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Research

Congeneric predators fill discrete niches created by the relative abundances of their prey species

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To what degree is niche partitioning driven by underlying patterns in resources such as food, rather than by competition itself? Do discrete niches exist? We address these questions in the context of Cooper's and sharp-shinned hawks, two broadly sympatric, North American, bird-eating raptors in the genus *Accipiter*. We find that the resource base, as quantified by body masses of birds at bird feeders, is approximately lognormal (smallest birds are most abundant), with lesser modes (peaks) in abundance at larger body mass. The predators appear to exploit peaks in the resource base, with sharp-shinned hawks focusing on small prey items (median of 26.5 g), and Cooper's hawks taking prey from the two most abundant peaks (both the small body mass peak and a lesser peak at medium body mass ~90 g). We tested the ability of citizen scientists to distinguish these notoriously similar species, and we determined the influence of potential false positive detections on our conclusions. We find that citizen scientists struggle to distinguish these predators from one another, and 18% of Cooper's hawks were identified as sharp-shinned hawks, while 27% of sharp-shinned hawks were identified as Cooper's hawks. Yet, simulations show that this uncertainty did not jeopardize our qualitative conclusions.

Keywords: *Accipiter*, adaptive landscape, citizen science, false positive, macroevolution, niche partitioning

Introduction

A central tenet of ecology is that two sympatric species cannot occupy the same niche indefinitely, and that one or both species must either undergo character divergence or suffer extinction (Chesson 2000). Early work on the nature of niche partitioning focused on how and why niche partitioning might happen (MacArthur and Levins 1967, MacArthur 1970, Tilman 1982). More recent work often focuses on detecting evidence of niche competition (Miller et al. 2017b), with the assumption that evidence of niche partitioning indicates the workings of the ghost of competition past (Connell 1980). Researchers rarely consider the degree to which niche partitioning has

been facilitated by underlying patterns in the distribution of resources available to the organisms in question.

Even the nature of the niche has been a matter of discussion among ecologists since the term first entered the ecological lexicon (Grinnell 1917, Elton 1927, Hutchinson 1957, Whittaker et al. 1973, Chase and Leibold 2003, Ricklefs 2008). Less frequently discussed is whether a niche can be characterized independently of a consumer and the resources it uses – do discrete niches exist whether or not they are occupied? In practice, niches are often modeled as 'utilization functions' along continuous resource axes. A niche is therefore most easily defined when occupied, and empty niches are thus vague abstractions (MacArthur 1970, Lekevičius 2009, Ashby et al. 2017). The niche according to Hutchinson (1957), for example, is defined by such utilization functions in n-dimensional space, and thus potential niche space is essentially a uniform resource, which precludes the a priori identification of discrete niches. That said, Hutchinson (1957) himself referred in his seminal work to empty niches; simple niche definitions clearly have limitations. In practice, most ecologists recognize that available niche space is uneven; the concept of the adaptive landscape is evidence of this implicit understanding.

In birds, notable instances of convergence across continents suggest that selective pressures may drive species to fill remarkably similar ecological niches; sustained aerial foraging for invertebrates appears to have been the genesis of both swifts and swallows, for example Pigot et al. (2020). Such convergent events might be explained by synonymous resource availabilities across continents, where parallel variation in resource availability leads to parallel evolution across similar adaptive landscapes. In most cases, the high-dimensional nature of the niche makes the identification of discrete niches problematic (Winemiller et al. 2015, Pianka et al. 2017), but some guilds may partition resources along so few dimensions, or there may be such clear modes in the underlying distribution, that discrete niches are more apparent. Frugivores and granivores use well defined resources characterized by multimodal distributions (Boag and Grant 1984, Fleming et al. 1987). Thus, the adaptive landscape for a bird in one of these foraging guilds may be more rugged, with tall adaptive peaks and deep valleys between them, e.g. with peaks in gape width corresponding to modes in the distribution of fruit sizes (Wheelwright 1985). These modes in fruit and seed distributions could perhaps be considered discrete niches. Niche partitioning in these guilds might therefore be facilitated or even entirely driven by these underlying patterns in the resource base. However, cross-continental convergent events do not necessarily imply synonymous resources bases; theory predicts that the fewer the dimensions across which species can partition resource use, the more divergent they must be in order to coexist (MacArthur and Levins 1967, MacArthur 1968). If these species primarily divide resources along a single axis of variation (e.g. size of food items) this by itself can explain the clear steps between, for example, small, medium and large ground finches (*Geospiza fuliginosa*, *G. fortis* and *G. magnirostris*, respectively) (Boag and Grant 1984).

Like frugivores and granivores, because potential prey items are finite in diversity, carnivorous bird species may also face rugged adaptive landscapes (Thiollay 1985). If the adaptive landscape is shaped by prey body mass, then generally speaking there is more opportunity for smaller predators, since prey body mass distributions are often approximately lognormal (Mittelbach 1981, Reynolds and Meslow 1984, Eadie et al. 1987, Hoyle and Keast 1987, Cohen et al. 1993). Of course, there may be less pronounced peaks in abundance at larger body masses, offering alternative adaptive peaks towards which a predator might evolve, particularly if these larger bodied prey were easier to catch.

