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FORAGING OF GRAY SQUIRRELS ON AN URBAN–RURAL GRADIENT: USE OF THE GUD TO ASSESS ANTHROPOGENIC IMPACT[1]

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Abstract. Responses of organisms to urbanization may involve adjustments in behavior. To qualify such behavioral plasticity we measured the degree to which gray squirrels (*Sciurus carolinensis*) exploited sunflower seeds in pans distributed over an urban–rural gradient of 78 sites in Virginia. Our objective was to use squirrel GUDs as a functional, relativistic measure of the effects of urbanization. Results showed that a higher proportion of pans were foraged from and that the GUDs were lower (more seeds were removed) in relatively high-density urban and suburban areas than in more rural agricultural areas, or in relatively human-free forest controls. For sites near or within human settlements, GUDs were lower nearer to human-occupied structures than at a greater distance from them, where more squirrels were observed, and where the density of trees was higher; GUDs were higher where there was substantial ground cover and where domestic pets (i.e., cats/dogs) were present nearby. Squirrels living in close proximity to humans appear to be either more limited by food or less sensitive to predatory risk than those living in more natural areas. We argue that the GUD represents a valuable metric with utility for measuring the separate and combined impact of anthropogenic actions at the individual and population levels.

Key words: food limitation; giving-up density; gray squirrel foraging; human impact; predation on squirrels; Sciurus carolinensis; *urban–rural gradients.*

INTRODUCTION

There is much basic and applied interest in using urban–rural gradients to evaluate and understand ecological changes that accompany human settlement (see Matson 1990). Some ecologists (i.e., McDonnell and Pickett 1990) have argued that urbanization can be viewed as an "experimental manipulation," albeit one occurring at an unprecedented scale and intensity, and that many of the concepts and methods used to study basic ecological relationships may be applicable to understanding anthropogenic impacts. One paradigm that has particular appeal in studies of human impact is that of gradient analysis (Ter Braak and Prentice 1988). Because urbanization and human impacts are usually spatially ordered, from highly developed central core areas to less impacted areas at some distance, analyses of changes in the physical and biotic environments over a gradient of decreasing human impact can be performed (Matson 1990). And while a diversity of human activities may vary along the gradient, it is unlikely that all will vary coincidentally. This means that once an indicator variable has been identified, separate effects can be statistically separated and tested for significance.

The large spatial scale at which anthropogenic effects occur means that a hierarchy of ecological response variables from that of individuals to landscapes might be considered as indicators of human impact. Most ecological assessments of urban–rural gradients have tended to focus on phenomena at the population, community, ecosystem, or landscape scales (e.g., McDonnell and Pickett 1990). However, it is clear that the behavior of individuals may change in response to even the most uninvasive human activities (Cooke 1980, Skagen et al. 1991), and that these shifts in behavior may provide a mechanistic explanation for responses observed at the population or community levels (Wiens et al. 1993). Hierarchy theory (O'Neill et al. 1986), in fact, predicts that phenomena observed at one scale might be the result of processes operating at the next smaller scale.

In this paper we focus on habitat usage patterns of gray squirrels, and how these shift along a gradient of increasing urbanization. Theory predicts that individuals should always choose the best habitat available (Levins 1968). But quality is undoubtedly evaluated in a multidimensional and graded manner. Availability of food, safety, nest sites, and mates are all important elements of an animal's habitat. One means of studying the diverse inputs that go into habitat selection has been to measure the exploitation of artificial resource patches by foraging individuals (for reviews see Brown 1988, Newman 1991, Bowers et al. 1993). The underlying idea is simple: if foraging gain is a decelerated function of time spent exploiting patches, then giving-up densities, times spent in patches, and quitting harvest rates might provide important details concerning habitat suitability. The giving-up density (GUD: the density of resources in a patch at which foraging stops) provides a straightforward means of estimating quitting

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harvest rates, and is usually easy to measure in field situations (e.g., Whitham 1977, Hodges and Wolfe 1981, Nonacs and Dill 1990; for review see Brown 1988).

