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Food habits of a small Florida black bear population in an endangered ecosystem

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Abstract: The Highlands–Glades subpopulation (HGS) of Florida, USA, black bears (Ursus americanus floridanus) is small, genetically depauperate, and resides primarily within the endangered Lake Wales Ridge ecosystem, which has lost >85% of native habitat to land development. Habitat loss can reduce availability of critical natural foods and cause bears to increase reliance on anthropogenic foods (i.e., human-sourced); lands supporting the HGS are expected to lose >50% of remaining Florida black bear habitat in coming decades. We used scat analysis to describe seasonal food habits, investigate potential dietary responses to food shortages, and inform habitat conservation and human–bear conflict management. Florida black bears in the HGS mostly relied on native soft and hard mast and invertebrates, which are all available in endangered scrub habitat communities. Corn dispensed at hunter-operated feeding stations was a dominant food item in scats; and other alternative foods, such as citrus fruit and white-tailed deer (Odocoileus virginianus), were found in summer-collected scats when soft mast should have been prevailing. Results indicate bears may respond to soft mast shortages caused by mast failures or habitat loss by consuming anthropogenic foods (e.g., corn, deer chow, citrus fruit, and garbage), which could increase human–bear conflicts. Florida carpenter ants (Camponotus floridanus) appeared to provide a reliable compensatory food during such shortages, but they are arboreal and largely dependent on imperiled bear habitat for proliferation. We strongly suggest remnant scrub and other communities rich in soft and hard mast-producing flora be targeted for acquisition and protection to ensure persistence of Florida black bears in this diverse ecosystem. We also suggest non-lethal actions to mitigate bear habituation to anthropogenic foods be implemented to minimize human–bear conflicts and prevent unnecessary losses to the already small HGS. Our study should be repeated to investigate whether dietary shifts occur in response to impending habitat loss and to further inform population conservation, habitat protection, and conflict management.

Key words: anthropogenic, diet, Florida, Florida black bear, food habits, habitat fragmentation, habitat loss, human–bear conflict, Lake Wales Ridge, Ursus americanus floridanus

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Widespread habitat destruction caused by urban development, agriculture expansion, and other anthropogenic land uses subdivided a formerly contiguous statewide Florida black bear (Ursus americanus floridanus) population into 7 disjunct subpopulations with varying levels of connectivity among them (Dixon et al. 2007). State-level protection and habitat restoration efforts facilitated abundance increases and some range reoccupation by most Florida black bear subpopulations during the past decade (Humm et al. 2017). However, results from a recent non-invasive genetic spatial capture–recapture study that used sampling and analytical methods similar to those used by Murphy et al. (2016) indicated the Highlands–Glades subpopulation (HGS) in south-central Florida, USA, remains small (N = 98 bears) and genetically depauperate (effective population size [Nm] = 25 bears;

The HGS is supported by a mosaic of native habitat communities that are disjunctly arranged in the endangered Lake Wales Ridge ecosystem and adjacent areas across a primarily agricultural and urban landscape [Pearlstone et al. 1997; Maehr et al. 2004, Weekley et al. 2008 [Fig. 1]]. This includes federally endangered scrub communities that support numerous endemic and imperiled flora and fauna (U.S. Fish and Wildlife Service [USFWS] 1999). Although a hotspot for biodiversity [Noss et al. 2015], the endangered Lake Wales Ridge ecosystem has experienced a >85% area loss of native communities [Weekley et al. 2008], and lands occupied by the HGS constitute one of the most fragmented areas in North America with an established black bear population (Maehr et al. 2001, 2004). Nonetheless, the HGS has the potential to serve as a stepping stone that facilitates demographic and genetic connectivity between the southern-most Big Cypress subpopulation and all other Florida black bear subpopulations to the north [Dixon et al. 2007 [Fig. 1 inset]]. Central Florida is, however, expected to incur substantial anthropogenic development and the largest percentage of habitat loss (>50%) in the state in coming decades [Carr and Zwick 2016], and intervening habitat between those subpopulations is threatened by rising sea levels from climate change [Whittle 2009; Carr and Zwick 2016].

Contrary to all other Florida black bear subpopulations, management of the HGS has relied almost exclusively on anecdotal information (FWC 2012). A lack of scientific knowledge about HGS bear ecology has thwarted conservation efforts (Maehr et al. 2004) and thus possibly hindered resiliency of the HGS to impending habitat loss. Food habits studies are an important initial step toward a more comprehensive understanding of ecological relationships of bear populations [Beckmann and Berger 2003; Lesmerises et al. 2015; Costello et al. 2016]. For small or imperiled bear populations, such investigations may be vital for informing landscape-level conservation planning [Fortin et al. 2013; Ciucci et al. 2014]. Although habitat productivity and therefore food availability change dynamically because of natural ecological processes (e.g., transitions between seasons), anthropogenic land-use activities can permanently degrade important habitats and decrease availability of critical natural foods. Dietary studies can facilitate monitoring of bear population responses to landscape-level changes such as dietary shifts and increased reliance on human-sourced foods [Hopkins et al. 2014; Ditmer et al. 2016], and inform habitat and population conservation in areas where the loss of critical habitat is an imminent threat to long-term population persistence.