Members of the genus *Accipiter* are predatory raptors that primarily take other birds as prey items (Ferguson-Lees and Christie 2001). The genus contains approximately 50 species in the strict sense, although harriers (*Circus* spp.) appear to be embedded within the larger *Accipiter* radiation (Griffiths et al. 2007). Globally, many continents contain at least two sympatric *Accipiter* species, often more. This pattern is repeated on a number of large islands, including Madagascar, Sulawesi, the Moluccas, New Britain and others (Griffiths et al. 2007). Notably, co-occurring species tend to resemble each other in plumage but show notable interspecific differences in size. Of further interest, accipiters show pronounced reversed sexual dimorphism, and the ratios between male and female body masses exhibit fairly consistent patterns between continents (Dunning 2007). In this study we do not have data to address questions of sexual dimorphism, but we return briefly to the topic in the discussion. Regardless, the existence of consistent differences in body size between species on disparate continents and islands suggests that common trends in potential bird prey abundance distributions could provide adaptive landscapes conducive to generating size-structured *Accipiter* assemblages. If predator species tend to focus their efforts on prey items of suitable size, then two non-mutually exclusive possibilities are that prey species exhibit a multimodal body mass abundance distribution, in effect creating empty niches that accipiters have subsequently filled, or that predators largely partition resources along the finite axis of prey size, leading to strict limitations on the number and characteristics of coexisting predators.

Our study species, sharp-shinned *A. striatus* and Cooper's hawks *A. cooperi*, are sympatric across most of North America. Research to date suggests the larger Cooper's hawk focuses on larger bird prey, but also includes small mammals in some regions, and overlaps with sharp-shinned by regularly taking smaller bird prey (Reynolds and Meslow 1984, Roth and Lima 2006, Roth et al. 2006). To date, the studies that generated this information have been labor-intensive efforts undertaken by a small number of well-trained observers. However, these studies have also been spatially and temporally limited, and few have quantified the abundance of potential prey items, thereby precluding characterization of the underlying resource base. Addressing our study questions at the spatiotemporal scale of interest requires a massive field effort, which we achieve by partnering with tens of thousands of citizen (or 'community') scientists (Panter and Amar 2021).

Here we leverage data from Project FeederWatch (Bonter and Cooper 2012, Bonter and Greig 2021) to compare the menu of prey items to those actually taken by these accipiters. Distinguishing among these *Accipiter* species is a well-known identification problem, even for experienced ornithologists (Ferguson-Lees and Christie 2001). Experience varies widely among citizen scientists, and quantifying potential misidentification rates of these largely sympatric species is both an interesting research question in its own right, and of critical importance in understanding whether robust conclusions can be drawn. To address this, we directly probed the ability of citizen scientists to identify these species, and thereby provide a preliminary quantifications of potential false positives in citizen science data, i.e. the extent to which certain regionally plausible observations can nevertheless be wrong.

In this paper we address the hypothesis that the distribution of prey items is multimodal and generates a rugged adaptive landscape with peaks (niches) that have subsequently been settled by these accipiters, by deriving species-level resource utilization functions and comparing these to a resource axis defined by prey body mass. We further use this information to quantify relative risk of predation by accipiters on bird prey species across North America. Finally, we quantify the ability of observers to distinguish these visually similar prey species, and we use this information to assess the strength of our conclusions.

Methods

Description of the dataset

We used the interspecific-interaction dataset described in Miller et al. (2017a) to study the prey species consumed by Cooper's and sharp-shinned hawks throughout North America. These data were collected by citizen scientists observing bird feeders during the non-breeding season (November through late March or early April, depending on the year), as a supplement to the data collected by Project FeederWatch. This dataset contains 2178 observations of an avian predator successfully attacking and killing prey; of these, 1186 and 677 were depredation by Cooper's and sharp-shinned hawks, respectively (the remainder were by different predator species). The dataset has broad geographical coverage across much of North America (Fig. 1).

Calculating predator preferences

To calculate predator preferences, we began by extracting the numbers of birds of all species reported at each location during the count period for which a given predation event was observed. Counts of birds reported by participants in Project FeederWatch are the maximum numbers of individuals seen simultaneously of each species within each two-day count period. We rolled all of these reports up to species-level taxa, e.g. reports of 'dark-eyed junco (slate-colored)' were converted to 'dark-eyed junco' before calculations. In order to generate a list of expected prey items the hawks would have targeted if they sampled based purely on abundance at the feeders they visited, we used a functionally identical but modified simulation approach to that used in Leighton et al. (2018). Per checklist, we first removed the predator as a possible target, then simulated 10 000 predation datasets identical in dimension and per-checklist predation events to those in the observed predation dataset, where the probability of interaction between any two species was proportional to their relative abundances during the count. In other words, each
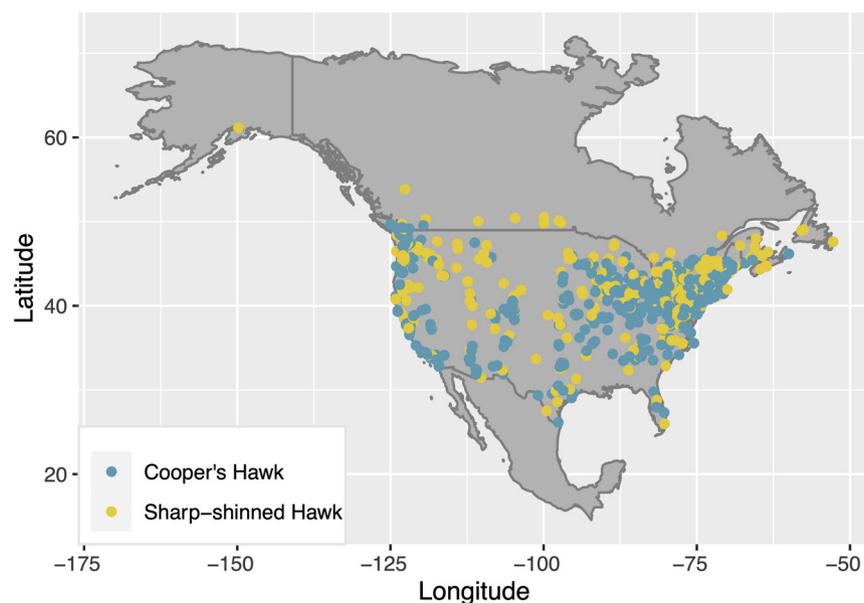

