS, $n = 274/68$; Bayesian 95% credibility intervals for DSR differences do not cross zero). The importance of hawk presence to hummingbird success was further illustrated in 2008 when four active hawk nests were destroyed by predators. When the DSR of hummingbird nests in the four plots before hawk nest failure was compared with that of hummingbird nests during the 2 weeks immediately after failure of the hawk nests, the survival of hummingbird nests (data from all four failed plots pooled) dropped to almost zero (0.9703 versus 0.9153 DSR; 32% versus 3% PPS, $n = 102/75$; Bayesian 95% credibility intervals for DSR differences do not cross zero).

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Fig. 1. Video-grab of a Mexican Jay removing the eggs from the nest (middle-lower right) of black-chinned hummingbird.

FORAGING PATTERNS OF JAYS IN RELATION TO HAWKS

The foraging height of jays was not associated with the location of hawk nests in plots with inactive nests, but jays foraged higher above the ground when closer to active hawk nests [analysis of covariance (ANCOVA), distance by raptor activity interaction, $F_{1, 341} = 36.4$; $P < 0.0001$; Fig. 3]. This behavioral shift in the presence of hawks creates a roughly cone-shaped space around active hawk nests, within which jays are infrequently detected (Fig. 2). The shape of this enemy-free space is due to the fact that jays are much safer from the hawks when they are at least as high above ground as the hawks, which hunt from perches within the canopy in horizontal or descending chases. An interannual comparison of jay foraging heights in seven plots (two reoccupied, four not reoccupied, and one occupied for the first time in 2009) demonstrated the effect of hawk presence on the spatial foraging habits of jays (Fig. 3).

HUMMINGBIRD SUCCESS IN RELATION TO HAWKS AND JAYS

A path analysis (Fig. 4), testing causal relationships between hawk presence, jay foraging, and hummingbird nest survival, supported two mechanisms responsible for this relationship: increase in jay foraging height near active hawk nests and affinity of hummingbirds for hawk nest sites. The indirect negative effects of hawks on jay foraging heights via decreased hummingbird nest dispersion (the path coefficient for this indirect effect is -0.021) were too weak to diminish the direct effects (0.37 path coefficient). This direct effect of hawks on jay foraging is very large in comparison to other trophic interaction effect sizes, and other effect sizes reported here are greater than or similar to most effect sizes reported in studies of trait-mediated indirect effects [for example, (22), also reviewed by (23)]. In this case, more than one-third of the variation in jay foraging is explained by raptor nest presence even when accounting for the effects of other relevant variables. Hummingbird nesting success in four plots where raptors did not return to nest showed the predicted interannual shift (0.9747 versus 0.9247 DSR; $P < 0.001$; 38% versus 5% PPS, $n = 73/35$). A comparison of hummingbird nesting success within the jay-free cone (Fig. 2 and fig. S1) versus nests associated with hawks (<300 m from active hawk nest) but outside the cone highlights the importance of nesting hawks to the reproductive success of hummingbirds (0.9827 versus 0.9577 DSR; $P < 0.001$; 52% versus 19% PPS, $n = 69/273$).

