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DNA SEQUENCING REVEALS PATTERNS OF PREY SELECTION IN MIGRATING SHARP-SHINNED HAWKS

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Abstract. Prey selection of migrating raptors has been documented only rarely. Here we used a genetic approach to identify avian prey of Sharp-shinned Hawks (*Accipiter striatus*) migrating through central New Mexico. We identified species by comparing profiles of a section of the 16S rRNA mitochondrial gene extracted from feathers of prey of known species to profiles from feathers of prey found on the feet and beaks of migrating hawks. We also quantified prey availability along the migration route with multi-year sampling by mist net at two sites near the raptor-sampling site. Sharp-shinned Hawks took most prey species in proportion to their availability, but they took some species, particularly medium-sized species, more frequently than expected. This pattern may indicate selection for energetically rewarding prey, or the pattern also could arise from differences between our sample of potential prey and the potential prey as viewed by the hawks themselves. The co-occurrence of migrating predators and their prey suggests interesting feedbacks that likely influenced the evolution of migration strategies of both hawks and songbirds in this area.

Key words: Sharp-shinned Hawk, Accipiter striatus*, predator–prey dynamics, migration strategy, optimal foraging, DNA barcoding, coevolution.*

Las Secuencias de ADN Revelan Patrones de Selección de Presas por Individuos Migratorios de *Accipiter striatus*

Resumen. La selección de presas por parte de rapaces migratorias ha sido raramente documentada. Aquí empleamos un enfoque genético para identificar las aves presa de individuos de *Accipiter striatus* migrando a través de Nuevo México. Identificamos las especies comparando los perfiles de una sección del gen mitocondrial ARNr 16S extraído de plumas de presas de especies conocidas con los perfiles de plumas de presas encontradas en las patas y picos de los halcones migratorios. También cuantificamos la disponibilidad de presas a lo largo de la ruta migratoria con muestreos multianuales con redes de niebla en dos sitios cercanos al sitio de muestreo de las rapaces. Los individuos de *A. striatus* tomaron la mayoría de las especies de presas en proporción con sus disponibilidades, pero tomaron algunas especies, particularmente especies de tamaño intermedio, más frecuentemente que lo esperado. Este patrón puede indicar la selección de presas energéticamente más provechosas, o el patrón también podría emerger de diferencias entre nuestro muestreo de presas potenciales y las presas potenciales desde la perspectiva de los halcones. La presencia conjunta de depredadores migratorios y de sus presas sugiere retroalimentaciones interesantes que probablemente influenciaron la evolución de estrategias migratorias de los halcones y las aves canoras en esta área.

INTRODUCTION

Birds use a variety of strategies to meet the energetic demands of migration (Bairlein and Gwinner 1994). Food is not always available along migration routes, so some birds store energy in fat reserves built up prior to migration (Blem 1980). Others meet energy demands by alternating bouts of fueling at stopover sites with flights between stopover sites (Schaub et al. 2008). Less commonly, food may be well distributed along the route, enabling opportunistic foraging along the way (Bairlein and Gwinner 1994).

Many migratory raptors fall into this latter category, especially those that specialize on avian prey (Dekker 1980, Moore et al. 1990, Yosef 1996, Ydenberg et al. 2007). Although migrating raptors may use wind lift and thermals to reduce energetic expenditures (Kerlinger 1989), the acquisition of food energy is crucial for fueling flapping flight and surviving the migratory journey. Because many potential prey along the migratory route also are migrating (Ydenberg et al. 2007), the foraging tactics of migrating raptors must be integrated with other objectives such as minimizing time or energy (Alerstam and Lindstrom 1990, Spaar

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et al. 1998) as well as responsive to the migration and risk-avoidance strategies of the prey.

Despite the potential for predator–prey interactions to influence migration strategies, we know little about the prey selection of most migrating raptors. This lack of knowledge is primarily technical in origin, as standard methods for identifying raptors' prey selection, such as collecting prey remains at nests, cannot be used during migration (Stahlecker et al. 2009). Brief observations of passing migrants typically reveal that migrating raptors have distended crops and therefore do forage en route, but observations that enable us to quantify prey selection during migration are rare (but see Dekker 1980).