Figure 1. Map of North America, with points placed on the locations of feeders at which *Accipiter*-depredation events were observed and reported to the FeederWatch interactions dataset. Yellow points reflect successful depredation events by sharp-shinned hawks (n = 677), blue represent predation events by Cooper's hawks (n = 1186).

simulation we created a mock interaction dataset informed by the abundances of the relevant species in each checklist, and we created 10 000 such datasets. We then replaced those randomly selected 'predators' (which were, of course, usually non-predatory common feeder birds) with the actual reported predator species, and used these simulated predation datasets to quantify predator preference and resource availabilities. We combined this information with prey species' average natural log-transformed body masses (Dunning 2007) to derive prey-size probability density functions for each predator, and compared these expected (available) resource utilization curves to those derived from what was actually consumed.

We also used the simulated predation datasets to quantify predator selectivity for prey species by deriving standardized effect sizes for each unique predator–prey interaction. These were defined as the differences between the actual numbers of that prey species taken by that predator and the mean expected numbers, divided by the standard deviations of those expected numbers. For example, if the expected numbers of American goldfinches *Spinus tristis* targeted in total by sharp-shinned hawks across three simulated predation dataset were 12, 10 and 11, but sharp-shinned hawks had actually targeted 20 American goldfinches in the dataset, then the standardized effect size for this interaction would be $(20–11)/1 = 9$, where 11 and 1 are the mean and standard deviation, respectively, of the expected number of targeted American goldfinches. In this example, the large positive standardized effect size (> 1.96) would indicate that the American goldfinch was targeted at a higher rate by sharp-shinned hawks than expected by their abundances at feeders where sharp-shinned hawks hunt.

Testing whether the resource base is multimodal

To test whether the resource base was multimodal, we employed Hartigans' dip test for unimodality on the vector of body masses from the simulations described above for both individual predator species and the combination data from both *Accipiter* species (Hartigan and Hartigan 1985). To compare distributions between prey availability and resource utilization functions, we used Kolmogorov–Smirnov tests (Massey 1951).

Relative risk of predation for prey species

We used the predator–prey specific standardized effect sizes described above to make a preliminary assessment of the factors that influence predation risk, and we put this information in an evolutionary context by displaying values on a phylogeny and calculating the phylogenetic signal associated with predation risk. Although this approach stops short of modeling what factors are correlated with predation risk, it provides a quantitative framework for future research. The phylogeny we used for these analyses was a maximum clade credibility tree derived from Jetz et al. (2012), modified with the R package (<www.r-project.org>) 'addTaxa' (Mast et al. 2015) to bind in tips for woodhouse's scrub-jay *Aphelocoma*

woodhouseii and Pacific wren *Troglodytes pacificus* as sister to California scrub-jay *Aphelocoma californica* and winter wren *Troglodytes hiemalis*, respectively. We used 'phytools' (Revell 2012) for the phylogenetic visualizations and signal calculations (Pagel 1999).

Assessing the impact of observer misidentification

Cooper's and sharp-shinned hawks are broadly sympatric throughout North America and are notoriously difficult to distinguish from each other. Thus, it is likely that some observations of these species in citizen science datasets in fact represent the other species (i.e. they are false positives of the species in question). This confusion is true even for experienced observers, and we therefore assumed it was true for the citizen scientists who observed predators' attacks. However, we were unsure of how frequent misidentification might be, and how inaccurate citizen scientists could be before it would jeopardize the strength of any conclusions we might come to. To address these issues, we administered a photo identification quiz to FeederWatch participants. Participants were recruited via an email sent out to all active FeederWatchers. Thus, while quiz-takers are not guaranteed to be the same participants who collected the original data, they were recruited from the same pool of citizen scientists. In general, little is known about rates of false positives in citizen science initiatives (Ruiz-Gutierrez et al. 2016). Thus, as a point of comparison, we also administered the same quiz to expert reviewers (highly skilled birdwatchers responsible for ensuring data quality) from the eBird citizen science platform (Sullivan et al. 2009). For both pools of quiz-takers, we matched their provided usernames against non-public datasets to confirm to which pool the participant belonged.

Participants were asked to identify 20 photographs of hawks. We designed the quiz such that five photos of each of seven regular feeder-visiting raptor species formed the pool from which the 20 photographs were selected. We used the Macaulay Library as the source of photographs, chosen to illustrate a range of plumages (juvenile and adult) and behaviors (flying and perched) for each species. For each photograph, quiz takers were asked to identify the bird as one of the following species: sharp-shinned hawk, Cooper's hawk, northern goshawk *A. gentilis*, red-tailed hawk *Buteo jamaicensis*, red-shouldered hawk *B. lineatus*, Merlin *Falco columbarius* and American kestrel *F. sparverius*. Some participants took the quiz multiple times (presumably growing accustomed to quiz material in the process), so we subset the returned quizzes to only the first quiz taken by a participant. Of the 4674 returned complete quizzes, 2018 represented the first quiz taken by a FeederWatcher. Based on this sample, we derived a confusion matrix that summarized the rates of correct and incorrect Cooper's and sharp-shinned hawk identifications by FeederWatch participants. Similarly, 165 confirmed expert reviewers took the quiz at least once, and we used these results to derive a comparable confusion matrix.

