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Too risky to settle: avian community structure changes in response to perceived predation risk on adults and offspring

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Predation risk is widely hypothesized as an important force structuring communities, but this potential force is rarely tested experimentally, particularly in terrestrial vertebrate communities. How animals respond to predation risk is generally considered predictable from species life-history and natural-history traits, but rigorous tests of these predictions remain scarce. We report on a large-scale playback experiment with a forest bird community that addresses two questions: (i) does perceived predation risk shape the richness and composition of a breeding bird community? And (ii) can species life-history and natural-history traits predict prey community responses to different types of predation risk? On 9 ha plots, we manipulated cues of three avian predators that preferentially prey on either adult birds or offspring, or both, throughout the breeding season. We found that increased perception of predation risk led to generally negative responses in the abundance, occurrence and/or detection probability of most prey species, which in turn reduced the species richness and shifted the composition of the breeding bird community. Species-level responses were largely predicted from the key natural-history trait of body size, but we did not find support for the life-history theory prediction of the relationship between species' slow/fast life-history strategy and their response to predation risk.

1. Introduction

Understanding factors determining community structure has long been a focus of ecology. Predation risk was proposed in early theoretical models as one critical force driving the patterns and dynamics of animal communities [1,2], and its role has subsequently been supported in a variety of ecological systems. Most empirical tests, however, have focused on aquatic systems and, to a lesser extent, terrestrial invertebrate systems (earlier studies reviewed in [3]). Tests of whether predation risk can structure terrestrial vertebrate communities remain scarce: there are relatively few observational studies (e.g. [4–8]) and even fewer experimental tests (e.g. [9,10]).

Predicting the effects of predation risk on structuring prey communities can be facilitated by understanding how species' traits may influence risk perception and the costs and benefits of responding to such risk. Both theoretical and empirical studies suggest that life-history and natural-history traits are linked to animals' sensitivity to predation risk [11]. Life-history theory predicts that compared with shorter-lived and more fecund species (aka 'faster' species), longer-lived and less fecund species (aka 'slower' species) should value future reproduction over current reproduction because they have higher residual reproductive value (*sensu* [12]) [13]. Consequently, when faced with the

trade-off between their own survival and that of their offspring, slower species should value their own survival over that of their offspring, while the opposite is expected of faster species [14]. Empirical work with a variety of taxa confirms these predictions for reproductive behaviours [15,16]. In addition, natural-history traits such as body size, competitive advantage and social behaviour can often predict prey response to predation risk [2,11,17]. Nonetheless, experimental tests of whether species' traits can predict community changes to variation in perceived predation risk remain rare.

We present a community-level, experimental study to test the effects of different types of predation risk on forest birds of the southeastern United States. We ask: (i) can perceived predation risk shape breeding bird community structure? And (ii) can key life-history and natural-history traits predict prey response to perceived risk, and hence help to explain community responses in terms of species richness and composition? We manipulated cues of three avian predators that preferentially prey on either adult birds or offspring, or both adult and offspring, and conducted repeated community surveys to characterize species- and community-level responses. We tested for the effects of perceived predation risk on community richness and composition by estimating the abundance and/or occurrence of target species. We further tested for the relationship between species response and slow/fast life-history trait and body size as predictors that may explain community responses to perceived predation risk.

2. Material and methods

(a) Study area

We conducted fieldwork in the sandhill habitat of north-central Florida (29.4° N, 82.0° W), situated within the Ordway-Swisher Biological Station, a 3700 ha managed research preserve, between late February and mid-August 2010. Forest vegetation was dominated by longleaf pine *Pinus palustris* and to a lesser extent American turkey oak *Quercus laevis*, with wiregrass *Aristida beyrichiana* in the understorey. Other typical species included a variety of oaks, herbs and grasses [18]. These habitats received prescribed burning in units of approximately 20 ha every 2–5 years to maintain longleaf pine- and wiregrass-dominated conditions.