The GUD of a forager that is behaving optimally and according to the rules of rate maximization should correspond to a harvest rate that balances marginal profits with the various marginal costs of foraging (Brown 1988). Theoretically, the point at which foraging stops can be used as a measure of the marginal net profit in a priori hypothesis testing: that is, if all costs and benefits have been appropriately measured, an optimal, unvarying GUD is predicted.

Differences in GUDs have been used as a measure of spatial or temporal differences in predatory risk (Newman et al. 1988, Bowers 1990, Kotler 1992), "missed opportunity costs," the marginal/net harvesting rate, or some combination of these and other factors that collectively define aspects of an organism's environment (Brown 1988, 1989, Bowers et al. 1993, Kotler et al. 1993, Bowers and Adams-Manson 1994). While GUDs are typically used to test for a specified effect, because they are sensitive to multiple inputs and directly reflect net energy intake, they provide a quantitative and relativistic measure of how individual organisms view their environment (Bowers et al. 1993). In short, GUDs have practical utility, a well-developed conceptual basis, and provide insights into how individuals relate to their environment—important ingredients for measurement endpoints in ecological monitoring and assessment work (Suter 1993).

One goal of our study was to quantify individualistic responses of gray squirrels (*Sciurus carolinensis*) to a gradient of increasing human habitation using the GUD approach. Gray squirrels are ecologically, economically, and aesthetically important (Flyger 1970), they commonly occupy the whole urban–rural gradient, and they have been the focus of many GUD types of foraging studies (Lima et al. 1985, Lima and Valone 1986, Newman and Caraco 1987, Newman et al. 1988, Bowers et al. 1993). Despite their apparent tolerance for humans, no study that we know of has explained if gray squirrels have benefited or suffered as a result of increasing human influence. A second goal was to identify the sign and pathway by which certain human impacts affect squirrel foraging behavior. We view our efforts as a test case to see if GUDs can be used as a measurement endpoint over which human impacts can be evaluated. The null hypothesis was that the foraging behavior of squirrels (as measured through GUDs) would not differ over the urban–rural gradient. Deviation from this null will be used to make inferences concerning human impacts on both squirrel behavior and their populations.

STUDY SITE AND METHODS

Research was conducted at 78 sites in a 500-km^2 area that included three counties in northern Virginia, USA (Frederick, Clarke, Fouquier counties) that are in and adjacent to the northern Shenandoah Valley. This region supports an urban-to-rural mixture of human settlements: from relatively high-density urban areas (Winchester: $\approx$250 persons/km^2); to smaller towns (Berryville and Boyce: $\approx$100 persons/km^2); to rural and agricultural/forested areas ($<$1 person/km^2); with some protected forests where human inhabitants are absent.

Site selection was determined by enlisting research volunteers from the general public. Volunteers were recruited through: (1) letters of inquiry sent to members of the "Friends of the State Arboretum," a support organization associated with the Blandy Experimental Farm of the University of Virginia (that served as headquarters for the project); (2) an article describing the project published in a local newspaper (*The Winchester Star*); and (3) by word of mouth. Participation was limited to volunteers who had observed at least one squirrel on their property during the last year, and who also had at least one tree $>$15 cm in diameter. In addition to the 64 volunteer sites, we established an additional 10 sites at Sky Meadows State Park, Fouquier County, Virginia as being representative of a natural forest, in a "control" situation (i.e., $\approx$5 km from all human habitation, and where hunting was not allowed), and an additional 4 sites in a wooded section of a 200-ha park within the city limits of Winchester.