We assessed the impact of observer misidentification on our conclusions of niche partitioning by using the

FeederWatch-participant-specific confusion matrix to add noise to the recorded predator observations. For simplicity, all non-focal predator species were lumped into a single category. For each of 1000 trials, the predator in each predator–prey interaction was potentially switched to another species with a probability defined by the confusion matrix. The probability density function analyses described above were then re-run for each of these 1000 trials in order to create sets of results that depicted how different our results could have reasonably been.

Results

Calculating predator preferences

Generalizing across the prey of both predators, larger-bodied prey species were less abundant than smaller-bodied prey (black, gray lines in Fig. 2). The overall pattern of potential prey abundance as a function of body mass followed a lognormal distribution with its peak around 26 g, although there was a notable, secondary peak around 105 g, corresponding to prey size around the size of blue jays, *Cyanocitta cristata*, mourning doves, *Zenaida macroura* and common grackles, *Quiscalus quiscula*, all common feeder birds. This secondary mode in the distribution meant that prey body mass exhibited multimodal distributions in abundance at feeders visited both by sharp-shinned and by Cooper's hawks (p-value for both Hartigans' dip tests were < 0.001).

Cooper's hawks exhibited a strongly bimodal resource utilization function, with broad overlap with sharp-shinned at lower prey mass, but an additional peak for prey of larger mass (thick blue line in Fig. 2). Thus, the body mass of prey items consumed by Cooper's hawks differed notably from what was locally abundant (thick gray line in Fig. 2) and, accordingly, the Kolmogorov–Smirov test of difference between these two distributions was highly significant (p < 0.001). The median of the Cooper's hawk resource utilization function was 50.8 g. Medians for bimodal responses are rather inadequate descriptive statistics. Thus, put differently, Cooper's hawks tended to exploit prey around the size of dark-eyed juncos (*Junco hyemalis*, 19.5 g), and also prey around the size of mourning dove (118.9 g) and California and Gambel's quails (*Callipepla californica*, 165.7 g and *C. gambelii*, 166.0 g). Cooper's hawks focused on prey that were on average 15% of their body mass.

Sharp-shinned hawks showed a strong tendency to focus on small prey items (thick yellow line in Fig. 2). The median of the resource utilization function of sharp-shinned hawks was a prey mass of 26.5 g. This is identical to the median body mass of prey items at the feeders that sharp-shinned hawks visited, and while the general shape of the sharp-shinned hawk resource utilization curve roughly mirrored that of prey abundance (thick black line in Fig. 2), a Kolmogorov–Smirov test comparing these two distributions revealed a statistically significant difference between these two distributions (p = 0.0001). This was due to a tendency for sharp-shinned hawks to focus on smaller prey items at a rate that exceeded
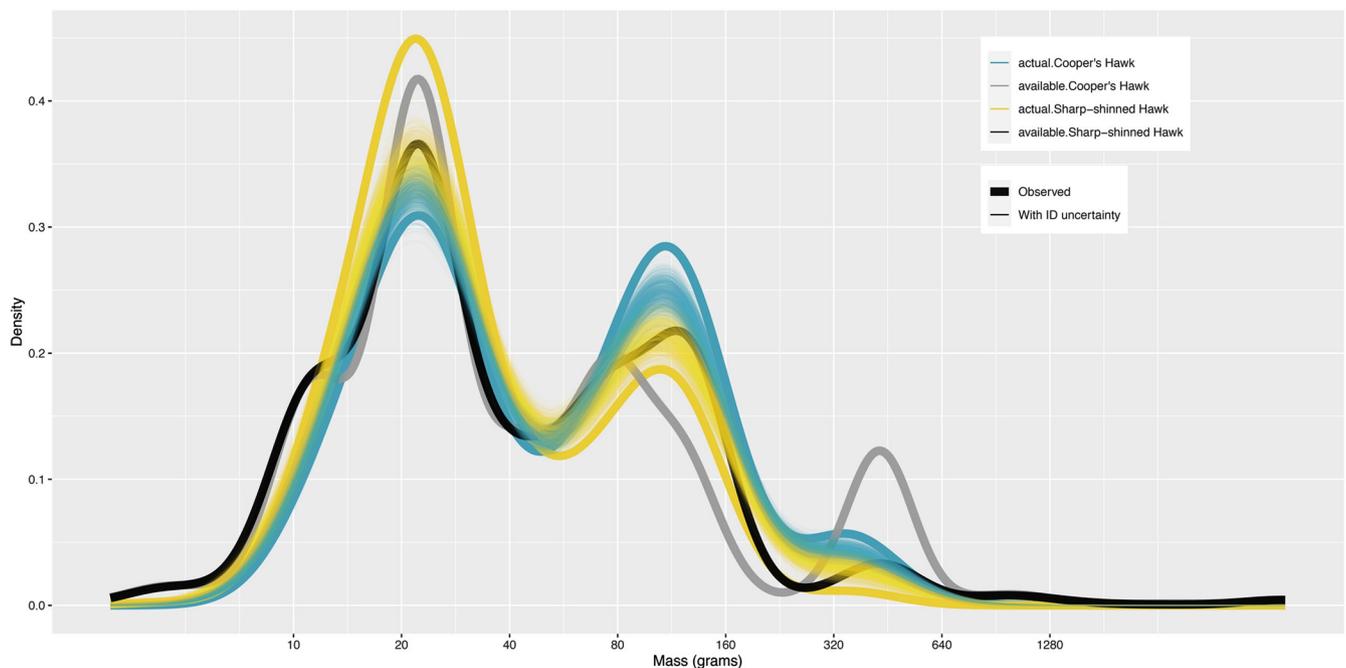

