# COMPARATIVE DIET ANALYSIS OF BARN OWL (*TYTO ALBA*) AND LONG- EARED OWL (*ASIO OTUS*) IN A HABITAT ISLAND IN NORTH-CENTRAL TEXAS

# Jaime E. Jiménez<sup>1,2,\*</sup>, Matthew K. Jones<sup>1</sup>, Kaitlyn Stoddart<sup>1</sup>, Sentell Dickson<sup>1</sup>, Abigail Chapman<sup>1</sup>, Jaime L. Baxter-Slye<sup>1,2</sup>, and Kenneth L. Steigman<sup>1,2</sup>

<sup>1</sup>Department of Biological Sciences, University of North Texas, Denton, TX 76203 <sup>2</sup>Advanced Environmental Research Institute, University of North Texas, Denton, TX 76203 \*Corresponding author; Email: Jaime.Jimenez@unt.edu

Abstract.–Predator-prey interactions often define the coexistence of species in space and time. In this research, we are filling a regional gap in knowledge of diet composition of the barn owl (Tyto alba) and the long-eared owl (Asio otus). The study was conducted at the Lewisville Lake Environmental Learning Area (LLELA), a patch of tallgrass prairie and post oak forest surrounded by areas with large anthropogenic modifications in north-central Texas. We examined the remains found in owl pellets collected September 2016 to March 2017. Small mammals, mainly rodents, constituted 100% of the T. alba and 98.5% of the A. otus diet. The hispid cotton rat (Sigmodon hispidus) was the most common prev detected (68.2% for T. alba and 89.0% for A. otus). Diet niche breadth of T. alba was broader than that of A. otus (0.47 and 0.06, respectively), whereas mean prev size was smaller in the T. alba diet. Diet overlap between these owls was high (0.96), likely because they hunt similarly at night, on the wing, and the prey species have limited diversity. Most rodents eaten were juveniles and the sex ratio of prey was even in both owls' diets. We highlight the value of conducting studies in such a unique and relatively pristine environment in the face of multiple threats. Additionally, although the occurrence of A. otus is rare and infrequent in the study area, we were still able to detect a difference in diet between the ubiquitous T. alba and A. otus.

Keywords: predator-prey, small mammals, owl pellet, prairie

The study of predator-prey relationships and interactions among members of the same guild are central topics for understanding the functioning of biotic communities and the biogeographical distribution of species (Root 1967). Adding to this complexity, human impacts on ecosystems disrupt these interactions, as well as the

Recommended citation:

Jiménez, J.E., M.K. Jones, K. Stoddart, S. Dickson, A. Chapman, J.L. Baxter-Slye & K.L. Steigman. 2020. Comparative diet analysis of Barn Owl (*Tyto alba*) and Long-eared Owl (*Asio otus*) in a habitat island in north-central Texas. Texas J. Sci. 72: Article 5. https://doi.org/10.32011/txjsci\_72\_1\_Article5

stability and resilience of natural communities (Chapin et al. 2000). For example, native species are generally drawn into areas isolated from human activities in regions that otherwise are affected by human presence. Aside from the local resident species, those migratory in particular, seek out these patches temporarily to use their resources while traveling or for overwintering. A problem that can arise under this scenario is the occurrence of ecological traps; that is, patches that are attractive to individuals, but ultimately negatively affect their fitness due to low patch quality and overload of other pressures (e.g., concentration of predators) that make these patches unsustainable (Donovan & Thompson 2001).

Although studies on community structure of vertebrate predators and their prey are extensive in north-temperate regions (Jaksic et al. 1992), studies in the southern United States are lacking. In particular, interactions between migratory and resident raptors in Texas, one of the main migratory routes of birds, have been scarcely studied. Likewise, little is known about the prey populations of vertebrate predators in northern Texas (Dalquest 1968; Schmidly & Bradley 2016) beyond their presence and the fact that they are changing in distribution (Hunsaker et al. 1959; Hart 1972; Austin & Kitchens 1986; Cleveland 1986; Tumlison et al. 1993; Green & Wilkins 2010), population dynamics (Wilkins 1995), and habitat relationships (Hanchey & Wilkins 1998). In this study, we examined the diet of two owl species, the barn owl (Tyto alba) and the long-eared owl (Asio otus), in a protected habitat island of vegetation in the Dallas-Fort Worth Metropolitan (DFW) area and compared their winter trophic ecology through remains found in pellets. Studies from other areas have shown that these medium-sized owls have similar trophic ecologies. Both species hunt mainly small mammals while flying low to the ground over grasslands during the night (Marti 1969). However, differences in morphology, migratory patterns, and nesting behavior exist. Tyto alba is larger (weight range: 400-560 and 420-700 g for males and females, respectively, Marti et al. 2020) than A. otus (weight range: 220-305 and 260-435 g for males and females,

