CHANGES IN RACCOON PARASITE COMMUNITIES IN RESPONSE TO AN EXPERIMENTAL MANIPULATION OF RESOURCE AVAILABILITY

by

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ABSTRACT

The role of social interactions among hosts in structuring their parasite communities was examined by experimentally increasing contact rates in raccoons, *Procyon lotor*, by altering resource availability. Two populations of raccoons in southern New York were trapped and monitored using radio telemetry during 1999 and 2000 to determine baseline levels of social interaction and parasite community structure. In 2001, the experimental site was perturbed with the addition of clumped food resources, while the control site was provisioned with equal quantities of dispersed food resources. This experimental design allowed for two controls: temporal (before and after the perturbation) and spatial (experimental site vs. control site). Remote photography showed that the mean number of animals aggregating at the food resources in the experimental site was higher than the mean number of animals associating together in the control site, thus contact rates between individuals were higher in the experimental site in response to the perturbation. Ectoparasites showed positive, neutral, and negative correlations with increased raccoon sociality. Across the endoparasite community, prevalence of infection increased as a result of increased raccoon sociality, while the effects on individual parasites were less straightforward. Overall, these results support the hypothesis that intraspecific variation in parasitism can be accounted for by intraspecific variation in degree of sociality. Further, these results suggest that anthropogenic changes which alter resource availability can have important consequences for disease transmission in wildlife.

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INTRODUCTION

Increased disease transmission is often hypothesized to be a principal cost of group living (Alexander 1974, Freeland 1976, Hamilton 1987, Sherman et al. 1988), and is therefore a potentially important force in shaping the evolution of social organization. The relationship between disease transmission and social structure is driven by the increased proximity among hosts in social groups compared to solitary hosts, resulting in increased contact rates and opportunities for disease transmission (Kuris et al. 1980). Conversely, group-living can also decrease the risk of infection through socially mediated avoidance behaviors (e.g. allopreening, Brooke 1985, Clayton 1991, allogrooming Freeland 1981, Hart and Hart 1988), or dilution effects which reduce the probability of any particular host in a group being singled out for infection (Hamilton 1971, Mooring and Hart 1992).

Ultimately, selection should favor those traits that allow individuals to avoid, minimize, or eliminate parasitic infections. A body of evidence supports the idea that parasites are capable of exerting selective pressures on hosts through a range of fitness effects (see Scott 1988, Hart 1990, Lehmann 1993, Møller et al. 1993 for reviews). If social aggregations of hosts result in transmission opportunities then parasites should be able to exert selective pressures on host social structure.

Several studies have investigated the relationship between social behavior and parasite transmission, often with contrary results. In species of colonial swallows, field studies have shown that the percentage of nests infested with fleas, swallow bugs, mites, and blow fly larvae increases with colony size (Hoogland and Sherman 1976, Brown and

Brown 1986, Møller 1987, Shields and Crook 1987); however no relationship has been found between colony size and tick infestation in swallows or another species of cooperatively breeding bird, skuas (Büttiker 1969, Hemmings 1989). A positive relationship has been observed between colony size and flea ectoparasitism in black-tailed prairie dogs (Hoogland 1979), while no relationships have been observed between flea, lice, or mite loads and group size in marmots (Arnold and Lichtenstein 1993, Van Vuren 1996). In a single study on feral horses conflicting results were found where increasing group size was correlated with increased abundance of endoparasites yet decreased harassment by ectoparasitic flies (Rubenstein and Hohmann 1989). Thus parasites may respond differently to a given degree of sociality within a host species.

Interspecific studies have also generated conflicting results. In North American passerines group living is correlated with increases in the prevalence of feather mites yet shows no relationship with the abundance of hippoboscid flies (Poulin 1991a). Paired comparisons of congeners found that colonial birds had a higher prevalence of lice and blood parasites than solitary birds (Rózsa et al. 1996, Tella 2002). Similarly, group size was positively correlated with infection by mosquito-borne *Plasmodium* in Amazonian monkeys (Davies et al. 1991). However, Freeland (1977) observed that primates formed polyspecific groups during periods of peak biting fly activity, suggesting that such associations may reduce the number of bites received by individual monkeys. No relationships have been found in comparative studies between host sociality and parasite richness in ectoparasites and Australian passerines (Poiani 1992), endoparasites and Soviet birds (Gregory et al. 1991), or ectoparasites and group-living fishes (Poulin 1991b). However, a field study of several primate species found some positive

relationships between the richness of endoparasitic protozoans and primate group size (Freeland 1979).

In a meta-analysis of several published studies, Côté and Poulin (1995) found consistent positive correlations between host group size and prevalence and intensity of contagious parasites, whereas for mobile parasites (e.g. those transmitted by volant vectors), larger groups had lower intensities of parasitic infection. The rationale for analyzing these kinds of parasites separately is that contagious parasites, those that require contact among hosts for their transmission, should be more affected by host sociality than mobile parasites, which are thought to be largely independent of proximity between hosts. Most of the studies cited above have looked at contagious parasites, and those that have looked at mobile parasites have yielded positive, negative, and neutral correlations between group size and infection (positive: Davies et al. 1991, negative: Duncan and Vigne 1979, Rubenstein and Hohmann 1989, neutral: Poulin 1999, Poulin 1991a). Moore et al. (1988) add that parasite life cycle should be taken into consideration, and hypothesized that monoxenous parasites, which require only one host to complete their lifecycle, should be more affected by host sociality than heteroxenous parasites which require several host species.

Thus the association between parasite infection and host sociality is more complex than a simple direct relationship, and is determined by several ecological, behavioral, and life history factors of both the host and parasites. When approached from the parasite community level the situation becomes even less clear, such that to understand the interactions between parasite communities and degree of host social interaction requires an experimental approach that manipulates host social structure while

simultaneously examining a broad array of parasites with diverse life cycle and transmission dynamics.

One way to manipulate host social structure in order to conduct such an experiment is to alter the timing, abundance and distribution of resources. The effect of clumped resources on social behavior or density of hosts occurs in nature through the utilization of ephemeral or localized resources (e.g. fruiting trees, water), and in human altered environments through the utilization of resources like refuse piles, dumpsters, hand outs, etc. For example, in a review of pathogens and the evolution of primate sociality, Freeland (1976) noted that reports of intergroup friendly or sexual interactions were largely attributable to shared usage of clumped resources such as water holes in the dry season or artificial feeding areas.

The presence of clumped resources encourages the reuse of habitats by large numbers of animals, which can lead to contamination of the environment with pathogens. Several observational and experimental studies have shown that animals tend to avoid such habitats, often by switching resting, feeding, or nesting sites frequently, and that these behaviors are related to levels of parasitism (e.g. primates Freeland 1980, Hausfater and Meade 1982; swallows Barclay 1988; badgers Butler and Roper 1996; bats Lewis 1996; sheep Hutchings et al. 2001). These avoidance behaviors can have important fitness consequences. For example, contamination of the environment from prolonged use can lead to juveniles being exposed to lethal doses of pathogens prior to the development of immunological competence (Freeland 1976).

Here, I use raccoons as a model system for exploring the relationship between degree of host social interaction and parasitism. The goal of this work is to address how

a shift from a solitary, low contact rate lifestyle to one of increased sociality and high contact rates influences parasite communities. I tested the hypothesis that increasing social interaction increases disease transmission by manipulating host social structure and contact rates through provisioning with clumped resources while simultaneously monitoring parasite communities.

HOST-PARASITE STUDY SYTEM

Raccoons, *Procyon lotor*, provide an ideal host study system to address questions concerning parasite-host interactions because they are widespread and abundant, they have a flexible social structure amenable to manipulation, a diverse and well-known parasite fauna, and harbor several diseases relevant for conservation biology and human health. Raccoons occur from southern Canada to Panama and are common throughout their range, reaching extreme local densities higher than 125 raccoons/km^2 in urban areas, but more normally range from 0.9 to 55.6 raccoons/km^2 (Kaufmann 1982, Rosatte et al. 1991, Riley et al. 1998). The presence of high density raccoon populations in close proximity with humans facilitates field work on raccoons, yet also has implications for the transmission of disease from raccoons to humans or domestic animals (Jenkins et al. 1988). In addition, dense populations are at a higher risk of epizootic outbreaks of contagious diseases such as rabies and canine distemper (Riley et al. 1988).

There is a wide range of inter and intraspecific variation in social organization among the order Carnivora (Macdonald 1983). For example, while largely considered solitary, raccoons exhibit a high degree of social flexibility. The home ranges of adult females tend to overlap extensively, and home ranges of males may also overlap with little evidence of territoriality (Steuwer 1943, Johnson 1970, Urban 1970, Fritzell 1978). Gehrt and Fritzell (1998b) observed that spatial groups of 3 or 4 males occupy overlapping territories, and that overlap is significantly higher within groups than between groups. There have also been reports of complex social interactions such as dominance hierarchies and neighbor recognition in captive males (Barash 1974, Ough

1982), and dominance hierarchies among free ranging raccoons at feeding stations (Sharp and Sharp 1956, Totton 1997). Among populations of some solitary carnivore species, social groups may arise partially as a result of spatiotemporal variations in resource availability, a well-documented phenomenon (Macdonald 1983). Raccoons have been observed to form groups in response to localized food resources such as particular fruiting trees, water, or feeding stations (Tevis 1947, Sharp and Sharp 1956, Seidensticker et al. 1988, Totton 1997). Communal denning has also been observed in raccoons, often in places where the availability of suitably secure and warm dens are a critical and potentially limited resource (Twichell and Dill 1949, Whitney and Underwood 1952, Mech and Turkowski 1966, Mech et al. 1966, Fritzell 1978, Schneider et al. 1971, Rabinowitz and Pelton 1986, Seidensticker et al. 1988, Gehrt and Spencer 1990, Enders and Smith 1993, Walker and Sundquist 1997, Gehrt and Fritzell 1998 a, b). Therefore, it may be possible to influence the degree of raccoon social interactions and contact rates by manipulating the abundance, timing, and distribution of resources.

The extensive raccoon literature is split between studies concerning their biology and ecology and studies focusing more narrowly on parasitology and disease (a search for "raccoons" in the last 37 years of the Journal of Parasitology alone generated 59 articles). Such interest is fueled by the presence of some key raccoon diseases of particular importance to conservation biology and human health such as the raccoon rabies virus, canine distemper, and the raccoon roundworm, *Baylisascaris procyonis*. The abundance and high density of raccoon populations relative to other wild carnivores makes them potentially important reservoir hosts for these and other generalist pathogens that may spill over to infect wildlife, domestic animals, and humans (Funk et al. 2001).

Thus the protocol for identifying raccoon parasites is well established, and many regional faunas are well known (e.g. southeastern U.S.: Harkema and Miller 1964, Bafundo et al. 1980, Smith et al. 1985, Cole and Shoop 1987; mid-western U.S.: Snyder and Fitzgerald 1985, Robel et al. 1989; western U.S.: McNeil and Krogsdale 1953, Hamir and Snyder 1999; southern Canada: Butterworth and Beverly-Burton 1981, Hoberg and McGee 1982, Ching et al. 2000). However, most raccoon parasitology on the raccoon in the northeastern United States has focused on *Baylisascaris procyonis* alone (Stone 1983, Ermer and Fodge 1986, Kidder et al. 1991).

MATERIALS AND METHODS

DESCRIPTION OF STUDY SITE

The study area, Black Rock Forest, is located in the Hudson Highlands of southern New York, approximately 80 km north of New York City on the west side of the Hudson River (Figures 1,2). Black Rock Forest is a 1500 hectare reserve that has been managed for forestry research since 1928, and protected as a natural area since 1989. Currently the forest is managed by the Black Rock Forest Consortium, a group comprised of several private and public institutions which promote scientific research and education.

Black Rock Forest is contiguous with New York state park land and forested land managed by the U.S.M.A.West Point Military Reservation. Historically, the forest was cleared for timber and agriculture in the 18th and 19th centuries. The dominant habitat type is second growth mixed-hardwood deciduous forest. Oaks (*Quercus rubra* and *Quercus prinus*), maples (*Acer saccharum* and *Acer rubrum*), beech (*Fagus grandifolia*), and birch trees (*Betula lenta* and *Betula alleghaniensis*) are the dominant tree species. Several wetland areas and man-made reservoirs occur throughout the forest, therefore water is probably not a limiting resource as has been observed or suspected for raccoon populations in other sites (Steuwer 1943, Kaufmann 1982, Kissell and Kennedy 1992, Gehrt and Fritzell 1998b; Figure 2).