Figure 2. Observed versus available resource utilization functions for sharp-shinned and Cooper's hawks, as illustrated using kernel density estimates of prey abundance as a function of the natural logarithm of prey body mass. Observed values (thick blue and yellow lines) are based on reported depredation events at feeders. Available values (black and gray lines) are based on the abundances of prey species at the feeders visited by the predators in question. The thinner lines, which look light shading in the figure, depict the range of potential alternate distributions of these resource utilization functions after incorporating identification errors by participants.
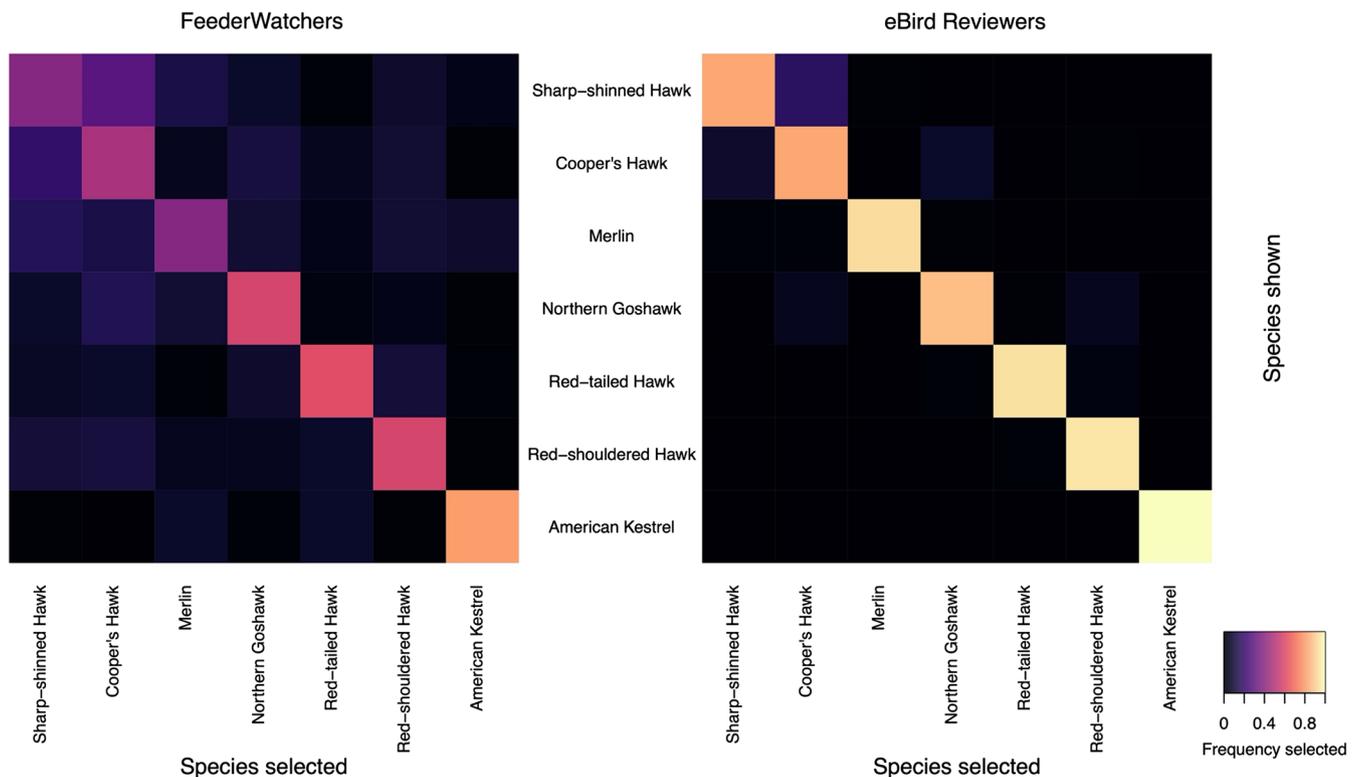
Figure 3. Heat maps of the species-level confusion matrices illustrating misidentification rates by FeederWatchers and expert eBird reviewers on the quiz. The true species that was presented in the photograph is shown along the rows, while the answer provided by participants is shown along the columns. Colors are comparable between heat maps. The brighter the color, the more frequently participants provided that answer. Example conclusions that can be seen in the figure include: reviewers generally scored better than FeederWatchers on the quiz (overall brighter colors along the diagonal); FeederWatchers were best able to identify American Kestrel to species; FeederWatchers periodically confused red-shouldered and red-tailed hawks; and quiz-takers from both groups most frequently confused sharp-shinned and Cooper's hawks.

their relative abundance at feeders. Prey species such as dark-eyed junco, pine grosbeak *Pinicola enucleator*, mourning dove, European starling *Sturnus vulgaris* and downy woodpecker *Dryobates pubescens* were targeted at particularly high rates, as quantified by their standardized effect sizes (Fig. 4). Using the average body mass of sharp-shinned hawks, these predators focused on prey that were on average 34% of the hawk's size.

Relative risk of predation for prey species

Qualitatively, factors aside from body mass explained some of the variation in predation risk (Fig. 4). For example, many finches (but not members of the genus *Spinus*), sparrows and other nine-primaried oscines (encompassed by the bottom four silhouettes in the figure) seemed at particular risk of depredation by sharp-shinned hawks, whereas chickadees and nuthatches appeared to be at a much lower risk. The phylogenetic signal of these patterns was not significant (Pagel's lambda = 0.06, p = 1). Quail and doves, on the other hand, seemed to be at particular risk of depredation by Cooper's hawks, and these patterns exhibited significant phylogenetic signal (Pagel's lambda = 0.64, p < 0.001).