respectively, Marks et al. 2020). *Tyto alba* is resident in Texas and breeds there, nests and roosts in old tree cavities, and lives solitarily during the winter, most commonly roosting in red cedars (*Juniperus virginiana*, K. Steigman, pers. observ.). *Asio otus* is an open-cup nester, breeds in northern North America, and uses communal roosts in red cedars during the winter (Fitch et al. 2003). Historic documentation of *A. otus* indicates that wintering roosts of this species have only occurred every 10 to 15 years in north Texas (Pulich 1988). The Lewisville Lake Environmental Learning Area (LLELA) seems the ideal place to examine the trophic ecology of *T. alba* and *A. otus* to understand how these owls coexist during the winter in this relatively small patch of native vegetation surrounded by development.

# MATERIALS & METHODS

Owl pellets were collected at LLELA. This protected area, south of Lewisville Lake, surrounded by the city of Lewisville and north Dallas suburbs, covers 809 ha. The study site includes one of the last remaining Blackland Prairie ecosystems that once covered a portion of Texas (Riskind & Collins 1975). This area supports characteristic eastern Cross-Timbers and the bottomland hardwood forest vegetation as well as patches of tall grass prairie in a relatively flat landscape. The Elm Fork of the Trinity River runs through LLELA, creating aquatic ecosystems such as wetlands, ponds, and creek drainages (Williams & Hudak 2005). Through prescribed burns and mechanical means, sections of LLELA are maintained as grassland. Prescribed burns are installed annually, on small acreages across the grasslands each year to provide a mosaic of burned, unburned, and regrowth areas preserving adequate habitat structure for a diverse grassland species' life histories. Climate is subtropical; summers are hot (21-27°C) and winters are cool (10-16°C), with 890 mm per year of precipitation (Bailey 1995).

We opportunistically collected barn owl pellets under three nest boxes and long-eared owl pellets under two red cedars, from September 2016 through March 2017. We made visual confirmation of both species roosting at the collection sites, with 12 long-eared owls perched in the red cedar site, and multiple barn owls perched on the nest boxes. Pellets were autoclaved, dried, and dissected. We identified small mammal bone remains to genus or species level under a dissecting microscope by comparison to voucher specimens from the UNT Elm Fork Natural History Museum collection, mammalian species entries (Whitaker 1974; Wiley 1980; Cameron & Spencer 1981; Spencer & Cameron 1982; Lackey et al. 1985; Eshelman & Cameron 1987; McCay 2001), and published guides (Elbroch 2006; Álvarez-Castañeda et al. 2017). When bones were absent, we assigned coarse hair found in pellets to Sigmodon (Schmidly & Bradley 2016). When possible, we distinguished juveniles from adults by their smaller sizes, unworn molars, and/or lack of suture closures of the cranial bones and epiphyses of the long bones (Dickman et al. 1991; Elbroch 2006; Trejo & Guthmann 2003; Álvarez-Castañeda et al. 2017). When we found pelvises, we were able to assign gender by visually assessing the pelvis bone shape following Dunmire (1955) and Dickman et al. (1991).

To compare owl diet diversity, we followed the standardized version of Levins' niche breadth (1968) as proposed by Colwell & Futuyma (1971). We assessed diet similarity between the owl species with Pianka's niche overlap index (1973). To examine the importance of biomass contributed per prey category, we computed the percent biomass of prey by using available weights from the literature for adults (Joule & Cameron 1975; Nowak 1999). For juveniles, we estimated half of these weight values. We calculated the geometric mean weight of small mammal prey (GMWP) taken by the owls according to Jaksic & Braker (1983) to decrease the biases due to small or large sample sizes of certain prey items. We followed methods described in detail by Marti et al. (2007).

