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Altered parasite assemblages in raccoons in response to manipulated resource availability

Abstract The role that host aggregation plays in structuring parasite assemblages was examined by experimentally increasing the contact rates of raccoons, *Procyon lotor*. Two populations of raccoons in southern New York were monitored for 2 years to determine baseline levels of host interaction and to identify the parasite assemblage. In the third year of the study, one population was provisioned with the addition of clumped food resources, while the other was provisioned with equal quantities of dispersed food resources. Remote photography showed that raccoons aggregated at clumped resources but not at dispersed resources, and therefore contact rates between individuals were higher in the site with clumped resources. There were no differences in parasitism between the sites prior to resource augmentation. Among ectoparasites, there were no significant changes in the prevalence or abundance of any species in response to the perturbation. In contrast, across the endoparasite assemblage within and across hosts, the prevalence of infection increased as a result of increased host contact. Strong increases in the prevalence of a few directly transmitted species and slight increases among most species lead to increased evenness in parasite prevalence, suggesting that parasites in this system are transmission limited. In addition, the number of parasite species per host (the parasite infracommunity) was higher in the clumped-resource population. These endoparasite results suggest that intraspecific variation in the species richness of parasite communities of individual hosts, and the prevalence of parasitic species in host populations as assessed across entire parasitic assemblages, is robustly influenced by intraspecific variation in the degree of host contact. Further, these results suggest that anthropogenic changes which alter resource availability may have important consequences for disease transmission in wildlife.

Keywords Community structure · Resource manipulation · Contact rates · Disease transmission · *Baylisascaris procyonis*

Introduction

Parasites and diseases can have dramatic affects on individual hosts and host populations, with repercussions for processes occurring at the community level (Anderson and May 1979; Moore 2001; Mouritsen and Poulin 2002). However, hosts can affect parasites at several scales as well. For example, individual hosts may alter their behavior to minimize the possibility of infection by parasites, and once infected, to minimize or eliminate parasitic infections (Kiesecker et al. 1999). At the level of host populations, fluctuations in host numbers can result in the loss of parasite populations as contact rates between infected and susceptible individuals drop below thresholds allowing parasite persistence (Freeland 1979; Anderson 1991). Given that individual hosts may harbor multiple species of parasites, and the broader assemblage of parasites found within an entire population of hosts is even more diverse, how do changes in host population ecology influence communities of parasites?

For many parasites, transmission is dependent on the rate at which individual hosts come into contact with

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one another. Host contact rates can be influenced by an array of variables such as habitat quality, host behavior, and local carrying capacity (Anderson and May 1979, 1991; Anderson et al. 1981). Consequently, contact rate is difficult to quantify, leading many investigators to use social structure or degree of sociality as a proxy for contact rate. Cross-species comparative analyses suggest that parasites can exert selective pressures on host social structures (Davies et al. 1991; Hochberg 1991) and intraspecific studies generally show positive correlations of host group size, number of parasite species per host, and infection intensities (Keymer and Read 1991; Møller et al. 1993). The fundamental underpinning of these relationships is increased contact within host aggregations allowing increased opportunities for parasite transmission among hosts.

If host contact plays a fundamental determinative role in the dynamics of parasite populations, then ecological factors that alter host contact should influence the structure and diversity of parasite assemblages. It is unlikely that increasing contact rates between hosts will uniformly increase the prevalence (percentage of hosts infected; Bush et al. 1997) of all parasites found in the community, as the transmission of many parasitic species is indirect and mediated by intermediate hosts, and for some species the relationship between host aggregation and parasitism may be inverse due to dilution or detection effects (Rubenstein and Hohmann 1989; Mooring and Hart 1992; Côté and Gross 1993). Nonetheless, we predict that a shift in a host population from a low-contact lifestyle to a higher contact lifestyle will cause the prevalence of parasitic species in the community across all hosts to increase overall, with this change driven by increased prevalence of direct-transmission species. At the same time, increased prevalence at the host community level should translate to increased species richness within individual hosts.

To explore the synergism between parasite assemblages and the behavioral ecology of the host, we experimentally manipulated raccoon (*Procyon lotor*) contact rates while simultaneously examining a broad array of their parasites. One way to manipulate host contact rates is to alter the timing, quantity, and distribution of resources, as in many species there is a close relationship between resource availability and animal aggregation (Carr and Macdonald 1986). While often considered solitary, raccoons exhibit a high degree of social flexibility, and aggregations of individuals form in response to localized resource availability (Gehrt and Fritzell 1998; Totton et al. 2002). By provisioning a host population with clumped resources we increased raccoon aggregation size, and thus contact rates. Monitoring a diverse group of parasites at two organizational scales before and during the manipulation allowed us to test the following hypotheses: (1) species richness within individual hosts (the parasite infracommunity) will increase and (2) the prevalence of parasites across the entire host population (the parasite component community) will increase with increased host contact.

