

COMPARATIVE DIETS OF ADULT AND YOUNG THREE-TOED WOODPECKERS IN A EUROPEAN ALPINE FOREST COMMUNITY

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Abstract: We studied year-round food preferences of the three-toed woodpecker (*Picoides tridactylus*) from 1994 to 2000 in Berchtesgaden National Park, Germany. We color-banded 52 birds for individual recognition, and we radiomarked 25 adults from this sample. We analyzed 142 feces of 30 adults and 588 feces of 40 nestlings from 15 nests. Additionally, we took samples from 20 trees recently used for foraging in 10 woodpecker territories to estimate local prey availability. Based on relative abundance and relative frequency of food items (i.e., importance value), overall diet composition of adult three-toed woodpeckers was dominated by spiders (Araneidea), larvae of longhorn beetles (Coleoptera, Cerambycidae), and bark beetles (Coleoptera, Scolytidae). Adults ate longhorn beetle larvae primarily during nesting, while imagines (fully developed adults) and larvae of various bark beetles appeared to be the main food resource outside the nesting season. Nestling diet was dominated by spiders and longhorn beetle larvae that were gathered 247 ± 122 m ($\bar{x} \pm$ SD) from the nest. Our results demonstrated that consumption of bark beetles by three-toed woodpeckers varies throughout the year, being lowest during the nesting season, while longhorn beetle larvae are preferred throughout the year. Securing habitat requirements of both bark and wood-boring beetle communities is a critical step to maintaining viable three-toed woodpecker populations.

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The three-toed woodpecker responds both numerically and behaviorally to bark beetle outbreaks. Dement'ev (1966) called the three-toed woodpecker "one of the most beneficial birds of taiga forests" based on analysis of stomach contents. In North America (Baldwin 1968, Koplín 1968, Koplín and Baldwin 1970, Massey and Wygant 1973) and Europe (Wasilewski 1969, Scherzinger 1998), three-toed woodpeckers have been considered an important vertebrate predator of bark beetles. However, most of these studies were conducted during relatively high bark beetle population densities and did not consider diet preferences of the bird in relation to its breeding cycle. Any attempt to quantify impacts of this woodpecker on beetle populations (Koplín 1972, Bütler and Schlaepfer 2003) should necessarily consider dietary preferences across seasons and between age classes under varying beetle densities.

The diet of adult three-toed woodpeckers has been studied throughout the species' breeding range using stomach contents (Hogstad 1970, Otvos and Stark 1985, Murphy and Lehnhausen 1998), droppings (Pechacek and Kristin 1993), and recently used bark patches (Fayt 1999). Only a few detailed studies have addressed the composition of

arthropod prey brought to nestlings. Despite limited nest sample sizes, results from fecal and neck-collar samples collected in Switzerland (Ruge and Havelka 1993; R. Hess, Unterägeri, unpublished data) and Germany (Pechacek and Kristin 1996), together with anecdotal observations (Lanz 1950, Schifferli and Ziegeler 1956), suggest that bark beetles comprise a small portion of the nestling diet.

We suggest several reasons why bark beetles may account for the relatively low proportion of the nestling diet. Adult woodpeckers may adjust their foraging behavior to secure the energetic requirements of their offspring and compensate for their increased daily energetic expenditures during reproduction. Due to their relatively small size, bark beetles may represent less profitable food for the demanding and fast-growing chicks than larger alternative prey. For example, bark beetles of all developing stages reach a body length of about 0.6 cm while the body size of alternative prey items brought to the offspring (mostly longhorn beetle larvae and spiders) reaches 1.3 cm (Pechacek and Kristin 1996). This suggestion assumes size dependence in the nutritional value of arthropod prey and predicts that bark beetles should be less abundant in the diet of offspring and adults than expected from their availability on foraging trees. Inversely, outside the nesting season, adult woodpeckers should rely on bark beetles according to their availability. Selection for more profitable prey increases in

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birds while feeding nestlings (Newton 1967, Green 1978), and adults in a number of species select larger food items for their nestlings than they eat themselves (Bryant 1973, Davies 1977, Bishton 1986, Brandl et al. 1994).

Alternatively, reduced bark beetle consumption during nesting may result from low beetle densities between outbreak periods when other food is easier to obtain. Bark beetle consumption should then be reduced not only during the nesting season, but also throughout the year. Bark beetle outbreaks are brought on by a combination of persisting warm air temperatures (>16 °C to emerge from hibernation in Mar or Apr; Lobinger 1994) and superabundance of breeding substrates (i.e., coniferous trees with defects in water regime through damage by storms, avalanches, hail, etc.; Schwenke 1996). During an outbreak, bark beetles are abundant and easily available by the time woodpeckers are rearing their young in June. Outbreaks may last several years if the supply by damaged trees remains high. Eventually, the bark beetle population will collapse due to increasing competition for breeding substrate; this may be hastened by wet and/or cold weather (Schwenke 1996). Thus, bark beetle outbreaks occur randomly, and three-toed woodpeckers likely exploit more predictable food resources to bridge the gap between outbreaks. However, under very high bark beetle densities (i.e., >35 maternal galleries/0.1 m² of bark [Niemeyer et al. 1995]) coinciding with the nesting period, three-toed woodpeckers may favor bark beetles despite their small size (Sevastyanov 1959, Pechacek and Kristin 1993, Murphy and Lehnhausen 1998).

We conducted a 7-year study to describe habitat use and prey collected by three-toed woodpeckers during the nesting and non-nesting periods. We collected fecal pellets to estimate diet preferences of adult birds and to compare these preferences with food items brought to their nestlings. Furthermore, we quantified prey availability on foraging trees among different woodpecker territories. Our objectives were to (1) determine food preferences of young and adult three-toed woodpeckers under low bark beetle population density, (2) ascertain whether seasonal variation occurs in food preferences, and (3) assess whether diet preferences reflect changes in prey availability or energetic requirements.