#### RESULTS

In total, we collected 15 and 114 pellets that rendered 23 and 138 prey items for T. alba and A. otus, respectively. Tyto alba had a higher mean number of prev per pellet ( $\bar{x} = 1.53 \pm 0.22$  (SE), n = 15) than A. otus ( $\bar{x} = 1.21 \pm 0.03$  (SE), n = 114; Mann-Whitney U = 682.5, P = 0.049). Tyto alba included only three mice species in its diet (100% of total prey by number), whereas A. otus preyed on four rodent species (98.6% of total prey by number), one insectivore (0.73%) and one unidentified passerine bird (0.73%). By far the most common prey by number taken by both T. alba and A. otus was the hispid cotton rat (Sigmodon hispidus), constituting 68.2 and 89.0% of their identified small mammal prey, respectively (Fig. 1). Baiomys taylori constituted 18.2% and Reithrodontomys fulvescens made 13.6% of the Tyto alba diet. For A. otus, Peromyscus sp. constituted 5.1%, R. fulvescens 2.9%, B. taylori 2.2%, and Cryptotis parva 0.7% of small mammal prey (Fig. 1). In each owl species' pellets we found one unidentified rodent.



Figure 1. Small mammal species proportions in the diet of *Tyto alba* (n = 22) and *Asio otus* (n = 136) during the winter at LLELA, north-central Texas.

When biomass was considered, accounting for age, *S. hispidus*, the largest mammal identified, represented even a higher percentage of the diet in both species (*T. alba* 93.1% and *A. otus* 96.3%, Fig. 2). The smaller-sized mammals decreased significantly as contributions to the diet in both owls when comparing frequency of prey to biomass of prey (from 31.8-7.0% in *T. alba* and from 11.0-3.4% in *A. otus*). The GMWP eaten by *T. alba* was smaller than that of *A. otus* (back transformed: 27.4 g vs. 43.4 g; Mann-Whitney U = 1,151, P = 0.007).

Standardized by the number of prey categories, niche breadth of *T*. *alba* was broader (Colwell and Futuyma's  $B_{sta} = 0.468$ ) than that of *A*. *otus* ( $B_{sta} = 0.055$ ), but diet overlap between owls was high (Pianka's O = 0.96). Given that *S. hispidus* represented over 65% of the prey by number in each owl diet, we examined age and gender breakdown of this species. Juveniles constituted 100% of *S. hispidus* preyed upon by *T. alba* and 96.6% preyed upon by *A. otus* (Fig. 3). The majority (80.3%) of *A. otus* pellets containing *S. hispidus* lacked pelvic bones,



Figure 2. Frequency and biomass composition of small mammal prey eaten by *Tyto alba* (n = 22) and *Asio otus* (n = 136) at LLELA, north-central Texas.



Figure 3. Age and gender of *Sigmodon hispidus* eaten by *Tyto alba* (n = 15) and *Asio otus* (n = 117) at LLELA, north-central Texas.

preventing us from assigning gender. Of those that we could identify, the ratio of males to females was 12:13. In contrast, we sexed the majority (60.0%) of *S. hispidus* prey found in *T. alba* pellets. Of these, the ratio of males to females was 4:5 (Fig. 3).

#### DISCUSSION

Although our study is limited in scope in time, space, and sample sizes, to our knowledge, this is the first study on the trophic ecology of *T. alba* and *A. otus* in north Texas. Small mammal species made up over 90% of both *T. alba* and *A. otus* diets by number and by biomass. The scarcity of shrews and birds in their diets might be the result of our small sample size, particularly for *T. alba*, for which we collected less than one-seventh of the number of pellets of *A. otus*. These prey items only showed up in the diet of *A. otus*.

*Prey composition.*—Our results are in line with most studies that show that these owls feed almost exclusively on small mammals, mainly rodents (Marti 1969; 1974; 1976; Goyer et al. 1981; Marks & Marti 1984; Eckert & Karalus 1988; Khalafalla & Iudica 2010), particularly in terms of biomass (Voight & Glenn-Lewin 1978; Grant et al. 1985; Baker 1991; Marti et al. 1993). The dominance of *S. hispidus* in the owls' diets agrees well with similar studies in Kansas (Maccarone & Janzen 2005), the Panhandle of Texas (Baker 1991), central Texas (Grant et al. 1985), west Texas (Noland et al. 2013), east Texas (Parmalee 1954), northern Mexico (González-Rojas et al. 2017), Louisiana (Marra et al. 1989), and the Gulf Coast (Raun 1960; Otteni et al. 1972; Goyer et al. 1981).