Materials and methods

Study site and host organism

Field work took place at Black Rock Forest, a 1,500 ha reserve in the Hudson Highlands of southern New York near Cornwall and West Point, which is part of a larger, heavily forested region of protected state and federal lands. The forest is mixed-hardwood deciduous, dominated by oaks (*Quercus* spp.), maples (*Acer* spp.), beech (*Fagus grandifolia*), and birch (*Betula* spp.). Wetlands, lakes and ponds occur throughout the forest, thus water is probably not a limiting resource for raccoons.

Raccoons were trapped and monitored from two neighboring populations (Glycerine Hollow and Jim's Pond), each inhabiting areas of ca. 4 km^2 each, and delineated by watershed boundaries, reservoirs, and rocky outcrops. Glycerine Hollow is a watershed located in the southeastern part of the forest while Jim's Pond encompasses the southwestern portion of the forest. No evidence of animals moving between the sites was observed during the study through either trapping or radio-telemetry. Over the course of the study, there were slight increases in the densities of both populations, but there were no significant differences in the sizes of the populations across sites, suggesting that the addition of clumped resources (as described later) did not influence population size (M.E. Gompper and A.N. Wright, in press).

Permanent traplines were established in each site by placing box traps (no. 207.5 Tomahawk live-traps) at 100 m intervals along 2.5 km stretches of forest roads. Trapping occurred for 2–4 weeks/site every summer and every fall (two times per year) over the course of the study (3.5 years). A total of 84 raccoons were trapped and processed during 2,082 trap nights between summer 1999 and summer 2002. Raccoons were anesthetized and ear-tagged, allowing data collection on age (from tooth wear, body size, reproductive status, and capture history), weight, basic morphology, and overall health and reproductive condition. Thirty-eight adult raccoons were radio-collared, with telemetry efforts designed for collection of feces from den sites and to assess whether animals were sharing dens.

Parasitology: data collection

Ectoparasites were sampled by standardized collection with a flea comb in ten strokes along an animal's back from the base of the neck to the base of the tail, followed by examination under a dissecting microscope. Animals were also checked visually for the presence of ectoparasites. Numbers of lice, fleas, replete (engorged with blood) ticks, and non-replete ticks were recorded as an estimate of ectoparasite abundance (the number of individuals of a particular parasitic species on a single host; Bush et al. 1997). A distinction was made between

replete and non-replete ticks because replete ticks may be a better indicator of long-term parasitism since they have been on the animal for a longer period; e.g., in the case of adult *Dermacentor variabilis*, ca. 7–10 days (Allan 2001).

Endoparasites were identified from fecal samples found in traps with known individuals and from fresh (<12-h old) feces found at den sites of known, radio-located animals. Latrines, which are common elsewhere (e.g., Page et al. 1998), were rarely found in Black Rock Forest. Samples were immediately stored in 10% formalin. Qualitative analyses to identify endoparasite species present in each sample were conducted by fecal floatation using standard sugar and zinc sulfate centrifugation techniques (Bowman 1999). All endoparasite identification was performed by personnel at the Cornell University Veterinary Diagnostic Laboratory, Ithaca, NY, USA. Using ova identification to determine the infection status of an individual host is sometimes problematic because of temporal variation in ova output. For this study this was less of a concern because multiple samples/individual (mean $\pm$ SE $= 2.23 \pm 0.32$; range $= 1$–15) were collected, sampling of the sites occurred at similar times within and between years, and cross-site sampling strategies were identical. Thus, for the comparisons we make, the risk of false negatives is approximately equivalent at both sites during any given sampling period.

