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Relative Impacts of Habitat and Geography on Raccoon Diets

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ABSTRACT.—We compared relative impacts of habitat type vs. location in the diet of a generalist omnivore, the raccoon (*Procyon lotor*). Raccoon diets were analyzed from 161 scat samples collected in a marine coastal habitat over 13 mo. We used a suite of statistical tools including univariate indices of diversity, descriptive statistics, niche similarity analyses, and two contrasted randomization algorithms with Monte Carlo to test whether raccoons maintained similar diets in different habitats. We compared these results to raccoon diet studies in geographically distant locations with similar habitats to relevant studies conducted geographically closer but with different habitats. Logistic regression analyses revealed that among habitat similarity, geographic closeness, and diet diversity (*i.e.*, relative dietary specialization of each population), only habitat similarity significantly (and positively) influenced probability of observing a greater-than-expected diet similarity. This demonstrated that raccoons in similar habitats had similar diets, with substitution of ecologically equivalent prey species.

INTRODUCTION

Diet analysis is necessary to understand the natural history of a single species, food webs, and impacts of species on the environment (Valentini *et al.*, 2008). For example, diet studies allow biologists to quantify ecological interactions among species by identifying quantities and diversity of food items consumed (Litvaitis, 2000) and to estimate effects of population size changes of predator and prey. Additionally, some species rarely are encountered in the wild, making them difficult to study, but their scat can provide biologists with many insights about their habits (Chame, 2003; Gompper *et al.*, 2006; Valentini *et al.*, 2008). Finally, diet breadth can be a key factor in determining invasiveness of alien species (NRC, 2002;

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Blackburn *et al.*, 2009). However, few techniques are available for statistically robust comparisons of diet data (Luiselli, 2006, 2008).

Diets of members of a population may vary temporally due to changing nutritional needs or availability of seasonal resources. If the diet of a predator species is inflexible, its diet may not differ even between spatially distant populations. Our objective was to use robust statistical techniques to characterize diets of a generalist omnivore, raccoons (*Procyon lotor*), across a large spatial range in different and similar habitats and to investigate quantitatively whether raccoon diets are influenced more strongly by geography or habitat. If raccoons are entirely generalists/opportunists, generally eating the most abundant food resources, we hypothesized that (1) raccoon diets would depend largely on local habitat type, hence their dietary spectrum would considerably vary geographically if the sites had different habitats; (2) in seasonal environments (such as temperate regions where food availability typically changes dramatically from season to season (*e.g.*, Herrera, 1982; Lechowicz, 1995) we would observe similarly dramatic changes in raccoon diet composition among seasons; and (3) raccoon diets would be very similar among sites with the same habitats during the same seasons even if they were geographically distant.

Raccoons range from southern Mexico to the southern boreal forest limit of Canada, and from coast to coast of North American coasts. In the 20th Century they expanded their range into high elevations, deserts, islands off the coast of the U.S., and into Canada (Seton, 1953; Lotze and Anderson, 1979; Gehrt, 2003; Larivière, 2004). They also have been introduced into parts of Russia (Aliev and Sanderson, 1966), many parts of Europe (Lutz, 1984; Cirovic and Milenkovic, 2003) and Japan (Asano *et al.*, 2003). Thus, they currently exist in a large range of habitats and occupy an enormous geographic range.

Their large original range and subsequent expansion occurred in part because raccoons are ecological generalists and readily adapt behaviorally to new habitats (Chamberlain *et al.*, 2002; Larivière, 2004). In most of their range, raccoons live in hardwood forests close to water where tree cavities are numerous (Goldman, 1950; Seton, 1953; Nowak, 1999). Raccoons also inhabit edge habitat (Stuewer, 1943; Seton, 1953; Gehrt, 2003), marshes and mangrove swamps (Cagle, 1949; Bigler *et al.*, 1981), prairies (Geis, 1966; Fritzell, 1978; Larivière, 2004), coastal habitats (Ivey, 1948; Platt *et al.*, 2000; Carrillo *et al.*, 2001), and have very successfully colonized suburban (Hoffman and Gottschang, 1977; Compton, 2007) and urban habitats (Schinner and Cauley, 1974; Rosatte *et al.*, 1991; Hadidian *et al.*, 2010).