In studies north of this range, the representation of small mammal species in the diet of both owl species change. The northern extent of the range of S. hispidus occurs in Kansas (Cameron & Spencer 1981). *Microtus* spp. dominates the prey composition found in owl pellets in Iowa (Voight & Glenn-Lewin 1978), Idaho (Marks & Marti 1984; Marti et al. 1993), Pennsylvania (Khalafalla & Iudica 2010), Utah (Smith et al. 1972; Marti 2010), Colorado (Marti 1969), and northern Kansas (Wooster 1936; Young et al. 2005; but see Kaufman et al. 2010). These rodents are found across the midwestern United States and into Canada (Stalling 1990). Thus, a distinction in owl prey composition of *Microtus* spp. in the northern United States, and S. hispidus in the southern United States exists. Rainey & Robinson (1954) found similar occurrences of S. hispidus and M. ochrogaster in Douglas County, Kansas, indicating that a convergence of the two rodent species' ranges occurs there. Korschgen & Stuart (1972) found similar results of the codominance of these two mice in the diet of A. otus in Cass County, Missouri. In studies west of Texas, in the deserts of New Mexico for A. otus (Jorgensen et al. 1998) and Arizona for T. alba (Brown 1995), Dipodomys spp. constituted the dominant prey of the owls. Sigmodon arizonae and Perognathus spp. were also abundant in A. otus in Arizona and in T. alba in New Mexican deserts, respectively (Franzreb & Laudenslayer 1982; Marti et al. 1986). Perognathus spp. was likewise most abundant in the Panhandle of Texas (Stickel & Stickel 1948). These studies reflect the usefulness of

owl pellet research as tools for mapping small mammal distributions, as their representation in the diet agrees with the distribution of the prey (Wooster 1936; Stickel & Stickel 1948; Baker 1991).

Franzreb & Laudenslayer (1982) found that T. alba preved preferentially on juvenile S. arizonae in Arizona whereas Raun (1960) found the opposite for S. hispidus in Texas. Our age analysis of S. hispidus showed that juveniles were overwhelmingly dominant in the diet of T. alba and A. otus. Sigmodon hispidus grows to adult size quickly, within 100 days (Cameron & Spencer 1981), but the ossification of the epiphyses does not occur in this time. Bones with adult-like size, but juvenile epiphyseal ossification were recorded as juvenile. The large occurrence of juveniles in the owl diets in our study is not necessarily a representation of preference for smaller prey; instead, it is possible that the owls pursue large, naive juveniles for an ideal ratio of caloric intake versus difficulty of capture. Due to the short length of this study, it is unknown whether the pellets were collected during a peak breeding cycle of the rodents (Abuzaineth et al. 2011), which might be another explanation for the abundance of juveniles compared to adults.

There appears to be no preference by either owl species in the selection of small mammal prey by sex (Dickman et al. 1991) in contrast to the findings of Lyman et al. (2016) for *T. alba* preying on *Microtus* and *Peromyscus*. A surprisingly small number of studies have been conducted that address age and sex of prey taken by these raptors. These components could provide meaningful insight into the role of raptors as drivers of the populations of small mammals.

*Diet metric comparison.*—The diets of *T. alba* and *A. otus* were composed mainly of a few species of rodents, particularly *S. hispidus*, as estimated both by frequency of occurrence and biomass of prey. The fact that these owls prey exclusively on small vertebrates of similar size explains the close correlation between frequency and biomass ingested, as reported in other studies (Marti et al. 1993; Noland et al. 2013, but see Otteni et al. 1972). In contrast, when owls prey on items of diverse body sizes the most frequent prey is not

always the one with the largest biomass (González-Rojas et al. 2017). The number of prey per pellet in our study is in line with other research (Khalafalla & Iudica 2010); that is, *T. alba* had higher average prey per pellet than *A. otus* (i.e., 1.53 vs 1.21, respectively).

Although T. alba, which is the larger predator in body size, is often reported to consume larger prey than A. otus (Marti 1969; 1974; Marks & Marti 1984; Marti et al. 1993), our data show a larger GMWP in A. otus (i.e., 27.4 g vs. 43.4 g, respectively). This might be explained by segregation of hunting habitat types by the owls. Pellets of T. alba were collected under a few nest boxes in an open field, whereas pellets of A. otus were collected under red cedars in a scrubby habitat. The profile of prey sizes might have been different in these two habitat types. Sigmodon hispidus, the most common and largest prey found by body size, prefers matted cover (Stickel & Stickel 1949; Cameron & Spencer 1981; Hanchey & Wilkins 1998), similar habitat to where A. otus roosted. Noland et al. (2013) reported that A. otus preved on higher than expected prev weight, attributing this to the fact that owls consumed mainly S. hispidus, the largest and most abundant prey at their site. Therefore, our GMWP findings might be the result of differences in hunting habitat types, rather than evidence that T. alba prefers smaller prey. This analysis assumes each owl species conducts the majority of its hunting in areas with close proximity to their roosts; this may or may not be the case.