Resource manipulation experiment

From summer 1999 to summer 2002 animals were trapped and monitored via telemetry in both sites. In summer 2001, resource manipulation commenced. Glycerine Hollow was provisioned with clumped food resources (to induce spatial aggregation) while Jim's Pond was provisioned with equal quantities of dispersed food resources (to control for feeding the animals without influencing spatial aggregation, as described hereafter). Thus the dispersed-resource site is not a perfect (i.e., un-manipulated) control, however, our experimental design allows for temporal (before and after provisioning), and spatial (clumped-resource experimental site vs. dispersed-resource quasi-control site) comparisons. Two feeding stations were established in the clumped-resource experimental site, each with a large pile of cracked corn (~11 kg/station) maintained ad libitum. The dispersed-resource control site was provisioned with equal amounts of corn placed in multiple small stations (0.5 kg/pile) along the trap-line. Analyses of morphometric data collected from trapped animals and denning data collected from radiocollared animals indicate no cross-site differences in body size or in contact rates away from the feeding stations (i.e., no increase in communal denning) as a function of the experimental design (Wright 2002; unpublished data).

Resource visitation by raccoons was monitored with CamTracker II motion-sensitive infrared still cameras which were checked weekly for the duration of the experiment. In the experimental site, each feeding station had a single camera permanently focused on the corn. The dispersed-resource control site was monitored by randomly circulating nine cameras throughout the site. Each camera station was baited once with cat food and moved to another randomly selected location once triggered. During these periods, cat food was also added to the feeding stations in the clumped-resource site such that the quantity of added food was always equal for both sites. This design controlled for effects of feeding without inducing host aggregation since the food available at any one feeding station in the control site was small in quantity and temporally and spatially unpredictable.

We scored photos for the number of adult raccoons and the number of adults plus cubs. In the fall it became difficult to differentiate cubs and adults, and cubs often foraged alone. Thus fall and winter analyses treated all raccoons as adults. Most raccoons were not individually recognizable, and so independence of photographs was difficult to assess. We used a time lag of 60 min to differentiate independent photographs; for each photograph examined, all other photographs within ± 60 min were treated as non-independent, with aggregation size quantified as the maximum number of individuals observed in the photographic series. Mann–Whitney U tests were used to assess differences in aggregation sizes between sites.

Parasitology: data analyses

To test whether the number of individual ectoparasites per host (abundance) changed with increased host contact, we used repeated measures ANOVA (Stewart-Oaten et al. 1986; Smith 2002). Since sites were sampled twice per year for 3.5 years there are seven sampling periods which were treated as a random factor nested within (i.e., the sampling period occurred in) the time before or after the perturbation began. In cases where the same individual was sampled repeatedly in a particular sampling period the mean number of ectoparasites observed for that individual during that period was used.

For both ectoparasites and endoparasites, we tested whether the richness of parasite species within hosts (the parasite infracommunity) changed with increased host contact. We used unpaired t tests to compare the mean number of parasite species per raccoon in each site before and after the perturbation began. In cases where one individual was sampled several times in a particular year its fecal sample results were pooled such that the maximum number of species was recorded to represent the parasite fauna of that animal for the year.

To test whether the prevalence (percentage of hosts infected) of individual parasite species changed with increased host contact, we used χ^2 or Fisher's exact tests

(depending on sample size) to compare the prevalence of individual parasite species before and after the perturbation in each site. Because there were three analyses per parasite species (control site before vs. after; experimental site before vs. after; control site after vs. experimental site after), we use a Bonferroni correction to set $\alpha = 0.05/3 = 0.017$. Thus values of $P < 0.017$ are deemed significant, and values of $0.05 > P > 0.017$ are deemed approaching significance.

At the parasite assemblage level, we were interested in how the prevalence of all endoparasite species in an entire host population changed with increased host contact. For this component community-level comparison, we used paired t tests where the paired comparisons were between the prevalence of endoparasite species present in at least one of the groups being tested. Non-parametric univariate kernel density curves were used to visualize changes in the prevalence of the parasite component community.

Results

Host aggregations

Mean aggregation size at the clumped resources in the experimental site was significantly larger than in the control population, regardless of whether cubs were excluded or included in the analyses (Fig. 1). A total of 890 photos were obtained from the experimental site

from two feeding stations, and 44 photos were taken in the control site from 47 stations. Although there were more cameras operating in the control site, fewer photos were obtained than in the experimental site since the small quantities of bait would disappear as soon as the site was visited by an animal, and so only one photograph per site was included per analysis. Excluding cubs, animals in the control site were always solitary, while in the experimental site the range of adults per photo was 0–5 (experimental site: mean $\pm$ SE $= 1.44 \pm 0.03$, $n = 442$, $P = 0.001$). Including cubs, the range of aggregation sizes in the control site was 1–5, and in the experimental site was 1–8 (control site: 1.14 ± 0.15, $n = 26$; experimental site: 1.85 ± 0.06, $n = 451$; $P < 0.001$).