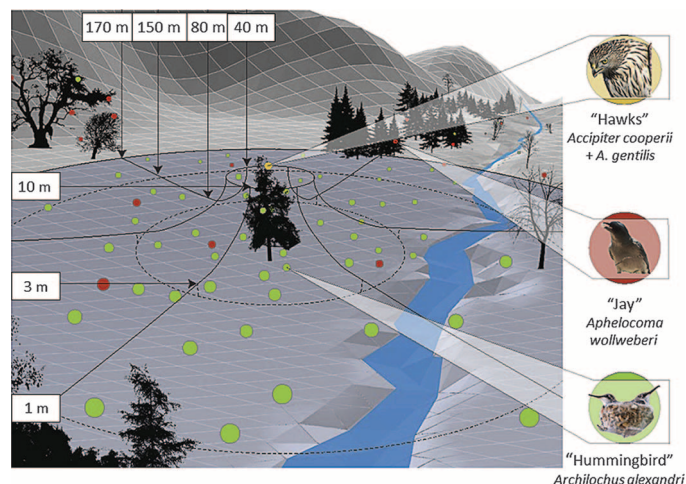


Fig. 2. Stylized graphical model of cone-shaped space surrounding active hawk nests, within which hummingbird nests had significantly higher survivorship. Data on the locations of jays in relation to each plot's hawk nest were pooled across plots and were used to generate the shape of the cone, using the lowest individual jays detected during the study and superimposed on a fictional landscape representative of the study area. Yellow, hawk nest; green, successful hummingbird nest; red, depredated hummingbird nest.

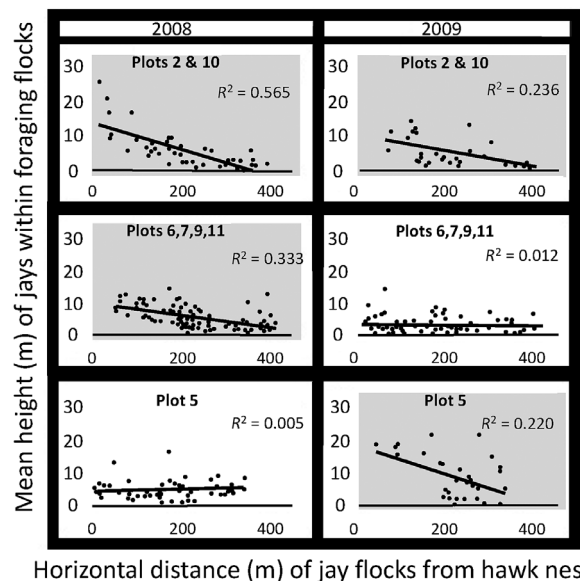


Fig. 3. Interannual comparisons of jay foraging patterns in study plots, illustrating the effect of raptor presence on the spatial distributions of foraging jays. Each point represents the mean height above the ground of individual jays within a single flock. Plots with active hawk nests are shaded gray. Upper panels show pooled data from two plots that were occupied in both years, middle panels represent four plots that were not reoccupied in 2009, and bottom panels show one plot occupied for the first time in 2009. ANCOVA with all plots and years combined revealed a significant interaction ($F_{1, 341} = 36.4$; $P < 0.0001$) between distance to a raptor nest and activity of the raptor (presence/absence). Plots that were unoccupied for the duration of the study are not illustrated.

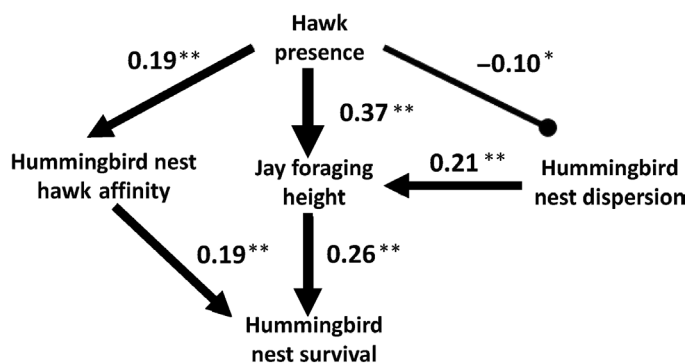


Fig. 4. Path analysis results (model fit $\chi^2 = 3.6$; $df = 4$; $P = 0.46$) for the proposed causal relationships between raptor presence, jay foraging height, and hummingbird responses. “Hawk affinity” was measured as distance to the hawk nest; “hummingbird dispersion” was a measure of dispersion determined using the nearest-neighbor value, R (larger values indicate less clumping); “hummingbird nest survival” was the daily survival rate (DSR). Arrows indicate positive causal relationships; the bullet-headed line indicates a negative causal relationship. Numbers next to lines are significant path coefficients ($*P < 0.05$, $**P < 0.001$). The path coefficient from hummingbird dispersion to survival was small (0.01) and not significant ($P > 0.6$); thus, the model fit was improved when it was excluded. An identical model using jay dispersion instead of hummingbird dispersion was a poor fit to the data (model significantly different from the data: $\chi^2 = 15.5$; $df = 4$; $P = 0.004$).