The niche breadths of the owls in LLELA align with other studies that reflect the generalist behavior of *T. alba* (Smith et al. 1972; Marra 1989; Khalafalla & Iudica 2010) versus the specialist behavior of *A. otus* (Marti 1976; Janes & Barss 1985; Kaufman et al. 2010, but see Marks & Marti 1984). The large diet overlap found between the owls by Khallafa & Iudica (2010) in Pennsylvania agrees with our results from LLELA (i.e., O = 0.96), which might reflect the limited diversity of small mammal prey available in the field, in contrast to the low overlap and high diversity of prey reported in Idaho by Marks & Marti (1984) and Marti et al. (1993).

Temporal and spatial consideration complicates the interpretation of our results (Marti 1969). First, small mammal biogeographic distributions change over time (Austin & Kitchens 1986; Cleveland 1986), making meaningful interpretation difficult when examining results from studies conducted in different decades. Second, several prey species show significant cycles of population abundances from season to season (Otteni et al. 1972; Grant et al. 1985) and from year to year (Raun 1960; Korschgen & Stuart 1972; Grant et al. 1985; Young et al. 2005). Third, microhabitat preferences of small mammals create differences in relative abundances of species within small areas (Stickel & Stickel 1949; Fast & Ambrose 1976; Marks & Marti 1984; Grant et al. 1985; Wilkins 1995; Hanchey & Wilkins 1998; Lyman 2012). Fourth, habitat succession from one stage to another over years also changes the species composition of prey (Fitch et al. 2003). Studies conducted at our spatial-temporal scale, in one location during one winter, are not comprehensive in accounting for all this complexity. Additionally, this study did not account for the presence and potential interactions between these two owls and other nocturnal and diurnal raptors, as well as with carnivores and snakes.

Thus, there are many caveats and assumptions that we hope will be clarified with more long-term research, across seasons and years, with larger sample sizes, and the assessment of the availability of prey in time and space. Considering the diverse community of predators and prey at LLELA and the fact that the area represents one of the few remaining, lightly impacted Blackland Prairie remnants, future research will help to better understand the ecological interactions of a biome that once dominated the landscape of north Texas.

*Conservation implications.*—Although LLELA currently supports a good representation of the original vertebrate species of the Blackland Prairie (Wilkins 1995; Schmidly & Bradley 2016), it is surrounded by recent development and likely behaves as an 'island.' This prevents sensitive species, such as large predators that require large hunting areas, from maintaining sustainable populations. It also prevents the exchange of local populations with other similar ecosystems. This island context attracts several migratory species that have limited

options for pristine stopover and refueling habitats along their routes due to the anthropogenic transformation of the landscape. The increased influx of migratory species could put stress on this small habitat island that would not exist if conserved areas were more common in the region.

These two owl species may be affected by urbanization in different ways. While both species prey mainly on rodents, the barn owl is known to nest and hunt in close proximity to human activity, which may allow it to hunt successfully on exotic rodent species in urban areas. However, although close to human dwellings, we did not detect this behavior in our study, but it rather preyed on native rodents. Conversely, the long-eared owl is a more secretive species that seeks cover in wooded areas and does not venture much into human developments. Urbanization may have negative effects on long-eared owl habitat quality. At our study site we have only detected this owl sporadically.

The LLELA is designated as protected land by the local government, but there are many threats that may compromise the integrity of its biota, such as economic development on the land, industrial pollution of air and water, recreational and research use, isolation from other similar undeveloped areas, species erosion, etc. These dangers emphasize the need for conservation of this unique site. This scenario also emphasizes the value in studying LLELA as a relative pristine environment now as its future is uncertain.

## ACKNOWLEDGMENTS

We appreciate the help of J. H. Kennedy for allowing us access to specimens under his care at the Elm Fork Natural Heritage Museum at UNT. J. P. Bednarz and E. G. Zimmerman provided professional insight towards identification of skulls. C. Ramírez and C. Antkowski helped with pellet dissections. The editor of the journal and two anonymous reviewers made comments that improved the quality of this research.