In addition to raccoons, the carnivore fauna of the forest includes black bears *Ursus americanus*, coyotes, *Canis latrans,* gray foxes, *Urocyon cinereoargenteus*, otters, *Lutra canadensis*, long-tailed weasels, *Mustela frenata*, striped skunks, *Mephitis*

mephitis, and feral cats, *Felis catus*. Opossums, *Didelphis virginianus*, are abundant. Less common are bobcats, *Felis rufus*, red foxes, *Vulpes vulpes*, mink, *Mustela vison*, and fisher, *Martes pennanti*. The forest is open to the public and their domestic dogs for recreation; however there have been no feral dogs inhabiting the forest since the arrival of the coyote in the late 1980's (Brady 1994, Gompper 2002). There is a deer-hunting season in the fall but no trapping or hunting of raccoons takes place.

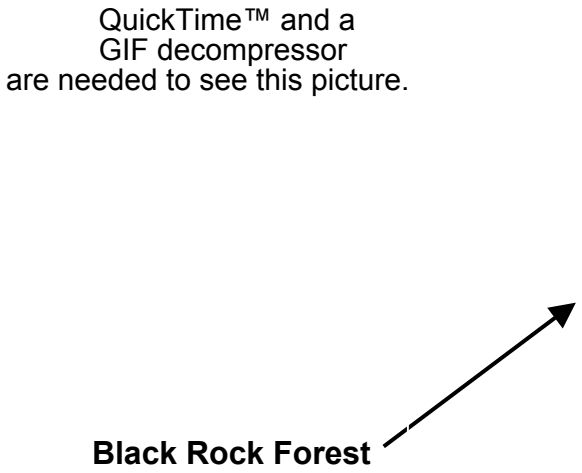

Figure 1: Location of Black Rock Forest in the Hudson Highlands, southern New York, U.S.A. (http://www.blackrockforest.org)

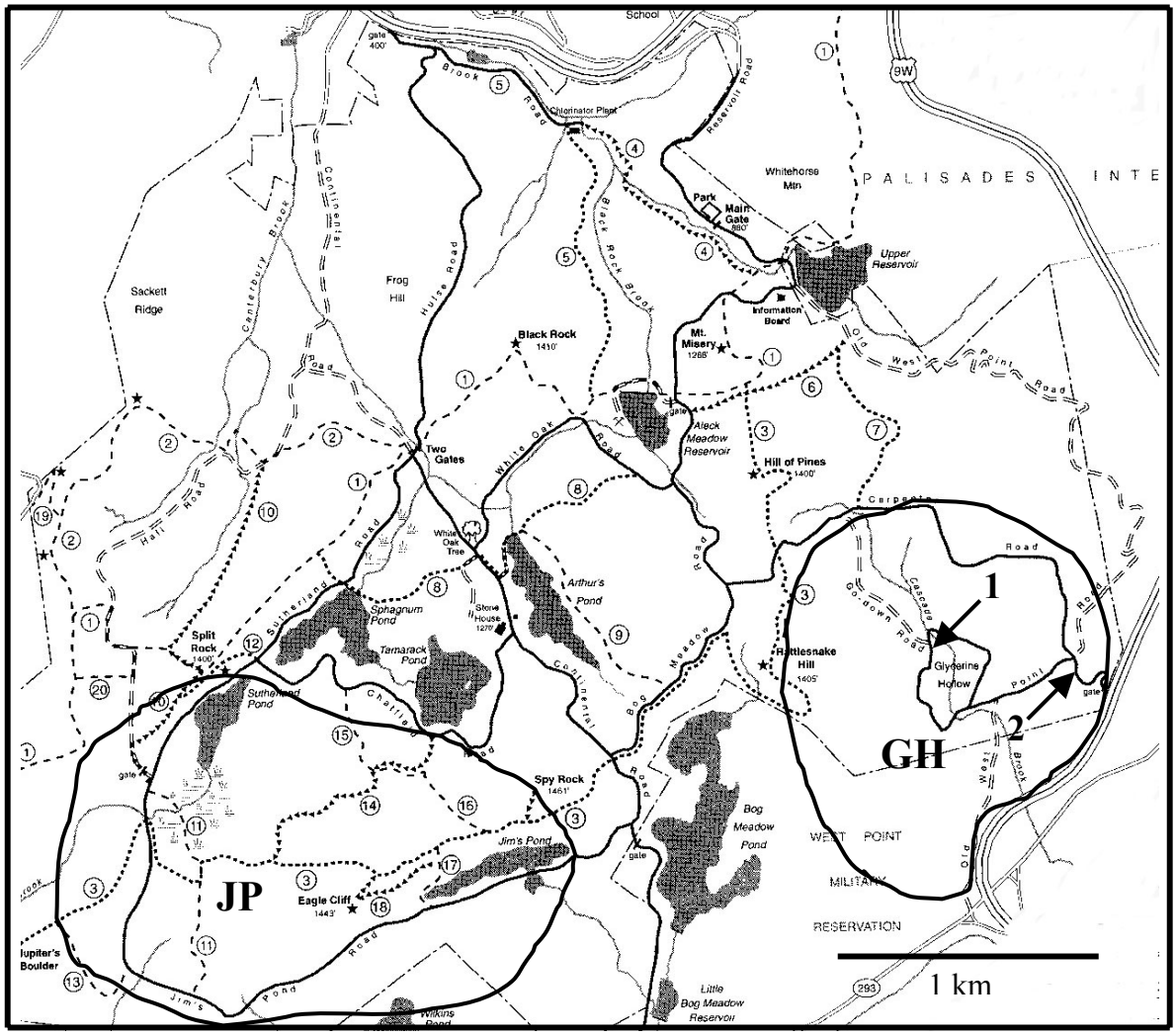

Figure 2: Map of Black Rock Forest with approximate boundaries of study sites JP (control site) and GH (experimental site) outlined. Arrows 1 and 2 show the location of the feeding stations in GH. Trapping occurred in each site along the main forest roads. (Schuster and Murray 1995, adapted from Karnig 1991).

Raccoons were trapped and monitored in two neighboring populations separated by watershed boundaries, reservoirs, and rocky outcrops. The experimental site, Glycerine Hollow (hereafter GH), is a bowl shaped watershed located in the southeastern part of the forest (elevation range ~260-430 m, Figure 2). GH is skirted on its southern edge by New York State Highway 9W, opposite which is a golf course and additional second growth forest managed by the West Point Military Reservation. The control site, Jim's Pond (hereafter JP), encompasses the southwestern portion of the forest and is also bordered by West Point Military Reservation land (elevation range ~350-440 m, Figure 2). The closest human habitation is at least 1.5 kilometers away from either site. While the two study populations are contiguous, no evidence of animals moving between these two sites was observed during the course of the study through either trapping efforts or radio telemetry.

TRAPPING AND PROCESSING RACCOONS

Permanent traplines were established in each site by placing Tomahawk box traps at100 m intervals and 25-50 m into the forest on alternate sides of forest roads (GH n=26-30 traps, JP n=23 traps). Trapping and processing of animals followed an approved animal care protocol (Columbia University IACUC Protocol No. 343A). Animals were anesthetized with an intramuscular injection of 10 mg/kg Ketamine Hydrochloride, a dissociative anesthetic, and 0.1 mg/kg Xylazine, an alpha-2 agonist sedative. Supplemental doses of Ketamine Hydrochloride equal to approximately one half the initial dose were administered as necessary to maintain anesthesia. The average time for anesthesia to take effect was 8.23 ± 0.69 minutes (n=30), and the average time that

animals were handled was 19.11 ± 0.83 minutes (n=89). Anesthetized animals' eyes were immediately lubricated with Puralube Vet Ointment upon handling to prevent desiccation. Temperature, respiration rate, and heart rate were monitored while animals were anesthetized (Osofsky and Hirsch 2000).

All animals were ear-tagged (Hasgo Tag Company, 100S-3 or NASCO rototags), weighed, and head-body and tail lengths were measured (Appendix I). Overall health and reproductive condition was noted. Age was approximated as juvenile, young adult, or adult from tooth wear, body size, and reproductive status (Grau et al. 1970). A skin biopsy, (approximately 4 mm^2), was collected from the outer thigh of each animal and stored in ethanol for future genetic analyses.

PARASITOLOGY

To monitor changes in parasite communities, parasitism was assessed at multiple levels based on the definitions of Bush et al. (1997) (Table 1). Ectoparasites were assessed from trapped animals, while endoparasites were assessed from fecal samples of trapped animals and from fresh (<24 hours old) feces found near radio-located animals.

Ectoparasites were sampled by standardized collection with a flea comb in ten strokes down each animal's back from the base of the neck to the base of the tail. Numbers of lice, fleas, replete ticks (those engorged with blood), and non-replete ticks were recorded from each hair sample as an estimate of ectoparasite abundance, and the presence or absence of ectoparasites was used to calculate ectoparasite prevalence. A distinction was made between replete and non-replete ticks since replete ticks may be a better indicator of actual parasitism since they have been on the animal for a longer

period of time. Animals were also checked visually for the presence of ectoparasites, particularly on the face and ears, and numbers of replete and non-replete ticks were recorded.

Feces were collected for endoparasite analysis and immediately stored in 10% formalin. Most samples were collected from scats found in traps with known individuals, some were collected directly from trapped animals using a fecal loop, and some were from den sites of radiocollared animals. Latrines, which are common elsewhere (Giles 1939, Yeager and Rennels 1943, Stains 1956, Kennedy et al. 1991, Page et al. 1998) were not found in Black Rock Forest. Fecal samples were processed by the Cornell University Veterinary Diagnostic Laboratory, Ithaca, NY. Qualitative analyses, which identified the endoparasite species present in each sample, were conducted using fecal flotation techniques (Bowman 1995). Endoparasite prevalence was calculated from this data.

TABLE 1: Parasitological Variables

Prevalence	Number of hosts infected with one or more individuals of a particular parasite species (or taxonomic group) divided by the number of hosts examined for that parasite species. (Often reported as a percentage)
Intensity	Number of individuals of a particular parasite species in a single infected host, i.e., the number of individuals in an ***infrapopulation***. (Always >0)
Abundance	Number of individuals of a particular parasite in/on a single host *regardless of whether or not the host is infected*. (≥0)
Mean Abundance	Total number of individuals of a particular parasite species in a sample of a particular host species divided by the total number of hosts examined (infected + uninfected)
Infrapopulation	All individuals of a species of parasite in an individual host at a particular time.
Infracommunity	A community of parasite infrapopulations in a single host.

Definitions from Bush et al. 1997

RADIO TELEMETRY

Adult animals were radiocollared with either AVM Instrument Company, LTD D-collars or Telonics, INC MOD-210 collars and monitored using an AVM LA12-Q Portable Telemetry Receiver and 3-element collapsible antenna. The switch from AVM to Telonics collars was necessary as many of the AVM collars failed prematurely (mean ± S.E. 106.59 ± 19.50 days, range 0-432 days, see Table 3 in Results). The goal of radio telemetry efforts was to determine social interactions among individuals, in particular, whether animals were denning or traveling together.

The topography of the study sites resulted in a high degree of error in using triangulation alone to locate study animals because the hilly, rocky terrain interfered with radio signals. Radio tracking was instead carried out by first scanning for all collared animals from several localities in a particular site, and then from a rough triangulation tracking individual animals to their actual den sites. The following characteristics of daytime den sites were recorded: type of den (e.g. rock den, tree cavity, tree branch, tree species, etc.), direction of slope, GPS coordinates, and the presence or absence of other animals in the den (Appendix II). While the error associated with triangulation was too large to reliably pinpoint animal location, triangulation was useful for determining when animals were not together. When triangulation implied that animals were together direct tracking verified or refuted the association.

PERTURBATION EXPERIMENT

From the summer of 1999 through February 2002 animals were trapped and monitored via radio telemetry in both sites. In the summer of 2001 the experimental

manipulation commenced. One site, GH, was provisioned with clumped food resources while the control site, JP, was provisioned with equal quantities of dispersed food resources. This experimental design allowed for two controls: temporal (before and after the perturbation), and spatial (experimental site vs. control site). Two large piles of corn (~11 kg) were maintained ad libitum at two sites in GH (Figure 2). These feeding stations were initially surrounded with a ring of fencing approximately 1.5 meters in diameter with gaps large enough to allow raccoons access to the corn while excluding other animals such as turkey and deer. Eventually, however, these fences were damaged by bears and subsequently removed since deer were rarely observed at the feeding stations (Figure 3). The control site was provisioned with either equal amounts of corn as GH thrown in handfuls into the forest from an ATV (e.g. one 23 kg. bag of corn would be split evenly between the two sites), or with single cans of cat food (5.5 oz.) used to bait the camera traps. In the latter case cans of cat food were also added to the feeding stations. It was necessary to use cat food in the control site because its odor aided in attracting animals to the cameras, while it was more practical to use corn in the experimental site because of its persistence. Food resources were replenished approximately once a week.

Utilization of the food resources was monitored using remote photography. CamTracker II infra red cameras were set up at each feeding station in GH generating photographic data on the numbers of animals aggregating at the food resources. Cameras were checked weekly for the duration of the experiment with film reloaded as necessary.