Limited availability or accessibility of natural foods because of habitat quality and quantity issues can increase the probability that bears exploit anthropogenic foods [Benson and Chamberlain 2005; Merkle et al. 2013; Ditmer et al. 2016], which are human-sourced foods made available to bears via human activities (e.g., agriculture, hunting, and urban development; Oro et al. 2013). Consumption of anthropogenic foods by bears is associated with human–bear conflicts; therefore, food habits studies can also inform conflict management (Greenleaf et al. 2009; Hopkins et al. 2014). Human–black bear conflicts increased rapidly throughout Florida over the past decade, particularly in the central portion of the state where multiple bear attacks on humans occurred in recent years, which prompted the state wildlife management agency to increase bear euthanasia in urban and exurban areas and implement a controversial legal harvest (FWC 2015). Although those are oft-employed agency management responses to chronic conflicts [Agee and Miller 2009; Penteriani et al. 2016], similar actions applied to the HGS could further reduce the number of black bears in this already small subpopulation.

To address said issues and provide managers with science-based information on HGS black bear ecology, we conducted a food habits study in which we collected and analyzed Florida black bear scats over a 2-year period. We also investigated whether a lack of natural foods in bear scats was associated with an increased occurrence of anthropogenic foods in scats. Our rationale was that, in the absence of direct measurements of natural foods availability (e.g., rigorous mast surveys; Ryan et al. 2007), an apparent replacement of natural foods with anthropogenic foods may suggest limited availability or accessibility of the former (Greenleaf et al. 2009; Merkle et al. 2013; Hopkins et al. 2014). Collectively, findings from our study should be useful for habitat and subpopulation conservation efforts and for human–bear conflict management in the HGS.

**Study area**

The 998-km² primary range of the HGS [Simek et al. 2005 [Fig. 1]] is located in Highlands and Glades counties of south-central Florida, where the climate is humid sub-tropical with hot, wet summers and mild, dry winters. Average elevation is 47 m above sea level, average annual
Fig. 1. Available habitat and primary range (Simek et al. 2005) of the Highlands–Glades subpopulation of Florida black bears (*Ursus americanus floridanus*) in south-central Florida, USA, where 166 bear scats were collected during 2004–2006 to describe food habits.

Approximately 36% (359 km$^2$) of lands within HGS primary range are considered potential Florida black bear habitat (Fig. 1). Many lands within primary range have been converted to agriculture (41%; 409 km$^2$), primarily citrus groves (12%; 120 km$^2$) and open pasture (23%; 230 km$^2$; FWC 2014). Twelve percent (120 km$^2$) of primary range has been developed as urban areas (FWC 2014); average human population density is 37 people/km$^2$ and the largest city is Sebring (10,331 people). Numerous

freshwater lakes and wetlands represent the remaining land area within primary range (11%; 110 km²).

Methods
Field sampling, scat classification, and food items identification

From May 2004 to April 2006, we collected Florida black bear scats opportunistically along roads and trails, at locations where bears were live-captured as part of a resource use study (Ulrey 2008, Guthrie 2012), and where otherwise we had permission to access bear-occupied lands (Fig. 1). We placed each collected scat in a sealed plastic bag labeled with the date of collection and Universal Transverse Mercator coordinates, and froze samples ≤4 hours post-collection. Scats decomposed rapidly in the hot, humid, and wet study area (W. A. Ulrey and J. M. Guthrie, personal observation); therefore, we presumed all collected scats reflected the month of defecation.

We classified scats into 3 seasonal periods that corresponded to Florida black bear biology and natural foods availability (FWC 2012): winter–spring (Jan–Apr), encompassing hypophagia when parturient females den and also when den emergence occurs; summer (May–Aug) during breeding season and soft mast ripening; and autumn (Sep–Dec) when hard mast becomes available and bears exhibit hyperphagia. We combined winter and spring into a single period because sample sizes for both seasons were independently small (n < 20 scats each season/yr) and because radiomonitoring data (n = 64 bears; 2004–2009) indicated many male and non-parturient female bears were winter-active (Ulrey 2008, Guthrie 2012).

We thawed and rinsed each scat through a single sieve (1.5-mm mesh) and then mixed the contents. We did not subsample for our analyses (e.g., Ciucci et al. 2014), but instead evaluated each scat in its entirety, hand-separating macro-categories (e.g., grasses, seeds, hair, and bones). We sorted and identified all food items to the lowest taxonomic resolution possible using field guides and identification manuals (e.g., Martin and Barkley 1961, Borden and White 1970, Peterson 1999, Marshall 2006). We identified seeds by comparing them with a reference collection from the study area (Archbold Biological Station). We identified arthropods to taxonomic order and to genus or species when possible; identifications were verified by a professional entomologist who was familiar with species in the study area (M. A. Deyrup, Archbold Biological Station). We classified all vegetation items (e.g., leaves, grasses, and forbs) into a single category (i.e., vegetation) because they typically have similar nutritional value (Dahle et al. 1998, Klare et al. 2011). We discarded black bear hair, which was presumably ingested by bears when grooming.