(b) Experimental design

In 24 plots, each with an area of 9 ha (300 × 300 m), we broadcast predator vocalization playbacks daily throughout the avian breeding season to increase the perceived predation risk of the prey bird community. We applied vocalizations of three species: Cooper's hawk *Accipiter cooperii* (Hawk hereafter), blue jay *Cyanocitta cristata* (Jay hereafter) and eastern screech-owl *Megascops asio* (Owl hereafter). In forested parts of the southeastern United States, all three species are important predators on other birds, and have discernible, relatively frequent vocalizations. Importantly, they represent contrasting types of predation risk to prey, spanning the gamut of being primarily an adult predator (Owl) or offspring predator (Jay), or both adult and offspring predator (Hawk), and differ in preferred prey species. The Cooper's hawk is a major predator of adult birds [19,20], and in our study site also regularly raids open-cup nests of passerines and accounts for the majority of nest predation for at least one species [21]. The blue jay is an important nest predator of open-cup-nesting birds, while its predation on adult birds is infrequently observed [22]. The Eastern screech-owl is primarily a predator of adult birds when it preys

on birds, and less frequently depredates nestlings. It targets mostly small birds, but occasionally attacks larger prey [23].

We assigned plots to one of four treatments (playback with Hawk, Jay or Owl vocalizations, versus no playback—i.e. Control; $n = 6$ per treatment) using a randomized block design, with care taken to ensure that plots within blocks were in a similar post-fire recovery stage with similar vegetation features. One round of bird community surveys in June of the year preceding treatments suggested no difference in plot-level species richness between treatments; hence a before–after design was deemed unwarranted and we proceeded to conduct our experiment within one breeding season. We delineated a central 4 ha (200 × 200 m) core within each plot, in which we applied predator vocalization playbacks and conducted bird surveys (see below). Each plot was at least 50 m from habitat edge, and spaced at least 200 m apart (at least 300 m apart for plot cores). We did not attempt to remove natural predators or eliminate predation events.

We used two playback stations on each plot's core area. Each playback station consisted of a portable CD player mounted in a camouflaged box at 3 m above ground wired to a deep-cycle marine battery and a timer [24,25]. Within plots, stations were spaced approximately 100 m apart and faced towards the plot centre. To minimize habituation to playback, we changed the location of stations biweekly throughout the breeding season (also see below). Control plots had stations that produced no sound, which were shifted in the same way as treatment plots. We chose to provide no sound for Control plots instead of using procedural playback control because of unknown effects from potential procedural control vocalizations (e.g. [25]). If species were responding similarly to playbacks in general (i.e. the rationale for using procedural playback controls), we would expect species to respond to all playback treatments in a similar way, but this was not observed (see §3).

We prepared unique playback files for each plot, with vocalization from no more than three predator individuals for each file to avoid mimicking the presence of too many predators [26]. Each playback file consisted of a 'primary' vocalization type (i.e. the most frequent vocalization used by the species, such as territorial calls), supplemented by a smaller amount of a 'secondary' vocalization type (i.e. vocalization that is less frequently used but that still advertises the presence and/or activity of the species). The amount of vocalization in each playback file and the amount provided daily on each plot were determined according to natural vocalization rates suggested by the original recordings and our field experiences. The daily amount of playback on each plot was 232 primary vocalizations plus 122 secondary vocalizations for the Hawk treatment, 720 primary vocalizations plus 160 secondary vocalizations for the Jay treatment and 260 primary vocalizations plus 144 secondary vocalizations for the Owl treatment. We circulated playback files between plots within a given treatment biweekly to further reduce habituation to playback. The detailed playback scheme is provided in electronic supplementary material S1. We played vocalizations daily from 5 March to 23 July, spanning the entire breeding season and the pre-breeding settlement phase of most bird species in this forest system [27].

We considered the following life-history and natural-history traits as relevant for predicting prey sensitivity to predation risk: annual fecundity, adult survival rate and adult body mass. Fecundity and adult survival are major components of species' slow/fast life-history strategy [28]. We considered body mass (proxy for body size) because the relative size of predator versus prey generally determines prey vulnerability [29,30]. As adult predators, Hawk is likely to favour medium-sized prey [17], whereas the smaller Owl probably prefers smaller prey [23]. Similarly for nest predation, body size may directly affect birds' vulnerability, because smaller birds may be less effective at deflecting larger predators [31].