Raccoons eat a wide variety of fauna and flora, including many species of berries, acorns (*Quercus* sp.), nuts, invertebrates, crayfish (Astacoidea), minnows (Cyprinidae), birds, reptiles, small mammals and many other items (*e.g.*, Hamilton, 1936; Stuewer, 1943; Baker *et al.*, 1945; Hamilton, 1951; Seton, 1953; Stains, 1956; Ewer, 1973; Greenwood, 1981; Gehrt, 2003; Tyler *et al.*, 2000). Raccoons are common predators of waterfowl eggs (Greenwood, 1981) and probably are the most common predators of turtle eggs in North America (Mitchell and Klemens, 2000). Raccoon diets have been evaluated in numerous studies (*e.g.*, Stuewer, 1943; Goldman, 1950; Ewer, 1973; Greenwood, 1982). Most indicate that seasonal food choices are based primarily on food availability; consequently, their diet changes throughout the year as foods become more abundant (Johnson, 1970; Fleming *et al.*, 1976; Gehrt, 2003). Despite the abundance of raccoon diet studies, we did not find any quantitative comparisons within or between studies; therefore, it is difficult to test hypotheses and evaluate patterns. Hoffman and Gottschang (1977) found that a suburban raccoon population ate mostly plant material, but cottontail rabbits (*Sylvilagus floridanus*), Norway rats (*Rattus norvegicus*), and refuse (items of human origin) also were eaten (Hoffman and Gottschang, 1977).

Most raccoon diet studies in marine coastal environments have occurred in the southeastern U.S. (Sanderson, 1987; Nowak, 1999). In coastal marine Louisiana, Fleming *et al.* (1976) reported crustaceans such as fiddler crabs (*Uca* sp.), blue crabs (*Callinectes sapidus*), and crayfish comprised 49% of raccoons' yearly diet. Oysters (*Crassostrea* sp.), clams (*Mercenaria mercenaria*), mussels (Mytilidae), snails, fish, and washed up debris also were reported. On St. Catherine's Island in Georgia, Harmon, and Stains (1979) reported that crustaceans were the most common food item in the diets, with fiddler crabs (*Uca* sp.) being the most common year-round crustacean, with *Panopeus* sp. and *Eurytium* sp. as secondary components. Cordgrass (*Spartina* sp.), and berries of yaupon (*Ilex vomitoria*), mistletoe (Santalaceae), and laurel cherries (*Prunus laurocerasus*), and greenbrier (*Smilax* sp.) were seasonally represented foods. On the Pacific coast of Costa Rica, Carrillo *et al.* (2001) reported that two species of crabs *Gecarcinus quadratus* and *Cardisoma crassum* were the most common food items in raccoon diets, followed by fruits. Other studies have concentrated on examining direct impacts of raccoons on prey species in marine coastal environments including eggs of diamondback terrapins (*Malaclemys terrapin* Feinberg and Burke, 2003; Butler *et al.*, 2004), spiny-tailed iguanas (*Ctenosura similes*) (Platt *et al.*, 2000), American crocodiles (*Crocodylus acutus*) (Fleming *et al.*, 1976; Platt *et al.*, 2000) and sea turtles (Ratnaswamy *et al.*, 1997).

MATERIALS AND METHODS

Study area.—Ruler's Bar Hassock (463 ha, 40°57'N, 73°50'W) is the largest island in Jamaica Bay, an oceanic bay in southwestern Long Island and within the political boundaries of New York City. Ruler's Bar Hassock consisted of open water and marshes with little upland until 1910–1938, when adjacent marshes were joined by being covered in dredge, and bridges were built connecting Ruler's Bar Hassock to the mainland. In 1950, 76% of Ruler's Bar Hassock became part of Jamaica Bay Wildlife Refuge (JBWR) with the rest of the island within the town of Broad Channel. The Ruler's Bar Hassock section of JBWR was managed for birds by planting food and cover species (Stalter and Lamont, 2002) including many plant species also favored by raccoons. Few or no raccoons existed on Ruler's Bar Hassock before the 1980s, but the island was colonized through deliberate human introductions and possibly natural dispersal of raccoons (Feinberg and Burke, 2003). Our study occurred within the JBWR section of Ruler's Bar Hassock, although Ruler's Bar Hassock raccoons could move freely in and out of JBWR. This part of Ruler's Bar Hassock contained upland habitats (113 ha), freshwater habitats (107 ha), estuarine habitats (98 ha), and developed lands (31 ha; Edinger *et al.*, 2008). Maritime conditions strongly influence Ruler's Bar Hassock plant communities; 89% of the non-aquatic habitat was either North Atlantic Low Salt marsh, Reed-grass Tidal marsh, Northern Tall Maritime Shrubland, or Successional Maritime Forest. Thus, we considered Ruler's Bar Hassock to be a marine coastal habitat.

Diet analysis.—We used scat analysis, a common method for carnivore diet studies, to investigate Ruler's Bar Hassock raccoon diets. We collected scats from Ruler's Bar Hassock once weekly and opportunistically from Jun. 2006 to Jun. 2007 (Rulison, 2009). We focused scat collection to within 10 m of the ocean shore line, which was commonly used by raccoons and contained many latrine locations. We placed scats in individual bags and froze them until examination.

For months when fewer than 15 samples were collected, all samples were dissected; for other months we randomly choose 15 samples. Each sample was thawed and dried at room temperature until the mass remained constant in subsequent measurements. Each sample

was weighed and then soaked in a water/detergent/alcohol solution for at least 24 h (McFadden *et al.*, 2006). Samples were sieved with a USA number 18 standard sieve (1 mm mesh opening), washed, and again dried to constant mass (McFadden *et al.*, 2006; Reed *et al.*, 2006). Food items were separated by use of forceps with the aid of a head loupe at 3× magnification or a dissecting microscope. Each food item was weighed to the nearest tenth of a gram and stored.