Data analyses

Seasonal sample sizes within a bear-year (i.e., May 2004–Apr 2005 and May 2005–Apr 2006) were relatively small, so we pooled season-specific data from both years. Most previous Florida black bear studies only used frequency of occurrence (FO) to describe food habits (Maehr et al. 2001), and an objective of our study was to compare food habits among subpopulations. Frequency of occurrence is also particularly appropriate for investigating diet diversity (Bojarska and Selva 2012), which was of importance for the HGS because of impending habitat loss and the associated potential decline of natural foods. Therefore, we calculated seasonal FO of each food item at the lowest identifiable taxon and seasonal FO of major food categories using the same method used by Ciucci et al. (2014) and Larson et al. (2015). We compared FO of the major food categories (soft mast, hard mast, invertebrates, vertebrates, vegetation, and anthropogenic) across seasons using a χ² test (Stenset et al. 2016). Data pooling was necessary, so we averaged FOs among seasons and calculated standard deviation as a measure of variance to provide a more reliable approximation of food item importance across a given year in the absence of volume-based metrics (Leger and Didrichsons 1994, Ciucci et al. 2014, Stenset et al. 2016).

To investigate whether a lack of natural foods in scats influenced the odds of a scat containing anthropogenic foods, we fit logistic regression models using maximum likelihood via the glm function in R (Cherry et al. 2016, R Core Team 2016). We used binary (i.e., 1 or 0) occurrences of food categories instead of FO because >1 item within individual categories was present in most scats and totals likely did not lack independence. We used anthropogenic foods as the response variable, season and natural foods categories as independent variables, and one level of each variable as a reference. We used Akaike’s Information Criterion corrected for small sample size (AICc) for model selection (Burnham et al. 2011), assigned significance to β estimates from the most parsimonious model if P < 0.05, and converted β estimates to odds ratios. We assessed goodness-of-fit of our top model using a le Cessie–van Houwelingen–Copas–
Fig. 2. Seasonal variation in frequency of occurrence (FO) of food item categories found in 166 Florida black bear (*Ursus americanus floridanus*) scats collected during 2004–2006 in the Highlands–Glades subpopulation of south-central Florida, USA. Results of $\chi^2$-tests comparing FO of food item categories among seasons are also presented. Categories were hard mast (Hard), soft mast (Soft), vegetation (Veg), invertebrates (Invert), vertebrates (Vert), and anthropogenic (Anthro).

Hosmer unweighted sum-of-squares test ([Hosmer et al.](1997)) via the R package rms ([Harrell 2017](https://www.bioone.org/journals/Ursus))

**Results**

During 2004–2006, we collected 166 Florida black bear scats, 27 (16.3%) of which were from 17 individual bears that were live-captured during our study period. We recorded 532 occurrences of 50 different native, non-native, and anthropogenic food items (Table 1): winter–spring scats contained 96 occurrences of 28 items, summer scats contained 151 occurrences of 35 items, and autumn scats contained 285 occurrences of 42 items. Seventeen (34.0%) of the 50 individual food items were present in scats from all 3 seasons.

We found significant FO differences among seasons for all natural foods categories but not anthropogenic foods (Fig. 2), and average annual FOs generally exhibited considerable variation (i.e., SD; Table 1). Among the major food categories, soft mast, invertebrates, and hard mast were dominant across a year. Oak acorns had the highest average annual FO among specific food items, followed by anthropogenic corn and native Florida carpenter ants (*Camponotus floridanus*). Oak acorns, Florida carpenter ants, and saw palmetto fruit had the highest FOs in winter–spring, summer, and autumn scats, respectively.

Feral hog (*Sus scrofa*), white-tailed deer (*Odocoileus virginianus*), and gopher tortoise (*Gopherus polyphemus*) remains in summer scats resulted in the highest seasonal FO for vertebrates. Among anthropogenic foods, corn was the most dominant across all seasons, followed by deer chow during winter–spring and citrus fruit during summer and autumn; we documented few occurrences of items indicative of garbage consumption (e.g., paper and plastic). The unweighted sum-of-squares test demonstrated adequate fit of the top regression model (SSE = 32.19; $Z = 1.00; P = 0.31$), which included both soft mast and vegetation as explanatory food categories (Table 2). Soft mast was the most important predictor of anthropogenic food occurrence in scats; the odds of a scat containing anthropogenic foods significantly increased in the absence of soft mast (Table 3).

**Discussion**

Across the southeastern United States, oak acorns provide the calories and macronutrients (e.g., crude fat) integral to black bear body fat accumulation during autumn hyperphagia ([Pelton 2001](https://www.bioone.org/journals/Ursus)), and our findings extend this generalization to the HGS. Carbohydrate-rich saw palmetto also fruits during autumn and is considered the single most important natural food item throughout the year.
Table 1. Frequency of occurrence of food items in Florida black bear (*Ursus americanus floridanus*) scats collected in the Highlands–Glades subpopulation of south-central Florida, USA, during the winter–spring (W), summer (S), and autumn (A) seasons of 2004–2006. Dashes (—) indicate the food item was not documented during that season, and # and \( n \) correspond to the total number of occurrences of each food item among all collected scats and the scat sample size, respectively.