(c) Data collection

We collected plot-level avian community data throughout the study using repeated transect surveys (6.00–11.00, 20 April to 21 July 2010) [32]. We surveyed each plot five times (approximately three weeks apart), except for three plots (one each for Hawk, Owl and Control) and two additional plots (one for Hawk and Jay each) for which surveys were halted after the second and third surveys, respectively, due to prescribed burning.

On the core 4 ha portion of each plot, we surveyed birds along two parallel transects placed 100 m apart, at a standard speed of 10 m min⁻¹ [32]. We recorded all adult birds seen or heard from the transect, the surveyor's location at the time of detection, and birds' angle and distance from the surveyor. We used bird records within the boundaries of each 9 ha plot to ensure adequate inclusion of plot resident birds exposed to treatments. Care was taken not to double count individuals. All surveys were conducted by the same person (F.H.; survey data are provided in electronic supplementary material S2).

We collected life-history and natural-history trait data on wild populations of prey from literature and other sources. Details on data, data sources and calculation of composite traits are provided in electronic supplementary material S4. A generally inverse relationship exists between fecundity and adult survival [33,34]; this relationship was supported by data on our study species ($r_{\text{Pearson}} = -0.44$). We thus used only annual fecundity to represent species' slow/fast life-history trait because the data are probably more reliable than survival estimates. There was no strong correlation between annual fecundity and body mass ($r_{\text{Pearson}} = -0.29$).

(d) Statistical analysis

We made the following predictions based on predator–prey and life-history theories. (i) Predator treatments should reduce plot-level species richness; (ii) treatments should alter community composition. In terms of species-level response to perceived predation risk that contributed to community changes, we predicted that (iii) slower species should respond more negatively to adult predation risk and faster species to offspring predation risk, and (iv) medium-sized species should respond more negatively to Hawk (than smaller and larger species) and smaller species to Owl (than larger species). We first analysed species response to treatment in abundance/occurrence and detection probability; from these results, we tested for community responses. We further tested the relationship between species response in abundance and key life-history and natural-history traits. We did all analyses using R v. 2.13.1 [35].

(i) Species-level response to perceived predation risk

To test for species plot-level abundance response to treatments, we used N-mixture models that explicitly account for imperfect detection [36]. Birds may respond to treatments with changes in detection probability (e.g. by reducing singing rates) rather than abundance. These two responses should be separated to understand how species respond, especially for making community-level inferences. N-mixture models separate these responses by separately parametrizing a *state* component that represents the abundance of animals, and an *observation* component that represents the detection of animals. The state and observation components then combine to specify the number of detected animals [36]. To separate effects of detection probability from population abundance, formulations of N-mixture models must make assumptions regarding population closure; that is, the extent to which the surveyed population size remains unchanged ('closed') across repeated surveys [37]. To avoid unsupported assumptions about population closure, we contrasted three model categories with decreasing strictness of population closure and increasing model complexity: (i) 'Closed' models (assuming

closure across all surveys) [38]; (ii) 'Robust Design' models (assuming closure within but not between clusters of survey periods, aka, 'primary periods'; *sensu* [39]) [38] and (iii) 'Open' models (assuming no closure across all surveys) [40].