## LITERATURE CITED

- Abuzaineth, A. V., N. E. Mcintyre, T. S. Holsomback, C. W. Dick & R. O. Owen. 2011. Extreme population fluctuation in northern pygmy mouse (*Baiomys taylori*) in southeastern Texas. Therya 2:37-45.
- Álvarez-Castañeda, S. T., T. Álvarez & N. González-Ruiz. 2017. Keys for identifying Mexican mammals. Johns Hopkins University Press, Baltimore, 528 pp.
- Austin, T. A. & J. A. Kitchens. 1986. Expansion of *Baiomys taylori* into Hardeman County. Southwest. Nat. 31:547.
- Bailey, R. G. 1995. Description of the ecoregions of the United States. Second edition. Miscellaneous Publication No. 1391. USDA Forest Service, Washington, D.C.
- Baker, R. H. 1991. Mammalian prey of the common barn owl (*Tyto alba*) along the Texas coast. Southwest. Nat. 36:343-247.
- Brown, N. L. 1995. Notes on the winter roost and diet of long-eared owl in the Sonoran Desert. J. Raptor Res. 29:277-279.
- Cameron, G. N. & S. R. Spencer. 1981. Sigmodon hispidus. Mamm. Species 158:1-9.
- Chapin, III, F. S., E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack & S. Díaz. 2000. Consequences of changing biodiversity. Nature 405:234-242.
- Cleveland, A. G. 1986. First record of *Baiomys taylori* north of the Red River. Southwest. Nat. 31:547.
- Colwell, R. K. & D. J. Futuyma. 1971. On the measurement of niche breadth and overlap. Ecology 52:567-571.
- Dalquest, W. W. 1968. Mammals of north-central Texas. Southwest. Nat. 13:13-22.
- Dickman, C. R., M. Predavec & A. J. Lynam. 1991. Differential predation of size and sex classes of mice by the barn owl, *Tyto alba*. Oikos 62:67-76.
- Donovan, T. M. & F. R. Thompson, III. 2001. Modeling the ecological trap hypothesis: a habitat and demographic analysis for migrant songbirds. Ecol. Appl. 11:871-882.
- Dunmire, W. W. 1955. Sex dimorphism in the pelvis of rodents. J. Mammal. 36:356-361.
- Eckert, A. W. & K. E. Karalus. 1988. The owls of North America. Weathervane Books, NY, 278 pp.
- Elbroch, M. 2006. Animal skulls: a guide to North American species. Stackpole Books, Mechanicsburg, xi+727 pp.
- Eshelman, B. D. & G. N. Cameron. 1987. Baiomys taylori. Mamm. Species 285:1-7.
- Fast, S. J. & H. W. Ambrose, III. 1976. Prey preference and hunting habitat selection in the barn owl. Amer. Midl. Nat. 96:503-507.
- Fitch, H. S., P. Von Achen & G. L. Pittman. 2003. Probable succession related prey changes of long-eared owls in Kansas. Kansas Ornithol. Soc. Bull. 54:42-43.
- Franzreb, K. E. & W. F. Laudenslayer, Jr. 1982. Composition and seasonal variation of the barn owl (*Tyto alba*) diet in Arizona. J. Raptor Res. 16:36-39.
- González-Rojas, J. I., H. Padilla-Rangel, I. Ruvalcaba-Ortega, M. A. Cruz-Nieto, R. Canales Del Castillo & A. Guzmán-Velasco. 2017. Winter diet of the long-eared owl *Asio otus* (Strigiformes: Strigidae) in the grasslands of Janos, Chihuahua, Mexico. Rev. Chil. Hist. Nat. 90:1-5.
- Goyer, N., A. L. Barr & A. R. P. Journet. 1981. Barn owl pellet analysis in northwestern Harris County, Texas. Southwest. Nat. 26:202-204.
- Grant, W. E., P. E. Carothers & L. A. Gidley. 1985. Small-mammal community structure in the postoak savanna of east-central Texas. J. Mammal. 66:589-594.