Figure 3: Set up of feeding stations. Camera is positioned approximately 3 meters away from the corn (Feeding Station 1 from Figure 2). Fencing was removed shortly after this photo was taken, Summer 2001.

The control site was monitored by randomly circulating 2 – 9 cameras (based on availability) throughout the site to determine group size of control animals. Cameras were set and baited with cat food to attract raccoons that were traveling or foraging normally. Cameras in JP were checked every 1-14 days. Once a camera had been triggered it was moved to another randomly selected spot off of the trapline excluding previously monitored areas. Even if a camera remained in a site for several weeks it was only baited once to prevent animals from habituating to a particular site. This setup allowed for controlling for the effect of feeding the animals yet did not perturb social structure since the control resources were unpredictable in time and space, and existed in small quantities.

STATISTICAL ANALYSES:

Paired t-tests were used to compare trap success between the two sites. Mann-Whitney U tests were used to compare group size between the sites after the perturbation from camera trap photos. Photos were scored for both the number of adult raccoons and the number of adults and cubs (Figure 4).

General Linear Model (GLM) analyses were used to compare the abundance of each type of ectoparasite before and after the perturbation. In cases where one individual was sampled repeatedly in a season the mean number of ectoparasites observed during that season was used. Fisher's exact tests were used to compare the prevalence of different types of ectoparasites between and within sites before and after the perturbation.

Unpaired t-tests were used to compare the mean number of endoparasite species per raccoon in each site before and after the perturbation. Paired t-tests were used to

compare differences in the community level prevalence of endoparasites between and within sites before and after the perturbation. Paired comparisons were between endoparasite species present in at least one of the groups being tested. In cases where one individual was sampled several times in a particular year the fecal sample results were pooled such that the maximum number of unique species were recorded to represent the parasite fauna of that animal for the year. Fisher's exact tests were used to compare differences in the prevalence of individual endoparasite species before and after the perturbation in each site, and to compare differences in the distribution of heteroxenous versus monoxenous species within each site before and after the perturbation.

Figure 4: Estimation of group size from remote photography. This photo shows two family groups plus an adult aggregating at a feeding station. Including cubs results in a group size score of 8, while excluding cubs results in a group size score of 3. Note also that the fencing did not prevent raccoons from gaining access to the corn (Feeding Station 2 from Figure 2).

RESULTS

SOCIALITY

A total of 79 individual raccoons were trapped and processed during 1,872 trap nights between summer 1999 and fall 2001 (Table 2). Similar trapping success at the two sites suggest similar population densities (Table 3). Thirty-eight adult animals were radio collared and tracked during the three years of the study (Table 4).

Radio telemetry in the years prior to the perturbation found that animals were usually solitary with the exception of mothers with cubs, and some communal denning that occurred primarily during the winter. Animals were found denning together on 6 occasions during the winter of 1999-2000 and three occasions during the winter of 2001-2002 (Table 5). The winter of 2000-2001 was plagued by technical difficulties with telemetry equipment; thus there is no good data from this season. Additionally, the deep snow packs present during the winters of 1999-2000 and 2000-2001 rendered GH inaccessible for radio telemetry work, and only a handful of animals were radiocollared in GH in each of those winters (1999-2000 n=2, 2000-2001 n=3, Table 4). A pair of females was found denning together on 4 occasions during the summer of 2001. This was the only case of radiocollared animals denning together outside of the winter months, and might be attributable to a mother-daughter association as one of the females was a reproductive adult and the other was a non-reproductive young adult. Two to four radiocollared animals occupied each communal den. All of the communal dens were similarly situated under large rocks and animals moved between specific den sites independently, with the exception of the female pair which were only found together.

TABLE 2: Summary of Trapping Effort and Success

Season	Site	# Trap Nights[1]	# New Animals	# Recaptures	# New/ #Trap Nights	# Recaps/ # Trap Nights
Summer 1999	GH	226	12	18	0.05	0.08
	JP	207	11	7	0.05	0.03
Fall 1999	GH	140	2	2	0.01	0.01
	JP	115	4	3	0.03	0.03
Summer 2000	GH	390	2	19	0.01	0.05
	JP	253	7	9	0.03	0.04
Fall 2000	GH	60	2	3	0.03	0.05
	JP	138	3	6	0.02	0.04
Summer 2001	GH	78	13	10	0.17	0.13
	JP	92	9	9	0.10	0.10
Fall 2001	GH	104	11	11	0.11	0.11
	JP	69	3	5	0.04	0.07

1 Trap night = (number of traps) x (number of nights of trapping)

TABLE 3: Paired t-tests comparing trapping success between GH and JP

Comparison	n	t value	Degrees of Freedom	*P* value
New GH vs. New JP	6	1.078	5	0.330
Recap GH vs. Recap JP	6	1.936	5	0.111
New GH vs. Recap GH	6	-0.714	5	0.507
New JP vs. Recap JP	6	-0.933	5	0.394

New=# New/# Trap Nights from Table 2, Recap=#Recaps/# Trap Nights from Table 2

TABLE 4: Summary of Radio Telemetry Monitoring

		Perturbation Experiment										
		Season(s) animal was radio-tracked										
ID	Sex	Fall 1999	Winter 1999/ 2000	Summer 2000	Fall 2000	Winter 2000/ 2001	Summer 2001	Fall 2001	Winter 2001/ 2002	# Dens Found*	# Collars worn*	Collar life span (days)*
JP 023	M	√	√	√	√					15	1	344
021	F	√	√	√						4	1	257
019	M	√	√	√						6	2	150, 45
024	M	√	√	√						0	1	262
035	F			√	√					6	1	130
037	F			√						0	1	Mortality[1]
032	F			√						3	1	26
015	M			√	√					1	1	14
033	M			√						0	1	51
018	F	√	√							1	1	98
022	M	√	√	√						2	1	179
030	M			√						0		0
034	M			√	√	√	√	√	√	3	3	415, 34, ongoing (T)
039	M				√					1	1	13
053	M						√			0		30
058	F						√			2	1	26
060	F						√			2	1	26
036	F			√	√	√	√	√	√	7	2	330, ongoing (T)
059	F						√	√	√	5	2	97+, ongoing (T)
031	M			√	√	√	√	√	√	6	3	202,65, ongoing (T)
075	F							√	√	0	1	ongoing
Total		6	6	14	7	3	7	5	5			

TABLE 4 Continued: Summary of Radio Telemetry Monitoring (*see below)

		Perturbation Experiment										
		Season(s) animal was radio-tracked										
ID Sex	Fall 1999	Winter 1999/ 2000	Summer 2000	Fall 2000	Winter 2000/ 2001		Summer 2001	Fall 2001	Winter 2001/ 2002	# Dens Found*	# Collars worn*	Collar life span (days)*
GH												
028	M			√						0	1	0
029	F			√						1	1	60
027	F			√						0	1	0
008	M			√	√					0	2	0, 197
026	F	√	√	√	√					8	1	348
007	M			√	√					15	1	75
006	M			√	√	√	√			1	2	0, 432
045	F						√			1	1	24
044	F						√			4		68
047	M						√			0	1	0
048	M						√	√	√	0	3	0,14, ongoing (T)
003	F			√	√	√	√	√	√	11	3	161+, 0, ongoing (T)
050	M						√	√	√	0	2	1, ongoing (T)
005	F	√	√	√	√	√	√	√	√	28	3	51, 145, ongoing
070	M							√	√	0	1	ongoing (T)
068	F							√	√	1	1	ongoing (T)
052	M							√	√	0	1	Mortality[2]
Total		2	2	9	6	3	8	7	7			

TABLE 4 Continued: Summary of Radio Telemetry Monitoring

Dens found: Number of times an animal was tracked to its daytime resting site.

Collars worn: Number of different radiocollars worn by an animal during the course of the study.

Collar life span: Number of days between first and last transmission picked up from a collar (collars were monitored for several months after the last registered transmission). Numbers separated by commas represent number of days for each collar worn. Numbers followed by a plus sign indicate that collars were operable for at least as many days reported (often these were collars removed prematurely for reasons other than collar operating condition). Ongoing: collars still in use at time of writing.

Mortality: animal died during the course of the study. 1-accidental trapping (study-related) mortality. 2-road kill on 9W

All collars are made by AVM Instrument Company unless denoted by (T) for Telonics, INC collars which were used during the end of the study.

TABLE 5: Summary of communal denning.

		Denning Group	
Site	Date	Males (ID)	Females (ID)
JP	11/8/99	023, 022	---
JP	11/13/99	024	018
JP	12/30/99	019, 022	021
JP	1/5/00	023, 720, 120	021
JP	1/6/00	023	021
JP	1/8/00	023, 022	---
JP	7/19/01	---	058, 060
JP	7/20/01	---	058, 060
JP	8/7/01	---	058, 060
JP	8/9/01	---	058, 060
GH	12/15/01	070	005
JP	1/12/02	034	059
JP	1/14/02	034	059

The perturbation experiment did not result in extended or summer communal denning, but it did result in animals aggregating at the food resources. During peak usage the resources at the feeding stations would be consumed within one week (e.g. early summer). An acorn masting event occurred during fall 2001, where acorn production increased from an estimated 4,910 acorns per acre in 2000, to 74,921 acorns per acre in 2001 (Brady 2002). During the acorn mast raccoons ceased using the corn resources, presumably since the abundant acorns were a higher quality or more accessible resource. Corn usage resumed to peak level during winter and spring 2002.

Remote photography results showed that the mean group size of animals aggregating at food resources in GH was significantly larger than the mean group size of unperturbed animals in JP regardless of whether cubs were excluded or included in the estimation of group size (Figure 5). Excluding cubs, animals in JP were always solitary, while in GH the range of animals per photo was 1-3 (JP mean ± S.E. 1 ± 0, n=37, GH mean ± S.E. 1.25 ± 0.018 n= 775, P=0.001; Figure 6). Including cubs, the range of group sizes in JP was 1-5, and in GH was 1-8 (JP mean ± S.E. 1.189 ± 0.122 n=37, GH mean ± S.E. 1.748 ± 0.043 n=794, P=0.000; Figure 6). Although there were more cameras operating in JP, fewer photos were obtained than GH since the constant movement of the cameras reduced the number of raccoon visits, and a large amount of film was spent on non-target wildlife attracted by the cat food.

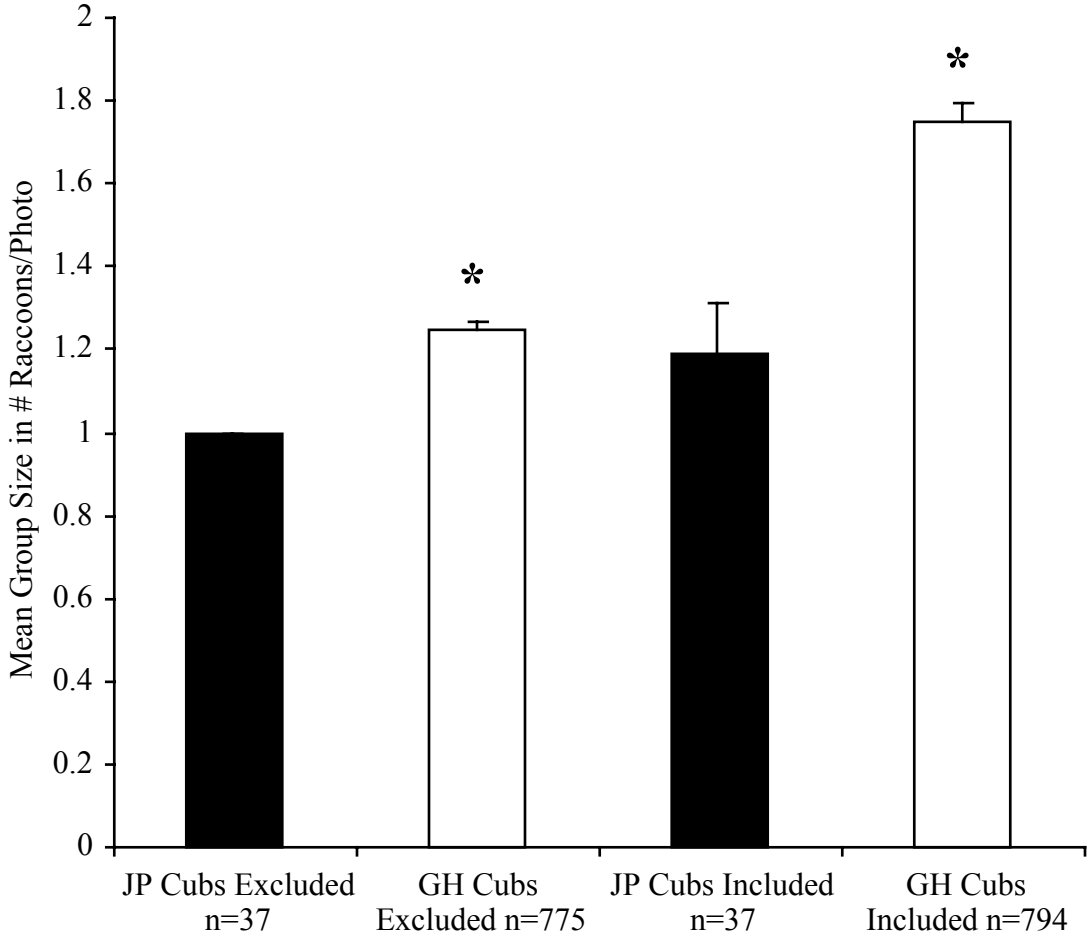

Figure 5: Estimation of group size from remote photography. Group size was estimated as the number of adult raccoons per photo (excluding cubs), and the number of raccoons per photo (including cubs). Mean group size was higher in the experimental site regardless of method of estimation. * Denotes significance at $P<0.01$