Ectoparasites

Over the course of the study 84 raccoons were captured and examined for ectoparasites on 115 occasions. Most hosts were infected by ectoparasites, primarily *D. variabilis* ticks, for which the raccoons are a principal host (Fish and Dowler 1989), as well as lice (*Trichodectes octomaculatus*) and fleas (*Chaetopsylla lotoris*). Due to variation in susceptibility of individual raccoons to the anesthetic, data sets for ten capture events were incomplete; 79 hosts were thoroughly and simultaneously examined for each of ticks, fleas and lice on 105 occasions. From the later group, 91% of hosts were infected
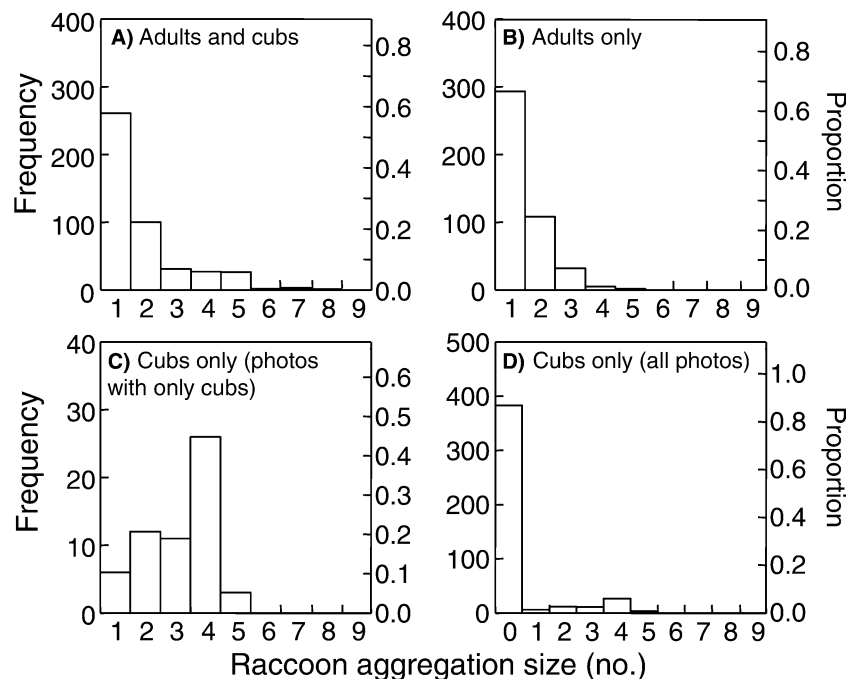

Fig. 1 Distribution of raccoon (*Procyon lotor*) aggregation sizes at the clumped-resource feeding stations in the experimental site. Y-axes represent numbers of independent photographs taken per aggregation size and relative frequency of each aggregation size. **a** Adults and cubs combined ($n = 451$ photographs); **b** adults only ($n = 449$ photographs); **c** cubs only, excluding photographs where no cubs were observed ($n = 58$ photos); **d** cubs only, including photographs with 0 cubs ($n = 451$ photos). Note different scales in the panels

by one or more species of ectoparasite, and the percentage of hosts infected with 1, 2, and 3 species of ectoparasite was 43%, 36% and 12%, respectively.

There were no differences in the mean number of ectoparasite species per host across the sites or over time in response to the perturbation (mean $\pm$ SE: control before 1.46 ± 0.14; control after 1.44 ± 0.19; experimental before 1.62 ± 0.16; experimental after 1.55 ± 0.15). Additionally, there were no significant differences (χ^2 tests; $P > 0.017$ for each comparison) observed in ectoparasite prevalence before or after the perturbation in either site (Table 1).

Ectoparasite abundance varied post-perturbation, however none of the changes in the abundances of the ectoparasite species were significant (Table 1; Electronic Supplementary Material S1). The abundance of lice increased dramatically in the Fall 2001 experimental population following the perturbation, with mean abundance approximately ten times greater than in the control site during that season, and more than double the abundance found at either site during any other period (Fig. 2). This increase relative to the control site was not, however, sustained into 2002 (Electronic Supplementary Material S1). For ticks there was a significant (MS = 78.3, $F_{1,5}$ = 13.8, $P = 0.006$) intra-period effect which was primarily a function of patterns of seasonal abundance of non-replete ticks (MS = 46.4, $F_{1,5}$ = 30.9, $P = 0.001$).