STUDY AREA

We conducted our study from 1994 to 2000 in Berchtesgaden National Park, Germany (47°32'N,

12°56'E; 600–2,700 m above sea level), where local bark beetle populations reached epidemic levels from 1992 to 1994 (Zierl and Siegrist 1999). Alpine forest dominated by Norway spruce (*Picea abies*) mixed with larch (*Larix decidua*) covered 8,100 ha of the park. Compared to the surrounding areas, which had been subjected to extensive forest management and supported on average <12 m³/ha of coarse woody debris (i.e., standing and down trees and logs; Burschel 1992), Berchtesgaden National Park had 30 m³/ha of coarse woody debris (Konnert 2000). Estimated densities of the three-toed woodpecker in the park ranged between 0.9 and 1.0 breeding pairs/km² (Pechacek 1995).

METHODS

Trapping and Marking of Birds

We trapped three-toed woodpeckers and marked them with serially numbered aluminum and colored plastic bands. We captured nestlings when they were 5–20 days old. We used a noose to pull nestlings out of the nest hole (Jackson 1982). We used mist nets to capture adult woodpeckers early in the nesting season (Apr–May) by inducing territorial responses from resident birds with a playback tape or by placing nets in the flight path to the entrance of the nest or roost cavity. Additionally, we used a trap door or a bag net at the nest or roost cavity.

Some adult woodpeckers also were fitted with a 1.5-g radiotransmitter (Typ BD 2G, Holohil Limited, Carp, Ontario, Canada). We glued radiotransmitters onto the upper base of the 2 central rectrices using a cyanoacrylate glue (Typ Stabiloplast No. 448, Renfert GmbH, Karlsruhe, Germany). Over the course of our study, we improved radiotransmitter attachment by using a series of nylon ties extending along 1 feather shaft and by cleaning the glued spot with 70% alcohol prior to attachment. The woodpeckers adapted well to the radiotransmitters, which weighed up to 2.5% of a bird's body mass, and the birds appeared to behave as unmarked individuals. However, we encountered problems with some of the transmitters (sudden molt of tail feathers, failure of glue holding the radiotransmitter, antenna breakage) within a few hours to several weeks after radiotransmitters were attached. In those cases, and after the expected 10-week life span of the radiotransmitters, we recaptured the birds whenever possible. Each woodpecker was radiomarked only once during the study to avoid pseudoreplication

due to repeated observations of the same individuals in multiple years. In 2 cases of re-mating after the presumed death of a mate, the “new” bird was trapped while its previously captured partner was not.

Radiotracking

We conducted radiotracking with portable B+R receivers (type 328080) and hand-held H-antennas (type HB 9 CV; Peter Reichenbach GmbH, Freiburg in Breisgau, Germany). We radio-tracked woodpeckers during daylight, starting the second day following trapping, using the homing-in method (White and Garrott 1990:42). We monitored movements of woodpeckers to locate defecating birds, find nests, and measure the distance between foraging sites and nests during the nestling period.

We defined a foraging site as a place to gather food for nestlings. We recorded locations of foraging birds when food gathered by a parent was not eaten but remained visible in the bill. We recorded Gauss-Krüger-grid coordinates superimposed on a 1:10,000 map. To provide accurate distance determination, we only analyzed observations that could be assigned to a 50-m radius. We attempted to obtain independent observations of food-gathering birds evenly distributed throughout our study period. Consecutive observations of the same woodpecker were separated by at least 1 hr to reduce the chance of autocorrelation (Swihart and Slade 1985). We considered locations to be spatially independent if the bird moved >100 m from its previous location (approx 30% of cases). We based this decision on the fact that the distance between consecutive locations at the 1-hr interval was usually at least 100 m.

Collecting and Analyzing Feces

We opportunistically collected nestling fecal samples that were carried out of cavities by parents while we observed activities at nests. We sampled feces up to 10 m around the nest tree after a parental bird, usually the male (approx 90%), dropped a fecal sack. We collected fecal samples from up to 5 pairs/year when the young were ≥ 10 days old. This was to assure that samples were evenly distributed over the second half of the nestling period. Earlier in the nestling period, fecal sacs were partially eaten by the adult (P. Pechacek, National Park Administration Berchtesgaden, unpublished data), and therefore, collecting a similar sample would have been less reliable. We counted the number of nestlings in each

nest either while banding young or—when we did not band young—by using a lighted mirror inserted into the entrance hole. We collected fecal samples of adults opportunistically throughout the year if we located woodpeckers while they were defecating. We also collected fecal samples while processing captured birds. We analyzed feces to estimate diet preferences during and outside the nesting season. We defined nesting from the first spring excavation recorded in the study area by the three-toed woodpecker in a given year (approx 15 Apr) to 15 September of that year.

Fecal samples were preserved in 70% alcohol and dissected using a microscope with 6–50X magnification. We identified food remains to the lowest possible taxonomic level using a comparative collection of arthropods. We based our determination on sclerotized chitin parts that were not affected by digestion (e.g., chelicers, mandible, legs, wings, head capsules). We used the term food object for everything found in fecal samples (e.g., 10 legs, 4 head capsules), and we classified these objects to food items (e.g., 3 insect families). We measured the frequency (%) with which a food item occurred in each fecal sample, and we calculated abundance of food items relative to the other items detected (%). In contrast to animal remains, abundance of plant parts in samples could not be accurately estimated (<1%) due to digestion. However, we believe we were able to determine the presence or absence of plant remains such as seeds or berries. We combined abundance and frequency of each food item using the formula:

$$(\text{relative abundance} + \text{relative frequency})/2$$

to estimate relative importance value (%) per food item (Pechacek and Kristin 1993). We calculated Shannon-Weaver's diversity (H') and Sheldon's evenness (e) values of the trophic niche (Mühlenberg 1993) based on food items detected in feces of woodpeckers if >2 feces per nest or bird were available. All fecal sample measurements on nestlings were averaged per nest, whereas measurements from adult feces were averaged per bird.

