Effects of resource availability and social aggregation on the species richness of raccoon endoparasite infracommunities

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Within populations the contact rate of hosts and infectious parasites is mediated by the interactions of resource availability, host density, and host behavior. Fluctuations in host density can result in the loss or extinction of a parasite population as contact rates between parasites and susceptible individuals drop below thresholds of parasite population persistence. Less understood is how changes in resources and the behavioral ecology of host populations affect parasites. We used food provisioning to experimentally assess the effects of resource availability and of inducing host aggregation on the endoparasite community of free-ranging raccoons. Twelve independent raccoon populations were subjected to differential resource provisioning for two years: a clumped food distribution to aggregate hosts (n = 5 populations), a dispersed food distribution to add food without aggregating hosts (n = 3), and a no food treatment (n = 4). Remote cameras indicated that aggregation sizes were three to four times greater in aggregated versus non-aggregated populations. We considered endoparasites with direct and indirect life cycles separately and determined the best-fit models of parasite species richness in relation to host aggregation, food supplements, and host age and sex. Social aggregation had a negligible impact on the species richness of directly or indirectly transmitted parasites. However, food additions decreased the number of indirectly transmitted parasite species by 35% in the oldest age classes. These results suggest that while resource availability can influence the transmission of indirectly transmitted parasites, an examination of additional factors will be necessary to understand the role of host contact and factors that shape the community structure of endoparasites in natural environments.

Parasite transmission within animal populations depends on the rate at which hosts come into contact with each other or the infectious stage of a parasite. Contact rates are mediated by resource availability and population density (Anderson et al. 1981), but relationships between host sociality, food resources, and parasite burden are difficult to quantify in free-ranging populations and are continually influenced by a wide range of factors, including host and parasite behavior, the ecological constraints and life history of each parasite, host demographics, and environmental conditions (Anderson and May 1991, Möller et al. 1993, Krasnov et al. 2002, Wilson et al. 2002). Attempts to address this complexity have resulted in a large number of comparative studies that assess host–parasite relationships between different host species. In contrast, few studies have examined the role of host or ecosystem attributes on parasite species richness within species (the parasite component community and infracommunity). There is a need to better understand this dynamic relationship, as generalized cross-species trends do not adequately describe and can contradict the known ecological relationships that may occur within a host population (Poulin 1997, Poulin and Mouillot 2004). In particular, consistent patterns of endoparasite species richness among mammal species have been shown to depend on the scale of study and ecology of individual hosts (Bordes and Morand 2008). Surprisingly, few studies have employed experiments to determine the intrinsic ecological relationships between a mammalian host and their endoparasite species richness in a natural setting.

Comparative studies have found that host traits such as longevity, size, social organization, density and life history can all correlate with parasite component community richness (Gregory 1997, Morand et al. 2000, Stanko et al. 2002, Nunn et al. 2003, Ezenwa et al. 2006). For example, among mammals, host density is positively correlated with parasite abundance and prevalence across a range of taxa (Arneberg et al. 1998). This makes intuitive sense as rates of contact frequently increase with density and result in greater parasite transmission. While such findings are important, they primarily inform our understanding of stable host–parasite relationships across multiple species and are limited in their ability to predict how alterations in the behavioral ecology of individual hosts will affect parasite communities in a particular ecosystem. For example, when examining a single host species within a site or region, one is asking a fundamentally different question – do alterations in contact or density within a particular species alter the parasite species richness of a population? Furthermore, how does any such relationship compare in importance to other host characteristics that may also influence the species richness of parasites, such as host sex or age? Such assessments are essential to understand.
the predominant factors that control parasite transmission and parasite species richness among host populations in their natural settings.

Here we examine factors that influenced endoparasite species richness of raccoons Procyon lotor. We considered two measures of species richness by evaluating parasites with direct and indirect life cycles separately. Those with direct life cycles are transmitted directly between raccoons via close contact or contact with feces or fomites. Some directly transmitted parasites can also be transmitted indirectly through a different host, although this is not required. Parasites with indirect life cycles must infect at least one additional host (often a prey species such as an insect or gastropod) before they can infect raccoons and complete their development and reproduction. Previous studies have observed only endoparasites with direct life cycles to correlate with, or respond to, changes in the behavioral ecology or density of hosts (Altizer et al. 2003, Wright and Gompper 2005). Indirect parasites are generally not thought to be as sensitive to alterations or behavioral differences in host ecology because they are constrained by an additional intermediate host.