Endoparasites

Fecal samples ($n = 129$) from 59 known raccoons and 14 unknown raccoons in known localities, yielded 14 species of endoparasites, with 13 species identified from each site (Table 2). Individual raccoons harbored 0–7 endoparasite species (infracommunity richness), and this number was significantly influenced by the experi-

mental perturbation. Excluding the experimental site after resource addition, the mean ($\pm$ SE) number of parasite species per host was 1.43 ± 0.21, with no significant differences as a function of site or timing (Fig. 3). Given the lack of significant differences in endoparasite infracommunity richness in the control site between years, these results were pooled (control before + control after = control all) for comparisons with the experimental site (control before 1.167 ± 0.45; control after 1.87 ± 0.29; $t = 1.374$, $df = 39$, $P = 0.177$; Fig. 3). After the start of resource additions, infracommunity richness in the experimental site doubled relative to the control populations to 2.86 ± 0.29 (Fig. 3). This value was significantly greater than that of both the control site (control all 1.56 ± 0.26, $t = 3.351$, $df = 75$, $P = 0.001$) and the experimental site before perturbation (experimental before 1.07 ± 0.36, $t = 3.515$, $df = 49$, $P = 0.0008$; Fig. 3).

Across the entire endoparasite assemblage, there were no significant differences in the prevalence of endoparasites when examined within the control population (control before vs. control after: $t = -1.048$, $df = 12$, $P = 0.315$), or when examined between the sites excluding the post-perturbation experimental population (control all vs. experimental before: $t = -1.614$, $df = 12$, $P = 0.133$). In contrast, endoparasite prevalence in the experimental site was significantly higher after the commencement of clumped resource augmentation compared to the control population (control all vs. experimental after: $t = -2.860$, $df = 13$, $P = 0.013$) and compared to the period prior to resource augmentation (experimental before vs. experimental after: $t = 3.205$, $df = 12$, $P = 0.008$). Fitting the distributions of prevalence levels across the component-community with kernel density curves reveals an increased evenness in the prevalence distribution following clumped resource augmentation in the experimental site (Fig. 4).

Table 1 Summary of ectoparasite prevalence (percentage of hosts infected out of the total examined) and abundance (mean $\pm$ SE number of individual parasites per host) in both sites before and after resource augmentation

	Control before		Control after		Experimental before		Experimental after	
	Prevalence	n	Prevalence	n	Prevalence	n	Prevalence	n
Fleas (*C. lotoris*)	46%	26	52%	25	57%	21	67%	33
Lice (*T. octomaculatus*)	35%	26	24%	25	19%	21	24%	33
Ticks (*D. variabilis*)	68%	28	77%	26	82%	27	65%	34
Replete ticks	54%	28	46%	26	56%	27	41%	34
Non-replete ticks	68%	28	62%	26	74%	27	59%	34
	Abundance	n	Abundance	n	Abundance	n	Abundance	n
Fleas (*C. lotoris*)	0.77 ± 0.31	26	0.48 ± 0.25	25	0.38 ± 0.20	21	0.33 ± 0.11	33
Lice (*T. octomaculatus*)	2.08 ± 0.59	26	2.40 ± 0.92	25	3.48 ± 0.88	21	5.88 ± 1.36	33
Ticks (*D. variabilis*)	8.43 ± 1.91	28	5.58 ± 1.33	26	6.41 ± 1.22	27	4.68 ± 1.17	34
Replete ticks	2.36 ± 0.69	28	1.35 ± 0.40	26	1.11 ± 0.27	27	1.74 ± 0.70	34
Non-replete ticks	6.07 ± 1.44	28	4.23 ± 1.11	26	5.30 ± 1.03	27	2.94 ± 0.93	34