The underlying theory (e.g., Charnov 1976, Brown 1988, Newman 1991) on which our study was based required that patches deplete, i.e., that as a forager removed resources, per-food-item search times increased, yielding a decelerated gain function. Under a constant rate of harvest, foragers should harvest all resources in a patch if they start to forage there at all (in the absence of satiation). By contrast, patches that deplete represent situations where graded behavioral responses can be measured (see Brown 1988). Other studies, in fact, have shown that gray squirrels foraging for sunflower seeds embedded in a matrix of sand or sawdust eat but do not cache the seeds, and that they experience a decelerated feeding curve (Newman et al. 1988, Bowers et al. 1993).

In our study GUDs were measured in round, plastic pans 35 cm in diameter with 10-cm sides; 200 graystripe sunflower seeds (*Helianthus annuus*) were mixed into 3 L of fine sand and the remaining seeds and husks removed after a 24-h period. The large volume of sand relative to the number of seeds produced search times for individual seeds that increased as pans became depleted (see Bowers et al. 1993). Using only 200 seeds per pan, and a single pan per site, guaranteed that squirrels would not become satiated on sunflower seeds alone.

Volunteers were provided packets of 200 pre-counted seeds, a sieve to remove the seeds from the sand, a supply of sand, a pan, and detailed instructions (descriptions of protocols). We asked that volunteers repeat the experiment at least three times per week be-

TABLE 1. Description of the variables used to characterize the environments at each of the 64 sites. Volunteers were asked (in a questionnaire) to describe their site in terms of the following:

Variable	Value/units	Description
Landscape type	City/town	Population density of 100–250 persons/km^2 (i.e., Winchester, Berryville)
	Suburban	Population density of 100–250 persons/km^2 but away from urban areas
	Agricultural	Low population density (<100 persons/km^2) with agricultural fields, pastures, or orchards nearby
	Largely forested	Low population density surrounded by mostly continuous forest
Distance to human domicile	Metres	Distance of pan to nearest human habitation
Distance to nearest road	Metres	Distance of pan to nearest paved road
Number of trees	Number	Number of trees >15 cm dbh within a 23 m radius of pan
Ground vegetation	Open	Mowed grass, open understory
	Covered	Bushy/shrubby, weedy; not open
Number of squirrels	Number	Maximum number of squirrels observed at one time during the last year
Pets	Present	Dogs/cats common at site
	Absent	Dogs/cats rare or absent at site
Bird-feeder	Yes	Bird-feeder at site during some time of year
	No	Bird-feeder absent
Chipmunks (*Tamias striatus*)	Present	Chipmunks present
	Absent	Chipmunks absent
Hunting	Allowed	Hunting on or near site
	Not allowed	No hunting

tween 1 July and 4 August 1994. After each 24-h trial, seeds were sieved from the sand, placed in a bag, and returned to the Blandy Farm for analyses. Every effort was made to standardize the protocols across sites. We also asked volunteers to characterize their site through a detailed questionnaire (see Table 1).

The mean and median number of uneaten seeds remaining after all 24-h trials at a site were used to estimate the GUD. Only trials where it was clear that squirrels had actually found and foraged from dishes were included. While birds sometimes removed seeds lying on the surface of the sand (typically no more than ≈10 seeds), the removal of such a small number of seeds should not affect the GUD for squirrels. We also tallied the proportion of trials at a site where squirrels did not forage from pans (if <10 seeds had been removed). We used the minimum and maximum number of seeds remaining in pans after squirrel visits as additional estimates of the GUD.

The mean, median, maximum, and minimum number of seeds remaining in dishes all correspond, in some manner, to the GUD for that site. Variation in these parameters across sites and over the urban–rural landscape provided the basis for testing effects of human habitation on squirrel behavior. We performed multiple regression analyses and ANOVA using various GUD and foraging parameters at a site as dependent variables, and the suite of variables listed in Table 1 as independent variables. To better meet assumptions of normality, count data were logarithmically and percent data arcsine transformed prior to analysis. Regression analyses included both forced entry to determine singular effects of certain variables, and stepwise analyses to determine relative and cumulative effects.