<table>
<thead>
<tr>
<th>Food item</th>
<th>W</th>
<th>S</th>
<th>A</th>
<th>Annual</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>#</td>
<td>n = 32</td>
<td>n = 39</td>
<td>n = 95</td>
<td>n = 166</td>
</tr>
<tr>
<td>Hard mast</td>
<td>79</td>
<td>50.0</td>
<td>5.1</td>
<td>51.6</td>
<td>35.6</td>
</tr>
<tr>
<td>Oak acorn (<em>Quercus spp.</em>)</td>
<td>63</td>
<td>50.0</td>
<td>2.6</td>
<td>47.4</td>
<td>33.3</td>
</tr>
<tr>
<td>Hickory nut (<em>Carya spp.</em>)</td>
<td>16</td>
<td>—</td>
<td>2.6</td>
<td>11.6</td>
<td>4.7</td>
</tr>
<tr>
<td>Soft mast</td>
<td>126</td>
<td>18.7</td>
<td>71.8</td>
<td>67.4</td>
<td>52.6</td>
</tr>
<tr>
<td>Saw palmetto (<em>Serenoa repens</em>)</td>
<td>61</td>
<td>3.1</td>
<td>10.2</td>
<td>56.8</td>
<td>23.4</td>
</tr>
<tr>
<td>Unknown fruit</td>
<td>25</td>
<td>12.5</td>
<td>20.8</td>
<td>10.5</td>
<td>14.6</td>
</tr>
<tr>
<td>Grape (<em>Vitis spp.</em>)</td>
<td>17</td>
<td>—</td>
<td>41.0</td>
<td>1.0</td>
<td>14.8</td>
</tr>
<tr>
<td>Gallberry (<em>Ilex glabra</em>)</td>
<td>7</td>
<td>3.1</td>
<td>2.6</td>
<td>6.3</td>
<td>4.0</td>
</tr>
<tr>
<td>Blueberry (<em>Vaccinium spp.</em>)</td>
<td>5</td>
<td>3.1</td>
<td>7.7</td>
<td>1.0</td>
<td>3.9</td>
</tr>
<tr>
<td>Blackberry (<em>Rubus spp.</em>)</td>
<td>4</td>
<td>—</td>
<td>7.7</td>
<td>1.0</td>
<td>2.9</td>
</tr>
<tr>
<td>Swamp tupelo (<em>Nyssa biflora</em>)</td>
<td>3</td>
<td>—</td>
<td>—</td>
<td>3.2</td>
<td>1.1</td>
</tr>
<tr>
<td>Cabbage palm (<em>Sabal palmetto</em>)</td>
<td>2</td>
<td>—</td>
<td>—</td>
<td>3.2</td>
<td>1.1</td>
</tr>
<tr>
<td>Dahan holly (<em>Ilex cassine</em>)</td>
<td>1</td>
<td>3.1</td>
<td>—</td>
<td>—</td>
<td>1.0</td>
</tr>
<tr>
<td>Brazilian pepper (<em>Schinus terebinthifolius</em>)</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>2.1</td>
<td>0.7</td>
</tr>
<tr>
<td>Vegetation</td>
<td>51</td>
<td>46.9</td>
<td>41.0</td>
<td>15.8</td>
<td>34.6</td>
</tr>
<tr>
<td>Leafy green vegetation</td>
<td>11</td>
<td>31.2</td>
<td>2.6</td>
<td>—</td>
<td>11.3</td>
</tr>
<tr>
<td>Vegetation (general)</td>
<td>12</td>
<td>9.4</td>
<td>15.4</td>
<td>5.3</td>
<td>10.0</td>
</tr>
<tr>
<td>Plant fiber</td>
<td>10</td>
<td>9.4</td>
<td>7.7</td>
<td>5.3</td>
<td>7.5</td>
</tr>
<tr>
<td>Grass</td>
<td>11</td>
<td>—</td>
<td>12.8</td>
<td>6.3</td>
<td>6.4</td>
</tr>
<tr>
<td>Palm heart (<em>Sabal palmetto or Serenoa repens</em>)</td>
<td>3</td>
<td>3.1</td>
<td>2.6</td>
<td>1.0</td>
<td>2.2</td>
</tr>
<tr>
<td>Ragweed (<em>Ambrosia spp.</em>)</td>
<td>2</td>
<td>—</td>
<td>—</td>
<td>3.2</td>
<td>1.1</td>
</tr>
<tr>
<td>Smartweed (<em>Polygonum spp.</em>)</td>
<td>1</td>
<td>3.1</td>
<td>—</td>
<td>—</td>
<td>1.0</td>
</tr>
<tr>
<td>Lichen</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>1.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Invertebrate (Arthropoda)</td>
<td>163</td>
<td>40.6</td>
<td>66.7</td>
<td>48.4</td>
<td>51.9</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td>79</td>
<td>12.5</td>
<td>61.5</td>
<td>28.4</td>
<td>34.1</td>
</tr>
<tr>
<td>Florida carpenter ant (<em>Camponotus floridanus</em>)</td>
<td>49</td>