Fig. 2 Variation in mean abundance of lice (no. of individual lice/host + 1SE) for control (*open bars*) and experimental (*filled bars*) sites over the course of the study (S summer, F fall). Resource addition began in summer 2001 (S2001)
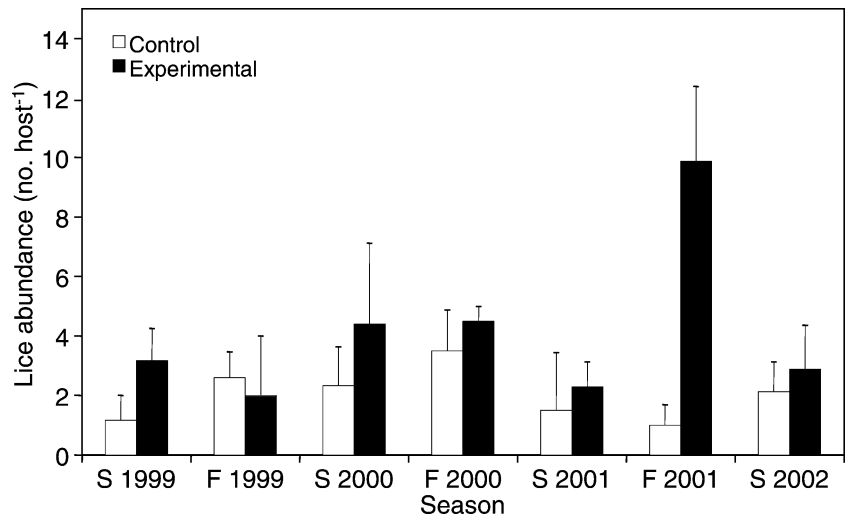

Table 2 Prevalence (percentage of hosts infected) of endoparasites within experimental (E) and control (C) populations, before (B) and after (A) resource augmentation, and significance values (*P*) for Fisher exact tests for comparison between treatments. Sample sizes (*n*) are numbers of individual hosts examined. C-all = CB + CA. Comparisons for which $P \leq 0.05$ are highlighted in bold, and species for which one or more comparisons differed by $P \leq 0.017$ are indicated with an asterisk

Parasite	Prevalence (% hosts infected)					Fisher's exact tests (*P* values)			
	EB (*n*=15)	EA (*n*=36)	CB (*n*=18)	CA (*n*=23)	C-all (*n*=41)	CB vs. CA	EB vs. EA	EA vs. CA	EA vs. C-all
Helminths									
Trematodes									
Alaria sp.	0.0	0.0	0.0	4.3	2.4	>0.999	NA	0.3898	>0.999
Digenea sp.	6.7	0.0	5.6	0.0	2.4	0.439	0.2941	NA	>0.999
Eurytrema procyonis	0.0	2.8	0.0	0.0	0.0	NA	>0.999	>0.999	0.4675
Nematodes									
*Baylisascaris procyonis**	0.0	44.4	0.0	17.4	9.8	0.1177	**0.0019**	**0.0482**	**0.0007**
Capillaria aerophilia	0.0	2.8	16.7	4.3	9.8	0.303	>0.999	>0.999	0.3638
Capillaria plica	0.0	11.1	5.6	13.0	7.3	0.6178	0.3067	>0.999	0.6993
Capillaria procyonis	0.0	30.6	5.6	39.1	24.4	**0.0251**	**0.0216**	0.5777	>0.999
Capillaria putorii	26.7	41.7	16.7	21.7	19.5	>0.999	0.3599	0.1608	**0.0465**
Crenosoma sp.	6.7	22.2	5.6	13.0	9.8	0.6178	0.2514	0.5017	0.2077
*Placoconus lotoris**	0.0	27.8	5.6	4.3	4.9	>0.999	**0.0216**	**0.0375**	**0.0097**
Strongyles sp.	13.3	0.0	5.6	0.0	2.4	0.439	0.0824	NA	>0.999
Acanthocephalans									
Macracanthorhynchus ingens	0.0	13.9	5.6	13.0	9.8	0.6178	0.3047	>0.999	0.7264
Protozoans									
Coccidians									
Eimeria nutalli	20.0	41.7	22.2	21.7	22.0	>0.999	0.2025	0.1608	0.0851
Eimeria procyonis	33.3	47.2	22.2	39.1	31.7	0.321	0.5361	0.5988	0.2415

Assessing the 14 species of endoparasites individually, two increased significantly in prevalence following the experimental addition of clumped resources (Table 2). *Placoconus lotoris* increased from 0–6% in populations without aggregations (control before, control after, and experimental before) to 28% in the experimental population post-perturbation (Table 2). Similarly, *Baylisascaris procyonis*, which was absent in both populations prior to resource augmentation and occurred in 17% of the control population after resource augmentation ($P=0.118$), increased to 44% prevalence in the experimental population ($P=0.002$). There was also a weakly significant increase in the prevalence of *Capillaria putorii* in the experimental site after the addition of resources ($P=0.047$). A fourth species, *Capillaria procyonis*, showed a weakly significant increase in prevalence at both sites over the course of the study (control site before vs. after $P=0.025$; experimental site before vs. after $P=0.022$). No other significant changes in prevalence of individual species were identified. Independent of the significance of change in individual parasites, and across all species, in the experimental site 11 species increased and two decreased in prevalence after the perturbation, while in the control site eight species increased and five species decreased in prevalence.