We identified prey items in several ways (Rulison, 2009). We created a reference collection from Ruler's Bar Hassock to help identify plant parts; seeds were identified using Martin and Barkley (2000). We identified mammal bones using Olsen (1964) and Elbroch (2006). Food items were identified to species where possible and also grouped into major taxonomic groups (mammals, birds, non-avian reptiles, fish, crustaceans, molluscs, insects, chelicerata, non-reproductive plant parts, mast [*i.e.*, berries, fruit, seeds, and nuts], soil, and refuse) to match classification systems used in other studies. Food item data were expressed as percent frequency of occurrence in scat samples. We calculated percent frequency of occurrence by counting number of times each prey species was identified within all scat samples during a particular time frame and dividing that number by total amount of scat samples for that time period.

We analyzed prey species richness with PRIMER (Version 6, Clarke and Gorley, 2006) to create a species-accumulation curve using the observed species data, as well as a non-parametric estimator first order Jackknife (Burnham and Overton, 1979; Heltshel and Forrester, 1983) to determine whether we sampled an adequate number of scats to characterize diets. We fit the species-accumulation and Jackknife curves with logarithmic curves, and then computed the equations for these curves.

We searched the published literature for other raccoon diet studies either geographically close (within 500 km of Ruler's Bar Hassock), or far (>500 km from Ruler's Bar Hassock). We searched similarly for raccoon diet studies from marine coastal habitats, which we defined as those within 3 km of an ocean shore. We re-categorized our data as necessary to match time frame and data formats of these other studies for comparisons.

Comparisons between seasons and with similar studies.—We classified Winter as Dec.–Feb.; Spring as Mar.–May; Summer as Jun.–Aug.; and Autumn as Sep.–Nov. (Rabinowitz and Pelton, 1986). We used three approaches to test for Ruler's Bar Hassock diet differences between seasons, and to compare Ruler's Bar Hassock diets with those from similar studies. First, where percent frequency of occurrence were sufficiently large in the Ruler's Bar Hassock data, we compared percent frequency of occurrence for specific prey types between seasons using two-tailed χ^2 tests. Second, we calculated Simpson's diversity indices (D). With this index, greater values correspond to wider dietary niche-breadth. We compared the D values of each pair of seasons using multiple two-tailed *t*-tests and applying Bonferroni corrections (Brower *et al.*, 1997). We also calculated the Simpson's diversity indices for the other raccoon diet studies that met our criteria, and compared D values. Third, we calculated the similarity in the utilization frequency of each food category in diets of two populations (or the same population between different seasons) using Pianka's (1986) symmetric equation. This equation yields values ranging from 0.0 (no similarity) to 1.0 (100% similarity). We contrasted the observed diet niche overlaps (similarity) between pairs of populations/studies with the mean simulated overlap resulting from 30,000 simulated pseudo-matrices generated by random Monte Carlo permutations (Gotelli and Graves, 1996) to test if any observed Pianka's similarities in quantitative diet composition (between seasons, and between sites) were from chance. To generate these pseudo-matrices, we used two contrasting algorithms, the randomization

algorithms RA2 and the RA3 of Lawlor (1980). RA3 conserves niche breadth for each seasonal sample (for Ruler's Bar Hassock seasonal comparisons), and for each site sample (for between-site comparisons) at each simulation, but destroys the resource utilization matrix's zero structure. RA2 relaxes niche breadth but conserves the resource utilization matrix's zero structure. The scopes of these two randomization algorithms differ. The RA2 procedure tests for intergroup differences in the frequencies of utilization of number of resources (prey types in our study), whereas RA3 tests for intergroup differences within the same resources (Luiselli, 2008). For instance, RA2 is more likely to uncover non-random differences in food composition of generalist predators like lizards (Luiselli, 2008), whereas RA3 is more likely to uncover food differences between more specialist predators such as snakes (Luiselli, 2006).

We used logistic regression models (forward conditional, casewise with Quasi-Newton as estimation method) to determine whether ecological correlates influenced food niche similarity. For each of the comparisons between sites/seasons performed, we used the results of Monte Carlo niche similarity analysis with RA2 and RA3 (entered in separate analyses) as dependent variables. For instance, when exploring correlates of greater-than-expected niche similarity with RA2, scores were 1 for the cases (=comparisons) that showed a significantly greater-than-expected observed similarity, and 0 for all the other cases. In all analyses, the covariates were geographic position (close = 1, distant = 0), habitat condition (1 = similar, 0 = different), and diet diversity (Simpson's D statistically different = 1, similar = 0).

Differences (between seasons and between sites) in the frequency of consumption of different prey items also were evaluated by two-tailed observed-versus-expected χ^2 tests. We used EcoSim 7.0 software (Gotelli and Entsminger, 2003) to generate Monte Carlo permutations of the observed data matrix.