We conclude that the presence of hawks at their nests has an indirect effect on the survival of hummingbird nests mediated by predator avoidance shifts in jay foraging behavior. We cannot rule out a variety of other mechanisms contributing to these patterns, some of which could be very complex, but we did reject two other possibilities. The “bottom-up” hypothesis that spatial abundance and dispersion of hummingbird nests explain variation in hummingbird nest survival (DSR) was not supported by the path analysis (Fig. 4). A similar path analysis allowed us to reject the hypothesis that jay dispersion affects raptors and hummingbird nests via the jay anti-predator defense response of mobbing hawks, which may increase with greater clumping (mob size) (Fig. 4).

MATERIALS AND METHODS

The work was carried out at the Southwest Research Station (31°53'N, 109°12'W, 1600 m above sea level), west of Portal in the Chiricahua Mountains, Cochise County, in southeastern Arizona. Hummingbird nests were searched for, individually numbered, and monitored in 800 × 200-m plots in riparian zones centered on six hawk nests identified as being currently active and six that had been active during the 2 years before our study but were inactive during the first year of the study. Habitat in this area is relatively uniform, with dominant tree species being juniper (*Juniperus deppeana*; Cupressaceae), oak (*Quercus* spp.; Fagaceae), and sycamore (*Platanus wrightii*; Platanaceae), ranging in height from 5 to 30 m. Below this broken canopy, the understory is fairly open, because of grazing practices, but includes scattered saplings of the aforementioned species as well as several other types of small shrubs. All areas were systematically searched in standardized criss-crossing patterns to ensure unbiased detection of hummingbird nests. Hummingbird and hawk nests were mapped with a GPS (Global

Positioning System), and their heights above the ground, other nest placement data (figs. S2 and S3), and their UTM (Universal Transverse Mercator) coordinates were used to calculate spatial relationships. The status of hummingbird nests (active or failed) was checked every 2 to 3 days, and DSRs and 95% confidence intervals were calculated using standard methods developed by Mayfield (24) and Johnson (25). To predict overall fledging success from DSRs, we used a 38-day nesting cycle, from laying of the first egg to fledging of both young. PPS was calculated as DSR raised to the number of days in the nesting cycle, predicting how many nests will survive to fledging. Comparisons of DSR values between samples of hummingbird nests (for example, nests associated with active versus inactive raptor nests) were compared using hierarchical nested Bayesian models described below. Relationships between jay foraging heights, distance to a raptor nest, and activity of the raptor nest (presence/absence) were examined with ANCOVA.

A hierarchical Bayesian model was used to examine the difference in hummingbird nest success between the presence and the absence of raptors, with individual DSR values for hummingbird nests nested within raptor nests. The same approach was used to compare DSR values for nests before and after raptor nests were destroyed. Priors were set at 0.5 for DSR for both the presence and the absence of raptors, assuming no previous knowledge of differences in nest success. Bayesian analysis produces statistics that estimate the probability of the hypothesis given the data $[P(\text{hypothesis})|\text{data}]$ and incorporates prior parameter estimates to create posterior probability distributions. To estimate model parameters, we used the Markov chain Monte Carlo (MCMC) simulation, where each step in the chain estimates the difference between DSR values for raptor or no-raptor nests based on the previous data. We used a 2000-step burn-in period followed by the 10,000-step MCMC to generate the posterior density distribution for the differences in DSR between raptor presence and absence. We calculated posterior probabilities of the null hypothesis (no difference in DSR) by quantifying the frequency that the difference was equal to or greater than zero in each step of the post-burn-in MCMC. For example, if DSR is greater when raptor nests are present (P) versus absent (A) across 99% of the post-burn-in MCMC steps ($P - A > 0$), we can conclude that the probability of no difference in nest success in the presence versus absence of raptors is 0.01. Bayesian analyses were performed in SAS v.9.4 using PROC GENMOD. For all raptor nests across years, the raptor presence minus absence DSR ($P - A$) 95% HPD (highest posterior density) was calculated as 0.11 to 0.27, indicating that the probability of no difference was far less than 5%. For the 2008 nests that were destroyed, $P - A$ 95% HPD values were 0.005 to 0.26, indicating that the probability of no difference was just less than 5%.