Fig. 3 Mean (± 1SE) number of endoparasite species per host (infracommunity richness) for control (*open circles*) and experimental (*filled circles*) sites before and after the start of resource augmentation. Infracommunity richness in the experimental population after resource addition increased significantly relative to both spatial and temporal controls
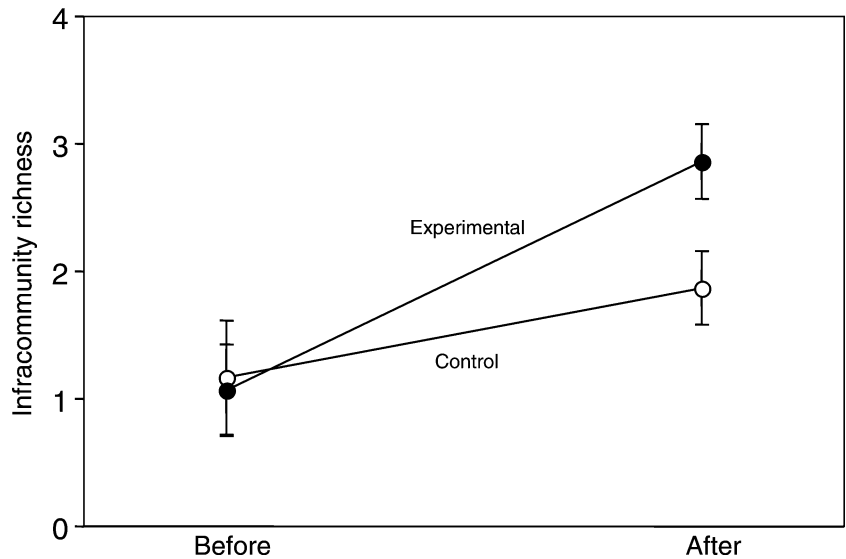
Fig. 4 Distribution of prevalence levels of endoparasitic species (*n* = 14) across all hosts (the component community) from the experimental site (subdivided into **a** before and **b** after resource augmentation periods) and **c** the control site (all years combined). **d** Three data sets (control site, experimental site prior to resource addition, and experimental site after resource addition) fitted with non-parametric univariate kernel density curves
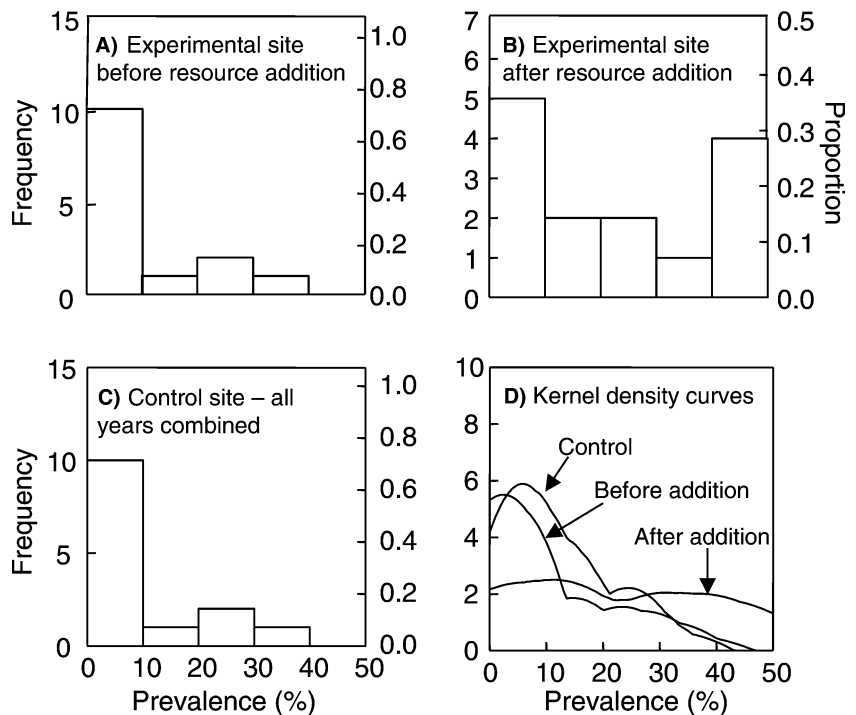
Discussion

We observed a rapid, complex response by the parasite fauna to increased host aggregation. While no significant changes were seen among the ectoparasite species, there was a doubling of the number of endoparasite species per raccoon (within-host parasite assemblage), and an increase in endoparasite prevalence across the entire endoparasite assemblage (among all hosts). Thus individual hosts were more likely to have multispecies infections when contact rates increased, and those multispecies infections involved a greater number of parasitic species. From a parasite perspective, endoparasite species within hosts became members of more diverse communities (the parasite infracommunity), and across hosts, endoparasites became members of a more evenly distributed community (the component community) as a result of enhanced contact rates.