- Green, N. S. & K. T. Wilkins. 2010. Continuing range expansion of the northern pygmy mouse (*Baiomys taylori*) in northeastern Texas. Southwest. Nat. 55:288-291.
- Hanchey, M. F. & K. T. Wilkins. 1998. Habitat associations of the small-mammal community in the Grand Prairie of north-central Texas. Texas J. Sci. 50:107-122.
- Hart, B. J. 1972. Distribution of the pygmy mouse, *Baiomys taylori*, in north-central Texas. Southwest. Nat. 17:213-214.
- Hunsaker II, D., G. G. Raun & J. E. Swindells. 1959. Range expansion of *Baiomys taylori* in Texas. J. Mammal. 40:447-448.
- Jaksic, F. M. & H. E. Braker. 1983. Food-niche relationships and guild structure of diurnals birds of prey: competition versus opportunism. Can. J. Zool. 61:2230-2241.
- Jaksic, F. M., J. E. Jiménez, S. A. Castro & P. Feinsinger. 1992. Numerical and functional response of predators to a long-term decline in mammalian prey at a semiarid neotropical site. Oecologia 89:90-101.
- Janes, S. W. & J. M. Barss. 1985. Predation by three owl species on northern pocket gophers of different body mass. Oecologia 67:76-81.
- Jorgensen, E. E., S. M. Sell & S. Demarais. 1998. Barn owl prey use in Chihuahuan Desert foothills. Southwest. Nat. 43:53-56.
- Joule, J. & G. N. Cameron. 1975. Species removal studies. I. Dispersal strategies of sympatric Sigmodon hispidus and Reithrodontomys fulvescens populations. J. Mammal. 56:378-396.
- Kaufman, D. W., G. A. Kaufman & D. E. Brillhart. 2010. Small mammals as winter prey of long-eared owls in Kansas. Trans. Kansas Acad. Sci. 113:217-222.
- Khalafalla, S. M. & C. A. Iudica. 2010. Barn and long-eared owl diets: a comparative study from central Pennsylvania and a key for identification of prey items. Northeast. Nat. 17:147-154.
- Korschgen, L. J. & H. B. Stuart. 1972. Twenty years of avian predator-small mammal relationships in Missouri. J. Wildl. Manag. 36:269-281.
- Lackey, J. A., D. G. Huckaby & B. G. Ormiston. 1985. *Peromyscus leucopus*. Mamm. Species 247:1-10.
- Levins, S. 1968. Evolution in changing environments. Princeton University Press, NJ. 132 pp.
- Lyman, R. L. 2012. Rodent-prey content in long-term samples of barn owl (*Tyto alba*) pellets from northwestern United States reflects local agricultural changes. Amer. Midl. Nat. 67:150-163.
- Lyman, R. L., A. E. Daskalakis-Perez, A. B. Daskalakis-Perez & E. A. Daskalakis-Perez. 2016. Sex ratio of rodents as barn owl (*Tyto alba*) prey. Amer. Midl. Nat. 176:152-157.
- Maccarone, A. D. & P. Janzen. 2005. Winter diet of long-eared owl (*Asio otus*) at an urban roost in Wichita, Kansas. Trans. Kansas Acad. Sci. 108:116-120.
- Marra, P. P., B. M. Burke & I. Albergamo. 1989. An analysis of common barn owl pellets from Louisiana. Southwest. Nat. 34:142-144.
- Marks, J. S. & C. D. Marti. 1984. Feeding ecology of sympatric barn owls and long-eared owls in Idaho. Ornis Scand. 15:135-143.
- Marks, J. S., D. L. Evans & D. W. Holt. 2020. Long-eared owl (*Asio otus*), version 1.0, *in* Birds of the World (S. M. Billerman, ed.). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.loeowl.01 (Accessed April 4, 2020)
- Marti, C. D. 1969. Some comparisons of the feeding ecology of four owls in north-central Colorado. Southwest. Nat. 14:163-170.