Sharp-shinned Hawks (*Accipiter striatus*) forage primarily on woodland and savanna birds (Bildstein and Meyer 2000) and are commonly seen over ridges at migration-monitoring sites throughout North America. In this study, we used a genetic approach (barcoding) to identify the prey taken by migrating Sharp-shinned Hawks. The technique involved collecting prey remains from the feet of hawks captured while passing a monitoring site and comparing nucleotide sequences extracted from these remains to reference samples collected from potential prey species in the area. We also compiled data on potential prey in the area where the hawks were migrating to examine prey selection in relation to prey availability.

METHODS

Researchers captured Sharp-shinned Hawks near Capilla Peak in the Manzano Mountains of central New Mexico at the long-term migration-monitoring site operated by HawkWatch International (Hoffman and Smith 2003). Sharp-shinned Hawks using this flyway originate in the Rocky Mountains from Alaska south through New Mexico and winter primarily in Mexico (Hoffman et al. 2002, Smith et al. 2003). Researchers lured migrating Sharp-shinned Hawks into stations with live lures and captured them in bow nets, mist nets, and dho-gaza nets (DeLong and Hoffman 1999, Hoffman et al. 2002). They fitted each hawk with an aluminum leg-band, identified its age and sex, and examined both the feet and beak for prey feathers stuck with dried blood (Fig. 1). If such feathers were present, researchers removed them and stored them in paper envelopes for later analysis.

Other researchers sampled potential avian prey in the area at two sites, one near the raptor-banding site at Capilla Peak (DeLong et al. 2005) and the other 35 km north of Capilla Peak in the foothills of the Manzanita Mountains near Coyote Springs. The mist-netting site at Capilla Peak was ~1 km from the primary raptor-banding site along the same ridge complex used by migrating raptors. Migrating raptors frequently passed through the netting area, hunted in the vicinity, and were occasionally captured in the mist nets. The Coyote Springs mist-netting site was in the same mountain range as Capilla Peak, with raptors known to pass through the area before arriving at Capilla Peak. Thus prey sampled

FIGURE 1. (A) A hatch-year Sharp-shinned Hawk captured at Capilla Peak in the Manzano Mountains, New Mexico, with distended crop, indicating recent prey capture and consumption. (B) Close-up of feet of the same bird, showing feathers of prey stuck to toes and talons. Photographs by Zachary M. Hurst.

from this area represented potential prey at a lower elevation shortly before the hawks arrived at Capilla Peak.

Rio Grande Bird Research operates the Capilla Peak songbird-banding site annually. Each year during this study they deployed up to 20 mist nets in a range of representative habitats (conifer and deciduous woodlands, meadows, and edge habitats) and opened the nets 1–2 days per week (DeLong et al. 2005). Sandia National Laboratories operates the Coyote Springs mist-netting site and during this study deployed 10 mist nets one day per week in a variety of habitats, including scattered pinyon–juniper (*Pinus edulis–Juniperus monosperma*) woodland and shrubland dominated by chamisa (*Ericameria nauseosa*) and four-winged saltbush (*Atriplex canescens*). At both sites, banders identified captured birds to species and weighed them to the nearest 0.1 g with an electronic scale.

Songbird sampling began in summer months, but for our analyses we used only data from September and October, which is the period when most Sharp-shinned Hawks migrate through the study area (DeLong and Hoffman 1999). We used songbird data recorded at Capilla Peak from 2000 to 2008 and at Coyote Springs from 2003 to 2010. These potential-prey datasets included 2621 birds banded at Capilla Peak and 1347 birds banded at Coyote Springs. Sampling bias was minimized because of our inclusion of two sites, our placement of multiple nets in a wide range of habitats at each site, and our sampling over 7–8 years. We used these datasets to generate relative abundances for potential prey species and mass-frequency distributions for all banded individuals at each site. For each potential prey species, we calculated the average body mass across all individuals captured at both sites and assigned the average mass for the species to individuals for which no mass was recorded.