For all models, we included treatment as the only candidate covariate for abundance (i.e. the state component of the N-mixture models). For detection probability (i.e. the observation component of the N-mixture models), we included treatment as the only candidate covariate, and additionally included time, Julian date and the quadratic term of Julian date of survey as nuisance covariates. We included quadratic term of Julian date because birds may be most detectable during territory establishment and more elusive during subsequent nesting activities [41]. Each model category thus had four candidate models. For each species, we started with Closed models, and moved to the next more complex model category only when the simpler models did not fit. We used two criteria to evaluate the fit of successfully converged models. First, because N-mixture models tend to overestimate abundance and underestimate detection probability when closure is inappropriately assumed [40], we accepted only models that produced estimates that largely aligned with our biological knowledge of the species (e.g. known territory sizes of species). Second, we accepted only models that produced estimates with coefficient of variation less than 5.0. For models that passed these two steps, we used Akaike's information criterion (AIC) to rank them, and accepted models from the lowest AIC until the cumulative model weight exceeded 0.95 [42]. Accepted models thus combined to form a 95% confidence model set that most probably approximated the observation [42]. For species that did not fit N-mixture models but were amenable to occurrence analysis (e.g. did not occur in all plots), we analysed their occurrence using similar hierarchical models [36], and the same model categories, structures and fitting process as the N-mixture models [43].

Of the total 36 breeding bird species detected during our study (including 24 prey species), we focused on 18 regular prey species that had at least 10 detections across all surveys on all plots combined (see electronic supplementary material S3 for species list). We fitted Robust Design models using our own R code and the 'unmarked' package (v. 0.9–4) for Closed and Open models. Detailed model specification is provided in electronic supplementary material S5.

(ii) Community-level response in terms of richness and composition

We tested for community-level response to treatments by (i) estimating species plot-level abundance from N-mixture model parameters and survey data [36], and (ii) constructing species richness and composition of the community on each plot. Because several species had competing models that indicated treatment effects on either abundance or detection probability (see §3 and electronic supplementary material S6), we conducted model averaging of the 95% confidence model set using the 'natural averaging' approach to estimate model parameters [42]. We further derived species plot-level occurrence state from abundance estimates (i.e. occurrence state = 1 if abundance was greater than 0). Details of species plot-level abundance estimation are provided in electronic supplementary material S5. Thirteen of the 18 focal species were fitted with N-mixture models (see §3 and electronic supplementary material S6), and thus had plot-level abundance estimates.

To analyse the response of bird community species richness to treatments, we tallied occurrence state across species to obtain plot-level species richness, with community defined as the collection of these 13 species. Because 10 out of these 13 species were best explained by Robust Design models (see §3 and electronic supplementary material S6), which stipulated two primary periods within which population was closed, each plot had two richness estimates, one for each primary period. We then used

generalized linear models (GLMs) with treatment as the only candidate covariate, using a log link, Poisson error distribution and an exchangeable correlation structure to account for the repeated measures of species richness within a plot (i.e. generalized estimating equations). We conducted analysis using the 'yags' package (v. 4.0-2.1), and used the quasi-likelihood under the independence model criterion (QIC) for model selection, selecting the models with the lowest QIC scores [44].

To analyse the response of bird community composition to treatments, we constructed community profiles using abundance estimates of the 13 species, with community defined as the collection of these 13 species. Again, each community had two profiles, one for each primary period. We then used two-dimensional, non-metric multidimensional scaling (NMDS [45]), and analysed treatment effects using analysis of similarity (ANOSIM) based on the Bray–Curtis dissimilarity index without transformation, with 1000 permutations [46,47]. After finding a treatment effect on community composition (see §3), we used the similarity percentage analysis (SIMPER) to evaluate which species contributed the most to community differences [48]. Species identified by SIMPER analysis would either be those with variable abundance within treatments, or those that contributed to between-treatment differences [49]. It was these latter species that we were interested in. We conducted analysis using the 'vegan' package (v. 2.1-19).

(iii) Relationship between life-history and natural-history traits and species response

We tested for the relationship between species life-history and natural-history traits and their responses to treatments that could explain community-level responses. Our interest was therefore on species responses in abundance. To obtain these response estimates from N-mixture models, we used the best-performing models (i.e. models for which $\Delta\text{AIC} \leq 2.0$ [42]), for a more accurate representation of species responses as strongly supported by data. For each species, if the model indicating a treatment effect on abundance was among the best-performing models, we used it (or the one with lower AIC if there was more than one model) to obtain species response estimates, in the form of the log ratio between the mean plot-level abundance of treatment over that of Control (see the electronic supplementary material, S5). Otherwise, the species response in abundance would be zero. We used linear regression to analyse the relationship between species response and traits; when regression assumptions were not satisfied, we used GLM with an identity link, gamma error distribution, on exponentiated (i.e. back-transformed) response data.