Assessment of Prey Availability

We used emergence traps to assess prey availability on foraging trees (Ausden 1996). Foraging trees were Norway spruce snags that were recently (i.e., within a month) used for foraging by marked three-toed woodpeckers. We obtained 0.5-m length

sections (samples) from <3 m above ground by cutting 20 foraging trees distributed over 10 territories of breeding woodpeckers (2 trees/territory). From each territory, we collected 1 sample that showed evidence of bark scaling or pecking, and another sample that displayed marks left by three-toed woodpeckers after excavating deeper in phloem or xylem. We collected samples on 19 June 2000 and placed each sample into a separate emergence trap for 4 months.

Our traps were transparent plastic cylinders equipped with a funnel and collecting bottle with preservative (salted water solution) below (Ausden 1996). The top of the cylinder was closed with a transparent plastic plate with 2 openings covered by gauze to prevent litter falling into the cylinder. Tree samples were laid on a wire mesh inside the trap. Invertebrate taxa hiding underneath the bark or emerging from pupae in dead wood fell into the funnel and the collecting bottle below. Traps were mounted on wooden stakes with rain covers and were left concentrated in a forest clearing in the study area.

We emptied traps between 29 June and 8 November 2000 at 14-day intervals. We identified collected invertebrates to order or family. From these samples, we estimated relative abundance of prey (%), Shannon-Weaver's diversity index, and Sheldon's evenness index. All measurements were averaged per woodpecker territory.

Statistical Analysis

Based on their ecology and general appearance, we categorized food items into 4 groups for statistical analysis: (1) Arachnoidea = spiders, (2) Cerambycidae larvae = longhorn beetle larvae, (3) Coleoptera = all other beetles, including bark beetles and longhorn beetle imagines, and (4) miscellaneous items. We used parametric tests when assumptions about normal distribution were met. When the level of measurement was ordinal or less, we used nonparametric tests. We used Wilcoxon rank-difference tests over Mann-Whitney *U*-tests in cases when the compared variables were dependent. Results were considered 2-tailed at $P < 0.05$. Standard deviations (SD) are given with means (\bar{x}) unless otherwise stated.

RESULTS

We trapped 14 male and 18 female adult three-toed woodpeckers, and we radiomarked 11 males and 14 females of this sample. Additionally, we captured 20 nestlings from 10 cavities.

We estimated distance between foraging sites

and 12 nests from a mean of 43 (range = 13–88) observations/radiomarked bird. A minimum of 35 chicks from monitored nests were fed prey gathered by 22 parents (10 males, 12 females) in an average median distance of 247 ± 122 m ($\bar{x} \pm$ SD) around the nesting cavity. Interquartile range of this distance varied between 140 ± 72 m and 402 ± 205 m, whereas the average maximum distance to deliver prey from the foraging site to the nest was 794 ± 316 m.

Adult Diet

We collected 142 fecal samples between 1995 and 1999 during 2 non-nesting and 3 nesting seasons. We collected 48 feces from 5 woodpeckers in both nesting and non-nesting periods (14 feces during nesting, 34 during non-nesting), 56 feces from 15 woodpeckers during nesting, and 38 feces from 10 woodpeckers during non-nesting. We detected no differences among years when we summarized contents of feces to food groups; thus, for 3 woodpeckers, we pooled feces collected from 2 different years to increase the total sample from a given individual woodpecker.

Year-round Period.—Feces of 30 adult woodpeckers contained 447 identifiable food objects that we classified into 27 food items (Appendix A). These included 1 non-arthropod order (Gastropoda) and 8 arthropod orders including 11 families. We also found 1 plant species (Norway spruce seeds), and we estimated that at least 2 more animal orders were present including at least 15 more families representing a total of about 58 species. We calculated year-round diversity of the trophic niche based on detected food items in 13 cases represented by 11 birds. Diversity was 1.55 ± 0.40 , whereas evenness averaged 0.80 ± 0.10 per bird.

Woodpecker ($n = 142$ feces from 30 adults) diets were dominated by spiders, longhorn beetle larvae, and bark beetles. Relative abundance of food groups differed between the nesting and non-nesting season (Friedman test: non-nesting season: $\chi^2 = 20.7$, $df = 3$, $P \leq 0.001$; nesting season: $\chi^2 = 30.4$, $df = 3$, $P \leq 0.001$). The diets of males ($n = 16$) and females ($n = 14$) were not significantly different during the non-nesting season (Arachnoidea: $F = 0.7$, $P = 0.409$; Cerambycidae larvae: $F = 2.5$, $P = 0.139$; Coleoptera: $F = 0.2$, $P = 0.693$; miscellaneous: $F = 0.0$, $P = 0.948$), or the nesting season (Arachnoidea: $F = 1.3$, $P = 0.263$; Cerambycidae larvae: $F = 2.7$, $P = 0.117$; Coleoptera: $F = 0.4$, $P = 0.516$; miscellaneous: $F = 9.9$, $P = 0.333$). In both periods, the miscellaneous group was the least abundant (Fig. 1).