Using untrained volunteers in scientific research is somewhat unconventional and has certain problems, ranging from an uneven distribution of sites across the landscape, to inconsistencies in protocol and in filling out the questionnaire. However, it should be noted that conducting a study on this scale and of this magnitude would have been impossible without volunteer help. In any event, taking multiple observations over a large number of sites should to some degree compensate for any irregularities. Data were excluded from the analyses if there appeared to be a question concerning the way they were collected.

RESULTS

Our data base included a total of 78 sites over which GUDs were measured for 578 24-h trials. While 27% (156) of the trials failed to record squirrel activity, every site appeared to record at least one GUD for gray squirrels. We restricted most of our analyses to 59 sites that had all requisite data recorded, and where all protocols appeared to be followed. In all but three cases, adjacent sites were separated by at least 0.5 km and therefore are expected to be largely independent. However, the different analyses often included variable numbers of sites, depending on whether omitted/missing data was pertinent or not to that analysis. For the principal set of 59 sites, 27% (16) were in cities/towns, 15% (9) in suburban areas, 14% (8) near human dwellings in agricultural areas, 12% (7) near human-occupied structures embedded in forests, and 17% (10) were in forest control areas away from all human settlements (Table 2). In no case were all 200 seeds removed from a pan during a 24-h period.

There were a number of differences in GUDs among the landscape types (Fig. 1); the most noticeable differences involved city/town and suburban sites vs. the

TABLE 2. Various estimated measures of foraging summarized for sites within certain landscape type classifications. (See *Study site and methods.*)

Landscape type	Number of sites	Giving-up density				% pans
		Mean ± 1 SD	Median ± 1 SD	Low ± 1 SD	High ± 1 SD	found ± 1 SD
City/town	16	43.7 ± 27.9	38.4 ± 42.7	8.8 ± 9.0	111.7 ± 55.9	93 ± 09
Suburban	9	48.1 ± 39.2	38.4 ± 40.9	6.9 ± 8.3	119.2 ± 65.0	82 ± 22
Agricultural	8	108.0 ± 68.5	105.8 ± 80.3	77.4 ± 77.4	162.4 ± 37.9	57 ± 30
Forest (near human)	7	52.3 ± 53.0	50.6 ± 68.2	9.3 ± 11.9	107.4 ± 82.0	64 ± 36
Other†	5	60.4 ± 37.8	43.2 ± 49.3	12.0 ± 8.3	137.2 ± 68.3	82 ± 24
City park	4	122.5 ± 53.2	122.3 ± 55.9	88.3 ± 61.2	157.0 ± 54.2	61 ± 36
Forest (control)	10	99.0 ± 60.2	97.6 ± 63.8	72.9 ± 64.2	132.8 ± 67.9	38 ± 49

† Sites not easily classified as one of the landscape types enumerated.

forest control (Table 2). ANOVA (with multiple range tests) showed that pans in the city/town category were visited more often than those in the agricultural or either of the forested landscape types; pans in suburban areas, forests near human habitation, or in the "other" category were visited more frequently than those in the forest control ($F_{6,61} = 5.62$, $P < 0.01$). There were also landscape differences in the degree to which squirrels exploited pans. Specifically, squirrels in cities/towns and suburban areas removed significantly more seeds (lower GUDs) than those in the agricultural, park, or forest control areas (Table 2; $F_{6,52} = 3.53$ for the mean, $F_{6,52} = 2.99$ for the median, and $F_{6,56} = 6.08$ for the lowest number of seeds remaining, all $P < 0.01$). There were no differences in the maximum number of seeds remaining in exploited dishes along the urban–rural gradient.