We conducted the analysis using two approaches: (i) by comparing how response to individual predator types related to traits; and (ii) by first calculating the pairwise difference in a species's response to different predator types (Hawk–Jay, Hawk–Owl and Owl–Jay), then comparing how this pairwise difference related to traits. The second approach was necessary for assessing the sensitivity to different types of predation risk within a species (e.g. risk against its own survival versus that of its offspring). We excluded the brown-headed cowbird *Molothrus ater* from analysis because it is a nest parasite with extremely high fecundity, which probably makes it respond to predation risk in a different way than other species [50].

All linear regressions included annual fecundity and body mass in the global models. We additionally included a quadratic term of body mass in the global models involving Hawk treatment because the Cooper's hawk probably prefers medium-sized prey over small or big prey when it preys on adult birds [17]. We log-transformed fecundity and body mass to reduce the influence of extreme trait values. We used the Akaike's information criterion corrected for small sample size (AICc) and chose the best model with the lowest AICc scores [42].

3. Results

Out of the 18 focal species, we were able to analyse abundance response to perceived predation risk for 13 species, and occurrence response for one other species. Eleven of these species responded to treatments by exhibiting altered abundance, occurrence and/or detection probability, mostly in negative ways, although some unexpected positive responses also occurred, especially under Hawk and Jay treatments (see electronic supplementary material S6 and S7). N-mixture and occurrence models further suggested that of the 11 species with significant responses to treatments, one responded in abundance, one in occurrence, three in detection probability and the other six species in either abundance or detection probability according to similar AIC values of competing models (see electronic supplementary material S6).

Confirming prediction (i) that perceived predation risk should lower plot-level species richness, Jay and Owl treatments significantly reduced plot-level species richness by 6.7 per cent ($\beta = -0.069$, s.e. = 0.031, $p = 0.025$) and 11.7 per cent ($\beta = -0.124$, s.e. = 0.028, $p < 0.001$), respectively. Hawk treatment marginally reduced plot-level species richness by 6.5 per cent ($\beta = -0.067$, s.e. = 0.038, $p = 0.078$; figure 1a). Confirming prediction (ii) that perceived predation risk should alter community composition, treatments strongly shifted community composition: for both primary sampling periods, ordinated community profiles showed distinct clusters for all treatments and Control (figure 1b,c). ANOSIM suggested a strong treatment effect on community dissimilarity for both primary time periods ($F_{3,20} = 3.52$, $p = 0.001$ and $F_{3,15} = 2.93$, $p = 0.001$, respectively). SIMPER analysis identified these dissimilarities to be predominantly driven by species exhibiting abundance responses to treatments according to N-mixture models (table 1).

Contrary to prediction (iii) that slower species should respond more negatively to adult predation risk and faster species to offspring predation risk, we did not find support for a relationship between species response to treatments and fecundity. On the other hand, our results confirmed prediction (iv) that body size could predict species response to perceived predation risk, but only under Owl treatment (figure 2). Smaller-bodied species showed a marginally stronger negative response to the Owl treatment compared with larger-bodied species ($\beta = 0.327$, s.e. = 0.159, $p = 0.066$; figure 2a). In addition, smaller-bodied species showed a marginally stronger negative response to the smaller-bodied Owl than to the larger-bodied Hawk, whereas the opposite applied to larger-bodied species ($\beta = -0.329$, s.e. = 0.171, $p = 0.087$; figure 2b). We found no relationship between species response to Hawk treatment and prey body size.