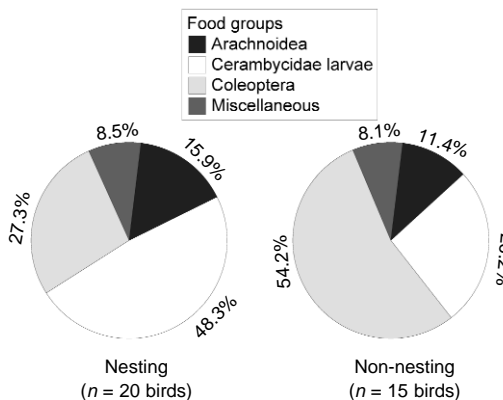


Fig. 1. Food groups in feces of adult three-toed woodpeckers in nesting and non-nesting seasons in Berchtesgaden National Park, Germany, 1995–1999. Shown are total numbers of relative abundance representing 14 females and 16 males. Number of feces per woodpecker ranged 1–13 during non-nesting (n = 72) and 1–20 (n = 70) during nesting. The feces of 3 females and 2 males were sampled in both seasons.

Nesting Period.—We identified 176 food objects during the nesting period. The number of food items per bird averaged 3.6 ± 3.9 (n = 20), and woodpeckers mainly preyed on longhorn beetle larvae (>63% importance value). Based on 70 feces from 20 woodpeckers, Arachnoidea and Coleoptera were preyed on equally (Wilcoxon test: $Z = -0.5$, $P = 0.645$). Abundance of the Cerambycidae larvae prey group in feces was significantly higher during nesting than during non-nesting (Mann-Whitney U-test: $Z = -3.1$, $P = 0.002$).

Non-nesting Period.—We found 271 food objects in feces collected during the non-nesting period. The number of food items discovered per bird averaged 6.4 ± 2.7 (n = 15). Imagines and larvae of various bark beetles appeared to be the major prey taken and made up 34% of the importance value of total prey, followed closely by longhorn beetle larvae (>25% importance value). Based on 72 feces from 15 individual woodpeckers, the abundance of Arachnoidea and Cerambycidae larvae did not differ significantly during the non-nesting

period (Wilcoxon test: $Z = -1.5$, $P = 0.139$). Abundance of the Coleoptera prey group was significantly higher during non-nesting than nesting (Mann-Whitney U-test: $Z = -3.3$, $P = 0.001$).

Nestling Diet

We collected 588 fecal samples from 40 10- to 24-day-old nestlings from 15 three-toed woodpecker nests between 1994 and 2000. Nests contained an average of 2.7 ± 0.6 (range = 2–4) young, and we collected an average of 39.2 ± 31.4 (range = 3–124) samples per nest.

Feces of nestlings contained 2,302 food objects that were classified into 57 food items (Appendix B). These included 1 non-arthropod order (Gastropoda), 13 arthropod orders from 23 families, and 1 plant species (Norway spruce seeds). Based on our feces analysis, we estimated that at least 3 more arthropod orders were present, including 19 more families representing about 76 species. Feces composition calculated per nest was dominated by spiders of the order Araneidea ($35.2 \pm 8.6\%$ importance value) and larvae of longhorn beetles ($26.4 \pm 10.1\%$ importance value).

Relative abundance of prey in 12 nests with >7 fecal samples was not equally distributed in the nestling diet (Friedman test: $\chi^2 = 27.2$, $df = 3$, $P \leq 0.001$; Fig. 2). Arachnoidea were fed to chicks more than Cerambycidae larvae (Wilcoxon test: $Z = -2.4$, $P = 0.015$), whereas the group containing miscellaneous items was preferred over Coleoptera (Wilcoxon test: $Z = -2.0$, $P = 0.041$). Samples were collected during the 1994–2000 nesting seasons, and we found no differences among years (Arachnoidea: $F = 0.9$, $P = 0.502$; Cer-

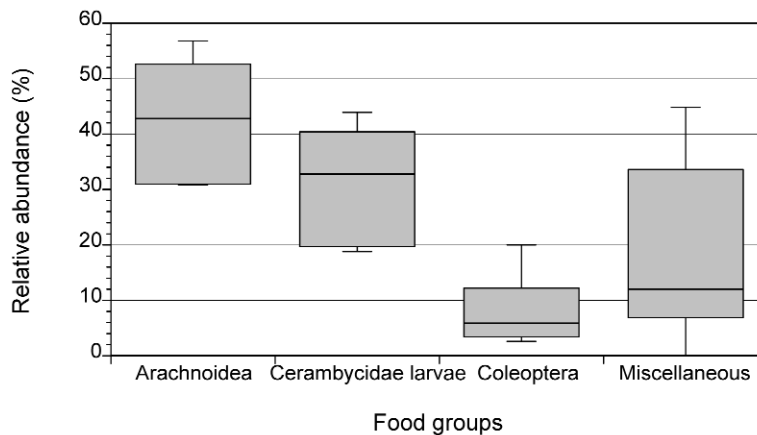


Fig. 2. Box plot of food groups found in feces of 31 nestlings of the three-toed woodpecker from 12 nests with 8–124 fecal samples (47.8 ± 30.7 [$\bar{x} \pm SD$] fecal samples/nest) in Berchtesgaden National Park, Germany, 1994–2000.

ambycidae larvae: $F = 0.5$, $P = 0.711$; Coleoptera: $F = 1.3$, $P = 0.352$; miscellaneous: $F = 2.3$, $P = 0.134$).