<td>12.5</td>
<td>48.7</td>
<td>28.3</td>
<td>29.2</td>
</tr>
<tr>
<td>Acrobat ant (<em>Crematogaster spp.</em>)</td>
<td>7</td>
<td>3.1</td>
<td>15.4</td>
<td>—</td>
<td>6.2</td>
</tr>
<tr>
<td>Bumble bee (<em>Bombus spp.</em>)</td>
<td>5</td>
<td>—</td>
<td>12.8</td>
<td>—</td>
<td>4.3</td>
</tr>
<tr>
<td>Unknown bee</td>
<td>5</td>
<td>3.1</td>
<td>7.7</td>
<td>1.0</td>
<td>3.9</td>
</tr>
<tr>
<td>Unknown ant</td>
<td>11</td>
<td>—</td>
<td>2.6</td>
<td>2.1</td>
<td>1.6</td>
</tr>
<tr>
<td>Yellow jacket (<em>Vesula spp.</em>)</td>
<td>1</td>
<td>—</td>
<td>2.6</td>
<td>—</td>
<td>0.9</td>
</tr>
<tr>
<td>Guinea wasp (<em>Polistes exclamans</em>)</td>
<td>1</td>
<td>—</td>
<td>2.6</td>
<td>—</td>
<td>0.9</td>
</tr>
<tr>
<td>Coleoptera</td>
<td>43</td>
<td>25.0</td>
<td>12.8</td>
<td>25.3</td>
<td>21.0</td>
</tr>
<tr>
<td>Unknown beetle</td>
<td>17</td>
<td>28.1</td>
<td>10.2</td>
<td>17.9</td>
<td>18.7</td>
</tr>
<tr>
<td>Weevil (<em>Curculio spp.</em>)</td>
<td>15</td>
<td>15.6</td>
<td>—</td>
<td>10.5</td>
<td>8.7</td>
</tr>
<tr>
<td>Scarab beetle (<em>Scarabaeidae</em>)</td>
<td>2</td>
<td>6.2</td>
<td>7.7</td>
<td>6.3</td>
<td>6.7</td>
</tr>
<tr>
<td>Bess bug (<em>Odontotaenius disjunctus</em>)</td>
<td>9</td>
<td>6.2</td>
<td>5.1</td>
<td>—</td>
<td>3.8</td>
</tr>
<tr>
<td>Unknown arthropod</td>
<td>20</td>
<td>9.4</td>
<td>20.5</td>
<td>12.6</td>
<td>14.2</td>
</tr>
<tr>
<td>Isoperta</td>
<td>13</td>
<td>3.1</td>
<td>12.8</td>
<td>7.4</td>
<td>7.8</td>
</tr>
<tr>
<td>Subterranean termite (<em>Rhinotermitidae</em>)</td>
<td>8</td>
<td>3.1</td>
<td>5.1</td>
<td>5.3</td>
<td>4.5</td>
</tr>
<tr>
<td>Unknown termite</td>
<td>5</td>
<td>—</td>
<td>7.7</td>
<td>2.1</td>
<td>3.3</td>
</tr>
<tr>
<td>Metastigmata</td>
<td>5</td>
<td>—</td>
<td>2.6</td>
<td>3.2</td>
<td>1.9</td>
</tr>
<tr>
<td>Tick (<em>Ixodidae</em>)</td>
<td>5</td>
<td>—</td>
<td>2.6</td>
<td>3.2</td>
<td>1.9</td>
</tr>
<tr>
<td>Odonata</td>
<td>1</td>
<td>3.1</td>
<td>—</td>
<td>—</td>
<td>1.0</td>
</tr>
<tr>
<td>Dragonfly (<em>Anisoptera</em>)</td>
<td>1</td>
<td>3.1</td>
<td>—</td>
<td>—</td>
<td>1.0</td>
</tr>
<tr>
<td>Diptera</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>1.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Unknown fly</td>
<td>1</td>
<td>—</td>
<td>—</td>
<td>1.0</td>
<td>0.3</td>
</tr>
<tr>
<td>Vertebrate</td>
<td>30</td>
<td>6.2</td>
<td>23.1</td>
<td>15.8</td>
<td>15.0</td>
</tr>
<tr>
<td>Mammalia</td>
<td>21</td>
<td>6.2</td>
<td>20.5</td>
<td>11.6</td>
<td>12.8</td>
</tr>
<tr>
<td>Feral hog (<em>Sus scrofa</em>)</td>
<td>4</td>
<td>—</td>
<td>7.7</td>
<td>1.0</td>
<td>2.9</td>
</tr>
<tr>
<td>White-tailed deer (<em>Odocoileus virginianus</em>)</td>
<td>3</td>
<td>—</td>
<td>7.7</td>
<td>—</td>
<td>2.6</td>
</tr>
<tr>
<td>Unknown hair or tissue</td>
<td>4</td>
<td>3.1</td>
<td>—</td>
<td>3.2</td>
<td>2.1</td>
</tr>
<tr>
<td>Nine-banded armadillo (<em>Dasypus novemcinctus</em>)</td>
<td>4</td>
<td>—</td>
<td>2.6</td>
<td>3.2</td>
<td>1.9</td>
</tr>
<tr>
<td>Raccoon (<em>Procyon lotor</em>)</td>
<td>6</td>
<td>3.1</td>
<td>—</td>
<td>2.1</td>
<td>1.7</td>
</tr>
</tbody>
</table>