4. Discussion

(a) Effect of perceived predation risk on community structure

Our study suggests that perceived adult and offspring predation risks strongly shaped the structure of breeding bird communities, by reducing species richness, shifting community composition, and generally reducing species abundance and/or occurrence. These results add evidence for the role of

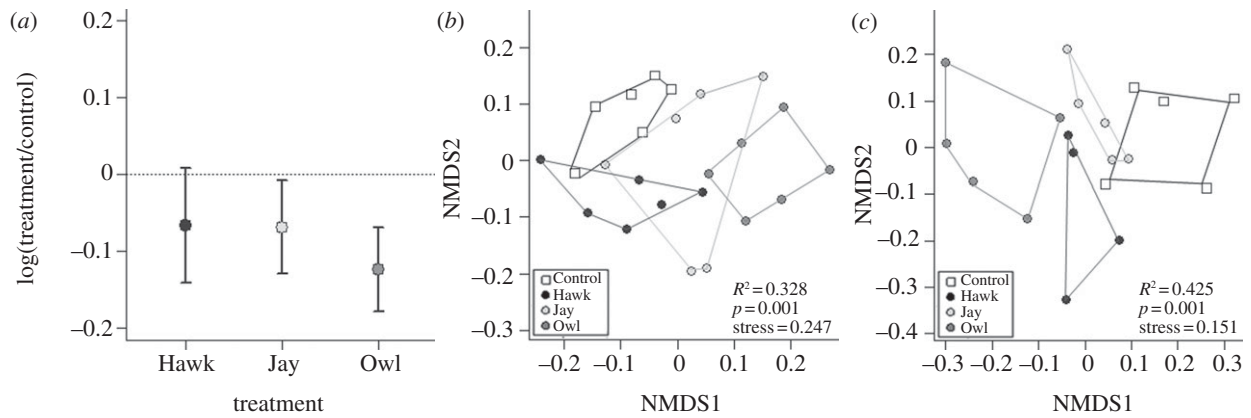


Figure 1. Treatment effects on community structure, in terms of species richness and composition. (a) Effects of playback treatments on plot-level species richness as estimated by N-mixture models. Effects are presented as the log of treatment-level species richness ratio (± 1.96 s.e.) between treatment and Control. (b,c) Two-dimensional NMSD and ANOSIM of Bray–Curtis community similarity index among plots for (b) the first time period and (c) the second time period. For the second time period, five plots were lost due to prescribed burning, including two for Hawk, and one each for Jay, Owl and Control. All analyses were based on model-averaged estimates from the 95% confidence model set.

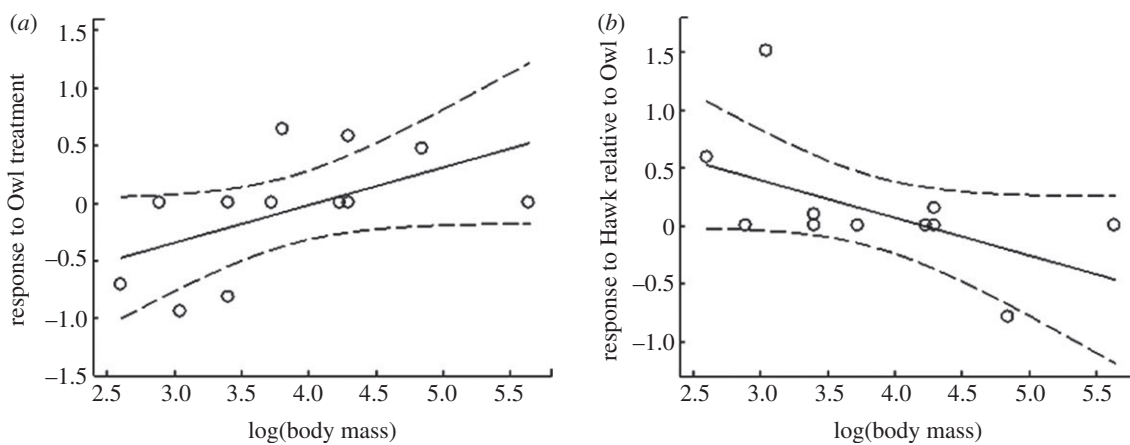


Figure 2. Relationship between species response to treatments in abundance and body size (estimates and model predictions, $\pm 95\%$ CI). (a) Species response to the Owl treatment in relation to body mass. (b) Difference in species response to the Hawk and Owl treatments in relation to body mass. For both analyses, brown-headed cowbird was excluded from analysis, and $n = 12$.