Assessing the impact of observer misidentification

Of the 4674 quiz responses we received, 2018 were from confirmed participants of Project FeederWatch, 165 were confirmed expert eBird reviewers and 14 were both FeederWatchers and eBird reviewers. On average, eBird reviewers correctly identified 90% of photographs, while FeederWatchers correctly identified 54%. Reviewers correctly identified sharp-shinned and Cooper's hawks more frequently than FeederWatchers, but both groups confounded these two species more than other species (Fig. 3). FeederWatchers correctly identified 45% of sharp-shinned and 53% Cooper's hawk photos to species. Because our intentions were simply to provide a point of comparison for the identification skills of FeederWatchers and to understand more about potential rates of false positives in citizen science initiatives, we do not explore the similarities and differences between these citizen scientists further here. We used heatmaps to visualize the confusion matrix derived from the quiz results of FeederWatchers (Fig. 3). Adding this noise into our initial estimates to account for *Accipiter* identification uncertainty reduced the niche separation between the predators (thin blue and yellow lines in Fig. 2). However, the overall pattern of sharp-shinned hawks focusing on small prey, and
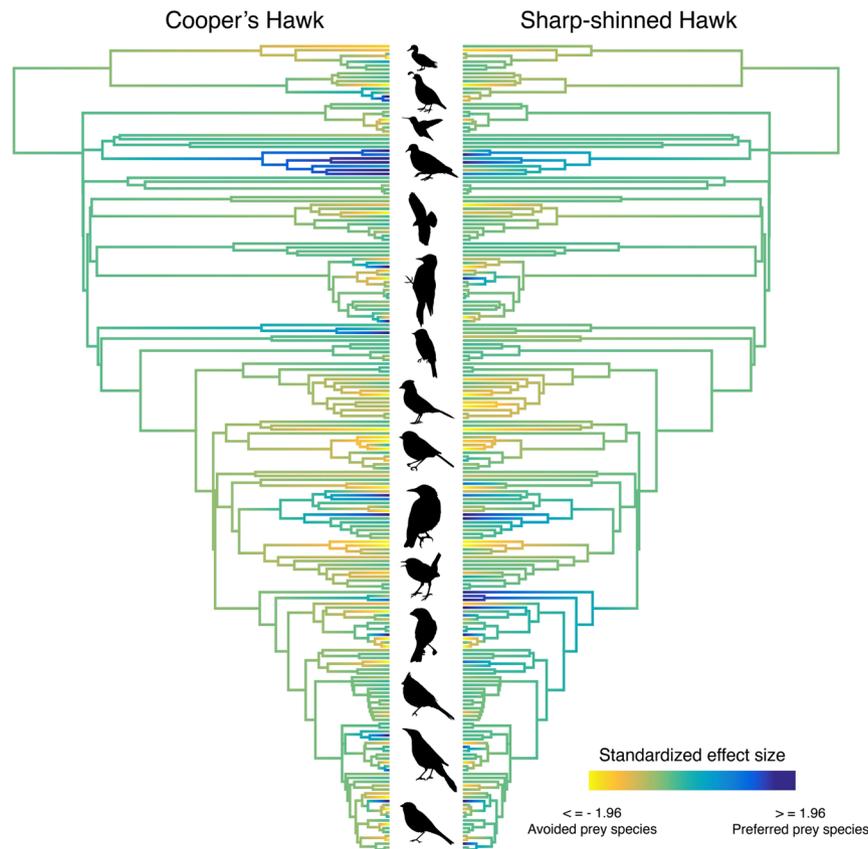
Figure 4. The standardized effect sizes (SES) of the predator–prey interactions between Cooper's and sharp-shinned hawks and potential prey species. Deep blue corresponds to species that were targeted at much higher rates than would be expected based on their abundances at feeders visited by the relevant predator species, whereas yellow corresponds to species that were targeted at much lower rates than would be expected. Sixteen species encountered by sharp-shinned hawks were never reported from feeders visited by Cooper's hawks, whereas 36 species encountered by Cooper's hawks were never reported from feeders with sharp-shinned hawks. These species were assigned the average SES across the relevant predator's range to facilitate arranging the trees in mirror fashion. Colored phylogenies created with *phytools* (Revell 2012), all bird silhouettes except northern cardinal *Cardinalis cardinalis* obtained from phylopic.org, used under Creative Commons licenses. These are used as indications of major clades in the phylogenies. From top to bottom, these are: Anatidae, Odontophoridae, Trochilidae, Columbidae, Accipitridae, Picidae, Tyrannidae, Corvidae, Paridae, Sturnidae, Troglodytidae, Fringillidae, Cardinalidae, Icteridae and Passerellidae. Northern cardinal silhouette created from a photograph by Brad Imhoff, Macaulay Library 185472461.

of Cooper's hawks exhibiting a bimodal resource utilization function remained evident in spite of the uncertainty in identification of predator species.

Discussion

In this study we defined resource utilization functions for the two broadly sympatric species of North American, bird-eating *Accipiter* species, the Cooper's hawk and sharp-shinned hawk. We also quantified prey availability for these hawks and compared availability and use to understand niche partitioning between them. Finally, we sought to quantify the rate at which these species may be confused for one another by citizen scientists, and to thereby understand the ramifications such misidentification might have on our conclusions. We found that the prey base, as defined by the abundance distribution by mass of potential prey species, is approximately

log-normal. However, prey availability was significantly multimodal: small-medium birds, e.g. those around the size of house finches, were by far the most common, but there was an additional peak in abundance of birds around the size of jays and grackles, and perhaps another, smaller peak in abundance of birds around the size of ducks, grouse and large pigeons (e.g. *Columba livia*, Fig. 2). Finally, while citizen scientists regularly confounded the study species, the rates at which they did so were not so high as to jeopardize our qualitative conclusions.