In all analyses, statistical tests were two-tailed and $\alpha = 5\%$. Variables were tested for normality and homogeneity of variances were examined with Levene's test (Zar, 1999). When variables were non-normal, non-parametric tests were used. These statistical analyses were performed with Statistica 6.0 software (Statsoft Inc., 2001).

RESULTS

We analyzed 161 scat samples, 19 from Spring, 61 from Summer, 41 from Autumn, and 40 from Winter. We identified 10 invertebrate species, 11 vertebrate species, and 18 plant species, plus sand, stones, and refuse (anthropogenic) items. Both species-accumulation and Jackknife curves indicated that another 10 scat samples would have been required to add an additional prey species (Fig. 1), and the Jackknife curve indicated that if we had collected an additional 200 or 300 samples, 3–9 species would have been added to the prey species list.

Differences in prey frequency.—The most abundant item by mass was bird feathers ($\bar{x} = 3.70$ g/scat), followed by crustaceans ($\bar{x} = 3.29$ g/scat), fish ($\bar{x} = 2.89$ g/scat), mast ($\bar{x} = 2.61$ g/scat) and soil ($\bar{x} = 2.27$ g/scat). Refuse ($\bar{x} = 0.05$ g/scat) and insects ($\bar{x} = 0.07$ g/scat) were the least abundant by mass (Table 1).

The most frequently consumed foods by percent frequency of occurrence were crustaceans, occurring in 127 samples (79% frequency of occurrence), plant parts in 88 samples (55% frequency of occurrence), and mast in 63 samples (39% frequency of occurrence; Table 2). Molluscs and insects also were abundant in samples. Terrapin remains were found in six scat samples; five were egg shell fragments and two included bones and scutes of hatchling terrapins (one contained both). Refuse, soil, and chelicerata

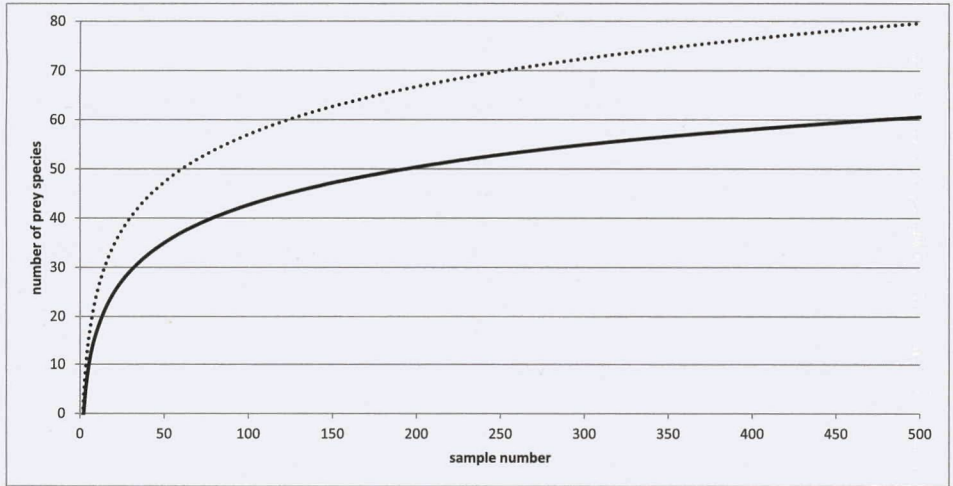


FIG. 1.—The projected prey species—accumulation curves generated for 500 samples from the prey species identified in raccoon (*Procyon lotor*) scats at Ruler's Bar Hassock, New York. The black and dotted curves were generated with actual species observed data (species-accumulation) and jackknife techniques respectively

(ticks (Ixodidae)) and horseshoe crab (*Limulus polyphemus*) were found in 4%, 6.5%, and 3% of the samples, respectively.

Crustaceans (specifically *Uca pugnax*) were the most common items by percent frequency of occurrence during every season. Plant material and mast were second and third most frequent items in the Summer and Autumn, respectively. During the Spring mammals and molluscs were the third most frequent items after crustaceans and plant material; during Winter molluscs were the third most frequently item found (Table 2).