Table 1. Bird species that combined to contribute greater than or equal to 50 per cent of the community dissimilarities (based on SIMPER analysis).

species	contribution (%)						abundance response to treatment ^a
	first period			second period			
	Hawk	Jay	Owl	Hawk	Jay	Owl	
summer tanager <i>Piranga rubra</i>	17.3	9.9	20.1	13.9	—	8.8	−0.72 (Hawk); −0.82 (Owl)
pine warbler <i>Dendroica pinus</i>	10.9	15.6	16.3	16.3	14.3	36.7	−0.71 (Owl)
Eastern bluebird <i>Sialia sialis</i>	10.4	—	—	11.7	9.5	—	−0.92 (Owl)
mourning dove <i>Zenaidura macroura</i>	10.0	13.9	14.1	—	14.1	—	0.57 (Jay)
red-headed woodpecker <i>Melanerpes erythrocephalus</i>	9.4	10.5	—	—	—	—	0.73 (Hawk); 0.71 (Jay)
yellow-throated vireo <i>Vireo flavifrons</i>	—	9.0	—	—	15.1	8.4	−1.16 (Hawk); −1.34 (Owl)
Bachman's sparrow <i>Peucaea aestivalis</i>	—	—	—	9.8	—	—	−0.94 (Owl)

^aResponse is represented in the form of the log ratio of mean plot-level abundance between treatment and Control (see electronic supplementary material S4 and S5). Only responses with $p < 0.1$ are presented, with italic indicating $p < 0.05$.

predation risk in structuring ecological communities, particularly terrestrial vertebrate communities, for which there are very limited experimental tests (e.g. [9,10]).

Factors affecting community assembly typically act via two mechanisms: (i) by altering species colonization through habitat selection; and (ii) by altering species key

demographic rates post-colonization [51]. Because our study spanned one breeding season, the observed community changes should predominantly be the result of community-wide alteration in avian habitat selection under heightened perception of predation risk. Owing to its direct fitness impacts, predation risk (both on adult birds and offspring) is often considered to be a central factor governing avian breeding habitat selection [4,5,10,52,53]. Our study adds strong experimental evidence for consistent effects at the community level.

Our findings also suggest that perceived predation risk could affect avian communities in ways other than habitat selection [54]. At least three and up to nine of the 13 focal species exhibited altered, generally lower, detection probabilities under heightened perception of predation risk (see electronic supplementary material S6). A variety of behavioural adjustments could have caused this result; for example, reduced singing and/or calling rates, and more cryptic activities. Such behavioural changes have been noted elsewhere [55,56], and could comprise effective anti-predator strategies, especially when shifting habitat is not possible or optimal [57]. In addition, demographic rates of prey populations, such as reproductive output, are likely to respond to increased perception of predation risk [52,58–60]. These behavioural shifts could potentially exert strong and profound effects at the population and community levels, beyond those of habitat selection [55,60].

While negative response to perceived predation risk was prevalent among prey species, there were some unexpected responses of species to perceived predation risk, especially under Hawk and Jay treatments (see electronic supplementary material S7). Several mechanisms involving potentially complex inter- and intra-specific interactions could be involved in such ‘unexpected effects of predation risk’ (*sensu* [3]). First, prey live in a multi-predator world, where response to one predator is influenced also by risks from other predators [61]. Some avian predators could potentially provide protection against other predators via intra-guild predation [3,62], and may be sought as neighbours by their prey [63,64]. This mechanism could be involved in many of the non-negative responses of prey species towards the Hawk treatment. Second, when competition exists among prey, negative effects of predation risk on the competitively dominant prey may release the poor competitor via the ‘keystone predator effect’ (*sensu* [65]) [3]. This is well documented in aquatic systems [66,67], and has been shown in some vertebrate studies [68]. Third, when habitat availability is limited, part of the population would be forced to settle in suboptimal habitats, causing the apparent absence of predation risk effects, while prey may have a range of other negative responses with resulting fitness consequences [69]. Lastly, the fact that the Jay treatment had the highest number of unexpected prey responses (see electronic supplementary material S7) may involve the blue jay being a heterospecific attractant for at least some of the prey species [70]. Highly active, aggressive and vocal, the blue jay may provide potential benefits to some prey species that override the predation risk it poses, such as reducing predation risk from other predators, indicating habitat quality and/or mitigating competition.