Our objective was to experimentally assess the effects of food resources and social aggregation on endoparasite prevalence and species richness. The experimental design consisted of a clumped food distribution to aggregate hosts, a dispersed food distribution that added the same amount of food but did not aggregate hosts, and a no food treatment. Food additions and aggregation were predicted to affect parasites with direct and indirect life cycles in a different manner. Many comparative studies have suggested that the diversity of food intake, food resources, and differing levels of social contact can impact the prevalence and abundance of parasites (Kuris et al. 1980, Pacala and Dobson 1988, Poulin 1995, Gregory 1997, Morand et al. 2000, Altizer et al. 2003, Nunn et al. 2003, Ezenwa et al. 2006). We hypothesized that parasite species richness of directly transmitted species would increase in aggregation treatments due to higher contact between hosts and infected feces near areas of aggregation. However, we expected the number of indirectly transmitted species to decline in aggregated treatments, and in food-augmented populations, because it would decrease the need to search for other food sources, including alternative hosts that are necessary to obtain indirectly transmitted species.

Material and methods

Study design

Raccoons were sampled from March to November in 2006 and 2007 at 12 sites in central Missouri, USA. All sites were located on forested state, federal, or university conservation or research areas within 60 km of Columbia, Missouri. Sites consisted of second growth oak Quercus spp. and hickory Carya spp.) forest with a maple Acer spp. and cedar Juniperus virginiana understory. Sites were considered independent of each other; over the course of four years we marked > 700 individuals and none were recaptured at any of the other study sites (Monello and Gompper 2010).

Sites were assigned to differential resource provisions for two years: a clumped food pile to aggregate hosts (n = 5 aggregated populations), a dispersed food distribution to control for the effects of food without aggregating hosts (n = 3 control with food), and a no food treatment (n = 4 control without food). Treatments were assigned randomly to sites within geographically defined site subsets that were used to assure that treatments were interspersed. The aggregated sites were maintained by placing 35 kg of dried dog food in the same location each week. Control with food sites were provisioned by placing food in multiple 0.25 kg piles (~140 week⁻¹) that were randomly located throughout each 4 km² study site. All provisions were maintained from January through September in 2006 and 2007.

Remote film cameras were used to monitor feeding station use, rates of contact, and raccoon aggregation sizes in treatment and control sites with and without food. One camera was maintained from January to August at each permanent feeding station in aggregated sites. Five cameras were maintained in control sites with and without food for 10-15 days during both the spring and summer. Cameras were placed in front of a small pile of food (control with food) or bait (control without food) and relocated every five days. Aggregation size was recorded as the maximum number of raccoons, excluding cubs, observed per night at each site. We assigned a categorical variable for short-term contact while at the feeding station of 0 (no contact within the ca 16m² camera range) or 1 (contact with conspecifics within the range) (Gompper and Wright 2005). Instantaneous contact rates were assessed for each site by quantifying the percent of camera days with photos that had > two raccoons, excluding cubs.

We calculated population density of each site by estimating adult population size in 2007 using closed population models in Popan-5 (Arnason and Schwarz 1999), and divided these values by the effective trapping area (Kenward 1985). We estimated the effective trapping area by multiplying the linear length of the trapline by a buffer of ∼2 of the annual home range of raccoons (Kenward 1985) from a subset of the sites in this study (Wehtje and Gompper 2011). We used the residuals from a linear regression of body mass on body size to assess the relative body condition of each individual (Schulte-Hostedde et al. 2005), with higher values indicating better body condition.

Raccoons were trapped for >10 days at each site three times per year between March and November. Tomahawk traps were baited with mackerel and checked daily. Raccoons were immobilized with ketamine hydrochloride and xylazine (Evans 2002), tagged with metal ear tags, weighed, sexed and aged by body size, genital morphology, and tooth eruption and wear (Grau et al. 1970). Animals were categorized into one of four age classes; I = 5–14 months, II = 15–38 months, III = 39–57 months, or IV = over 58 months. We rarely detected endoparasites in cubs (<5 months; Monello 2009) and they were not included in our analyses.

Fresh feces was collected from within or below traps, homogenized, and stored in 10% formalin. Endoparasite ova and oocysts were identified by standard fecal floatation procedures using sugar and zinc sulfate centrifugation techniques (Bowman 1999). Only one sample per animal was included in this study. When multiple samples of an individual were obtained due to recapture events, one sample was randomly selected for analysis. Although using additional
samples may give a more accurate parasite species richness index for an animal, we did not include them because it would have resulted in a disproportionately larger sampling effort for animals that were recaptured. We assumed that by using one sample per individual and sampling each area with equal effort across seasons, the likelihood of finding parasites in fecal samples would be equal across all individuals, sites, and treatments.