Crustaceans, mast, molluscs, and plant material were the only food categories that occurred with sufficient frequency to test for significant differences in frequency

TABLE 1.—Total mass, frequency of occurrence of each prey type and average mass of each item in raccoon (*Procyon lotor*) scats at Jamaica Bay Wildlife Refuge, Rulers Bar Hassock, New York, all data combined

Items type	Total mass (grams)	Times in samples	Average mass (gm) per scat sample
Crustaceans	418.04	127	3.29
Molluscs	60.88	40	1.52
Cheliceratas	1.34	5	0.27
Insects	2.2	32	0.07
Fishes	57.73	20	2.89
Terrapins	4.57	8	0.57
Birds	55.64	15	3.70
Mammals	55.70	21	2.65
Plants	47.19	88	0.54
Mast	164.49	63	2.61
Soil	22.68	10	2.27
Refuse	0.31	6	0.05

TABLE 2.—Frequency of occurrence of raccoon (*Procyon lotor*) scats containing each food item type in each season at Jamaica Bay Wildlife Refuge, Rulers Bar Hassock, New York

Category	Food item	Autumn	Winter	Spring	Summer	Year average
Crustaceans	Atlantic marsh fiddler crab (<i>Uca pugnax</i>)	54	75	67	51	59
Crustaceans	Brachyura sp.	49	43	20	31	38
Molluscs	Quahog (<i>Mercenaria mercenaria</i>)	15	15	40	15	17
Molluscs	Ribbed mussel (<i>Geukensia demissa</i>)	2	30	20	0	11
Molluscs	Moon snail (<i>Polinices heros</i>)	2	0	0	0	1
Molluscs	Mud snail (<i>Nassarius obsoletus</i>)	2	3	0	2	2
Chelieratas	Horseshoe crab (<i>Limulus polyphemus</i>)	0	0	20	3	3
Chelieratas	Tick (Ixodidae)	0	0	7	0	1
Insects	Insects	22	8	13	28	20
Fishes	Fishes	2	15	20	0	12
Chelonians	Terrapin egg (<i>Malaclemys terrapin</i>)	2	5	0	5	4
Chelonians	Terrapin hatchling (<i>Malaclemys terrapin</i>)	2	0	0	0	1
Birds	Birds	10	10	7	10	9
Birds	Bird eggs	0	0	0	2	1
Mammals	Small mammals	0	10	27	7	9
Mammals	Raccoon hair (<i>Procyon lotor</i>)	0	10	7	5	6
Plant material	Assort. twigs	5	3	0	11	6
Plant material	Assorted leaves	2	0	0	5	2
Plant material	Roots	0	3	0	0	1
Plant material	Beach grass/common reed (<i>Ammophila breviligulata</i>) <i>Phragmites australis</i> leaves and stems	27	53	40	33	37
Plant material	Bayberry (<i>Myrica pensylvanica</i>) leaves	12	30	20	3	14
Algae	Red algae (Rhodophyta)	2	13	7	0	4
Algae	Sea lettuce (<i>Ulva lactuca</i>)	5	8	0	3	4
Mast	American Holly (<i>Ilex opaca</i>)	0	3	0	0	1
Mast	Autumn Olive (<i>Elaeagnus umbellate</i>)	32	5	13	0	10
Mast	Bittersweet (<i>Celastrus orbiculatus</i>)	0	10	0	0	3
Mast	Buckthorn (<i>Rhamnus</i> sp.)	0	3	0	0	1
Mast	Chokeberry (<i>Aronia</i> sp.)	5	0	7	0	2
Mast	Dogwood (<i>Cornus</i> sp.)	0	0	0	2	1
Mast	Grape (<i>Vitis</i> sp.)	20	5	0	0	6
Mast	Mulberry (<i>Morus</i> sp.)	0	0	0	43	16

TABLE 2.—Continued

Category	Food item	Autumn	Winter	Spring	Summer	Year average
Mast	Prickly pear (<i>Opuntia humifusa</i>)	0	5	0	0	1
Mast	Raspberry (<i>Rubus</i> sp.)	2	0	0	5	2
Mast	Salt-spray rose (<i>Rosa rugosa</i>)	0	3	0	0	1
Mast	Unknown seeds	5	3	0	2	1
Fruit	Sunflower seed (<i>Helianthus</i> sp.)	0	0	7	0	1
Soil	Stone	0	0	0	2	1
Soil	Soil	2	3	7	10	6
Refuse	Refuse	2	5	0	5	4

individually among seasons (Table 2). Frequencies of crustaceans ($\chi^2_3 = 18.04$, $P < 0.001$), mast ($\chi^2_3 = 23.41$, $P < 0.001$), and plant material ($\chi^2_3 = 15.18$, $P = 0.002$) varied significantly among seasons, but mollusc frequency did not vary significantly among seasons ($\chi^2_2 = 2.40$, $P = 0.49$).

Simpson's Index of Diversity D for all seasons combined was 0.83. Among all possible two-season comparisons of Ruler's Bar Hassock raccoon food-species diversity, only the difference between Spring and Autumn ($t_1 = 1.81$, $P < 0.007$) was significant. High Pianka (1986) niche overlap among all four seasons ($O = 0.80$) indicated that raccoon diets in the different seasons were significantly more similar than would be expected by chance (\bar{x} of simulated overlap values = 0.130, $s^2 = 0.0016$, $P < 0.001$, calculated using the RA2 algorithm; \bar{x} of simulated overlap values = 0.469, $s^2 = 0.0015$, $P < 0.001$, calculated using the RA3 algorithm, see Gotelli and Graves, 1996).