- Marti, C. D. 1974. Feeding ecology of four sympatric owls. Condor 76:45-61.
- Marti, C. D. 1976. A review of prey selection by the long-eared owl. Condor 78:331-336.
- Marti, C.D. 2010. Dietary trends of barn owls in an agricultural ecosystem in northern Utah. Wilson J. Ornithol. 122:60-67.
- Marti, C. D., J. S. Marks, T. H. Craig & E. H. Craig. 1986. Lon-eared owl diet in northwestern New Mexico. Southwest. Nat. 31:416-419.
- Marti, C. D, K. Steenhof, M. N. Kochert & J. S. Marks. 1993. Community trophic structure: the roles of diet, body size, and activity time in vertebrate predators. Oikos 67:6-18.
- Marti, C. D., M. Bechard & F. M. Jaksic. 2007. Food habits. Pp. 129-151, *in* Raptor research and management techniques (D. M. Bird and K. L. Bildstein, eds.). Institute for Wildlife Research, National Wildlife Federation, Washington, D.C., 462 pp.
- Marti, C. D., A. F. Poole, L. R. Bevier, M. D. Bruce, D. A. Christie, G. M. Kirwan & J. S. Marks. 2020. Barn owl (*Tyto alba*), version 1.0, *in* Birds of the World (S. M. Billerman, ed.). Cornell Lab of Ornithology, Ithaca, NY. https://doi.org/10.2173/bow.brnowl.01 (Accessed April 4, 2020)
- McCay, T. S. 2001. Blarina carolinensis. Mamm. Species 673:1-7.
- Noland, R. L., T. C. Maxwell & R. C. Dowler. 2013. Food habits of long-eared owls (*Asio otus*) at a winter communal roost in Texas. Southwest. Nat. 58:245-247.
- Nowak, R. M. 1999. Walker's mammals of the world. Volumes I and II. Sixth ed. Johns Hopkins University Press, Baltimore, lxx+1921 pp.
- Otteni, L. C., E. G. Bolen & C. Cottam. 1972. Predator-prey relationships and reproduction of the barn owl in southern Texas. Wilson Bull. 84:434-448.
- Parmalee, P. W. 1954. Food of the great horned owl and barn owl in east Texas. Auk 71:469-470.
- Pianka, E. R. 1973. The structure of lizard communities. Ann. Rev. Ecol. Syst. 4:53-74.
- Pulich, W. 1988. The birds of north central Texas. Texas A&M University Press, College Station, 472 pp.
- Rainey, D. G. & T. S. Robinson. 1954. Food of the long-eared owl in Douglas County, Kansas. Trans. Kansas Acad. Sci. 57:206-207.
- Raun, G. G. 1960. Barn owl pellets and small mammal populations near Mathis, Texas, in 1956 and 1959. Southwest. Nat. 5:194-200.
- Riskind, D. H. & O. B. Collins. 1975. The Blackland Prairie of Texas: conservation of representative climax remnants. Pages 361-367, *in* Prairie: A multiple view (M. K. Wali, ed.). University of North Dakota Press, Grand Forks, 433 pp.
- Root, R. B. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. Ecol. Monographs 37:317-350.
- Schmidly, D. J. & R. D. Bradley. 2016. The mammals of Texas. Seventh ed. University of Texas Press, Austin, xxvi+694 pp.
- Smith, D. G., C. R. Wilson & H. H. Frost. 1972. Seasonal food habits of barn owls in Utah. Great Basin Nat. 32:229-234.
- Spencer, S. R. & G. N. Cameron. 1982. *Reithrodontomys fulvescens*. Mamm. Species 174:1-7.
- Stalling, D. T. 1990. Microtus ochrogaster. Mamm. Species 355:1-9.
- Stickel, W. H. & L. F. Stickel. 1948. Mammals of northwestern Texas found in barn owl pellets. J. Mammal. 29:291-293.
- Stickel, W. H. & L. F. Stickel. 1949. A *Sigmodon* and *Baiomys* population in ungrazed and unburned Texas prairie. J. Mammal. 30:141-150.

- Trejo, A. & N. Guthmann. 2003. Owl selection on size and sex classes of rodents: activity and microhabitat use of prey. J. Mammal. 84:652-658.
- Tumlison, R. V., R. Mcdaniel & J. G. Duffy. 1993. Further extension of the range of the northern pygmy mouse, *Baiomys taylori*, in southwestern Oklahoma. Southwest. Nat. 38:285-286.
- Voight, J. & D. C. Glenn-Lewin. 1978. Prey availability and prey taken by long-eared owls in Iowa. Amer. Midl. Nat. 99:162-171.
- Whitaker, Jr., J. O. 1974. Cryptotis parva. Mamm. Species 43:1-8.
- Wiley, R. W. 1980. Neotoma floridana. Mamm. Species 139:1-7.
- Wilkins, K. T. 1995. The rodent community and associated vegetation in a tallgrass Blackland Prairie in Texas. Texas J. Sci. 47:243-262.
- Williams, L. L. & P. F. Hudak. 2005. Hydrology and plant survival in excavated depressions near an earthen dam in north-central Texas. Environ. Geol. 48:795-804.
- Wooster, L. D. 1936. The contents of owl pellets as indicators of habitat preferences of small mammals. Trans. Kansas Acad. Sci. 39:395-397.
- Young, E. A., M. N. Harding, M. Rader & L. Wilgers. 2005. Notes on food habits of wintering long-eared owls in north-central Kansas. Kansas Ornithol. Soc. Bull. 56:25-28.