Differences between Diet of Young and Adults

The mean number of food items in feces of young (per nest) was higher (11.9 ± 6.3 ; $n = 15$) than that found in feces of adults during nesting (3.6 ± 3.9 ; $n = 20$; Mann-Whitney U -test: $Z = -4.0$, $P \leq 0.001$). Prey diversity did not differ between nestlings ($H' = 1.64 \pm 0.49$; $n = 15$) and their parents ($H' = 1.71 \pm 0.46$; $n = 5$; Mann-Whitney U -test: $Z = -0.6$, $P = 0.570$). Species evenness, however, was lower in nestlings ($e = 0.69 \pm 0.12$) than in adult birds ($e = 0.81 \pm 0.10$; Mann-Whitney U -test: $Z = -2.1$, $P = 0.032$).

Comparing the relative abundance of the 4 food groups found in feces of 14 adult woodpeckers and their 23 nestlings, parents fed their offspring significantly more Arachnoidea ($42.5 \pm 11.0\%$ relative abundance) than they ate themselves ($13.2 \pm 13.6\%$ relative abundance; Wilcoxon test: $Z = -2.5$, $P = 0.012$). Conversely, the relative abundance of Cerambycidae larvae was significantly lower in feces of young ($26.2 \pm 13.2\%$) than in feces of parents ($63.3 \pm 32.3\%$; Wilcoxon test: $Z = -2.2$, $P = 0.025$). We found no significant differences in feces composition between parents and their young when we compared the relative abundance of Coleoptera ($14.9 \pm 21.1\%$ vs. $17.8 \pm 15.8\%$; Wilcoxon test: $Z = -1.0$, $P = 0.327$) and miscellaneous items ($16.4 \pm 15.6\%$ vs. $5.7 \pm 12.8\%$; Wilcoxon test: $Z = -1.3$, $P = 0.207$). However, focusing on the relative abundance of the miscellaneous group, we found a significant difference between nestlings and adults when we ignored their relationship (i.e., considering nests and birds regardless of paired young-parent combinations). Relative abundance of miscellaneous items in all 15 nests averaged $18.3 \pm 14.3\%$, whereas the relative abundance of miscellaneous items found in feces of all 20 adults averaged $2.9 \pm 9.4\%$ (Mann-Whitney U -test: $Z = -4.1$, $P \leq 0.001$).

Prey Available on Foraging Trees

Samples from 20 snags recently used for foraging in 10 territories of the three-toed woodpecker were inhabited by about 9,630 (45%) springtails (Collembola), about 10,130 (48%) individuals from the order Acari, and by 1,573 other invertebrates (7%). We excluded springtails and Acari from the further analysis because they were obviously too small to be a consequential food for the three-toed woodpecker.

We classified trapped invertebrates into 32 taxa categories from 19 orders and 20 families. Except for molluscs (Gastropoda) and earthworms (Lumbricidae), catches included arthropods. The number of invertebrate taxa that emerged from foraging trees (16.8 ± 2.4) was significantly higher than the number of food items detected in feces of adults during nesting (Mann-Whitney U -test: $Z = -4.4$, $P \leq 0.001$) and non-nesting ($Z = -4.1$, $P \leq 0.001$). However, the difference was not significant when we compared number of potentially available prey taxa with food items detected in feces of young birds (Mann-Whitney U -test: $Z = -1.9$, $P = 0.061$).

Emergence trap samples were dominated by various undetermined beetle larvae (<0.2 cm body size), flies (Diptera), and bark beetles. Relative abundance of all taxa categories varied among sampled territories as revealed by their summarization to food groups (Friedman test: $\chi^2 = 24.8$, $df = 3$, $P \leq 0.001$). Arachnoidea and Cerambycidae larvae both were less abundant than Coleoptera (Wilcoxon test: $Z = -2.8$, $P = 0.005$, and $Z = -2.8$, $P = 0.005$) and miscellaneous items (Wilcoxon test: $Z = -2.8$, $P = 0.005$, and $Z = -2.8$, $P = 0.005$).

We tested for differences between prey availability on foraging trees and prey consumed. Cerambycidae larvae were significantly more abundant in feces of both nestlings and adults throughout the year than available on foraging trees (Table 1). Conversely, the food group containing miscellaneous items was always significantly less abundant in feces than on foraging trees. Arachnoidea were eaten by adults in proportion to their availability on foraging trees, but nestlings were fed with spiders more than would be expected based on availability. Coleoptera were consumed significantly less than expected by both young and adult woodpeckers during nesting, but equal to expectation during the non-nesting season by adults.

DISCUSSION

Adult Diet

We found significant seasonal differences in three-toed woodpecker diets. During nesting, woodpeckers primarily preyed on longhorn beetle larvae (>63% importance value). Consumption of bark beetles made up >34% of importance value during non-nesting, but bark beetles were rarely eaten during nesting (<10% importance value). Thus, contrary to earlier reports from Russia (Sevastyanov 1959), Germany (Pechacek and Kristin 1993), and Alaska (Murphy and Lehnhausen 1998), our results indicate strong seasonal variation in the

Table 1. Food groups found in diets of three-toed woodpeckers compared to those available in woodpecker territories in Berchtesgaden National Park, Germany, 1994–2000. Shown are relative abundances (%) of food groups obtained by analysis of feces of nestlings and adults that were compared by Mann-Whitney *U*-test with relative abundances of food groups found on 20 foraging trees (2 per territory). Three-toed woodpecker diet was based on feces of 40 nestlings from 15 nests (\bar{x} = 39.2 feces/nest, range = 3–124; n = 588) and on feces of 30 adults (14 females and 16 males). Adult feces were represented by 70 feces (range = 1–20 feces/bird) from the nesting season and 72 feces (range = 1–13 feces/bird) from the non-nesting season. Feces of 3 females and 2 males were sampled in both seasons.