We found five other raccoon diet studies that were either geographically close to Ruler's Bar Hassock or were conducted in marine coastal habitats. Hamilton (1936, 1940, 1951) fit the first criterion and Harmon and Stains (1979) and Munsher (2007), fit the second criterion; these five also presented their data in sufficient detail for comparison with Ruler's Bar Hassock data. Ivey (1948), Grimm and Whitebread (1952), Whitney and Underwood (1952), Fleming *et al.* (1976), McComb (1980), Dunn and Chapman (1983), and Carrillo *et al.* (2001), fit one or both criteria but did not present data in a manner that could be used for our comparisons.

Hamilton (1940) collected scats on 14 Jul. and then through the month of Sep. Relevant Ruler's Bar Hassock D-values varied significantly from those from his 14 Jul. through Sep. combined samples ($t_1 = 6.22$, $P < 0.005$). In contrast, the moderate Pianka niche overlap between the Ruler's Bar Hassock samples and Hamilton's 14 Jul. through Sep. combined samples ($O = 0.43$) did not differ statistically from that expected by chance (\bar{x} of simulated overlap values = 0.479, $s^2 = 0.0187$, $0.35 < P < 0.65$ when calculated with the RA2 algorithm, and \bar{x} of simulated overlap values = 0.185, $s^2 = 0.0357$, $0.12 < P < 0.87$ when calculated with the RA3 algorithm).

We found that Hamilton's (1951) scat samples collected Apr.–Oct. did not have significantly different D values from Ruler's Bar Hassock from that time period ($t_1 = 2.24$, $P > 0.25$). The two data sets are similar except for the relative frequencies of crustaceans. However, we found low Pianka niche overlap between the Ruler's Bar Hassock samples and Hamilton's (1951) samples ($O < 0.01$). This value is much less than expected by chance using the RA2 algorithm (\bar{x} of simulated overlap values = 0.514, $s^2 = 0.0144$, $P < 0.001$) but

TABLE 3.—Summary of all raccoon (*Procyon lotor*) diet comparisons indicating geographic proximity and habitat similarity) and comparative statistics.
RBH = Ruler's Bar Hassock

	Geographically close	Similar habitat	Simpson	RA2	RA3
RBH Summer	X	X	NS	Sig high overlap	Sig high overlap
RBH Summer	X	X	NS		
RBH Summer	X	X	NS		
RBH Spring	X	X	Sig diff		
RBH Spring	X	X	NS		
RBH Autumn	X	X	NS		
Hamilton 1940 Jul.–Sep.	X		Sig diff	NS	NS
Hamilton 1951 Apr.–Oct.	X		NS	Sig low Overlap	NS
Hamilton 1936 Nov.–Jan.	X		NS	NS	NS
Munscher 2007 Feb.–Nov.	X	X	NS	NS	Sig high overlap
Harmon and Stains 1979 Spring		X	NS	NS	NS
Harmon and Stains 1979 Summer		X	NS	Sig high overlap	Sig high overlap
Harmon and Stains 1979 Winter		X	NS	Sig high overlap	Sig high overlap

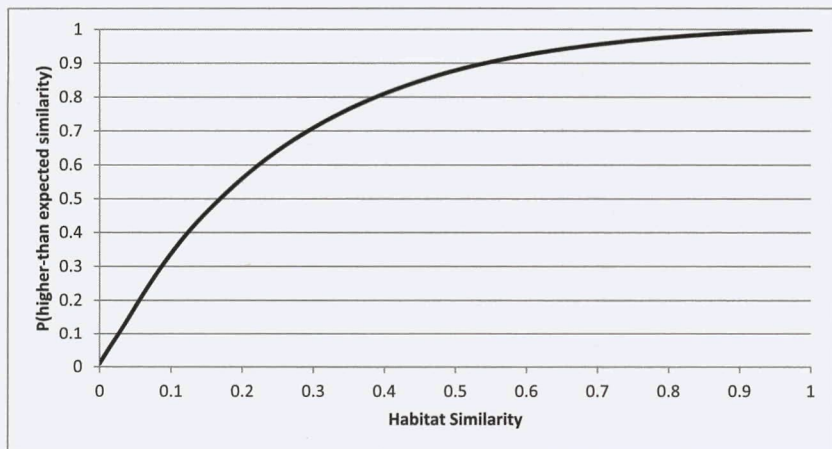


FIG. 2.—Logistic regression of effect of habitat similarity (0 = different; 1 = similar) on probability of getting a greater-than-expected Pianka's similarity value with RA2 algorithm after 30,000 Monte Carlo simulations. Note that probability of observing a very high diet similarity between seasons/sites increases dramatically with habitat similarity

not different than expected by chance using the RA3 algorithm (\bar{x} of simulated overlap values = 0.131, $s^2 = 0.0355$, $0.35 < P < 0.66$).