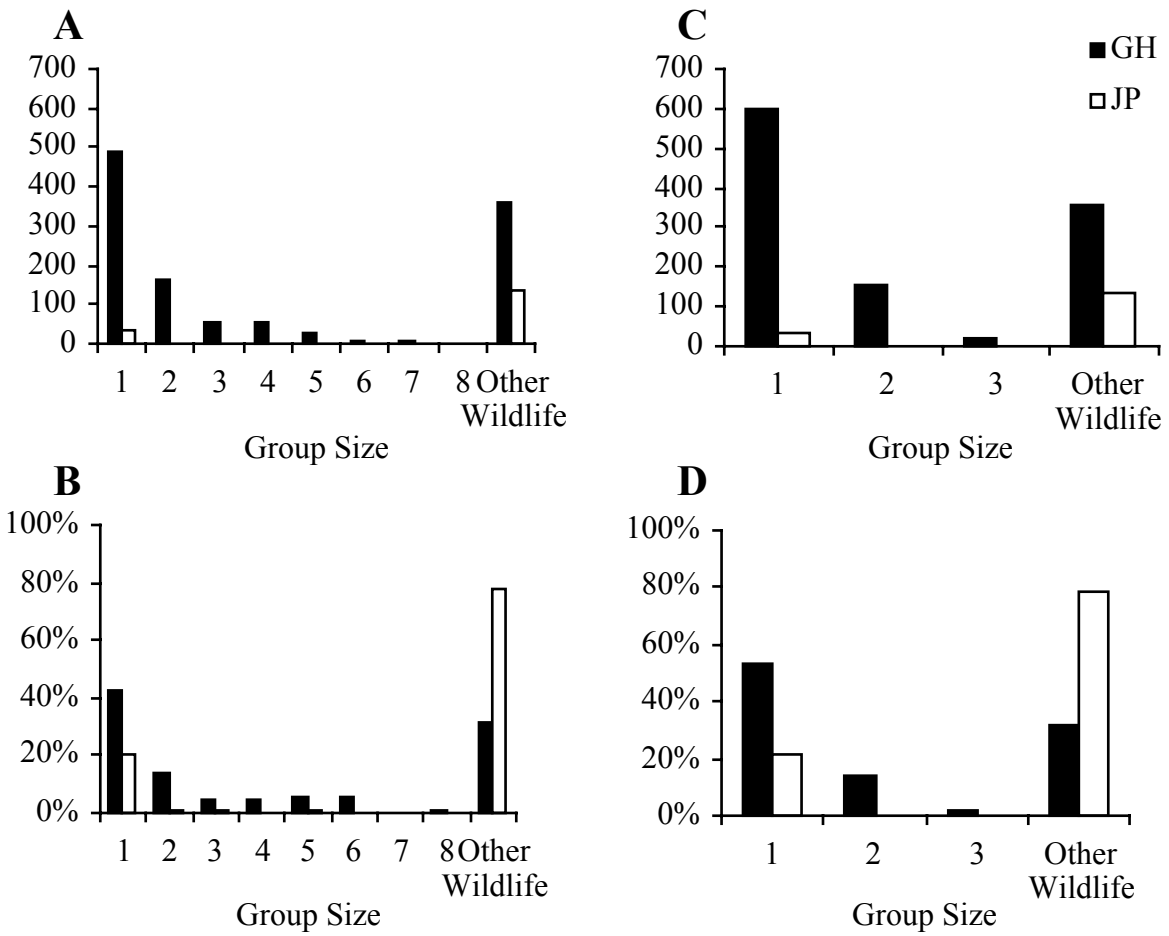

FIGURE 6: Remote photography results for the estimation of group size after the perturbation. Figures 6A and 6B show the distribution of group sizes if cubs are included in the estimation. Figures 6C and 6D show the distribution of group sizes if cubs are excluded from the estimation. In both cases, the mean group size is significantly higher in GH in response to the perturbation compared to JP, the control site.

ECTOPARASITES:

The mean abundance of lice increased after the perturbation in GH (GH n=25, JP n=17, *P*=0.029; Figure 7). There were no significant changes in the mean abundance of fleas or replete ticks (Figure 7). Mean tick abundance, measured as the average number of replete + non-replete ticks per host, was significantly higher before the perturbation in both sites, however this effect is due to a significant difference in the numbers of non-replete ticks alone (Figure 7). Numbers of non-replete ticks were significantly higher in JP than in GH before and after the perturbation, and higher in both sites during the first two years of the study (Before: JP n=28, GH n=27, *P*=0.001; After: JP n=18, GH n= 26, *P*=0.004; Figure 7). A significant seasonal effect influenced numbers of non-replete ticks, with intensities highest in the summer (Before: JP n=28, GH n=27, *P*=0.000; After: JP n=18, GH n= 26, *P*=0.000), but was not significant for the other ectoparasites.

The prevalence of replete ticks was significantly higher in GH before the perturbation compared to after (GH Before prevalence=55.6%, n=27; GH After prevalence=23.1%, n=26, *P*=0.024; Table 6). No significant differences were found between the prevalence of any other ectoparasites before or after the perturbation in either site (Table 6).

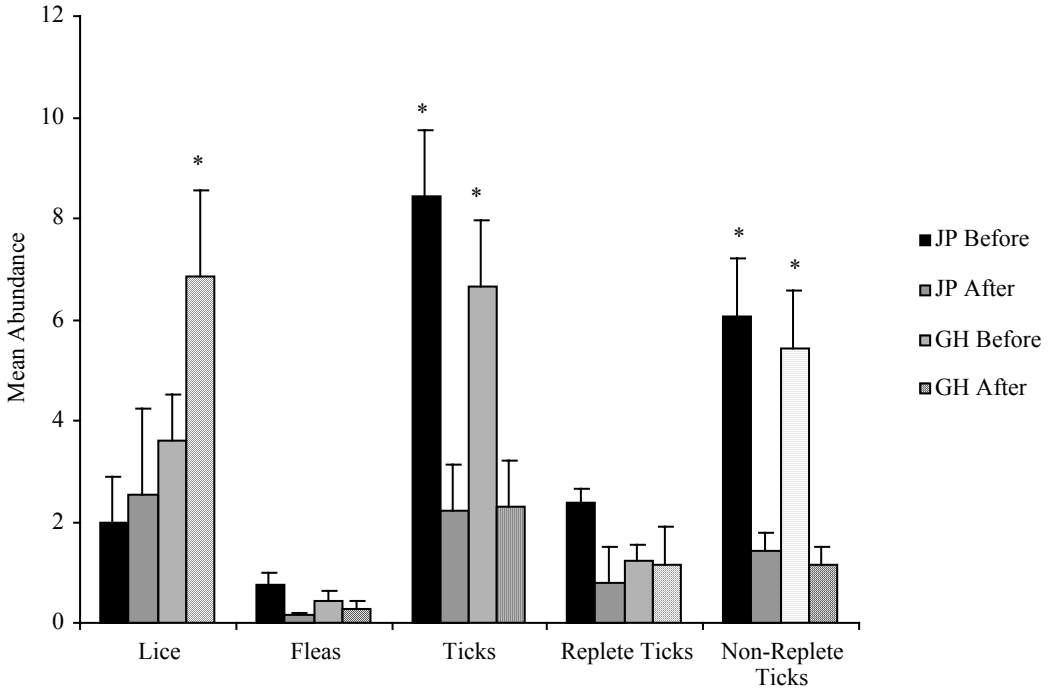

FIGURE 7: Mean abundance (average number of ectoparasites per host) in each site before and after the perturbation. Mean abundance of lice was significantly higher in response to the perturbation compared to both controls. Numbers of Ticks (Replete plus Non-Replete) were significantly higher in the years prior to the perturbation, due to the contribution from Non-Replete Ticks. * Denotes significance at the P=0.05 level.

TABLE 6: Prevalence of ectoparasites within and between sites before and after the perturbation

Ectoparasite	Site	Prevalence[1]	Prevalence[2]	JP Before vs. JP After *P* value	GH Before vs. GH After *P* value	JP After vs. GH After *P* value
Lice	JP Before	14/28	50%	>0.999	0.360	0.178
	JP After	7/15	46.7%			
	GH Before	12/21	57.1%			
	GH After	18/25	72%			
Fleas	JP Before	9/28	32.1%	0.719	0.711	0.686
	JP After	3/14	21.4%			
	GH Before	5/21	23.8%			
	GH After	4/25	16%			
Ticks	JP Before	17/28	60.7%	0.512	0.063	0.318
	JP After	11/15	73.3%			
	GH Before	13/25	52%			
	GH After	17/21	80.9%			
Replete Ticks	JP Before	15/30	50%	>0.999	0.024*	0.098
	JP After	8/16	50%			
	GH Before	15/27	55.6%			
	GH After	6/26	23.1%			
Non-Replete Ticks	JP Before	20/30	66.7%	0.534	0.166	0.758
	JP After	9/16	56.3%			
	GH Before	19/27	70.4%			
	GH After	13/26	50%			

1 Prevalence = (number of infected hosts)/(total number of hosts examined)

2 Prevalence = % hosts infected

* Denotes significance at the *P*=0.05 level

ENDOPARASITES:

Eighty-eight scats were analyzed from 55 individuals, yielding 13 species of helminths and protozoans (Table 7). A total of 11 endoparasite species were identified in GH and 12 were identified in JP. The two sites shared ten species, but *Capillaria aerophilia* and *Alaria sp.* were absent from GH, and *Eurytrema procyonis* was absent from JP; these species were found at low prevalence when they did occur. Unidentified trematodes of the order Digenea were found in both sites.

Due to small sample sizes in 1999 and 2000, these years were pooled to assess endoparasite prevalence and community richness before the experiment. Plotting the mean number of endoparasite species found with the addition of each sample to the pool, (generated from plotting the relationship between sample order and number of endoparasite species for10 random iterations of sample order), suggests that endoparasite sampling over the three years of the study and both sites combined accounts for the majority of endoparasite species present in Black Rock Forest (Figure 8). The degree of sampling in either site similarly appears to be representative of the majority of the endoparasite fauna (Figure 9). As these curves plateau it suggests that additional samples will not result in the discovery of large numbers of novel endoparasite species (Colwell and Coddington 1994). The equation for the best-fit line in Figure 8 is:

$$y=3.11(\ln x) + 0.65$$

This equation can be used to estimate species diversity. For example, if a total of 200 samples were collected, the number of endoparasite species found is estimated to be 17 species. Thus, more than doubling sampling effort from 88 to 200 samples would only

TABLE 7: Endoparasite life history.

Parasite Species	Infection site	Life cycle[1]	Transmission mode	Intermediate hosts
Helminths				
Trematodes				
Alaria sp.	Intestine	heteroxenous	Ingestion of intermediate host	Snails, amphibian larvae
Flukes(Order Digenea)		heteroxenous	Ingestion of free-living stage or intermediate host	Snails
Eurytrema procyonis	Pancreas	heteroxenous	Ingestion of intermediate host	Snails
Nematodes				
Capillaria plica	Bladder, Urinary Tract	heteroxenous	Ingestion of intermediate host	Earthworms
Capillaria procyonis	Alimentary tract	heteroxenous	Ingestion of intermediate host	Probably Earthworms
Capillaria putorii	Intestine, Stomach	heteroxenous	Ingestion of intermediate host	Probably Earthworms
Crenosoma sp.	Lungs	heteroxenous	Ingestion of intermediate host	Slugs
Baylisascaris procyonis	Intestine	monoxenous	Fecal-oral contact	
Capillaria aerophilia	Bronchi	monoxenous	Fecal-oral contact	
Placoconus lotoris	Intestine	monoxenous	Ingestion or transmammary	
Strongyloides sp.	Small intestine	monoxenous	Free-living larvae penetrate host skin or transmammary	
Acanthocephalans				
Macracanthorhynchus ingens	Intestines	heteroxenous	Ingestion of intermediate host	Millipedes
Protozoans				
Coccidians				
Eimeria nutalli	Small intestine	monoxenous	Fecal-oral contact	
Eimeria procyonis	Small intestine	monoxenous	Fecal-oral contact	

Data from: Chandler 1942, Pence and Meinzer 1979, Bafundo et al. 1980, Butterworth and Beverly-Burton 1981, Kazacos 1989, Bowman 1995.