Food groups	Prey available		Prey in diet											
			Nestlings				Adults							
	\bar{x}	SD	\bar{x}	SD	Z	P	\bar{x}	SD	Z	P	\bar{x}	SD	Z	P
Arachnoidea	8.6	6.0	42.3	10.5	-4.2	0.000	15.7	23.1	-0.5	0.622	15.9	24.7	-0.3	0.730
Cerambycidae larvae	4.8	5.8	28.4	11.1	-3.7	0.000	63.9	33.9	-4.0	0.000	24.9	21.2	-2.5	0.011
Coleoptera	42.2	12.5	11.2	16.1	-3.7	0.000	17.5	26.1	-3.1	0.002	50.6	26.9	-1.0	0.318
Miscellaneous	44.5	12.9	18.3	14.3	-3.3	0.001	2.9	9.4	-4.6	0.000	8.5	9.7	-4.1	0.000
Total	100.0		100.0				100.0				100.0			

food preferences of the three-toed woodpecker. The observed increase in bark beetle consumption during the non-nesting season, when bark beetles were at low densities during study, contradicts our working hypothesis that a low proportion of bark beetles in the diet of juveniles results from a low availability of bark beetles in the environment.

Nestling Diet

Nestling diet was dominated by spiders and longhorn beetle larvae (altogether >65% of the importance value), whereas bark beetles were negligible (<4% of the importance value). Our results were consistent with previous findings from Germany and Switzerland that spiders and large longhorn beetle larvae dominate the diet of juvenile three-toed woodpeckers (Ruge and Havelka 1993; Pechacek and Kristin 1996; R. Hess, Unterägeri, unpublished data). These investigators showed that food of nestlings did not differ substantially from their parents during nesting.

Nestling diet varied considerably among territories, mainly through variation in the miscellaneous category. In some nests, nestlings were fed more often with tipulids (Diptera, Tipulidae) and (but less often) with ants (Hymenoptera, Formicidae) and other flies than nestlings from other nests. We found the frequency of tipulids to be particularly high, as they were detected in 45–59% of fecal samples, but their relative abundance in feces made up only 12–16%. Ruge and Havelka (1993) also reported high numbers of the Tipulidae in the diet of young three-toed woodpeckers.

Prey Selection

The three-toed woodpecker displayed selective food habits for large prey (1–2 cm of body size) in a manner similar to the green woodpecker

(*Picus viridis*; Rolstad et al. 2000). Throughout the year, longhorn beetle larvae seemed to be the most important prey for the woodpeckers. These larvae were eaten by juvenile and adult birds 5.9 and 5.2–13.3 times, respectively, more than their availability on foraging trees would suggest. Conversely, smaller prey such as bark beetles (approx 0.6-cm body size), undetermined small larvae (<0.2 cm), and members of the order Procoptera (<0.3 cm) were eaten only rarely. During nesting, the relative abundance of Coleoptera (including bark beetles) in the diet of young and adults was 3.8 and 2.4 times lower than available, respectively. However, outside the nesting season, their abundance in the adults' diet did not differ significantly from their availability on trees. Hence, our results support our working hypothesis that nesting woodpeckers reduce their bark beetle consumption and switch to spiders and larger longhorn beetle larvae to secure the greater energetic requirements of the nesting period.

Possible Biases.—We acknowledge several potential biases that may have influenced our findings on prey selection. First, we estimated prey availability from arthropods found on trees in July 2000. We based this on the assumption that most arthropods found in the woodpecker diet were poor dispersers. Second, the availability of prey in sample trees may have been reduced before collecting, due to earlier woodpecker foraging activities. Third, the numbers of foraging trees sampled per territory (2) and length of trunk sections sampled (0.5 m) were limited. Fourth, tree sections were removed close to the ground (<3 m), but we observed woodpeckers foraging up to 20 m above the ground. Fifth, captures reflected the abundance of species susceptible to being caught in our emergence traps; whereas our captures

underestimated abundance of other species (some insects [e.g., beetles of the family Carabidae and ants] may have left tree sections before being “sealed” in a trap). Small and inconspicuous invertebrates may have remained undetected if they did not emerge from their pupae within the 4-month period in the emergence trap because samples were not dissected afterward. Finally, trunk samples were taken only from spruce snags, even though some (approx 5–10%) foraging observations were on other tree species (e.g., larch) or on living trees.

On the other hand, we were not concerned that our ability to detect food items in fecal matter of the three-toed woodpecker varied significantly among taxa. Although identification of soft microarthropods (e.g., small lepidopteran, coleopteran larvae) could have been affected by digestion resulting in an underestimation of their densities, their legs still would have been detected. Because three-toed woodpeckers eat few soft microarthropods, no significant differences between diet compositions quantified by neck collars versus analyzing feces have been found (Pechacek and Kristin 1996).

Flexible Feeding Strategy.—As demonstrated by Koplín (1972), energy expenditure related to cold winter temperatures was less important in the three-toed woodpecker than in other woodpecker species, possibly due to the three-toed woodpecker's association with the boreal environment. Thus, energy requirements of the three-toed woodpecker outside the nesting season may have been lower than during nesting, when additional energy was needed for territorial defense, nest building, mate guarding, and reproduction. During winter, foraging birds may trade-off preferences for energetically rewarding prey (longhorn beetle larvae), which were obtainable only after considerable investment of time, movement, and effort into searching, against less abundant and nutritional insect prey (bark beetles) that exhibit a clumped distribution. We observed that woodpeckers limited energetically costly flights during non-nesting by spending up to 3 hr searching for food on a single tree infested with bark beetles.