**Model selection**

We used information-theoretic model selection to evaluate the ability of treatments and host characteristics to explain the species richness of directly and indirectly transmitted parasites. To assess the importance of these factors on parasite infracommunities, we developed 13 candidate models that included aggregation, food supplementation, year, and host age and sex. The factors food and aggregation were considered separately to compare their relative importance. Year was only included when significant model effects were found (p < 0.05). Factor selection and a priori model formulation for experimental sites was based on previous findings from single parasite species and comparative studies of parasite species richness (Wilson et al., 2002), as well as data that indicated host age and sex to be important to the parasite burden of free-ranging raccoons (Monello and Gompper 2007, 2009, 2010).

We used generalized linear models with a normal distribution for model selection; previous work on this data indicated that endoparasite species richness was normally distributed for parasites with both direct (skewness = 0.155 ± 0.179; kurtosis = -0.493 ± 0.356) and indirect life cycles (skewness = 0.345 ± 0.179; kurtosis = -0.029 ± 0.356) (Monello 2009). We conducted a goodness-of-fit test to assess the ability of model factors to explain endoparasite species richness by comparing the global model against the intercept-only model (Franklin et al. 2000). We proceeded with model selection procedures only if global models provided a better fit than intercept-only models (α = 0.05). We calculated Akaike’s information criterion (corrected for small sample size; AICc) and ranked the models based on differences between the best approximating model and all other models (ΔAICc) in the candidate set. Models with a ΔAICc value ≤2 of the best-fitting model were considered to have empirical support as a best-fitting model. To better assess model structure and factors, we calculated the overdispersion parameter of the best-fit model for each ectoparasite species, model weight (i.e., the relative likelihood that a particular model is the best-fit model) and model-averaged estimates and odds ratios (± 95% CI) for each variable in the 90% confidence set of models (Σmodel weights >0.90; Burnham and Anderson 2002).

**Results**

Aggregation size of adult raccoons was greatest in sites with the permanent feeding stations (Kruskal–Wallis H = 230.948, DF = 2, p < 0.001; aggregated > control sites with food > control sites without food, all comparisons p < 0.006 based on Mann Whitney U-test), with up to 10 individuals simultaneously visiting the food plots in aggregated sites (mean number of individuals per photo ±95% confidence interval (CI); control without food = 1.00 ± 0.00; control with food = 1.16 ± 0.06; aggregated = 3.22 ± 0.19). Instantaneous contact rates for adults were 80% in aggregated sites (n = 358), 15% in control with food sites (n = 149), and 0% in control without food sites (n = 43). Individual opossums Didelphis virginiana were the only other animal that consistently used the food piles (>5% of camera nights), and this only occurred in the aggregated sites.

Raccoon density did not differ among treatments (Kruskal–Wallis H* = 1.10, DF = 2, p = 0.576), averaging 20.0 ± 4.9 (SE) in control without food sites (range 15.3 to 22.8, n = 4), 23.7 ± 5.1 in control with food sites (range 19.9 to 27.1, n = 3), and 22.0 ± 5.8 in aggregated sites (range 8.8 to 31.6, n = 5). Supplemental food increased the weight and improved the relative body condition of female raccoons (mean body condition ± 95% CI; control without food = -0.54 ± 0.21; control with food = -0.17 ± 0.16; aggregated = 0.03 ± 0.15), but no differences were observed among males (control without food = 0.26 ± 0.25; control with food = 0.40 ± 0.27; aggregated = 0.35 ± 0.17).

We observed 16 endoparasite species from 289 individual raccoons sampled during 2006–2007 (Table 1). The most common parasites were a capillarid roundworm Capillaria procyonii (prevalence = 86–90%) and the intracellular parasite Eimeria nutalli (prevalence = 81–91%). Five parasites detected in this study have been confirmed to reproduce in raccoons and have direct life cycles (E. nutalli, E. procyonii, Placoconus lotoris, Molinesus barbatus and Baylisascaris procyonii). We considered these five species to be directly transmitted and all other species to be indirectly transmitted. Of the

Table 1. Prevalence (% infected) of endoparasites detected among raccoons in control, control with food, and aggregated sites (n = number of individual raccoons).