1-Heteroxenous: indirect life cycle, parasite requires several hosts to complete development

1-Monoxenous: direct life cycle, parasite only requires one host to complete development

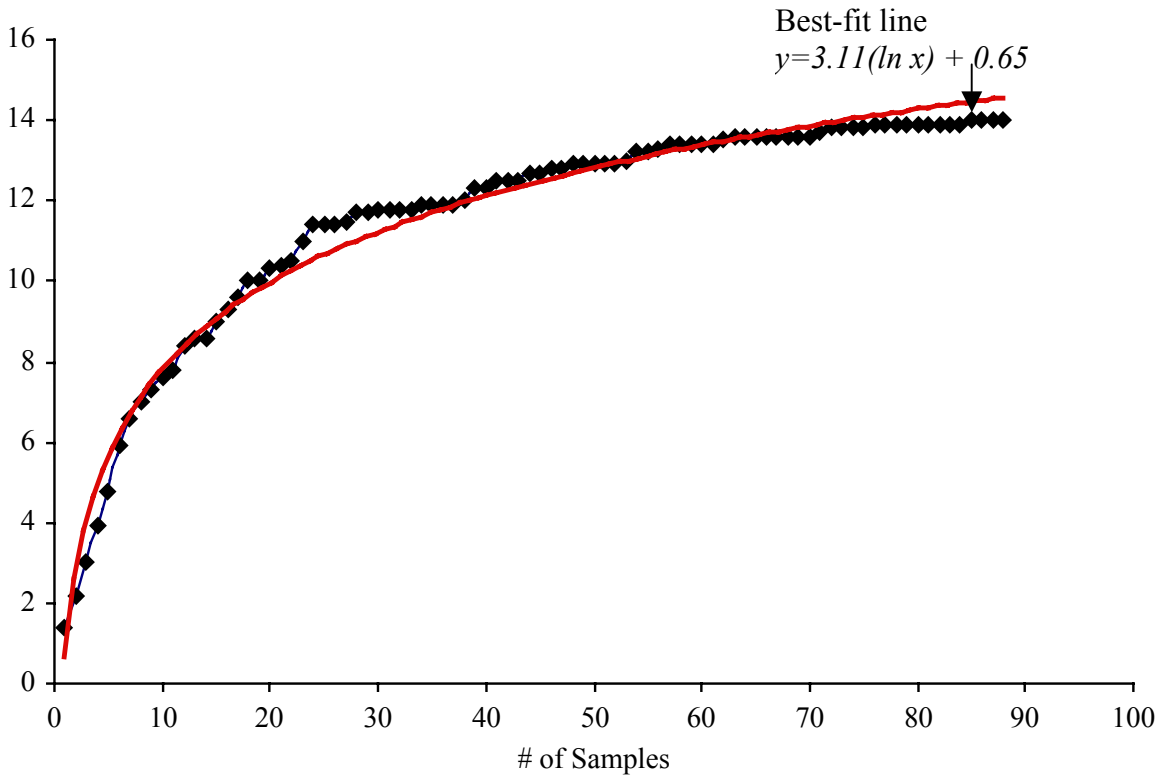

FIGURE 8: Species accumulation curve for endoparasite sampling in Black Rock Forest. Each point represents the mean number of species found as each new sample is added to the pool for 10 randomizations of sample order

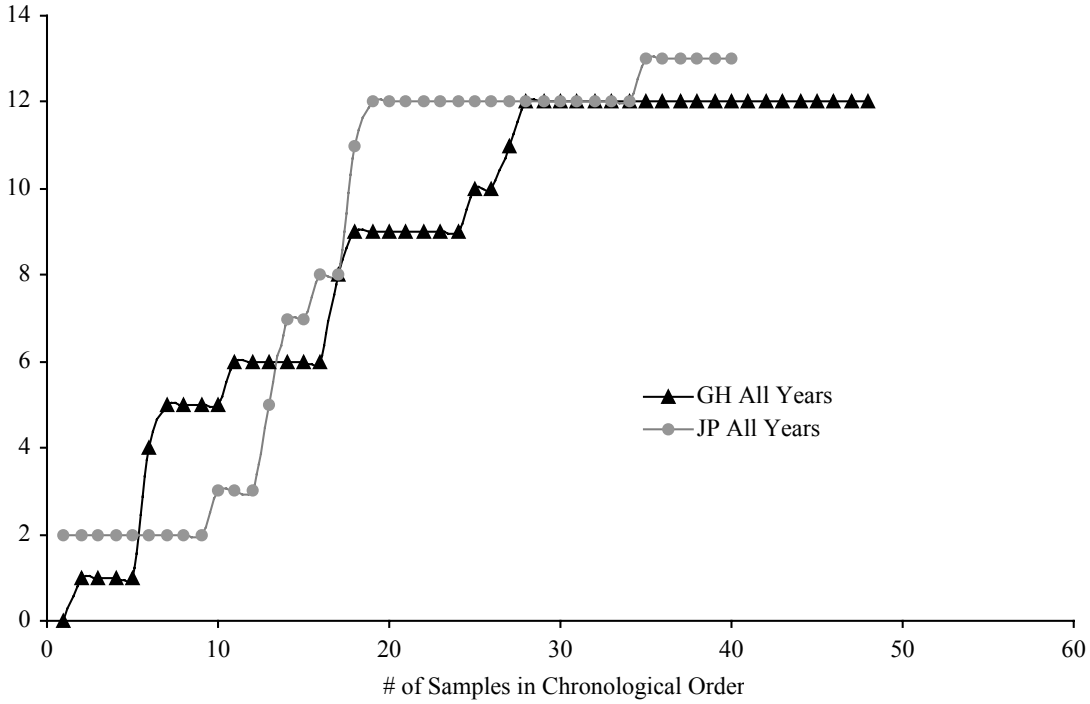

FIGURE 9: Sampling effort in GH and JP, all years combined. The number of species found as each new sample is added to the pool is plotted in the order that samples were collected.

increase endoparasite diversity by a few species which probably exist at very low prevalence anyway.

Individual raccoons harbored 0-6 endoparasite species (infracommunity size censu Bush et al. 1997, Table 2) (Figures 10, 11). Since there was no significant difference in mean number of endoparasite species per raccoon in JP between years, these results were pooled (JP Before + JP After = JP All) for comparisons with the experimental site (JP Before mean ± S.E. 1.211 ± 0.402 n=19, JP After mean ± S.E. 2.154 ± 0.317 n=13, *P*=0.099, Table 8). The mean number of endoparasite species was significantly higher in GH after the perturbation compared to both controls (GH Before mean ± S.E. 1.067 ± 0.358 n=15, GH After mean ± S.E. 3.056 ± 0.446 n=18 P=0.002; JP All mean ± S.E. 1.594 ± 0.280, GH After mean ± S.E. 3.056 ± 0.446 n=18 *P*=0.005; Table 8, Figure 12).

Since there was no significant difference in community level endoparasite prevalence within JP between years these results were pooled (JP Before + JP After = JP All) for comparisons to the experimental site (JP Before vs. JP After *P*=0.123; Figure 13, Table 9). Endoparasite prevalence at the community level was not significantly different between the two controls (GH Before vs. JP All *P*=0.287; Figure 14, Table 9). Endoparasite prevalence in GH was significantly higher after the perturbation compared to controls (GH Before vs. GH After *P*=0.007; Figure 15, Table 9; GH After vs. JP All *P*=0.008; Figure 16, Table 9).

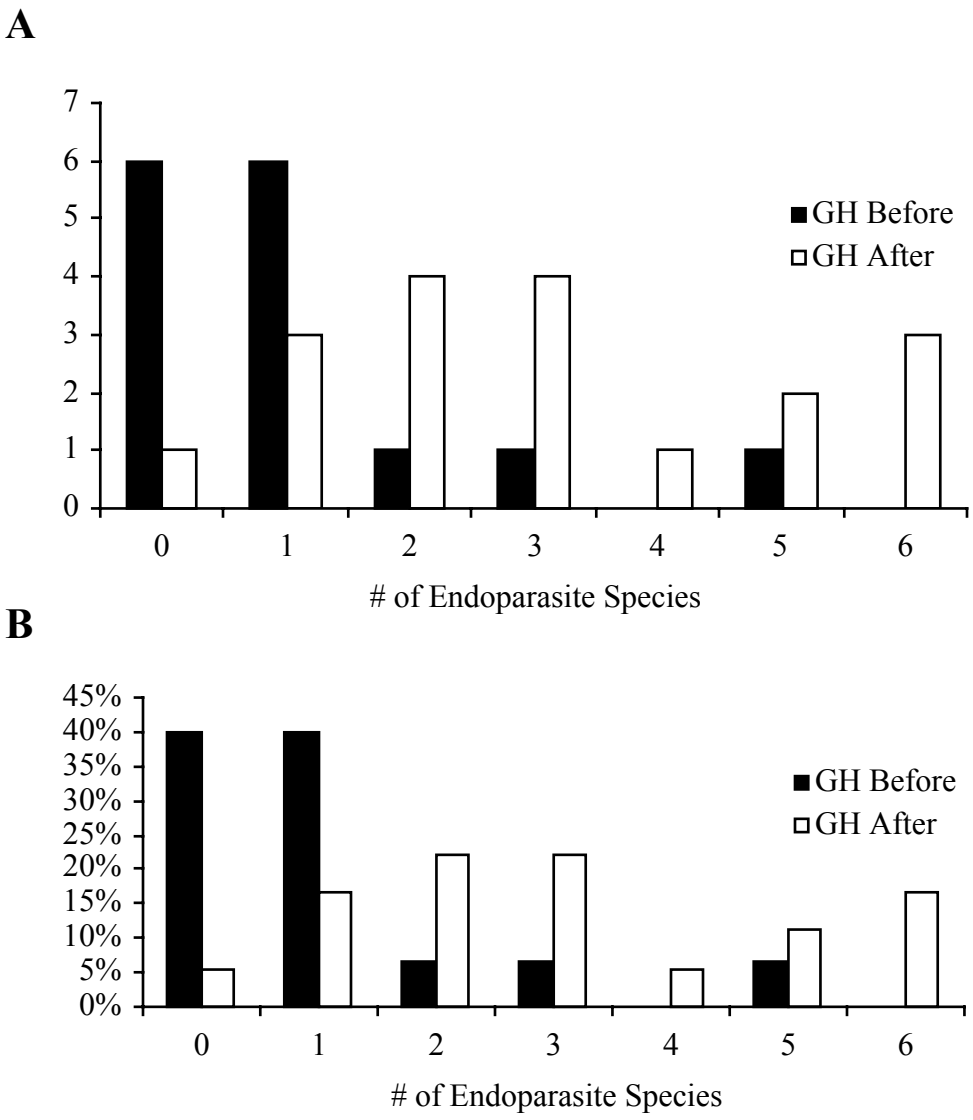

FIGURE 10: Endoparasite diversity within hosts in GH before and after perturbation, shown as A) the number of raccoons infected with 0-6 parasite species and B) the percentage of raccoons in the population infected with 0-6 parasite species.