A number of factors were subsumed under the general category of landscape type (Table 3). For example, sites in cities/towns and in suburban areas tended to be closer to human-occupied structures and roads, have more open understories and overstories (fewer trees and shrubs), and hunting was rarer than for agricultural or forested homesteads in more rural sites. More squirrels were observed at suburban and forested sites with adjacent human settlement than at sites in cities/towns, and the fewest were observed in agricultural areas that also had the fewest trees. The maximum number of squirrels observed at a site ($n = 16$) was within the city limits of Winchester, where there was an unusual number of large trees nearby ($n = 26$). Occurrence of pets, bird feeders, and chipmunks also varied among landscape types (Table 3). In general, squirrel abundance was highest at urbanized sites with high numbers of large trees, bird feeders, and where pets were absent.

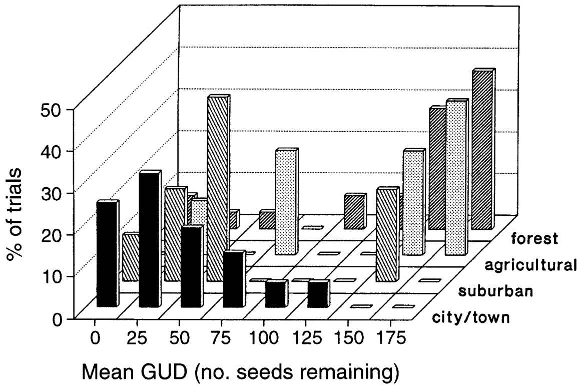

FIG. 1. Relative frequency distribution of mean GUDs for city/town ($n = 17$), suburban ($n = 9$), agricultural ($n = 8$), and forest ($n = 8$) sites. See Table 1 for definition of sites. Forest control and city park sites are not included.

To further investigate the absolute and relative roles of the various factors on foraging behavior we used regression analyses where: (1) each individual variable was entered separately; and (2) stepwise entry was used to treat all variables as a group. Analyses were restricted to the sites near human habitation (forest control and city park sites were omitted), and included the same suite of dependent variables as used in tests of landscape type differences (see Table 2).

The number of squirrels observed at a site was the most consistent and significant correlate of the maximum, minimum, median, and mean GUD (Table 4): where more squirrels were observed, GUDs were lower (more seeds were removed), and the proportion of unexploited pans was lower. Presence of pets at a site produced significantly higher mean, median, and maximum GUDs than when they were absent (Fig. 2); within more urban areas, pans nearer human-occupied structures, at sites with higher tree densities, and with little ground cover all had lower maximum GUDs.

Despite the marked differences in GUDs among landscape types (see Table 2), much of the variation in GUDs was accounted for by variables listed in Table 1. For example, specific features of sites collectively accounted for between 17% (low GUD observed at a site) and 54% (percentage of trials recording foraging) of the variation in foraging activity (Table 4). Sites near human habitation with more trees supported more squirrels ($r = 0.49$, df = 34, $P < 0.01$). While there was no relationship between the number of squirrels and "hunting/no hunting," or the number of squirrels and the distance from pans to the nearest human habitation (both $P > 0.20$), sites within more urban areas but farther from human habitations and where hunting was allowed recorded a lower proportion of squirrel visits (Table 4). The distance to human habitation was positively and the number of trees negatively correlated

TABLE 3. Characterization of habitat features of sites near human settlements listed by landscape type. See Table 1 for more information about the individual variables. Numbers following ± are 1 SD.

Variable	Landscape type: City/town	Suburban	Largely forested	Agricultural
Distance to house (m)[†]	11.8 ± 7.1	20.3 ± 15.1	40.7 ± 52.9	23.8 ± 18.7
Distance to road (m)[‡]	43.1 ± 66.2	33.2 ± 20.0	211.7 ± 124.0	236.9 ± 107.4
Number of trees[§]	11.6 ± 8.2	12.4 ± 10.0	49.7 ± 28.9	10.9 ± 7.2
Number of squirrels	4.3 ± 1.5	5.3 ± 2.3	5.8 ± 2.9	2.9 ± 2.2
% hunting[‖]	0	11	50	25
% pets[¶]	63	67	57	88
% bird-feeders[#]	81	100	100	88
% open ground cover[††]	82	83	75	50
% chipmunks[‡‡]	25	78	50	66

[†] Mean distance from pan to nearest human habitation.