We gathered reference feathers (all body feathers) from potential prey species captured at Capilla Peak or Coyote Springs or collected from the lures used to capture the hawks, and we stored the feathers in paper envelopes for later analysis. The reference feather set included 103 feathers from 57 species, representing broad coverage of the potential prey in the area. Some species were missing from the sample, including swifts, swallows, and hummingbirds, and although swallows and hummingbirds are sometimes taken as prey, they do not constitute a large part of the Sharp-shinned Hawk's diet (Joy et al. 1994). For most species we obtained feathers from two or three individuals to broaden the genetic sampling.

We sent feathers to Wildlife Genetics, Inc. (Nelson, British Columbia, Canada), who extracted DNA with Qiagen DNeasy tissue kits and used single-track (adenosine) sequence methods (Hahn et al. 1993) to create profiles for a section of the 16S rRNA mitochondrial gene. This gene is useful for species identification because of a combination of highly conserved and variable regions (Vences et al. 2005). The approach used short (210 ± 3 bp, depending on species) nucleotide sequences in a hypervariable region to differentiate species. The test works well with sparse genetic material because the short region amplifies strongly (Moura et al. 2011), which is important because feathers were frequently very small and therefore did not produce large amounts of genetic material. The profiles from the unknown samples could then be compared to those of the reference samples to identify the unknown prey species. Finally, we used chi-squared tests to compare the relative frequency of each species in the prey sample to that in the mist-net sample.

RESULTS

We collected prey-feather samples from 72 Sharp-shinned Hawks captured during autumn migration from 2004 to 2008. The genetics lab conclusively identified the species of 50 of these samples (Table 1). Two were Sharp-shinned Hawk feathers, which we eliminated from the analyses. The remaining 20 analyses were inconclusive, meaning the feathers were identified to less precise taxonomic levels, such as sparrow or woodpecker, or produced real unknowns, which were either atypical genetic variants of species sampled as part of the reference set or species not included in the reference set. Here we consider only data where the identity of the prey was confirmed to species.

The most commonly observed prey were the American Robin (*Turdus migratorius, n* = 9) and Hermit Thrush (*Catharus guttatus, n* = 7). Sharp-shinned Hawks took these species more frequently than expected given their abundance at the Capilla Peak and Coyote Springs sites (Fig. 2, Table 1). The hawks took some of the most common potential prey species, such as the Dark-eyed Junco (*Junco hyemalis*), Chipping Sparrow (*Spizella passerina*), and Wilson's Warbler (*Cardellina pusilla*), less than expected or in proportion to their abundance, and they took most other species in proportion to their abundance (Fig. 2, Table 1).

Species taken more often than expected tended to be relatively large (Fig. 3). Both of the two most common prey species were larger than most potential prey, and the hawks also took several other relatively large prey species, including the Western Scrub-Jay (A*phelocoma californica*), Western Tanager (*Piranga ludoviciana*), and Spotted Towhee (*Pipilo maculatus*).

Overall, patterns of prey selection with respect to potential prey were similar at Capilla Peak and Coyote Springs (Figs. 2 and 3). Some identified prey species do not typically occur at Capilla Peak but are more common at lower elevations, including the Ladder-backed Woodpecker (*Picoides scalaris*), Rock Wren (*Salpinctes obsoletus*), and Bullock's Oriole (*Icterus bullockii*). We also identified the House Sparrow (*Passer domesticus)* as prey of two hawks. House Sparrows are abundant as potential prey in the urban and near-urban savannas at lower elevations. Although we captured

TABLE 1. Species and frequency of prey identified with nucleotide sequence comparisons (barcoding) for Sharp-shinned Hawks migrating through the Manzano Mountains of central New Mexico, and comparisons to the relative abundances of prey species as documented by mist netting at Capilla Peak and Coyote Springs. Significant differences in relative abundance are in bold. Dashed cells indicate species that were not detected as potential prey at either site.