We also found no significant difference in D-values between Hamilton (1936) 10 Nov.–20 Jan. and Ruler's Bar Hassock during that time period ($t_1 = 0.034$, $P > 0.25$; Table 3). The moderate Pianka niche overlap between the Ruler's Bar Hassock samples and Hamilton's (1936) 10 Nov.–20 Jan. combined samples ($O = 0.469$) was not statistically different from that expected by chance (\bar{x} of simulated overlap values = 0.569, $s^2 = 0.0148$, $0.22 < P < 0.79$ when calculated using the RA2 algorithm, \bar{x} of simulated overlap values = 0.248, $s^2 = 0.0371$, $0.18 < P < 0.82$ when calculated using the RA3 algorithm).

We found no significant difference in D-values between relevant Ruler's Bar Hassock data and those from Munscher (2007) collected 7 Feb.–1 Nov. ($t_1 = 0.087$, $P > 0.25$). The two data sets are similar except for the relative frequencies of insects, plant material, and soil. There was high Pianka niche overlap between the Ruler's Bar Hassock samples and Munscher's (2007) samples ($O = 0.80$); although this value is not different than expected by chance (\bar{x} of simulated overlap values = 0.317, $s^2 = 0.0302$, $0.20 < P < 0.80$ when calculated using the RA2 algorithm) it is greater than expected by chance (\bar{x} of simulated overlap values = 0.686, $s^2 = 0.0104$, $P < 0.014$) when calculated using the RA3 algorithm.

There was no significant difference in D-values between relevant Ruler's Bar Hassock data and those from St. Catharine's Island, Georgia (Harmon and Stains, 1979) for their Spring (Mar. through May; $t_1 = 7.72$, $P > 0.25$), Summer (Jun. through Aug.; $t = 2.65$, $P > 0.25$) or Winter (Jan. and Feb.; $t_1 = 3.07$, $P > 0.25$; Table 3) samples. We found moderate Pianka niche overlap between the Spring Ruler's Bar Hassock samples and Harmon and Stains (1979) Spring samples ($O = 0.34$). This value did not differ from expected by chance (\bar{x} of simulated overlap values = 0.351, $s^2 = 0.0412$, $0.44 < P < 0.56$ when calculated using the RA2 algorithm; \bar{x} of simulated overlap values = 0.339, $s^2 = 0.0161$, $0.49 < P < 0.51$ when calculated using the RA3 algorithm). The Pianka niche overlap between the Ruler's Bar Hassock Summer samples and Harmon and Stains (1979) Summer samples ($O = 0.88$) was greater than expected by chance (\bar{x} of simulated overlap values = 0.251, $s^2 = 0.0448$, $P =$

0.008 when calculated using the RA2 algorithm; \bar{x} of simulated overlap values = 0.429, s^2 = 0.0016, $P < 0.001$ when calculated using the RA3 algorithm). The Pianka niche overlap between Ruler's Bar Hassock and Harmon and Stains (1979) Winter samples ($O = 0.55$) was greater than expected by chance (\bar{x} of simulated overlap values = 0.262, s^2 = 0.0044, $P < 0.001$ when calculated with the RA2 algorithm; \bar{x} of simulated overlap values = 0.127, s^2 = 0.0095, $P = 0.002$ when calculated with the RA3 algorithm).

Greater-than-expected similarity between diets was influenced positively only by habitat similarity for both RA2 and RA3 (RA2 – coefficient = 1.02, $P < 0.0001$, Table 3, Fig. 2; other variable coefficients: Simpson's D = 0.05, $P = 0.122$, Distance = 0.101, $P = 0.082$; overall model significance: $-2(\log\text{-likelihood}) = 5.55$, $P < 0.01$, odds ratio = 0.01, 75% percent of cases correctly classified). We have not reported details of the RA3 results for brevity as RA2 and RA3 largely agree (only one out of 15 cases differs). Only one case of significantly less-than-expected similarity was observed, and this coincided with an inter-seasonal comparison at the same study site (Hamilton, 1951, Table 3). Obviously, generalizations could not be conducted with only a single case. Overall, we concluded that inter-seasonal/inter-population differences in (Simpson's) diet diversity and (Pianka's) diet similarity are related slightly, with a slight tendency for closer populations to show more similar diets, and habitat similarity being the only factor influencing diet similarity.

DISCUSSION

Even though raccoons have diverse diets, few items are consumed year-round, because most diet items are only available seasonally (Lotze and Anderson, 1979). As would be expected of optimal foragers, raccoons become more selective as food availability increases (Lotze and Anderson, 1979; Gehrt, 2003). The most dominant items (both in terms of abundance and percent frequency of occurrence) in most studies are plant mast (*i.e.*, nuts, berries, and seeds) and arthropods (*i.e.*, Lotze and Anderson, 1979). This also was true at Ruler's Bar Hassock, where crustaceans (brachyuran crabs and *Uca pugnax*) and plant items were the most common diet items year-round. Similarly, Fleming *et al.* (1976) noted that decapods, specifically crayfish, fiddler crabs, blue crab (*Callinectes sapidus*), and shrimp were the major food items throughout the year in coastal marsh raccoons (*Procyon lotor megalodous*) in Louisiana. Barton and Roth (2007) and Munscher (2007) found similar results in coastal raccoon populations in Florida, where crustaceans and plants were the primary food items.