Sharp-shinned and Cooper's hawks appear to partition niche space, as defined by prey body mass, in a way that permits their coexistence. However, divergence between the predators is incomplete, and Cooper's hawks exploit prey in a bimodal fashion. While they often focus on larger prey items than sharp-shinned hawks, Cooper's hawks also broadly overlap with sharp-shinned hawks by regularly taking prey of smaller size (Fig. 2). Presumably, exploitation competition

from Cooper's hawks is a greater threat to sharp-shinned hawks than is the converse. Of course, smaller birds are more abundant, which therefore provides a larger resource base to divide between predators. Furthermore, at least during the breeding season, sharp-shinned hawks show a tendency to associate with coniferous and generally denser forests (Trexel et al. 1999), although during the non-breeding season both species associate with woodlands and urban areas where they overlap (Roth et al. 2008). Still, at the continental level it is clear that sharp-shinned is less of an urban denizen, even in the non-breeding season (see interactive habitat associations at Fink et al. 2021), and this tendency appears to influence the species selected as prey items by each – many of the species targeted by sharp-shinned, as measured by their standardized effect sizes, are infrequently found away from forests, including evening grosbeak *Coccothraustes vespertinus*, common redpoll *Acanthis flammea* and purple finch *Haemorhous purpureus* (Fig. 4). This habitat partitioning, although it is reduced in the wintering season (Roth et al. 2008, Fink et al. 2021), presumably further diminishes competition between the two predators.

The degree to which this spatial segregation may be driven by anthropogenic causes is of interest (Roth and Lima 2003, Millsap 2018). In particular, over the past few decades, Cooper's hawks have shown a remarkable ability to colonize urban areas (Boal and Mannan 1999, Stout and Rosenfield 2010, McCabe et al. 2018), such that at least some of these areas now function as source populations for surrounding non-urban habitats, especially in winter (Roth and Lima 2003, Roth et al. 2008, Millsap 2018). Sharp-shinned hawks can be found in urban areas (Viverette et al. 1996), but a rapidly increasing urban presence appears to be particularly pronounced in Cooper's hawks (other species, e.g. *A. nisus* are also increasing in urban areas, Bell et al. 2010). Of interest in that respect is the northern goshawk *A. gentilis*, which is generally a forest-based, non-urban species (although populations in Europe do use fragmented habitats to some degree, Squires et al. 2020). We did not quantify its resource utilization function here owing to the small sample size of observed depredation events by goshawks in our dataset. However, based on other studies, we know that the species tends to focus on larger prey than either Cooper's or sharp-shinned hawks, and regularly includes mammals in its diet (Reynolds and Meslow 1984, Boal and Mannan 1996). Like Reynolds and Meslow (1984), we conclude that sharp-shinned hawks appear to primarily select prey from the smallest, most abundant end of the prey availability axis, and that Cooper's hawks and northern goshawks focus on larger prey, with greater caloric rewards, but do occasionally take smaller prey (i.e. Cooper's hawks will regularly take sparrow-sized prey, and northern goshawks will regularly take dove-sized prey). Thus, while the increase in urban Cooper's hawks is likely driven primarily by large local abundances of appropriate dove-sized prey (Millsap 2018), this urban increase could also be fueled in part by competition 'from both sides' of the resource axis (if, for example, there is less non-urban habitat in general available to *Accipiter* species), which might have driven

Cooper's hawks, over a very short evolutionary timescale, to adapt to urban habitats. In that regard, exploring population connectivity between urban and rural populations is of particular interest – results to date suggest that urban populations are indeed a source for non-urban areas (Millsap 2018).

Relative predation risk for prey species appears only weakly related to body mass, and some species of appropriate body mass were targeted at notably low rates (Fig. 4). For example, Cooper's hawks showed a pronounced penchant for quail and doves, including the expanding, frequently urban-dwelling white-winged dove *Zenaida asiatica*. Sharp-shinned hawks favored nine-primaried oscines like sparrows and some finches, while seeming to eschew other, similar-sized passerines like chickadees and nuthatches. A number of previous studies have addressed the question of predation risk (Reynolds and Meslow 1984, Götmark and Post 1996, Roth and Lima 2003, 2007, Roth et al. 2006, Chamberlain et al. 2009). These studies found that predation risk is attributable to low foraging heights (Götmark and Post 1996), long distances to cover when foraging (Whitfield 2003) and not foraging in flocks (Cresswell 1994). Of these, our results suggest that foraging on the ground is particularly dangerous for prey species; when visiting feeders, doves, quail, sparrows and some finches all routinely forage on the ground. Distance to cover is presumably similar for all species visiting a given feeder, and therefore probably not a relevant factor in explaining variation in predation risk in our study. The relevance of flocking behavior is, with the current data, difficult to assess. It is possible, for example, that species like chickadees and nuthatches visit the feeder as part of mixed species flocks, with sentinels whose alarm calls reduce predation risks for flock members (Goodale and Kotagama 2008). Such questions await analysis with a more suitable dataset.