		Capilla Peak			Coyote Springs		
Prey species	n	Relative abundance	χ^2	P	Relative abundance	χ^2	P
American Robin *Turdus migratorius*	9	0.001	400.5	**<0.001**	0.028	36.1	**<0.001**
Brown-headed Cowbird *Molothrus ater*	1	—	—	—	—	—	—
Bullock's Oriole *Icterus bullockii*	1	—	—	—	—	—	—
Chipping Sparrow *Spizella passerina*	3	0.038	0.78	0.38	0.138	2.26	0.13
Dark-eyed Junco *Junco hyemalis*	6	0.317	8.05	**0.005**	0.106	0.17	0.68
Green-tailed Towhee *Pipilo chlorurus*	1	0.005	2.28	0.13	0.021	0.00	1.00
Hermit Thrush *Catharus guttatus*	7	0.049	9.10	**0.003**	0.009	64.7	**<0.001**
House Sparrow *Passer domesticus*	2	—	—	—	—	—	—
Ladder-backed Woodpecker *Picoides scalaris*	1	—	—	—	—	—	—
MacGillivray's Warbler *Geothlypis tolmiei*	2	0.031	0.18	0.67	0.008	5.63	**0.018**
Northern Mockingbird *Mimus polyglottos*	1	—	—	—	0.001	13.1	**<0.001**
Orange-crowned Warbler *Oreothlypis celata*	1	0.046	0.69	0.40	0.007	1.07	0.30
Red-breasted Nuthatch *Sitta canadensis*	1	0.017	0.04	0.85	0.003	4.14	**0.042**
Rock Wren *Salpinctes obsoletus*	1	0.000	26.3	**<0.001**	0.003	4.14	**0.042**
Spotted Towhee *Pipilo maculatus*	2	0.002	24.5	**<0.001**	0.029	0.26	0.61
Townsend's Warbler *Setophaga townsendi*	1	0.067	1.61	0.20	0.029	0.11	0.74
White-crowned Sparrow *Zonotrichia leucophrys*	1	0.013	0.20	0.66	0.013	0.25	0.62
Western Scrub-Jay *Aphelocoma californica*	2	0.001	52.7	**<0.001**	0.006	8.31	**0.004**
Western Tanager *Piranga ludoviciana*	2	0.002	28.5	**<0.001**	0.002	20.2	**<0.001**
Wilson's Warbler *Cardellina pusilla*	3	0.112	1.18	0.28	0.042	0.50	0.48

many Sharp-shinned Hawks by using House Sparrows as a lure, these two hawks were captured with Ring-necked Doves (*Streptopelia capicola)* as the lure species, so we concluded that these feathers represented real instances of predation. Female hawks took prey that averaged larger than prey taken by males ($t = 2.24$, df = 48, $P = 0.03$). Both sexes took small prey (down to 7 g), but males' prey was all less than ~80 g, whereas females' prey ranged up to ~92 g.

DISCUSSION

Many raptors hunt during the course of their migrations (Dekker 1980, Clark 1985, Candler and Kennedy 1995, Yosef 1996; Ydenberg et al. 2007). To fuel their journeys, regular foraging must take place, as hawks typically do not carry large fat reserves (DeLong and Hoffman 2004). At Capilla Peak, for example, Sharp-shinned Hawks carry only enough fat reserves to survive a few days of normal activity (DeLong and Hoffman 2004). Although we have seen many hawks at migration sites with distended crops that indicate recent foraging, previously only incidental observations of prey selection associated with such foraging have been documented. For example, we have observed migrating raptors taking prey at the Capilla Peak site, but rarely, and with identification of the prey species usually not possible.

Using nucleotide sequence comparisons (barcodes), we quantified prey selection of actively migrating Sharp-shinned Hawks (Table 1). Most of the prey species we documented have been reported as Sharp-shinned Hawk prey in previous studies that were focused on breeding or other seasons (Storer 1966, Duncan 1980, Reynolds and Meslow 1984, Joy et al. 1994). Typically, thrushes, warblers, and sparrows tend to be numerically important in the diet of the Sharp-shinned Hawk, which is consistent with our results. Although the American Robin and Hermit Thrush were the most common species in our migration sample, warblers and sparrows often surpassed them numerically outside of migration. We also detected three prey species previously unreported for the Sharp-shinned Hawk: Townsend's Warbler (*Setophaga townsendi*), Bullock's Oriole, and Ladder-backed Woodpecker.