[‡] Mean distance from pan to nearest paved road.

[§] Number of trees with dbh > 15 cm within 23 m of pan.

[‖] Percent of sites where hunting is allowed.

[¶] Percent of sites where dogs or cats are present.

[#] Percent of sites where birds are fed (summer or winter).

[††] Percent of sites where ground vegetation immediately around pan is mostly absent, low or mowed.

[‡‡] Percent of sites where chipmunks (*Tamias striatus*) are also present.

with the maximum number of seeds remaining in dishes where some squirrel activity was recorded: dishes closer to human habitations and where there were high densities of trees had more seeds removed (lower maximum GUDs).

DISCUSSION

There is one main result: squirrels in natural, more rural forests or at some distance from human settlements consistently foraged from fewer pans and had

TABLE 4. Results of simple and multiple regression analyses testing for relationships between the various independent variables and measurements of foraging activity (i.e., estimates of mean, median, low, and maximum GUD for a site and the percentage of trials squirrels failed to remove seeds from pans). Under each foraging metric are listed: (1) the amount of variation accounted for by each variable separately (R^2) and, in parentheses, the sign of the relationship, (2) the step at which that variable was entered into the multiple regression, and (3) the cumulative amount of variation explained (Cum. R^2) after entry. Only those variables showing significant correlations with foraging activity are included (i.e., distance from nearest road, and the presence/absence of chipmunks, are not included).

Dependent variable	Independent variables: Landscape type[†]	Pets (0 or 1)	Hunting (0 or 1)	Distance to habitation	No. trees	No. squirrels	Bird-feeder (0 or 1)	Ground cover
Mean GUD								
R^2	3 (+)	13* (+)	<0	<0	4 (−)	28* (−)	<0	2 (+)
Step	3	2	···	···	···	1	···	···
Cum. R^2	47	40	···	···	···	28	···	···
Median GUD								
R^2	<0	11* (+)	<0	<0	4 (−)	27* (−)	<0	<0
Step	···	2	···	···	···	1	···	···
Cum. R^2	···	42	···	···	···	27	···	···
Low GUD								
R^2	<0	2 (+)	<0	<0	<0	17* (−)	<0	<0
Step	···	···	···	···	···	1	···	···
Cum. R^2	···	···	···	···	···	17	···	···
Maximum GUD								
R^2	1 (+)	10* (+)	<0	1 (+)	11* (−)	8* (−)	<0	3 (+)
Step	2	···	···	3	1	···	···	4
Cum. R^2	19	···	···	27	11	···	···	34
% not foraged from								
R^2	13* (+)	1 (+)	28* (+)	15* (+)	2 (−)	15* (−)	2 (−)	3 (+)
Step	4	···	1	3	···	2	···	···
Cum. R^2	54	···	28	49	···	42	···	···

* $P < 0.05$.

[†] City, town, suburban = 1; agricultural, forested sites = 2.

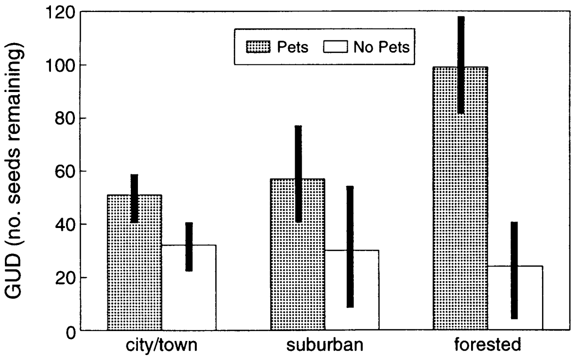

FIG. 2. Mean GUD (±1 standard error) for sites with and without pets for city/town, suburban, and forested sites near human habitation.

higher GUDs than those living in close association with humans. This pattern was apparent both in comparisons of city/town and suburban vs. forest control sites and over urban–rural sites with human habitations.