Changes in the endoparasite assemblage were a function of slight increases in the prevalence of many species, and strong increases in a few species. Of the species observed in the experimental site during the

study, 11 increased after the perturbation, while only two decreased. As a result, the endoparasite assemblage became more even, with fewer species found at low prevalence levels ($<15\%$ prevalence) and more species found at higher prevalence levels ($>30\%$ prevalence). These increases in prevalence as well as the doubling in infracommunity richness suggest that it is unlikely that strong interspecific interactions were excluding parasites from particular hosts. Rather, these findings imply that the low prevalence of many species prior to manipulation is at least partly due to lack of transmission opportunity, i.e., that parasites are transmission-limited in this system.

Of the two endoparasite species that showed significant increases in prevalence after perturbation of the experimental site, one is directly transmitted by ingestion of the parasite or vertical transmammary transmission (*P. lotoris*), and one is directly transmitted through fecal-oral contact (*B. procyonis*). Increased prevalence of *C. putorii*, which is likely transmitted indirectly through ingestion of intermediate earthworm hosts, was also observed, although the level of support in this case is weaker. The results of this study therefore indicate that changes that occur in parasite assemblages following increased host contact are driven primarily by strong shifts in a small number (here, ca. 15%) of directly transmitted species.

The mechanism(s) underlying the observed shifts in parasitism are unclear. However, provisioning with clumped resources achieved a localization of raccoon activities in a small area, and photographs of direct contact (including allogrooming) of individuals at the feeding stations implies that direct contact of hosts could be an important route underlying change in the parasite assemblage. Indirect transmission could also be occurring; the area around the feeding stations can be considered highly contaminated with fecal materials compared to other areas due to high raccoon traffic. Reuse of highly contaminated areas can result in increased parasite transmission (Barclay 1988; Lewis 1996), and may be another mechanism contributing to the shifts in endoparasites observed here.

While variation in ectoparasitism was observed over the course of the study, patterns similar to those seen for endoparasites were not detected. Given the different types of pressures associated with life inside and outside the host, in combination with the small number of ectoparasite species examined in depth, it is perhaps unsurprising that similar patterns were not observed. It may be that the population and community dynamics of ectoparasites occur over much different temporal and spatial scales than endoparasites, and consequently our experimental design was more appropriate for detecting patterns in the latter. Therefore, and despite the logistic efforts it would require, future studies of the sort presented here should consider increasing the duration of the experimental perturbation and the manipulation of multiple sites.

Humans purposely or accidentally manipulate resources for many species, and in some human-domi-

nated habitats a subset of species such as raccoons can occur at very high densities. If increased density or increased contact rates lead to increased disease transmission, then these habitats could become flash points for epizootics among subsidized species (Hartup et al. 1998; Daszak et al. 2000; Childs et al. 2001). Understanding how resource manipulations indirectly influence pathogen transmission and parasite community structure may give novel insights into how habitat alteration that leads to the expansion of subsidized species may also alter the disease ecology of the species. For instance, the changes observed in this study occurred in a region of older second growth forest that is currently minimally disturbed by humans. Raccoons achieve their highest densities ($>>50/km^2$; Prange et al. 2003) in residential and other human-dominated landscapes, partially because of the abundance of clumped resources such as human refuse. In these regions one might expect changes in the structure of raccoon parasite communities to occur that are similar to those observed in this study. Although the impacts of anthropogenic landscape changes on wildlife disease are poorly understood, it is presumed that habitat fragmentation and alteration influence disease emergence and dynamics as these changes affect host movement, density, and interspecific contact (Daszak et al. 2000). The results reported here support a general hypothesis that intraspecific variation in the size and structure of parasite assemblages among individual hosts or host populations can in part be accounted for by intraspecific variation in degree of host contact, suggesting that human impacts that alter resource availability may also indirectly alter disease transmission.

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