Table 1. Continued.

<table>
<thead>
<tr>
<th>Food item</th>
<th>#</th>
<th>W</th>
<th>S</th>
<th>A</th>
<th>Annual $\bar{x}$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>$n = 32$</td>
<td>$n = 39$</td>
<td>$n = 95$</td>
<td>$n = 166$</td>
</tr>
<tr>
<td>Reptilia</td>
<td>4</td>
<td>2.6</td>
<td>3.2</td>
<td>1.9</td>
<td>1.7</td>
</tr>
<tr>
<td>Gopher tortoise ($Gopherus polyphemus$)</td>
<td>4</td>
<td>2.6</td>
<td>3.2</td>
<td>1.9</td>
<td>1.7</td>
</tr>
<tr>
<td>Aves</td>
<td>5</td>
<td>1.0</td>
<td>1.0</td>
<td>0.3</td>
<td>0.6</td>
</tr>
<tr>
<td>Unknown feathers</td>
<td>5</td>
<td>1.0</td>
<td>1.0</td>
<td>0.3</td>
<td>0.6</td>
</tr>
<tr>
<td>Anthropogenic</td>
<td>75</td>
<td>40.6</td>
<td>35.9</td>
<td>23.2</td>
<td>33.2</td>
</tr>
<tr>
<td>Corn</td>
<td>41</td>
<td>40.6</td>
<td>28.2</td>
<td>18.9</td>
<td>29.2</td>
</tr>
<tr>
<td>Deer chow</td>
<td>13</td>
<td>31.2</td>
<td>7.7</td>
<td>1.0</td>
<td>13.3</td>
</tr>
<tr>
<td>Unknown grain</td>
<td>7</td>
<td>15.6</td>
<td>15.6</td>
<td>3.2</td>
<td>6.3</td>
</tr>
<tr>
<td>Citrus</td>
<td>12</td>
<td>10.2</td>
<td>7.4</td>
<td>5.9</td>
<td>5.3</td>
</tr>
<tr>
<td>Paper or plastic</td>
<td>2</td>
<td>3.1</td>
<td>1.0</td>
<td>1.4</td>
<td>1.6</td>
</tr>
<tr>
<td>Unknown food item</td>
<td>8</td>
<td>9.4</td>
<td>2.6</td>
<td>3.2</td>
<td>5.1</td>
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<tr>
<td></td>
<td></td>
<td>96.83</td>
<td>0.93</td>
<td>0.03</td>
<td>-96.37</td>
</tr>
</tbody>
</table>

$^a$Non-native natural food.

Florida black bear range (Maehr et al. 2001; Table 4). Collectively, energy-rich oak acorns and saw palmetto fruit dominated autumn scats in the HGS (~18,000–

Table 2. Logistic-regression model selection investigating whether a lack of seasonal occurrences of natural food categories in Florida black bear ($Ursus americanus floridanus$) scats influenced the odds of a scat containing anthropogenic foods for the Highlands–Glades subpopulation in south-central Florida, USA (2004–2006). We used anthropogenic foods as the response variable, and season and occurrence of soft mast (Soft), hard mast (Hard), invertebrates (Invert), vertebrates (Vert), and vegetation (Veg) as explanatory variables. We used occurrence of each natural foods variable as the reference level to evaluate non-occurrence. For brevity, only models ≤2 ΔAIC$_c$ are presented.

Table 3. Model-averaged coefficient estimates (β) from the top logistic-regression model predicting occurrence of anthropogenic food items in Florida black bear ($Ursus americanus floridanus$) scats collected in the Highlands–Glades subpopulation of south-central Florida, USA (2004–2006). Occurrence of each natural foods variable was used as a reference; thus, non-occurrence of those variables was estimated. Standard errors (SE), odds ratios (e$^β$), and their 95% confidence intervals, z-values, and the probabilities that β differed from 0 are also presented.
Table 4. Dominant food items in the annual diets of all 7 Florida black bear (Ursus americanus floridanus) subpopulations (Florida, USA), with foods listed in decreasing order of frequency of occurrence (FO). Sample sizes for each study area (n) and total number of unique food items found (#) are presented, as are FO values in parentheses. Modified from Maehr et al. (2001).

<table>
<thead>
<tr>
<th>Subpopulation</th>
<th>n</th>
<th>#</th>
<th>Food 1</th>
<th>Food 2</th>
<th>Food 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eglin&lt;sup&gt;a&lt;/sup&gt;</td>
<td>259</td>
<td>30</td>
<td>Beetles (46%)</td>
<td>Oak acorns (38%)</td>
<td>Saw palmetto fruit (17%)</td>
</tr>
<tr>
<td>Apalachicola&lt;sup&gt;b,c&lt;/sup&gt;</td>
<td>54</td>
<td>9</td>
<td>Swamp tupelo fruit (47.6%)</td>
<td>Bayberry fruit (21.2%)</td>
<td>Oak acorns (7.6%)</td>
</tr>
<tr>
<td>Osceola&lt;sup&gt;d&lt;/sup&gt;</td>
<td>703</td>
<td>27</td>
<td>Corn (29%)</td>
<td>Saw palmetto fruit (17%)</td>
<td>Blackgum fruit (11%)</td>
</tr>
<tr>
<td>Ocala–St. John&lt;sup&gt;e&lt;/sup&gt;</td>
<td>676</td>
<td>36</td>
<td>Oak acorns (59.6%)</td>
<td>Saw palmetto fiber (27.4%)</td>
<td>Sabal palmetto fruit (20.3%)</td>
</tr>
<tr>
<td>Chassahowitzka&lt;sup&gt;f&lt;/sup&gt;</td>
<td>212</td>
<td>20</td>
<td>Vegetation (76%)</td>
<td>Sabal palmetto fruit (70%)</td>
<td>Saw palmetto fruit (37%)</td>
</tr>
<tr>
<td>Highlands–Glades&lt;sup&gt;g&lt;/sup&gt;</td>
<td>166</td>
<td>50</td>
<td>Oak acorns (33.3%)</td>
<td>Corn (29.2%)</td>
<td>Florida carpenter ant (29.2%)</td>
</tr>
<tr>
<td>Big Cypress&lt;sup&gt;h&lt;/sup&gt;</td>
<td>739</td>
<td>44</td>
<td>Sabal palmetto fruit (29.4%)</td>
<td>Saw palmetto fruit (22.7%)</td>
<td>Brazilian pepper (22.1%)</td>
</tr>
</tbody>
</table>