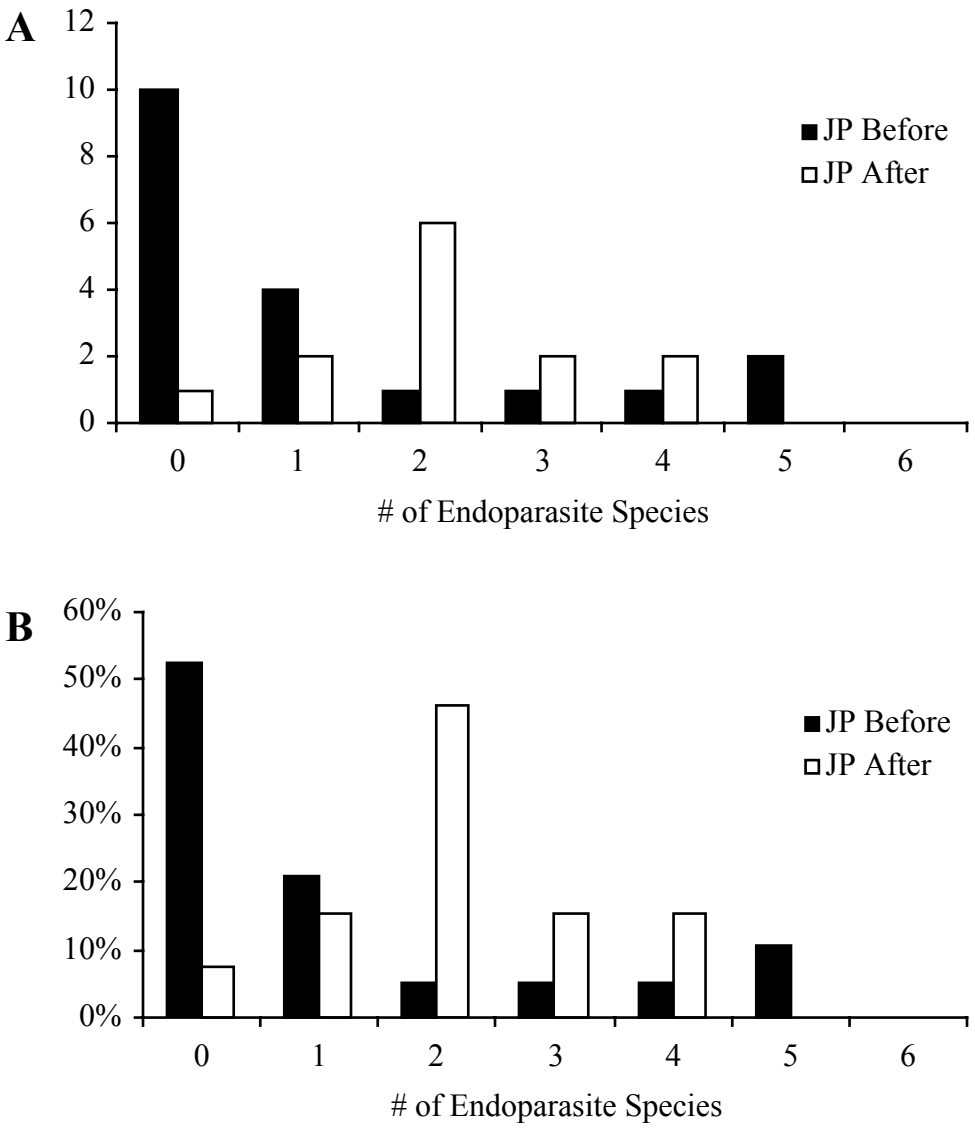

FIGURE 11: Endoparasite diversity within hosts in JP before and after perturbation, shown as A) the number of raccoons infected with 0-6 parasite species and B) the percentage of raccoons in the population infected with 0-6 parasite species.

TABLE 8: Unpaired t-tests comparing mean number of endoparasite species per raccoon

Comparison	Degrees of Freedom	t-value	*P* value
JP Before vs. JP After	30	1.705	0.099
GH Before vs. JP All	45	-1.105	0.275
GH Before vs. GH After	31	3.379	0.002*
JP All vs. GH After	48	2.919	0.005*

* Denotes significance at the $P<0.01$ level

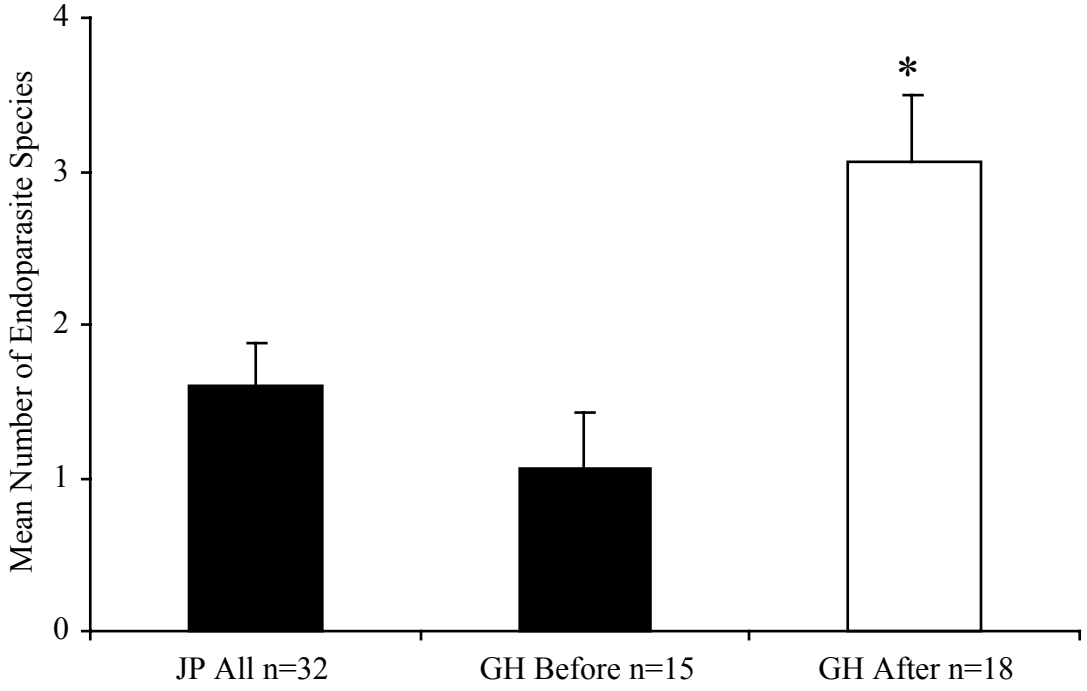

FIGURE 12: Mean number of endoparasite species per raccoon in each site before and after the perturbation. Endoparasite diversity was highest within hosts in GH in response to the perturbation. * Denotes significance at the $P<0.01$ level.

TABLE 9: Paired t-tests comparing endoparasite prevalence at the community level

Comparison	n	t value	Degrees of Freedom	*P* value
JP Before vs. JP After	13	1.664	12	0.123
GH Before vs. JP All	12	1.118	11	0.287
GH Before vs. GH After	12	-3.319	11	0.007
GH After vs. JP All	14	3.097	13	0.008

Paired comparisons were between endoparasite species present in at least one of the groups.
n=Number of endoparasite species compared

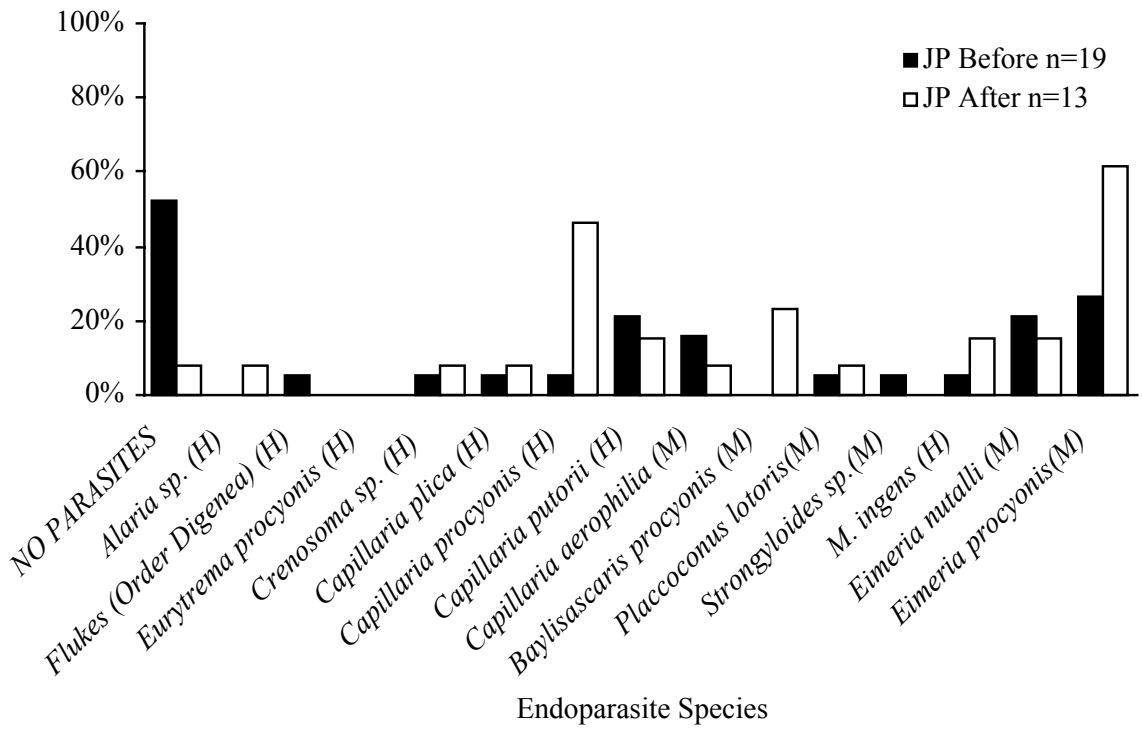

FIGURE 13: Endoparasite prevalence in JP before and after the perturbation. There are no significant differences in endoparasite prevalence between the years. Parasite life cycle is noted in parentheses as either (H) heteroxenous or (M) monoxenous.

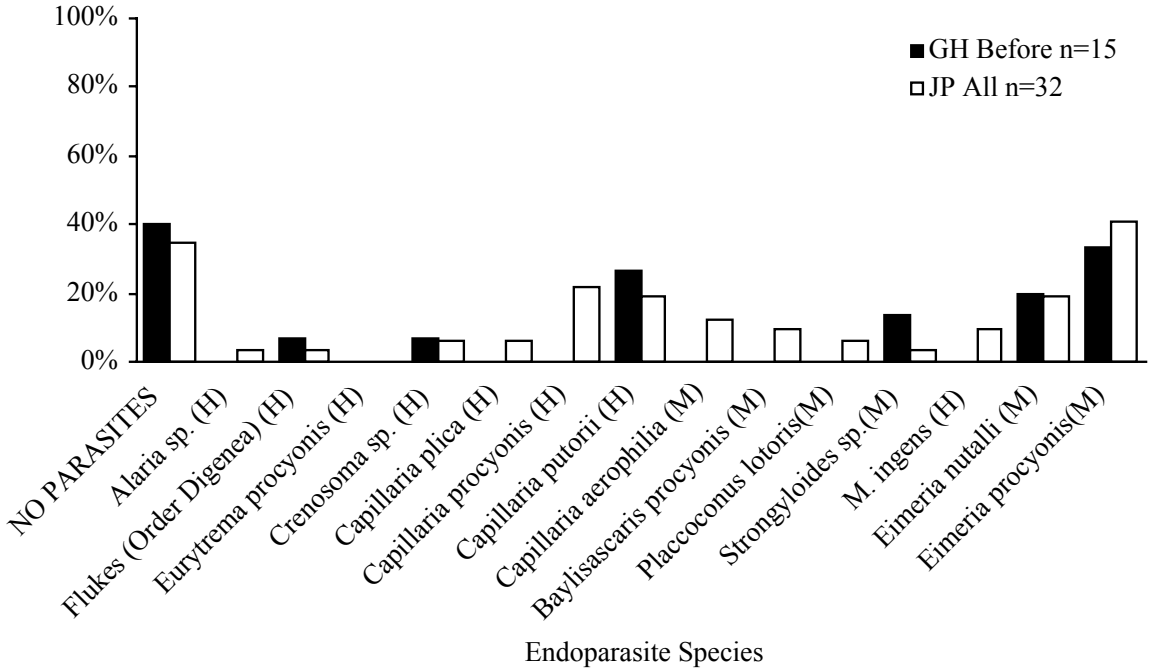

FIGURE 14: Endoparasite prevalence in the temporal and spatial controls. There are no significant differences in endoparasite prevalence between the controls. Parasite life cycle is noted in parentheses as either (H) heteroxenous or (M) monoxenous.