Jay foraging and description of enemy-free space

The location of jay flocks was marked with a GPS as described above. At the time of first detection of the flock, the height above the ground of all visible individuals was recorded. These foraging height measurements were used to calculate a mean foraging height for each flock (Fig. 3). Jay flocks were replotted every 15 min if they remained within the plot area. The jay-free cone in each plot with an active hawk nest was conservatively defined by the location of the lowest individual jays and closest (to the hawk nest) detected during the study. Similarly, the composite description of the enemy-free space around hawk nests was described by pooling the lowest and

closest jay sightings across all plots. Locations of all foraging jay flocks associated with an active raptor nest were used to graphically summarize the cone-shaped areas of enemy-free space with 3D mesh plots of three representative plots (fig. S1). The package “conproj” in R was used to assess the least-square fit of the nests to a cone shape, using a quadratic programming routine.

Dispersion of hummingbird nests

To categorize the distribution of hummingbird nests as clumped (versus random or hyperdispersed), we used nearest-neighbor analysis (26), with R values significantly less than 1, indicating a clumped distribution and variance calculated on the basis of year-to-year variation.

Analysis of direct and indirect effects of hawks on hummingbird nest survival

To examine the indirect effects of raptor presence or absence on hummingbird nest survival via hummingbird nest proximity to hawks, hummingbird nest dispersion, and jay foraging height, we used path analysis to test a previously hypothesized structure equation model (27). Path coefficients for direct effects were obtained from the structural equation model, whereas indirect effects were calculated as the product of direct effects in any given pathway. For our a priori specified structural equation model, we identified causal relationships to formulate a simple set of paths with one exogenous variable (hawk presence) predicting four endogenous variables (Fig. 4); no latent variables were used. Specifically, on the basis of literature (1–3, 5, 6, 9–19) and natural history, hawk presence was hypothesized to directly cause clumping of hummingbird nests around the nest (hawk affinity, measured as distance to the nest) and also cause increased clumping among nests (hummingbird dispersion, measured as the nearest-neighbor value, R) and an increase in mean height of jay foraging. Both hawk affinity and jay foraging height directly cause an increase in hummingbird nest survival (DSR). In addition, local clumping of hummingbird nests, closer to hawk nests, was hypothesized to decrease jay foraging height, despite increased risk from raptors. We tested the fit of this model using SAS protocols and selected the formulation of the reticular action model to define models. Starting values for the parameter estimates were determined by using a combination of three methods: observed moments of variables, the McDonald method, and two-stage least squares. The estimation method for the model was maximum likelihood, and the Levenberg-Marquardt algorithm was used to iterate solutions for optimization. The χ^2 for the absolute index was used to assess the fit of the model, with $P > 0.1$ (with 4 df) as an indication of a good fit to the data. Residuals met assumptions for multiple regression.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/1/8/e1500310/DC1>

Methods and Analyses

Fig. S1. Cone-shaped enemy-free space surrounding three representative active hawk nests.
Fig. S2. Photo of a hummingbird nest in situ showing variables measured to quantify nest microsite selection.

Fig. S3. Diagrammatic illustration of variables measured at each hummingbird nest to quantify nest site selection within the substrate tree.

Table S1. A review of the literature on protective nesting associations in birds indicating the species involved (if known) and the hypothesized mechanism by which the protected species benefits.

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Trait-mediated trophic cascade creates enemy-free space for nesting hummingbirds

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