Though squirrels were clearly present in relatively undisturbed forest areas, anecdotal observations suggest that squirrel density was much higher at sites near human settlements, and was especially high at heavily forested urban and suburban sites. Coincident with the gradient in squirrel density were differences in the ratio of exploited:unexploited pans (38% in the forest control vs. 57–93% for the other landscape types) and in GUDs that tended to be 2–3 times lower near human settlements than away. Other reports tend to support the notion that gray squirrels may be more abundant in urban than in rural or more natural settings. For example, Shuler (1969) reported that 100 gray squirrels were trapped at a single urban site in Lewisburg, Pennsylvania, and Flyger (1970) reported that up to 80 squirrels visited a single backyard feeder in Silver Spring, Maryland. Flyger (1959) estimated the density of squirrels in two small suburban woodlots in Baltimore at >12.5 individuals/ha. By contrast, Gorman and Roth (1989) found gray squirrel densities in a protected Delaware woodlot to vary markedly among seasons but averaged ≈7 individuals/ha, and Havera and Nixon (1980) reported gray squirrel densities of 1–2 individuals/ha in a mixed hardwood forest in Illinois.

A higher rate of finding pans and lower GUDs for urban than rural squirrels suggest that food availability alone probably cannot account for the differences in squirrel densities. More specifically, if food was generally more available in urban than rural environs, then GUDs at more urban sites should also be higher despite the apparently higher squirrel densities there. This clearly, was not the case. Rather, the pan data suggest that there are not more squirrels in urban environments because there is more food there. If anything, the data suggest that there is less available food, making for hungrier and more desperate urban squirrels. If there was some sort of equilibrium between squirrel abundance and food availability, then GUDs over the urban–rural gradient should have been similar.

Food supplementation experiments (Havera and Nixon 1980) have failed to increase gray squirrel densities as low as 1 individual/ha in a natural setting, suggesting that other factors may be involved in the regulation of densities along urban–rural gradients. One possible alternative is that predation by natural and human hunters may be higher in more rural than in human-dominated habitats. With higher rates of predation, squirrel densities may be lower and food more available on a per capita basis; also because of high predation risk, squirrels should be more cautious in more rural than in urban settings. Recording higher GUDs at rural forested sites is totally consistent with there being higher predation rates, fewer squirrels, and more available food there. These numerical and functional squirrel responses between sites with high and low predation risk are similar to that reported elsewhere for birds (e.g., Grubb and Greenwald 1982, Valone and Lima 1987).

One possible alternative explanation for the patterns reported here is that the unfamiliar sunflower seeds, sand, and pans may be less acceptable (or less attractive) to rural than to urban squirrels. The suggestion is that measures of foraging activity employed here may reflect behavioral responses to novel situations (and resources) rather than the marginal trade-offs on which the GUD approach is predicated. This, however, seems unlikely, in that squirrels inhabiting the control forest sites removed, on average, about one-half of the sunflower seeds in those pans foraged from. Clearly, sunflower seeds at high densities were not only acceptable but appeared to be quite attractive to rural squirrels and, as required under the GUD approach, became less attractive as seeds in pans became depleted. The fact that these squirrels did not depress seeds to as low a level as those in more urban environments does not indicate that sunflower seeds were less preferred, or had a different preference ranking, but rather that alternative, more profitable food items were probably available nearby.