The three treatments had different effects on bird community composition. Not only did they result in different community compositional shifts, but the degree to which

they affected species richness also differed: while Owl had the strongest negative effect on species richness, Hawk showed only a marginally significant effect. This differential response of prey community to different predator treatments should be understood in light of two issues. First, predators may have different influences on prey depending on their identity (as discussed above) and density [71,72]. A treatment (in our case vocalizations) of a naturally abundant predator species may elicit a proportionally minor increase in prey risk perception, whereas a similar treatment of a low-density predator may cause a disproportionately large increase in prey risk perception. We unfortunately lack data on the density for two of three predators, but would expect them to differ from each other. Understanding of prey response to different predators would benefit from future studies that look at how prey response to predation risk may be affected by predator density. Second, our analysis was on a subset of the prey bird community (i.e. the collection of 13 species that fitted N-mixture models, out of the 18 regular prey species, and the total of 24 prey species); the detected effects of predators thus may be different if we were able to include all prey species in the analysis. For example, analysis on the raw richness data of the 18 regular prey species (i.e. the number of species tallied from field surveys) suggested strong negative effects of all treatments (see electronic supplementary material S8).

(b) Response to perceived predation risk in relation to life-history and natural-history traits

Under the context of habitat selection, we did not find support for the life-history theory prediction that fecundity should predict species response to adult versus offspring predation risk. However, our finding that smaller-bodied species responded more negatively to vocalizations of the small-bodied Owl treatment supported the prediction that body size should determine prey sensitivity to adult predation risk (figure 2) [29,30].

The life-history trade-off between current and future reproduction of an organism broadly predicts greater aversion to adult predation risk over offspring predation risk for slower species, and the opposite for faster species [13,73]. Empirical tests in birds of this widely held prediction have largely focused on nest defence and other risk-taking behaviours around the nest, due to the obvious trade-off parents must make in those situations [14–16]. We designed this study to provide new types of support, by (i) assessing predation-risk sensitivity in the context of avian breeding habitat selection, a behaviour that operates over larger spatio-temporal scales with demonstrable population-level consequences [74]; and (ii) contrasting adult versus offspring predation risks under the same context. The latter is an essential aspect of testing this life-history theory prediction, but has only rarely been implemented within the design of single studies [15,16].

The lack of support for the above life-history theory predictions in the context of breeding bird habitat selection should be understood in view of the following issues. First, species may display sensitivity to perceived predation risk in ways other than habitat selection. This issue is suggested by their responses in terms of detection probability: at least three species in our analysis that had a zero response in abundance actually responded to perceived predation

risk with an altered detection probability (see electronic supplementary material S6). Therefore, the fact that life-history variation failed to predict species response to perceived predation risk in terms of habitat selection does not mean that this trait bears no relevance to species sensitivity to perceived predation risk in general. Second, different predator types may vary not only in the life-history stage they pose the most threat to, but some might also generally be more important predators than others. Different levels of predation risk posed by different predators therefore can also influence prey response. Third, compared with body mass data, the fecundity of our focal species had a much narrower range of variability, with 10 of the 12 species (i.e. excluding brown-headed cowbird) having fecundity values clustered around the middle approximately 34 per cent of the full range (see electronic supplementary material S4). This lack of variability in fecundity gradient probably reduced our ability to detect potentially existing relationships between fecundity and species response. Finally, compared with the body mass trait, which can be easily and reliably measured, the fecundity trait is much more difficult to estimate reliably for each species (e.g. data need to be collected over full breeding cycles). In addition, our design would have been stronger if we had reliably estimated vital rates for populations inhabiting our particular sites.

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