Our results indicate that migrating Sharp-shinned Hawks take most prey species in proportion to their abundance, regardless of whether they forage at higher-elevation sites such as Capilla Peak or at lower-elevation sites such as Coyote Springs. This result makes sense because accipiters tend to be strongly opportunistic hunters, as judged by their willingness to quickly

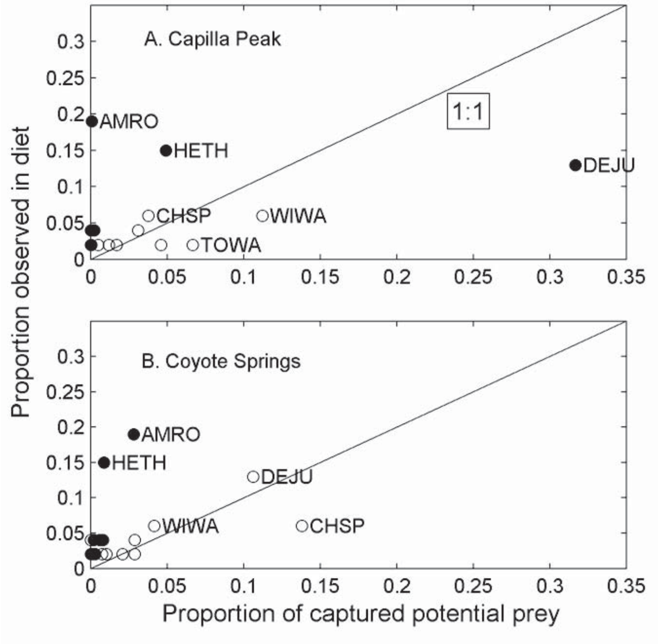

FIGURE 2. Comparison of the relative abundances of prey species observed in the diet of Sharp-shinned Hawks captured during autumn migration at Capilla Peak in the Manzano Mountains of central New Mexico in relation to the relative abundances of potential prey species as determined by mist netting at (A) Capilla Peak and (B) Coyote Springs. Points close to the 1:1 line indicate prey species taken roughly in proportion to their abundance, points well above this line indicate species taken more often than expected from their abundance (i.e., AMRO = American Robin and HETH = Hermit Thrush), and points well below this line indicate species taken less often than expected from their abundance (i.e., DEJU = Dark-eyed Junco). Other common species: WIWA = Wilson's Warbler, TOWA = Townsend's Warbler, CHSP = Chipping Sparrow. Black points indicate significant differences between observed and expected relative abundances.

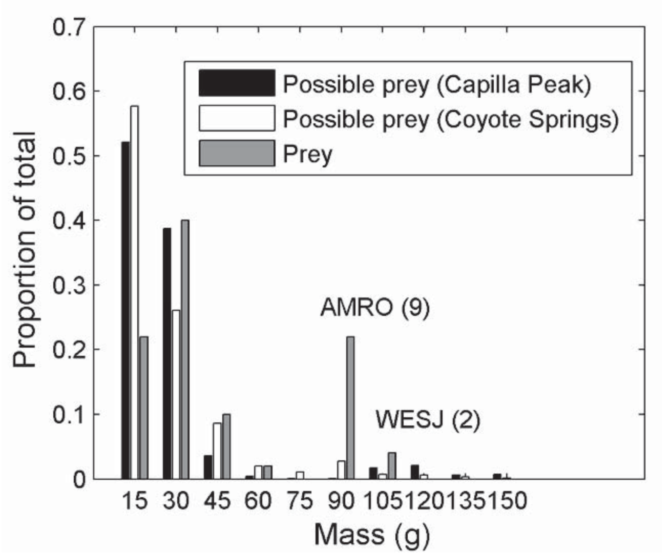

FIGURE 3. Mass distributions of prey taken by Sharp-shinned Hawks captured during autumn migration in the Manzano Mountains, New Mexico, compared to the mass distributions of potential prey as determined by mist netting at nearby Capilla Peak and Coyote Springs. Relatively heavy prey species (with number in sample in parentheses) are highlighted, including the American Robin (AMRO) and Western Scrub-Jay (WESJ). Labels on x axis indicate upper mass for bin in 15-g increments (e.g., 15 for 0–15 g).

change course and attack lures at banding stations and by the very long list of previously reported prey species (Reynolds and Meslow 1984, Joy et al. 1994). Nonetheless, deviations from this pattern were strong for the American Robin and Hermit Thrush, which were taken as prey more often than would be expected from their abundance at either site, by both males and females. Similarly, several other species, although not common in the diet, were taken more often than expected given their abundance. In nearly all of these cases, these species also were relatively large compared to the overall distribution of prey sizes available at both Capilla Peak and Coyote Springs (Fig. 3).