<sup>a</sup>Stratman and Pelton (1999)
<sup>b</sup>Maehr and Brady (1984)
<sup>c</sup>Based on analysis of stomach contents, not scats.
<sup>d</sup>Odbey et al. (2005)
<sup>e</sup>Roof (1997)
<sup>f</sup>Orlando (2003)
<sup>g</sup>This study
<sup>h</sup>Maehr (1997)

year-round and radiomonitoring data confirmed some HGS bears were winter-active during our study (Ulrey 2008; Guthrie 2012). Although oak acorns dominated winter–spring HGS scats, which exemplifies acorn overwintering, mast surveys conducted in the study area indicated acorn yields during our years of sampling were 54.8% higher than the 27-year average (1988–2014; Bowman 2015). Scrub communities contain 5 of the 7 oak species of the Lake Wales Ridge ecosystem and adjacent areas within HGS primary range (Abrahamson and Layne 2003), but substantial scrub has already been lost (Weekley et al. 2008). The magnitude of acorn overwintering that occurred is likely uncommon, and we therefore believe our annual acorn FO is an overestimate. Our short 2-year sampling period precluded an identification of the foods that winter-active Florida black bears may rely on during years of average or poor oak productivity, but winter–spring FOs suggest vegetation, anthropogenic foods, and invertebrates may be important.

Most green vegetation (e.g., leaves, grasses, forbs, etc.) generally is considered of tertiary diet importance to black bears in the southeastern United States because those items provide little nutritional value compared with other natural foods (Maehr et al. 2001, Inman and Pelton 2002). In contrast, anthropogenic foods are caloric-rich, typically require little energy expenditure to access, and are often exploited by bears when natural foods are scarce. Hunter-dispensed corn at feeding stations has the potential to sustain at least some winter-active bears, which could increase skeletal–lean body mass and improve individual fitness (Robbins et al. 2004, Steyaert et al. 2014). Bears can quickly habituate to corn and other anthropogenic foods, leading to increased human–bear conflicts that could endanger humans and cause financial losses. Florida black bears visiting feeding stations and depredating or damaging agricultural crops collectively account for a prominent human–bear conflict complaint in the area occupied by the HGS (FWC 2012). Citrus fruit is the most widespread agricultural crop in the Lake Wales Ridge ecosystem, groves of which were important predictors of female bear road-crossings in the HGS (Guthrie 2012). Despite the close proximity of numerous groves to established bear subpopulations, our study is the first to document citrus fruit in the diet of Florida black bears (Maehr et al. 2001). Although not seasonally or annually important, the limited macronutrients provided by citrus fruit (<1 g fat; <1 g protein; <12 g carbohydrates) are insufficient for supporting maintenance or growth of lean body mass in bears. Therefore,
the presence of citrus in summer scats anecdotally suggests higher quality natural foods were either limited in availability or inaccessible during summer (Costello et al. 2014). Blueberry and blackberry fruits that other Florida black bear subpopulations relied on during summer (Maehr and DeFazio 1983; Maehr et al. 2001) had nominal FO, whereas lower nitrogen grapes (Vitis spp.) had the highest FO among soft mast in summer scats. Interspecific competition for quality summer soft mast is extraordinary among vertebrates and could rapidly erode fruit availability despite high productivity (Inman and Pelton 2002). Heightened occurrence of vertebrate remains in summer scats further supports limited soft mast availability during our sampling. Those remains included white-tailed deer, indicating predation of neonates rather than kleptoparasitism of hunter kills or scavenging (Zager and Beecham 2006); and predation of neonate ungulates by black bears has been posited as a response to shortages of natural vegetal foods (Belant et al. 2006; Svoboda et al. 2011).

Other studies noted the impacts that soft mast shortages can have on black bear populations, such as depressed vital rates, and the relationship of shortages with human–bear conflicts (Inman and Pelton 2002; Obbard and Howe 2008; Romain et al. 2013). We found heightened dietary reliance on anthropogenic food sources as soft mast occurrence declined, a response that would increase human–bear conflicts assuming anthropogenic foods are a reliable proxy (Howe et al. 2010; Hopkins et al. 2014). Our FO estimates indicate corn is the most likely substitute for soft mast among anthropogenic food items, but human–bear conflicts at feeding stations located in rural areas may be less severe relative to those associated with other human-sourced foods (Merkle et al. 2013; Ditmer et al. 2016). Despite not collecting scats in the urbanized north-central part of HGS primary range where human population density is highest, we documented a few occurrences of garbage in scats. Bears frequenting urban areas to access garbage can result in conditioning to human presence, loss of fear of humans, and injured aggression toward humans (Pilstrom et al. 2014; Penteriani et al. 2016). Citrus fruit is Florida’s top cash crop (~US$1.10 billion income annually; Gitzen 2015); therefore, contentious and costly conflicts with humans could also develop if HGS bears increase citrus fruit consumption or cause damage to citrus trees.