MANAGEMENT IMPLICATIONS

The flexible feeding strategy of the three-toed woodpecker may result from seasonal changes in the energetic requirements of the bird and in the profitability of its prey, including changes in abundance, availability, predation effort, and nutritional value. Thus, we stress the need to secure habitat requirements of both bark and wood-boring longhorn beetles and associated arthropod communi-

ties, especially including spiders, as a critical step to maintaining viable three-toed woodpecker populations. Habitat for these saproxylic arthropods is composed of a considerable number of dead trees comprising a high diversity of decay stages. Sufficient supply of dead and dying trees in natural forests is guaranteed due to permanent impact of natural forces (e.g., wind, heavy snow) combined with competition of trees for resources. Diverse decay stages evolve automatically in the course of several years. In forests managed for timber harvest, where dead and dying trees generally are not desired, these patterns should be allowed close to three-toed woodpecker nesting sites. Based on the average distance for food gathering, dead trees should not be removed within a 250-m circle from nests. With respect to large seasonal home ranges of three-toed woodpeckers (Pechacek 2004), some dead tree patches should be allowed throughout woodpecker habitats. Most dead wood arthropods are poor dispersers; thus, dead trees should be distributed more evenly than clumped. Retaining and restoring areas with a diversity of dead coniferous trees in different decay stages will favor the coexistence of alternative prey for three-toed woodpeckers.

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(Appendices on next page)

Appendix A. Adult diet of the three-toed woodpecker obtained by analysis of feces of 14 females and 16 males in Berchtesgaden National Park, Germany, 1995–1999. Number of feces per woodpecker ranged 1–13 during non-nesting ($n = 72$) and 1–20 ($n = 70$) during nesting. Feces of 3 females and 2 males were sampled in both seasons.

Food item	Nesting season ($n = 20$)						Non-nesting season ($n = 15$)					
	Relative abundance (%)		Relative frequency (%)		Importance value ^a (%)		Relative abundance (%)		Relative frequency (%)		Importance value ^a (%)	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Gastropoda	0.21	0.93	0.38	1.72	0.21	0.96	0.00	0.00	0.00	0.00	0.00	0.00
Diplopoda	0.21	0.05	0.56	2.48	0.23	1.02	0.00	0.00	0.00	0.00	0.00	0.00
Araneidea	15.40	1.00	29.46	37.55	13.82	18.70	15.94	24.72	47.26	55.87	17.71	24.50
Opilioneida	0.29	0.10	0.81	2.67	0.34	1.12	0.00	0.00	0.00	0.00	0.00	0.00
Homoptera Aphidoidea	0.00	0.00	0.00	0.00	0.00	0.00	0.33	1.27	0.67	2.58	0.30	1.17
Coleoptera larvae	0.52	0.05	0.25	1.12	0.26	1.14	0.00	0.00	0.00	0.00	0.00	0.00
Coleoptera	0.45	0.10	1.27	3.94	0.50	1.53	0.58	2.25	1.03	3.97	0.61	2.38
Carabidae	2.32	0.35	5.37	12.61	2.45	5.69	2.15	3.82	11.07	26.17	2.86	4.80
Cerambycidae imagines	0.21	0.05	0.56	2.48	0.23	1.02	0.00	0.00	0.00	0.00	0.00	0.00
Cerambycidae larvae	58.15	3.05	84.64	32.32	57.44	35.21	23.97	20.40	62.27	38.65	24.62	17.86
<i>Rhagium</i> sp. larvae	5.79	0.15	7.38	23.20	5.93	22.36	0.96	2.53	1.94	5.19	1.06	2.79
Buprestidae larvae	1.42	0.15	5.50	22.35	1.79	7.01	3.25	6.01	16.29	34.60	4.23	8.26
Elateridae larvae	1.54	0.15	5.63	22.30	1.89	6.99	2.59	6.72	7.22	15.78	3.12	7.17
<i>Athous</i> sp.	0.83	0.09	5.00	22.36	0.97	4.35	0.00	0.00	0.00	0.00	0.00	0.00
Scolytidae imagines	6.68	0.30	11.13	30.61	6.66	22.46	7.02	8.30	26.91	39.50	7.20	8.28
Scolytidae larvae	2.48	0.25	8.02	23.07	2.40	5.58	18.23	26.47	28.11	39.55	13.30	18.51
<i>Ips typographus</i>	0.41	0.15	1.21	3.80	0.49	1.52	15.40	21.27	28.50	35.93	13.21	15.65
<i>Polygraphus</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	1.42	5.50	0.67	2.58	0.63	2.45
<i>Otiorrhynchus</i> sp.	0.38	0.10	0.81	2.67	0.37	1.17	0.00	0.00	0.00	0.00	0.00	0.00
<i>Byrrhus</i> sp.	0.21	0.05	0.56	2.48	0.23	1.02	0.00	0.00	0.00	0.00	0.00	0.00
Lepidoptera larvae	0.50	0.10	0.81	2.67	0.40	1.37	0.00	0.00	0.00	0.00	0.00	0.00
Formicidae	0.00	0.00	0.00	0.00	0.00	0.00	5.59	10.16	14.94	28.42	5.59	9.38
<i>Formica</i> sp.	0.86	0.15	1.83	5.76	0.79	2.56	0.51	1.15	2.06	4.33	0.91	1.99
Diptera imagines	0.92	0.25	2.30	7.57	1.01	3.18	1.22	4.29	7.33	25.76	1.53	5.04
Diptera larvae	0.00	0.00	0.00	0.00	0.00	0.00	0.85	2.37	2.44	6.48	1.14	3.07
Tipulidae	0.21	0.05	0.56	2.48	0.23	1.02	0.00	0.00	0.00	0.00	0.00	0.00
<i>Picea abies</i> seeds	3.52	11.50	1.36	4.57	5.38	14.67	1.90	5.09				
Total	100.00				100.00		100.00				100.00	

^a Combination of abundance and frequency calculated as a percent value of $\{(relative\ abundance + relative\ frequency)/2\}$.