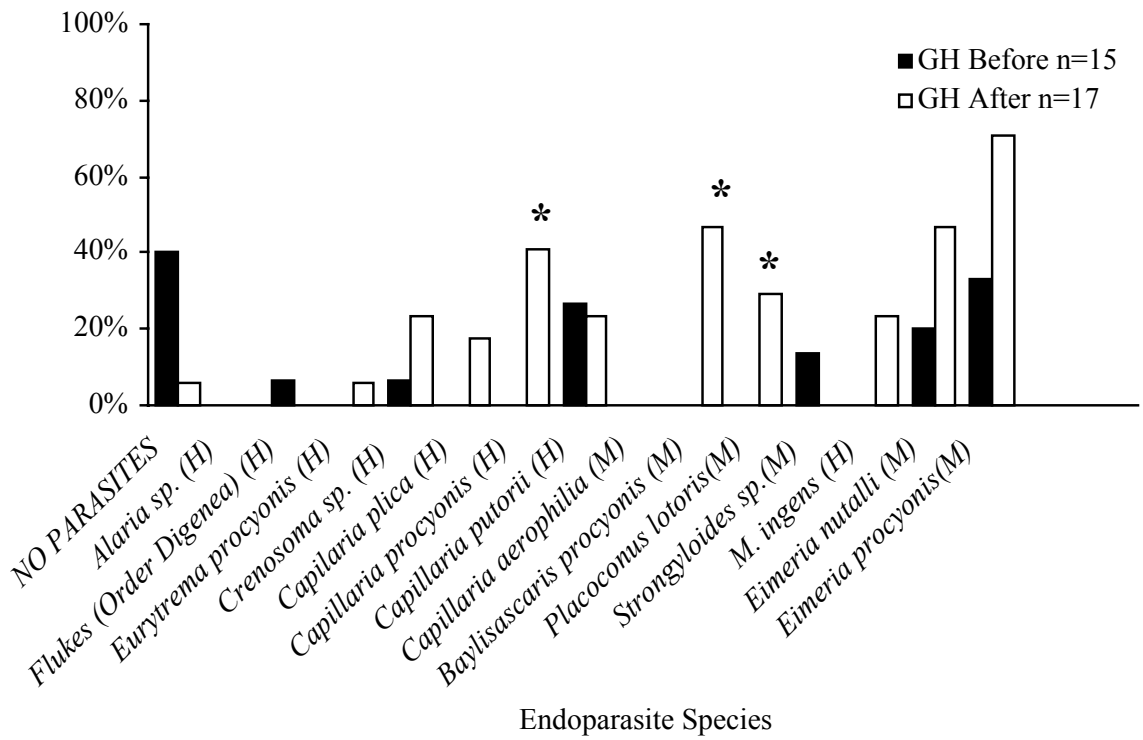

FIGURE 15: Endoparasite prevalence in GH before and after the perturbation. Three parasite species: *Capillaria procyonis, Baylisascaris procyonis,* and *Placcoconus lotoris* significantly increased in prevalence in response to the perturbation. At the community level, the prevalence of parasites overall increased in response to the perturbation.
* Denotes significance at the *P*=0.05 level. Parasite life cycle is noted in parentheses as either (H) heteroxenous or (M) monoxenous.

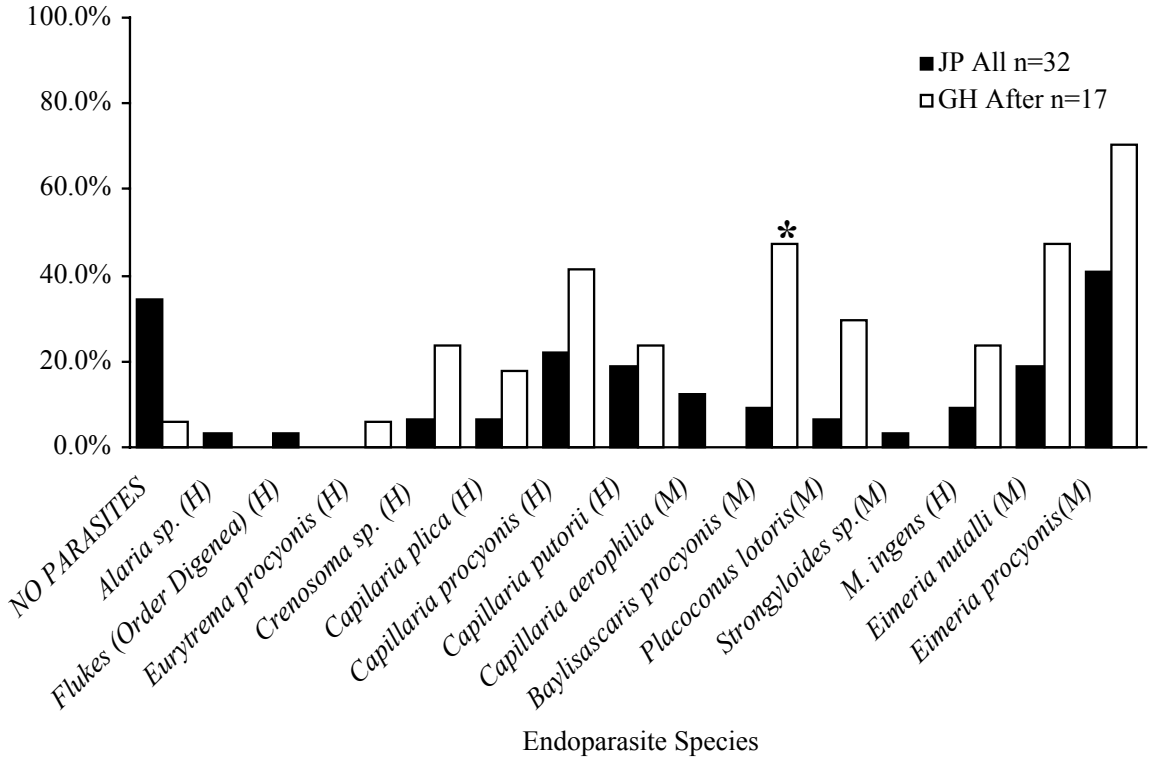

FIGURE 16: Endoparasite prevalence in the experimental site after perturbation compared to the control site. The prevalence of *Baylisascaris procyonis* increased significantly in the experimental site. Overall, the prevalence of endoparasites at the community level was higher in the experimental site after the perturbation compared to the control site. * Denotes significance at the *P*=0.05 level. Parasite life cycle is noted in parentheses as either (H) heteroxenous or (M) monoxenous.

Among individual endoparasite species, three where significantly more prevalent in GH following the experimental perturbation compared to before, and one was significantly more prevalent in GH following the experimental perturbation compared to the control site (Table 10). The prevalences of *Capillaria procyonis* and *Placcoconus lotoris* were significantly higher after the perturbation in GH compared to before (P=0.009 and 0.049, respectively; Table 11). The prevalence of *Baylisascaris procyonis* was significantly higher in GH after the perturbation compared to both controls (GH After vs. GH Before P =0.004, GH After vs. JP All P =0.01; Table 11). No other differences in individual species' prevalence were significant (Table 11).

The number of species and distribution of heteroxenous versus monoxenous species was the same for JP across years but changed after the perturbation in GH; however this difference was not significant (GH Before vs. GH After P>0.999; Table 12).

TABLE 10: Number of endoparasite species that were at a higher prevalence in each comparison. Numbers in parentheses indicate the number of species that occurred at a significantly higher prevalence.

	# Species at higher prevalence		# Species at higher prevalence
JP Before	5	JP After	8
GH Before	5	JP All	8
GH Before	3	GH After	8 (3)
JP All	3	GH After	10 (1)

TABLE 11: Comparison of individual endoparasite species prevalence between experimental and control treatments

Endoparasite Species	Site	Prevalence[1]:	Prevalence[2]:	GH Before vs. GH After *p* value	GH After vs. JP All *p* value
Alaria sp.	GH Before	0/15	0.0%		
	GH After	0/18	0.0%	---	>0.999
	JP All	1/32	3.1%		
Order Digenea	GH Before	1/15	6.7%		
	GH After	0/18	0.0%	0.456	>0.999
	JP All	1/32	3.1%		
Eurytrema procyonis	GH Before	0/15	0.0%		
	GH After	1/18	5.6%	>0.999	0.360
	JP All	0/32	0.0%		
Crenosoma sp.	GH Before	1/15	6.7%		
	GH After	4/18	22.2%	0.346	0.171
	JP All	2/32	6.3%		
Capillaria plica	GH Before	0/15	0.0%		
	GH After	3/18	16.7%	0.233	0.336
	JP All	2/32	6.3%		
Capillaria procyonis	GH Before	0/15	0.0%		
	GH After	7/18	38.9%	0.009*	0.325
	JP All	7/32	21.9%		
Capillaria putorii	GH Before	4/15	26.7%		
	GH After	4/18	22.2%	0.653	>0.999
	JP All	6/32	18.8%		
Capillaria aerophilia	GH Before	0/15	0.0%		
	GH After	1/18	5.6%	>0.999	0.642
	JP All	4/32	12.5%		
Baylisascaris procyonis	GH Before	0/15	0.0%		
	GH After	8/18	44.4%	0.004*	0.010*
	JP All	3/32	9.4%		
Placcoconus lotoris	GH Before	0/15	0.0%		
	GH After	5/18	27.8%	0.049*	0.083
	JP All	2/32	6.3%		
Strongyloides sp.	GH Before	2/15	13.3%		
	GH After	0/18	0.0%	0.199	>0.999
	JP All	1/32	3.1%		
Macracanthorhynchus ingens	GH Before	0/15	0.0%		
	GH After	4/18	22.2%	0.108	0.235
	JP All	3/32	9.4%		
Eimeria nutalli	GH Before	3/15	20.0%		
	GH After	7/18	38.9%	0.283	0.180
	JP All	6/32	18.8%		
Eimeria procyonis	GH Before	5/15	33.3%		
	GH After	11/18	61.1%	0.166	0.240
	JP All	13/32	40.6%		

1 Prevalence = (number of infected hosts)/(total number of hosts examined), 2 Prevalence = % hosts infected, * denotes significance at the *P*= 0.05 level for Fisher's exact tests.

TABLE 12: Numbers of heteroxenous and monoxenous species in each site before and after the perturbation

	GH Before	GH After	JP Before	JP After
# of Heteroxenous species	3	6	6	6
# of Monoxenous species	3	4	5	5
Total	6	10	11	11

DISCUSSION

The results of this study support the idea that parasite community structure is influenced by host social structure. Community level shifts in parasitism were observed in response to perturbation of raccoons by provisioning with clumped resources, which increased social interaction, and consequently contact rates, between hosts. This shift in community structure was a function of slight increases in many species, and strong increases in particular species. The shift occurred among both ectoparasites and endoparasites, and among species transmitted through both direct and indirect pathways.

ECTOPARASITISM

Most previous work exploring the relationship between host sociality and parasitism has focused on ectoparasites rather than endoparasites, as the transmission of contagious ectoparasites is thought to be more strongly determined by proximity among hosts (Moller et al. 1993). For the three ectoparasites studied here, positive, negative and neutral correlations were found between increased contact rate and the abundance of lice, ticks, and fleas, respectively. Lice (positively correlated with increased sociality) fit the host-proximity contact model best, as they are highly species specific and spend their entire life cycle on the host; thus their primary transmission route is dependent upon direct contact between hosts (Bowman 1995). Fleas, which showed no correlation with increased sociality, occurred at both low prevalence and low intensity relative to the other ectoparasites. Fleas have a multi-stage life history with several larval stages that do not live on the host, and adult stages display little tendency to move between hosts. Thus

transmission of fleas is not highly dependent upon direct contact between hosts but rather contact with resting sites where flea eggs and larvae have been developing. Thus the habitat of the flea is composed of a particular host and its particular burrow or nest (Krasnov et al. 2002). Since the raccoons in this study changed den sites often and rarely shared dens, contact with infected resting sites was rare. Since a shift in flea abundance and prevalence was not observed, it seems that social behaviors which merely increase contact with shared feeding sites is not sufficient to alter flea transmission and infection among hosts.

The observed decreases in tick prevalence and abundance in the experimental years of the study may be interpreted in two ways: either increased sociality decreased tick infection through allogrooming, or tick population dynamics are largely independent of raccoon sociality. Ticks can be removed by auto or allogrooming by hosts. Since the ease with which an ectoparasite can be removed is related to the ectoparasite's size, the efficacy of removing ectoparasites through grooming in decreasing order is replete ticks, non-replete ticks, fleas, and then lice. Presumably, the latter two ectoparasites are too small (<5 mm) to be effectively removed by raccoon grooming. The prevalence of replete ticks (the class of ectoparasites most easily removed by grooming) was significantly lower in the experimental site post perturbation (GH Before prevalence 55.6%, GH After prevalence 23.1%, P=0.024, Table 6). Thus fewer individuals were infected by engorged ticks, which may be evidence for grooming between hosts aggregating at the feeding stations. A similar conclusion was drawn in a previous study on coatis, *Nasua narica*, close relatives of raccoons, where solitary males had a higher

prevalence of replete tick infection than group-living females due to allogrooming within groups (Gompper in press).

However, coatis have a more complex social structure than raccoons, and allogrooming has been well-documented (e.g. Gompper 1996), whereas raccoons are largely considered solitary and allogrooming has not been directly reported. Some of the raccoons that were ear-tagged with large plastic tags were recaptured with chewing damage to their ear-tags, however, the observed decrease in replete tick prevalence is, at best, an indirect indicator of allogrooming. While the results for tick prevalence suggest the possibility of allogrooming among raccoons, the results for tick abundance do not. The decrease in abundance was only observed in non-replete ticks, not in replete ticks which are presumably easier to remove through grooming. Further, the decrease in tick abundance was similar across both the experimental and control sites (Figure 7). If decreased tick abundance is due to grooming, we would not expect to see a decline in tick abundance in the control site where animals are solitary. An alternative explanation is that tick population dynamics are fluctuating largely independently of raccoon social interactions, such that the experimental portion of the study happened to be carried out during a low tick year.