Whether or not the anthropogenic foods available to HGS bears can support a sufficient portion of the population necessary to ensure long-term persistence in the face of imminent habitat loss is unclear. Although nutrient-poor citrus fruit is incapable of doing so, carbohydrate-rich corn and deer chow are easily accessible and hunter-dispersed corn provided approximately 8,000% of the amount of hard and soft mast available to bears in Virginia, USA, during years of mast failures (Gray et al. 2004). Anthropogenic foods were, however, not among the most dominant summer-food categories in HGS scats. Invertebrates were the only category with consistently moderate to high FO across all seasons, a finding that was largely influenced by myrmecophagy of Florida carpenter ants during summer. Ants are a protein- and lipid-rich food that can support lean mass accumulation in bears if consumed in large, concentrated amounts, such as at formicaries (López-Alfaro et al. 2013). Studies of black and brown bear (U. arctos) populations elsewhere noted the importance of ants and other invertebrates, which are likely reliable food sources with minimal abundance fluctuations. Florida carpenter ants and weevils, including the giant palm weevil (Rhynchophorus cruentatus), are arboreal species that are acutely dependent on remaining bear habitat for proliferation (Tedder et al. 2012). Thus, impending habitat loss could also reduce populations of those important invertebrates and increase consumption of anthropogenic foods by HGS bears.

Much of the uncertainty in our results is a function of sampling duration, which was too short to account for super-annual mast fluctuations (Craighead et al. 1995), and small seasonal sample sizes of scats. Pooling within-season scats across years to overcome the latter issue resulted in sample sizes that were skewed toward autumn when bear food consumption and defecation rates are typically highest (Dahle et al. 1998; Ciucci et al. 2014), thereby attributing more weight to food items in autumn scats (i.e., pooling fallacy; Machlis et al. 1985; Leger and Didrichsons 1994). Therefore, FO probably overestimated the importance of smaller sized oak acorns while underestimating the importance of larger sized foods, such as vertebrates (Klare et al. 2011). Locations of our sample collections were also clustered in 3 areas of high Florida black bear use (Ulrey 2008; Guthrie 2012), which likely exacerbated said issue by violating the assumption of sample independence (Klare et al. 2011). Furthermore, because some natural foods are endemic to remnant habitat communities (e.g., scrub palmetto fruit) that are

difficult to access without substantial risk to bears (e.g.,
crossing roads) as a result of habitat loss and fragmenta-
tion (Guthrie 2012), our clustered sampling may not
have detected all of the foods consumed by bears. Al-
though increasing our winter–spring and summer scat
sample sizes would have been difficult because of the
small number of bears in the HGS, future dietary studies
should conduct sampling over a longer temporal period
(e.g., > 3 consecutive yr) to account for mast fluctuations
(Romain et al. 2013). Estimating volume-based metrics
in our study would have been unlikely to facilitate more
insightful comparisons among Florida bear subpopu-
lations, but should be used in conjunction with FO for
future studies to better approximate dietary importance
of specific food items (Klare et al. 2011; Ciucci et al.
2014; Stenset et al. 2016).

Management implications
Federally endangered scrub communities contain nu-
merous high-quality hard and soft mast–producing flora
(e.g., saw palmetto, blueberry, and 5 species of oak;
Abrahamson et al. 1984, Layne and Abrahamson 2010);
therefore, we suggest managers consider intensifying ef-
forts to protect remnant patches of scrub via state and
federal agency acquisition or conservation easements to
thwart further loss. Soft mast generally appears to be
the most important food category to Florida black bears
in the HGS, and the lack thereof is associated with in-
creased consumption of anthropogenic foods; therefore,
habitat conservation should also include other commu-
nities with quality soft-masting shrubs and plants, such
as flatwoods and sandhills (Abrahamson and Abraha-
msion 1989; Layne and Abrahamson 2010). An indirect
byproduct of these habitat conservation efforts is main-
tenance of arboreal Florida carpenter ant populations
for bears to consume during years of poor mast yields or
in the event that masting flora abundance and distribu-
tion is reduced by anthropogenic development. Although
hunter-dispersed corn at wildlife feeders provides a nu-
tritious, easily accessible supplemental food for bears,
such feeding could result in habituation and lead to bears
increasing exploitation of other anthropogenic foods that
are in closer proximity to humans (e.g., garbage) or are
agricultural commodities (e.g., citrus fruit). Small size of
the HGS should limit human–bear conflict management
to primarily non-lethal methods, so we suggest managers
increase public education and outreach (Pienaar et al.
2015) and expand agency-assistive anthropogenic-food–
management programs to the HGS area (Barrett et al.
2014). Finally, our samples were collected a decade prior
to present; therefore, we strongly suggest repeating our
study over a longer duration to investigate whether di-
etary shifts occur in response to impending habitat loss
and to further inform habitat and subpopulation conserv-
ation and human–bear conflict management.

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of the authors and do not necessarily reflect the views
of the University of Kentucky. Use of trade, product, or
firm names is for descriptive purposes only and does not
imply endorsement by the University of Kentucky.

Literature cited
ABRAHAMSON, W.G., AND C.R. ABRAHAMSON. 1989. Nutri-
tional quality of animal dispersed fruits in Florida sandridge
Vegetation of the Archbold Biological Station, Florida: An
example of the southern Lake Wales Ridge. Florida Scientist
47:209–250.
production for five oak species in xeric Florida uplands.
Ecology 84:2476–2492.
AGEE, J.D., AND C.A. MILLER. 2009. Factors contributing to-
ward acceptance of lethal control of black bears in Central
ARCHBOLD BIOLOGICAL STATION. 2010. Station fact
sheet: Archbold Biological Station. http://www.archbold-