It seems likely that the abundance of natural predators of squirrels may vary over human settlement gradients. In more urban areas, without strong predation pressure, the limiting factor for squirrels may be availability of trees that provide nest sites, food, and escape routes. This is consistent with the positive correlation between the number of squirrels observed at human-occupied sites and local tree density. That the control sites (with the highest tree densities) appeared to have low numbers of squirrels and the highest GUDs implies that a different set of rules may apply to squirrel populations in more natural settings. More specifically, sites near humans may represent refugia from natural predators, and along a gradient of increasing human presence, squirrel populations may shift from being predator-limited to food-limited. This scenario is consistent with observations by Cooke (1980) that passerine bird species living close to humans are less responsive to potential predators than those living in more rural areas. That squirrels often remove nearly all of the mast crop production of some urban trees (see Steele and Smallwood 1994) is further evidence that food may be limited in urban landscapes.

One test of whether food or predators limit squirrel populations would be through food addition experiments. Specifically, we predict that adding supplemental food may increase squirrel densities in urban but not rural sites. There is some support for this notion. Havera and Nixon (1980) reported a minimal squirrel response to the addition of cracked corn over three winters in a rural Illinois woodlot. By contrast, in our study we found the abundance of squirrels at 41 urban and suburban sites with bird feeders to be about twice that of the four sites without feeders (4.85 ± 2.3 vs. 2.25 ± 1.3 squirrels/site; mean ± 1 SD), a significant difference ($F_{1,43} = 4.92$, $P < 0.03$). Hence, there appear to be more squirrels where supplemental food is available (via bird feeders) than where it is not.

Further detail concerning responses of squirrels to predators comes from urban and suburban sites with and without domestic pets. Dogs and especially cats are occasional predators on urban squirrels (Powell 1982). Gustafson and VanDruff (1990) showed that the startle distance of gray squirrels in Syracuse, New York was ≈26 m for dogs and 13 m for humans, suggesting that squirrels probably view dogs as more of a threat than people. In our study we found that urban and suburban sites with pets had GUDs about twice that of sites without pets. Hence, there appears to be variability in predation risk among urban sites that parallels the larger scale trend between urban and the rural forest, control sites.

If squirrels are relatively more susceptible to predators in rural than in more urban settings, then there could be very different selective regimes over human settlement gradients. For example, an urban–rural shift in predation pressure has been invoked to account for the occurrence of more apparent melanistic morphs of gray squirrels in urban areas and their near absence in more rural forests. Such shifts can be dramatic: i.e., from populations composed of ≈60% of the melanistic form in and around Syracuse, New York, to <2% in surrounding rural areas (Creed and Sharp 1958). It may also be that in urban settings higher premiums are placed on individuals being adventurous than in more risky habitats with more predators. Bold and aggressive squirrels would have greater access to bird feeders and other food resources provided by humans than more timid individuals. And without predation to constrain the behavior, bold squirrels would leave more offspring, thereby perpetuating and enhancing that behavior. A corollary, then, is that shifts in GUDs with changes in predation risk may be greater for more timid squirrels in rural than for bold squirrels in urban sites (see Cooke 1980 for such a study on passerine birds). While others have studied squirrels in urban settings and found GUDs to be higher in areas of purportedly higher predatory risk (Lima et al. 1985, Lima and Valone 1986, Newman and Caraco 1987, Newman et al. 1988), it is intriguing to speculate that responses measured in these studies might be fairly subdued compared to what might have been measured for more rural, risk-prone squirrels. In short, urbanization may not only affect the numbers and foraging economics of squirrels but their general behavioral disposition as well.

Our goal in this paper has been to expand the suite of environmental inputs usually subjected to GUD analyses to include those factors that change over an urban–rural gradient of human habitation. In doing this we have created an inclusive context for integrating humans as explicit components of ecosystems. Our results provide an overall estimate of the aggregated human impact on squirrels, as well the relative impacts of particular human actions on both squirrel populations and the behavior of individuals. We believe studies like ours, where human impacts are considered in a broader conceptual framework of basic ecological responses, and according to well-developed ecological theories, offer great potential for measuring, understanding, and mitigating anthropogenic effects (see McDonnell and Pickett 1990).

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