Ticks are relatively free-ranging generalists compared to lice and fleas, thus they feed on and move actively between a variety of hosts, and are not directly transmitted among individuals. Additionally, tick population cycles have been observed to be associated with the timing of pulsed resources such as acorn masting events, which influence populations of rodent hosts in a cyclical fashion (Jones et al. 1988). It is therefore possible that tick population dynamics are responding to variables other than

raccoon sociality, such that 1999 and 2000 happened to be years of higher tick abundance irrespective of the experimental perturbation. Rogers et al. (1999) observed a similar relationship between tuberculosis in badgers, another facultatively social carnivore, where tuberculosis prevalence showed cyclical oscillations independent of badger group size. Thus, transmission dynamics may help explain the differences observed for lice infection, while the case for flea and tick infection is less clear.

ENDOPARASITISM

A more complex response was observed in the prevalence of endoparasites. Roughly equal numbers of monoxenous and heteroxenous life cycle endoparasites were compared, and no significant differences were observed in the numbers of direct versus indirect parasite species in each site in response to the perturbation. For the three endoparasite species that showed significant increases in prevalence before and after the perturbation in the experimental site, one was indirect with infection through ingestion of intermediate earthworm hosts (*Capillaria procyonis*), one was direct with infection through ingestion of the parasite or vertical transmammary transmission (*Placoconus lotoris*), and the other was direct with infection through fecal-oral contact (*Baylisascaris procyonis*). Thus the endoparasite results of this study do not support the hypothesis that direct transmission or monoxenous parasites are more influenced by host sociality than indirect transmission or heteroxenous parasites. However, the life history characteristics of these endoparasites are not well known, such that alternate transmission pathways may be viable. A better understanding of the ecology of these parasites in relation to raccoon hosts would perhaps clarify these relationships.

Endoparasite diversity was higher in the experimental years, and while this may be partially attributable to increased sampling in that year, the overall prevalence of parasites at the community level increased in response to the perturbation compared to both the temporal and spatial controls. Thus endoparasite species either increased or maintained prevalence in response to increased spatial overlap among hosts. No significant decreases in prevalence were observed for any endoparasite in response to the perturbation, although some low prevalence parasites were only detected in the early years or in only one site. Therefore endoparasitism is positively correlated with increased social interaction among hosts.

Small sample size may have limited the power of some of the statistical analyses between the before and after years since sampling was much more thorough in the experimental year. Low sampling in the before years may result in missing endoparasite species present in the population. Nonetheless, the temporal control is still informative, and is further bolstered by data from the spatial control.

The analyses conducted here assume independence of infection between the different parasite species. Individual raccoons harbored as many as 6 different endoparasite species. Such multiple infections may not be independent within an individual since physiological, immunological, or ecological factors may result in positive or negative associations between parasite species. For example, if two parasite species utilize a similar transmission route such as fecal-oral contact, than any host behavior that increases fecal-oral contact may similarly increase infection by both parasites (Howard et al. 2001). Additionally, immunocompromised individuals may be more susceptible to multiple infections (Cohen 1973, Molineaux et al. 1980), and

parasites may compete with each other within the host (Richie 1988, Koppenhöfer et al. 1995, Perlman and Jaenike 2001).

Most of the endoparasites identified in this study can be characterized as either heteroxenous with transmission through ingestion of an invertebrate intermediate host (usually snails or earthworms), or as monoxenous with transmission through fecal-oral contact. Thus the potential exists for positive associations between infections based on shared transmission routes. However, such non-independence should not be problematic for this study since the focus is at the parasite community level. Instead, interactions between parasite infections can be thought of as a partial mechanism by which altering host behavior resulted in community level shifts.

RACCOON SOCIALITY:

Provisioning with clumped resources increased the level of social interaction and degree of spatial overlap among raccoons. Previous to the perturbation, raccoons were not entirely asocial, as occasional communal denning occurred in both sites primarily during the winter, presumably as a thermoregulatory strategy (Seidensticker et al. 1988). Two to four animals were found denning together at a time; this is probably an underestimate of actual denning group size since raccoons without radiocollars could have been present in these dens. In order to detect a communal den using radio telemetry it is necessary that at least two of the denning animals be radiocollared. Thus our ability to find communal dens was limited by the small sample size and unequal sex ratios of animals radiocollared in any particular winter. Other investigators have encountered similar logistical difficulties associated with winter tracking; however published raccoon

studies that have incorporated year-round monitoring have reported communal denning of some kind.

Consequently, it is likely that winter communal denning occurs more frequently than the data here suggest. If communal denning is a thermoregulatory strategy than there is no reason a priori to assume that the need for such a strategy should differ between the two sites. Although data is sparse, it is assumed that the incidence of communal denning occurs at an equal frequency in each site. Thus, while there was already some level of social interaction in the study populations, provisioning still resulted in increased social interaction in the experimental site, resulting in a shift from a largely solitary, low-contact life style to a life style with increased proximity among hosts and a higher concentration of raccoon activity in a localized area over a greater portion of the year.

IMPLICATIONS FOR WILDLIFE DISEASE ECOLOGY:

The observed shifts in the parasite community happened rather rapidly in response to a relatively low level perturbation over a short period of time. Provisioning began in May 2001, yet animals ceased utilizing the resources in the fall due to the increased availability of acorns. The last fecal samples included in this study were collected that fall indicating that the effects of the perturbation were observed relatively quickly. This effect may be even more pronounced in extreme or marginal habitats where animals are particularly reliant on clumped resources over longer periods.

Provisioning with clumped resources achieved a localization of raccoon activities over a small area. Consequently, spatial overlap was highly concentrated even though any particular raccoon may not have come into direct contact with all of the conspecifics

in the population. As such, the area around the feeding stations can be thought of as being highly contaminated compared to other areas due to the high amount of raccoon traffic. Re-use of highly contaminated areas has been shown to result in increased disease transmission (e.g. Freeland 1976, Barclay 1988), and may be a partial mechanism through which shifts in parasitism occurred in this study.

A similar effect may occur in areas where raccoon and human distributions overlap, since raccoons achieve their highest densities in residential and other human-dominated landscapes, partially because of the abundance of clumped resources. The impacts of anthropogenic landscape changes on wildlife disease is not well known. It is presumed, however, that habitat alteration, destruction, and fragmentation impact disease emergence as these changes affect host movement and density (Dobson and May 1986, Daszak et al. 2001). It has even been suggested that human environmental modification may be the most significant driver of emerging infectious zoonotic diseases (Daszak et al. 2001). The results reported here support the hypothesis that human impacts which alter resource availability may have implications for disease transmission, as exemplified by the case of *Baylisascaris procyonis*.

Concern has been mounting over the threats posed by *B. procyonis* as an emerging zoonosis, with several authors warning that the risk of human exposure and infection may be higher than currently recognized (e.g. Kazacos and Boyce 1989, Sorvillo et al. 2002). While *B. procyonis* is benign in raccoon hosts, severe or fatal neurologic disease has been documented in over 50 species of mammals including humans (Kazacos 2001). Eleven human cases of *B. procyonis* infection have been reported to date, with eight in children under 10 years of age, and four resulting in

fatalities (Huff et al. 1984, Fox et al. 1985, Kazacos and Boyce 1989, Sorvillo et al. 2002). *B. procyonis* has also been implicated in the decline of the threatened Allegheny woodrat as raccoon populations have increased in woodrat habitats, a process facilitated by human encroachment (Balcom and Yahner 1996).

In this study, a substantial increase in the prevalence of *Baylisascaris procyonis* occurred in response to utilization of clumped resources by raccoon hosts, with prevalence increasing from 0% to 44.4% within the experimental site. Significant increases were also observed in *Placoconus lotoris* and *Capillaria procyonis*. However, the increase in *B. procyonis* is of particular interest because of its potentially detrimental effects on other wildlife, domestic animals, and human populations. Given the abundance and high density of raccoons in and around human habitation, and their utilization of clumped resources such as dumpsters in these habitats, these results suggest that similar increases in prevalence of *B. procyonis* may exist in these habitats.

This phenomenon may occur generally in wildlife living in close association with humans. For example, aggregations of birds at backyard bird feeders in residential areas have led to the emergence of bacterial disease and mycoplasmal conjunctivitis because of increased host density, contact rates, and species diversity at feeders (Hartup et al. 1998, Kirkwood 1998). Similarly, Rubin et al. (2002) found that bighorn sheep in urban habitats had higher parasite prevalence than a non-urban subpopulation due to smaller core activity areas and repeated use of selected areas.

The results reported here support the hypothesis that intraspecific variation in parasitism can be accounted for by intraspecific variation in degree of social interaction, as community level shifts in parasitism were observed in response to increased sociality

among raccoon hosts. Parasite life cycle and transmission dynamics may be important determinants of the strength and direction of this relationship. These results also have implications for the transmission of raccoon parasites in and around human habitation, and indicate that human impacts that modify resource availability may directly influence disease transmission in a broad range of taxa through similar mechanisms. Future research which utilizes a similar experimental approach while assessing a wide variety of parasites and other diseases will further elucidate the importance of resource availability and host social structure in disease transmission as it pertains to the evolution of sociality, conservation biology, and human health.

Appendix IA: Average weight, head body length, tail length, and neck curcum for animals trapped in GH by sex, age, and season.

Site	Sex	Age	Season	n	Weight (kg)	Head Body Length (cm)	Tail Length (cm)	Neck Curcum (cm)
GH	F	Adult	Fall	4	5.9			
				4		63.4		
				4			23.1	
				2				24.8
GH	F	Adult	Summer	13	4.6			
				10		57.7		
				11			24.8	
				4				23.0
GH	F	Juvenile	Fall	5	3.6			
				5		53.1		
				5			20.5	
				1				24.0
GH	F	Juvenile	Summer	4	3.5			
				4		55.4		
				4			23.6	
				3				21.0
GH	M	Adult	Fall	3	7.0			
				4		65.9		
				4			23.3	
				0				0
GH	M	Adult	Summer	17	5.5			
				17		62.4		
				17			25.2	
				6				23.8
GH	M	Juvenile	Fall	6	3.3			
				7		50.1		
				6			22.3	
				1				18.5
GH	M	Juvenile	Summer	5	3.9			
				5		60.5		
				5			23.9	
				2				20.8

Appendix IB: Average weight, head body length, tail length, and neck curcum for animals trapped in JP by sex, age, and season.

Site	Sex	Age	Season	n	Weight (kg)	Head Body Length (cm)	Tail Length (cm)	Neck Curcum (cm)
JP	F	Adult	Fall	4	5.7			
				4		59.9		
				4			20.6	
				0				0
JP	F	Adult	Summer	11	4.6			
				9		55.8		
				10			22.9	
				2				24.0
JP	F	Juvenile	Fall	1	3.9	54.0	19.0	0
JP	F	Juvenile	Summer	3	3.6			
				1		52.0		
				3			23.3	
				1				21.0
JP	M	Adult	Fall	8	6.9			
				7		66.7		
				7			21.0	
				0				0
JP	M	Adult	Summer	11	6.0			
				7		65.3		
				10			23.2	
				4				23.6
JP	M	Juvenile	Fall	3	3.8			
				1		53.0		
				3			23.5	
				1				24.0
JP	M	Juvenile	Summer	3	4.3			
				2		27.8		
				3			21.3	
				0				0

Appendix IIA: Summary of den characteristics for 162 raccoon dens found in Black Rock Forest

Den characteristics		Percentage of dens
Den Type (n=162)		
	Rock	45.1%
	Tree	40.1%
	Unidentified	14.8%
Type of Tree Den (n=65)	Exposed on branch	32.3%
	Inside hole/hollow	67.7%
Tree Species (n=65)	Oak (*Quercus sp.*)	26.1%
	Maple (*Acer sp.*)	32.3%
	Unidentified	41.5%
Scats found near dens (n=162)		23.5%
Slope (n=28)	S	7.1%
	SW	28.6%
	SE	35.7%
	NW	3.6%
	NE	3.6%
	W	10.7%
	E	10.7%

Appendix IIB: Den characteristics by site and season

		Den type				Direction of Slope							
Site	Season	# Rock Dens	# Exposed Tree Dens	# Dens in Tree Holes/ Hollows	# Unknown Den Type	S	SW	SE	W	NE	E	NW	#Dens with Scats
JP	Summer	28	Oak 2 Maple 0 Other 3	3 1 9	7	1	2	2	3				14
JP	Fall/ Winter	22											2
GH	Summer	23	Oak 7 Maple 5 Other 4	5 15 11	14	1	6	8		1	2	1	20
GH	Fall/ Winter	3					2	2					

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