A source of uncertainty in our conclusions is our focus on bird feeders, and on birds as prey. In some areas, mammals comprise a small but not insignificant proportion of Cooper's hawk diet (16% or less of total diet in 6 of 12 studies summarized in Rosenfield et al. 2020, but 29–70% in the remaining studies). Thus, the partial niche differentiation we detected here is liable to be larger in reality, as sharp-shinned hawks very rarely take mammals (Reynolds and Meslow 1984, Roth et al. 2006, Bildstein et al. 2020). Our focus on birds as prey likely explains the small average size of Cooper's hawk prey (15% of adult size in our study) as compared with previous studies that did include mammal prey (Lake et al. 2002, Rosenfield et al. 2020). While our focus on predation events near bird feeders somewhat limits our conclusions, we note that previous studies have found that accipiters appear to exploit feeders frequently but opportunistically, and that they do not depend on feeders (Dunn and Tessaglia 1994, Roth et al. 2008). Thus, our conclusions likely represent a limited but reasonable approximation of the prey availability and resource utilization functions at feeders in winter of these sympatric, size-differentiated *Accipiter* species across the continent of North America. We have conducted preliminary investigation of body mass distributions in winter in North America using eBird data (Sullivan et al.

2014, Johnston et al. 2021) – a non-feeder-focused sampling protocol – and found a similar size-abundance distribution, although feeders underestimate the regional abundance of large-bodied waterbirds like ducks and geese.

Another source of uncertainty in our conclusions was observer misidentification of predator species. Given that these accipiters are known to be difficult to distinguish from one another – indeed they are often lumped for analyses with FeederWatch data (McCabe et al. 2018, Bonter and Greig 2021) – we explicitly accounted for this uncertainty by testing observers on their ability to successfully identify the study species (Fig. 3). We found that our conclusions were robust to this source of error (thin lines in Fig. 2), and we suggest that an even more extreme rate of misidentification than what we observed would not dramatically alter our overall conclusions. A robust comparison of quiz misidentification rates between participant groups is beyond the scope of the current study, but based on a qualitative exploration of the results, photographs of juveniles and birds in flight appeared to present the most identification difficulty. FeederWatch participants would presumably score much closer to expert reviewers on their identification skills with common feeder birds. Unfortunately, our methodology is somewhat limited in that a photograph provides a static image an observer can study in detail, but lacks the size or behavioral characteristics observers might use in the field; the identification process is admittedly different between the photo versus field methods. Furthermore, it is entirely possible that a complex interaction exists between the predator identification provided by a FeederWatcher, and the prey species a predator was observed attacking. If so, the quiz approach would be unable to detect this bias. Nevertheless, our study is one of the first attempts to directly quantify these false positive rates in citizen science data, and we believe it offers a fairly accurate and somewhat cautionary perspective on the issue. Understanding the intricacies of the covariance of misidentification rates with observer expertise (Johnston et al. 2018) will likely prove important to future efforts to accurately use citizen science data for research.

Globally, the genus *Accipiter* contains repeated instances of broadly sympatric, similar looking species that differ notably in size. Repeated patterns in sexual size dimorphism also appear to exist (Dunning 2007). A number of competing hypotheses seek to explain *Accipiter* sexual dimorphism, including resource partitioning between the sexes and the utility of large female size for nest defense (Andersson and Norberg 1981, Kennedy and Johnson 1986, Boal and Mannan 1996). It seems possible that the distinct modes in resource use which we see here in Cooper's hawks may be due in part to partitioning of resources between the sexes (Millsap et al. 2013, Panter and Amar 2021), but we are unable to address that here. These repeated inter- and intra-specific patterns of body size raise the question of whether these recurrent *Accipiter* assemblages are composed of species that have converged in plumage but come from lineages distinguished by size (i.e. similarly sized species in different regions are more recently diverged from one another than are

differently sized species within regions), or whether these represent parallel regional radiations from an ancestral *Accipiter* that radiated into their modern, different-sized forms (i.e. differently sized species from the same region are more recently diverged from one another than are similarly sized species in different regions). These patterns also raise the question of whether co-occurring species exhibit similar plumages as a function of close evolutionary relationships, or whether there might be interspecific mimicry involved (Leighton et al. 2018, Miller et al. 2019).

While our study only examined two species of *Accipiter* hawks in North America, our findings lead to interesting conjectures about this genus of raptors around the globe. The aforementioned multimodal distribution in prey abundance by body mass may, if manifest on other continents, generate the rugged adaptive landscape that has led to these replicated patterns of *Accipiter* sympatry; there may well be discrete niches into which *Accipiter* species have evolved repeatedly across the globe. Alternatively, it is possible that a finite, log-normally distributed resource base such as the body masses of potential avian prey items leaves limited options for partitioning. It may simply be the case that, across the globe, two or more *Accipiter* species have found themselves in regional sympatry (either as the result of in-situ speciation or multiple colonizations), and that, given the limitations of the resource base and the lack of dimensions available for partitioning, only a handful of bird-eating predators are able to coexist (MacArthur and Levins 1967). Both of these mechanisms could be relevant, and we look forward to future studies, including sorely lacking phylogenetic work, that shed light on the relationship between resource use and availability in other sympatric *Accipiter* species. For now, we conclude that discrete niches do indeed exist for North American accipiter species, and that sharp-shinned and Cooper's hawks have filled these in a way that permits their coexistence; they do not display complete niche differentiation, but they show divergent resource utilization functions as quantified by prey body mass.

Author contributions

Eliot Miller: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Project

administration (equal); Software (equal); Validation (equal); Visualization (equal); Writing – original draft (equal); Writing – review and editing (equal). **Oisin Mac Aodha**: Formal analysis (equal); Methodology (equal); Resources (equal); Software (equal); Writing – original draft (equal); Writing – review and editing (equal). **Emma Greig**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **David Bonter**: Funding acquisition (equal); Project administration (equal); Resources (equal); Supervision (equal); Writing – original draft (equal); Writing – review and editing (equal). **Wesley Hochachka**: Formal analysis (equal); Funding acquisition (equal); Methodology (equal); Resources (equal); Supervision (equal); Validation (equal); Writing – original draft (equal); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.w6m905qs8> (Miller et al. 2022).

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