Sharp-shinned Hawks migrating through the Manzano Mountains therefore show some inclination to feed upon relatively uncommon and large prey. The reason for this is unclear, but we suggest four possibilities that are not mutually exclusive. First, these larger prey may be energetically more rewarding than smaller prey. Selecting larger prey would be consistent with an optimal foraging strategy whereby hawks maximize energy intake per hunting attempt or hunting time by focusing on larger prey (Charnov 1976). This strategy is most likely to be employed when prey are abundant because when prey are scarce, foragers should take whatever they can get. Gil and Pleguezuelos (2001) made a similar argument for the selection of relatively large prey by Short-toed Eagles (*Circaetus gallicus*) in Spain.

Second, it is possible that the selection of these larger, relatively uncommon prey species may be related to habitat use by the prey. Some of these prey species, including the American Robin, Western Scrub-Jay, and some towhees, often are found in woodland edges or shrublands rather than in closed-canopy forests. In these more open habitats, migrating hawks may more easily detect them, increasing their relative availability as prey. We think this possibility is less likely than the optimal-foraging possibility, because two other species that are common in the area, the Dark-eyed Junco and Chipping Sparrow, also are found in open and edge habitats in the area, yet they were taken either in proportion to their abundance or less than expected. Also, Hermit Thrushes typically are found in forest cover but were common prey.

Third, some size classes of prey may be easier to capture than others. Because of the potential effects of size-dependent escape speeds and maneuverability, it is possible that the size classes of prey Sharp-shinned Hawks selected were more vulnerable to predation than were either larger or smaller birds. We think this possibility also is unlikely, because smaller birds are often more numerically important in the Sharp-shinned

Hawk's diet during the breeding season (Joy et al. 1994), and maneuverability of both predator and prey is presumably similar at all seasons.

Fourth, it is possible that the data on potential prey are biased in some way. Mist netting may undersample some potential prey species, especially those that spend most of their time above the canopy where there were no mist nets to sample them. This may be most likely for American Robins, which sometimes pass through the sites in flocks above the canopy; however, this is not the case for Hermit Thrushes. Moreover, the robin's low abundance indicated by mist-netting data is qualitatively in agreement with our general observations in the study areas. On the other hand, many species may be well sampled by mist nets but appear relatively unavailable from the point of view of the hawks. This may be particularly true for small species, including warblers, vireos, and kinglets, many of which occur in dense vegetation at these sites. Such vegetation would make for difficult hunting and could mask the presence of many of these individuals to passing hawks. Thus, from the point of view of the hawks, the size distribution of potential prey may be somewhat less highly skewed toward small species than is shown in Fig. 3. Furthermore, the precise timing of passage of the Sharp-shinned Hawk and potential prey species could influence prey availability, but much additional sampling will be required for these finer-scale timing issues to be assessed.

The co-occurrence of migratory songbirds and bird-eating raptors at the Capilla Peak migration site may have led to co-evolution of migratory strategies. Predation risk should influence songbirds' migration strategies (Cimprich et al. 2005, Edelaar and Wright 2006, Ydenberg et al. 2007). Songbirds migrating through the Manzano Mountains may choose to forage or rest in relatively safe habitats such as dense oak woodlands, which would then alter the prey landscape for migrating hawks, perhaps inducing a reciprocal change in the hawks' strategy for hunting or migration. Alternatively, timing differences between songbirds and hawks may arise. Presumably, however, hawks could then adjust their timing to track that of their prey (Aborn 1994). In short, we suspect that the migratory strategies of raptors and songbirds reflect the presence of each other, but it is still unclear exactly how this plays out. Songbirds and raptors co-occur at other montane migration bottlenecks as well (Carlisle et al. 2004), suggesting that the problem of co-evolving migratory strategies may be integrated over broad geographical areas.

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