One noticeable seasonal shift involved consumption of mammals, especially muskrat (*Ondatra zibethicus*) kits and white-footed mice (*Peromyscus leucopus*). Small mammal remains composed 20% frequency of occurrence and 42% frequency of occurrence of Ruler's Bar Hassock raccoon diets in Winter and Spring respectively. Gehrt (2003) and Stains (1956) reported similar shifts whose cause was unknown.

An even more dramatic, but more easily explained, change in seasonal diets involved plant mast. Consumption of mulberries (*Morus* sp.; 43% frequency of occurrence) had the second greatest frequency of occurrence (after *Uca* sp.) during Summer when the mulberries were readily available on trees and on the ground. Raccoons switched to grapes (*Vitis* sp.) and autumn olive (*Elaeagnus umbellata*; 20% and 32% frequency of occurrence, respectively) in Autumn. Most of these diet adjustments coincided with the fruit-producing seasons for these plants. However, during Winter raccoons foraged on oriental bittersweet (*Celastrus orbiculatus*) berries and prickly pears (*Opuntia humifusa*), although both fruits were available earlier (prickly pears mature in the Summer and bittersweet in Autumn). These fruits might be less desirable than others available during Summer and Autumn, and so may not be eaten until more desirable foods are exhausted.

Although scat analysis is a common method for carnivore diet analysis, some food items are likely to be under-detected by this method. For example, Greenwood (1979) was unable to detect relevant residue in raccoon scat after feeding them earthworms and boned meat. Similarly, although we observed many raccoon-predated terrapin nests during their nesting season in Jun. and Jul., we found little evidence of terrapin eggs in raccoon scats, probably because raccoons typically only consume the liquid contents. Raccoons tend to eat more terrapin eggshells later in the nesting season (Feinberg and Burke, 2003; Burke *et al.*, 2009); we found evidence of this pattern in Ruler's Bar Hassock raccoon scats collected in Jul. Similarly, unless the shells of bird or other reptile eggs were consumed and not just the liquid contents, egg consumption would not be detected using scat analysis, thus these would be underrepresented in diet data. Probably the only available technique for identifying egg consumption in raccoon scat is DNA or molecular scatology (*e.g.*, Deagle *et al.*, 2005). We also noted that three of the four scat samples containing significant amounts of soil were collected in Jun. and Jul. We suggest that sand may have been consumed incidentally with terrapin eggs. Greenwood (1981) concluded this after observing soil in raccoon scats; further, he observed raccoons consuming earthworms and concluded that soil ingested also could be due to raccoon predation on earthworms. Therefore, sand may be an indirect indication of turtle egg and/or earthworm consumption.

With dietary generalists such as raccoons, a complete dietary list may not be possible. Our species-accumulation curves indicated, however, that we identified a large percentage of the Ruler's Bar Hassock raccoon prey species. More precise methods, especially more thorough identification of soft material, may add some additional prey species.

Raccoons at Ruler's Bar Hassock live on the edge of a major urban area; therefore, we predicted their diets might include items of human origin, such as trash or seeds from bird feeders (Hoffman and Gottschang, 1977). Exotic fruit, especially citrus, regularly wash up on Ruler's Bar Hassock shores due to religious ceremonies commonly performed in Jamaica Bay. We observed raccoon footprints on the shorelines daily. Nevertheless, the only anthropogenic items we found in Ruler's Bar Hassock raccoon diets were paper, small plastic items and what appeared to be cigarette filters, but it is not clear why raccoons would deliberately consume such items. We also may have underestimated the consumption of anthropogenic items if raccoons ate items that were not detectable in scats.

We compared Ruler's Bar Hassock raccoon diets among seasons and to other diet studies that were either from similar habitat type (coastal marsh) or close geographically. Major food types (crustaceans, mast, and plant material) were consumed in significantly different frequencies in different seasons at Ruler's Bar Hassock, but nevertheless, using three types of species diversity tests, we found high similarities between Ruler's Bar Hassock raccoon diets in the different seasons. These same analyses showed high similarities between Ruler's Bar Hassock raccoon diets and two geographically remote studies undertaken in similar marsh habitat. In contrast, we found both low similarity and some significant differences in diet between Ruler's Bar Hassock raccoons and raccoons from a series of sites geographically close but differing in habitat. These results suggest that habitat type overrides geographical proximity in determining raccoon diets. Thus, predictions of raccoon diets in any unstudied area would be optimized if based on studies of raccoons in similar habitat, even if spatially distant, instead of studies on closer populations, if habitats are different. Nevertheless, we suggest that the ability to exploit novel food resources in new habitats likely played a vital role in the recent successful expansion of raccoons, through natural dispersal in North America and human-facilitated introductions elsewhere.

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