Appendix B. Diet of juvenile three-toed woodpeckers (40 nestlings from 15 nests), obtained by analysis of feces ($n = 588$) in Berchtesgaden National Park, Germany, 1994–2000. Number of feces per nest averaged 39.2 (range = 3–124).

Food item	Relative abundance (%)		Relative frequency (%)		Importance value ^a (%)	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Gastropoda	0.29	0.62	1.31	2.79	0.41	0.83
<i>Julus</i> sp.	0.01	0.04	0.10	0.29	0.03	0.08
Chilopoda	0.02	0.07	0.17	0.48	0.05	0.15
Araneidea	41.08	11.65	78.29	26.73	35.23	8.62
Opilioneida	1.19	2.86	4.24	8.84	1.61	3.82
Phalangidae	0.02	0.07	0.20	0.57	0.06	0.17
Homoptera Aphidoidea	2.36	5.67	3.14	6.10	1.79	4.06
Heteroptera Pentatomidae	0.05	0.18	0.21	0.81	0.07	0.27
Psyllinea	0.39	1.53	0.58	1.63	0.51	1.45
Thysanura	0.02	0.07	0.20	0.57	0.06	0.17
Coleoptera	0.23	0.76	1.51	5.16	0.41	1.41
Carabidae	1.42	1.56	6.74	10.07	2.21	2.77
<i>Pterostichus</i> sp.	0.02	0.10	0.19	0.53	0.07	0.20
Pselaphidae	0.02	0.07	0.20	0.57	0.06	0.17
Cerambycidae imagines	0.05	0.18	0.21	0.81	0.07	0.27
<i>Rhagium</i> sp. larvae	2.26	3.67	6.52	10.16	2.45	3.88
Cerambycidae larvae	26.17	11.29	63.09	28.07	26.43	10.10

(continued on next page)

Appendix B. continued.

Food item	Relative abundance (%)		Relative frequency (%)		Importance value ^a (%)	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Buprestidae	0.05	0.21	0.51	1.45	0.16	0.46
Buprestidae larvae	0.27	0.52	0.92	1.73	0.32	0.64
Elateridae	0.02	0.07	0.17	0.48	0.05	0.15
Elateridae larvae	0.07	0.25	0.21	0.79	0.11	0.41
<i>Corymbites cupreus</i>	0.06	0.15	0.38	0.70	0.17	0.32
<i>Athous subfuscus</i>	0.02	0.07	0.20	0.57	0.06	0.17
<i>Athous</i> sp.	0.93	2.85	2.97	8.55	1.27	3.79
Curculionidae	0.28	0.57	1.19	2.40	0.37	0.75
<i>Otiorrhynchus</i> sp.	3.33	11.40	6.05	17.09	3.01	9.48
Chrysomelidae	0.04	0.14	0.16	0.60	0.05	0.18
Scolytidae	0.34	0.67	1.80	1.67	0.92	1.08
Scolytidae imagines	0.77	2.13	2.05	4.92	0.75	1.91
Scolytidae larvae	1.42	2.21	4.28	6.17	1.61	2.42
<i>Ips typographus</i>	0.43	1.16	1.17	3.23	0.41	1.12
<i>Ips</i> sp.	0.05	0.19	0.50	1.43	0.15	0.42
<i>Hylurgops</i> sp.	0.01	0.04	0.10	0.29	0.03	0.08
Anobiidae	0.04	0.15	0.18	0.68	0.05	0.20
<i>Epurea</i> sp.	0.03	0.11	0.30	0.86	0.09	0.25
<i>Byrrhus</i> sp.	1.14	3.07	3.26	8.93	1.47	4.02
Mecoptera Panorpa	0.38	1.33	1.56	5.43	0.46	1.61
Raphidioptera	0.08	0.20	0.33	0.87	0.10	0.25
Lepidoptera Psychidae	0.04	0.14	0.16	0.60	0.05	0.18
Lepidoptera larvae	0.05	0.21	0.51	1.45	0.16	0.46
Symphyta	0.02	0.07	0.17	0.48	0.05	0.15
Ichneumonidae	0.08	0.22	0.38	1.02	0.12	0.32
Vespidae	0.04	0.11	0.36	0.66	0.12	0.23
Formicidae	2.01	2.54	8.59	10.40	2.80	3.43
<i>Formica</i> sp.	2.03	4.40	6.73	7.66	4.07	5.25
<i>Camponotus</i> sp.	3.52	11.21	8.52	25.60	4.29	13.57
<i>Lasius</i> sp.	0.13	0.52	0.18	0.70	0.08	0.32
<i>Myrmica</i> sp.	0.16	0.43	0.53	1.42	0.19	0.51
Diptera	0.18	0.49	1.69	3.32	0.54	1.04
Diptera imagines	1.66	2.46	5.54	8.33	1.85	2.70
Diptera larvae	0.09	0.35	0.86	2.42	0.27	0.76
Tipulidae	3.91	5.63	15.54	21.22	4.92	6.56
<i>Tipula</i> sp.	0.28	1.07	2.32	6.56	0.71	2.02
Mycetophilidae	0.30	1.15	2.32	6.56	0.72	2.04
Brachycera	0.02	0.10	0.19	0.53	0.07	0.20
<i>Picea abies</i> seeds	0.12	0.48	0.30	1.16	0.13	0.50
Total	100.00				100.00	

^a Combination of abundance and frequency calculated as a percent value of $\{(relative\ abundance + relative\ frequency)/2\}$.