<table>
<thead>
<tr>
<th>Parasite Species</th>
<th>Control (n = 93)</th>
<th>Control w/food (n = 89)</th>
<th>Aggregated (n = 107)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Directly transmitted parasites</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eimeria nutalli*</td>
<td>81%</td>
<td>91%</td>
<td>88%</td>
</tr>
<tr>
<td>Placoconus lotoris</td>
<td>39%</td>
<td>36%</td>
<td>29%</td>
</tr>
<tr>
<td>Molineus barbatus*</td>
<td>43%</td>
<td>42%</td>
<td>31%</td>
</tr>
<tr>
<td>Eimeria procyonii*</td>
<td>35%</td>
<td>55%</td>
<td>50%</td>
</tr>
<tr>
<td>Baylisascaris procyonii</td>
<td>9%</td>
<td>16%</td>
<td>20%</td>
</tr>
<tr>
<td>Indirectly transmitted parasites</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Capillaria procyonii</td>
<td>90%</td>
<td>87%</td>
<td>86%</td>
</tr>
<tr>
<td>Capillaria puttor*</td>
<td>51%</td>
<td>51%</td>
<td>42%</td>
</tr>
<tr>
<td>Eurytrema procyonii*</td>
<td>52%</td>
<td>21%</td>
<td>25%</td>
</tr>
<tr>
<td>Capillaria plica*</td>
<td>25%</td>
<td>30%</td>
<td>23%</td>
</tr>
<tr>
<td>Crenosoma spp.*</td>
<td>23%</td>
<td>22%</td>
<td>14%</td>
</tr>
<tr>
<td>Physaloptera spp.*</td>
<td>15%</td>
<td>9%</td>
<td>19%</td>
</tr>
<tr>
<td>Atrotaenia procyonii*</td>
<td>1%</td>
<td>1%</td>
<td>1%</td>
</tr>
<tr>
<td>Maccacanthorhynchus ingens*</td>
<td>2%</td>
<td>2%</td>
<td>3%</td>
</tr>
<tr>
<td>Crazia spp.*</td>
<td>1%</td>
<td>1%</td>
<td>1%</td>
</tr>
<tr>
<td>Sarcocystis spp.*</td>
<td>0%</td>
<td>2%</td>
<td>0%</td>
</tr>
<tr>
<td>Alaria spp.*</td>
<td>1%</td>
<td>0%</td>
<td>0%</td>
</tr>
</tbody>
</table>

remaining 11 endoparasites, nine are known to only have an indirect life cycle, and two have unknown life cycles in raccoons (C. procyonis and Cruzia spp.). We considered both of these species to have indirect life cycles. When C. procyonis and Cruzia spp. were classified as directly transmitted, support for the model results reported below only increased. Thus, the classification of parasites and corresponding results of this study should be considered conservative.

Three of five directly transmitted parasite species declined in the presence of raccoon aggregation (Table 1; E. nutalli, P. lotorii and M. barbatus). Among the directly transmitted parasite species that increased due to aggregation, Fisher’s exact comparisons (with a Bonferroni correction factor) indicated there were no significant increases in prevalence (control vs aggregation treatments; B. procyonis p = 0.029, E. procyonis p = 0.045). Several indirectly transmitted parasite species exhibited declines when food was added (e.g. E. procyonis, Crenosoma spp., C. puttori; Table 1); however, only E. procyonis exhibited a statistically significant decline due to aggregation and food supplementation (control vs food supplementation or aggregation; E. procyonis p < 0.001, all other species and treatment comparisons p > 0.140; Table 1).

### Model selection

Goodness-of-fit tests that compared species richness in global and intercept-only models found a significant difference for parasites with a direct (likelihood ratio $\chi^2 = 39.217$, $DF = 7$, $p < 0.001$) and indirect life cycle (likelihood ratio $\chi^2 = 16.550$, $DF = 6$, $p = 0.011$). Year of sample collection had significant model effects on parasites with direct ($\chi^2 = 26.576$, $DF = 1$, $p < 0.001$) but not indirect life cycles ($\chi^2 = 0.126$, $DF = 1$, $p = 0.72$), and was therefore only included in model selection procedures of directly transmitted parasite species (Table 2). The mean number of directly transmitted parasite species was greater in 2007 (mean $\pm 95\%$ CI: 2.52 $\pm$ 0.17, $n = 140$) than 2006 (1.91 $\pm$ 0.16, $n = 149$), whereas the number of indirectly transmitted parasite species was similar in 2006 (2.40 $\pm$ 0.22, $n = 149$) and 2007 (2.46 $\pm$ 0.20, $n = 140$).

The best fit models of directly transmitted parasite species richness ($\Delta$AIC$_c$, of 0–2) all included age (Table 2; overdispersion of best-fit model $= 1.021$). Model averaged estimates and odds ratios indicated that age class III had $\sim 30\%$ greater species richness of directly transmitted parasites in the first year of the experiment (Table 3, Fig. 1a), but this effect only occurred in sites with food additions (Fig. 1b). When age class III was examined by treatment in 2006, results indicate the increased in species richness of directly transmitted parasites primarily occurred in aggregated sites (mean $\pm 95\%$ CI: aggregated $= 3.10 \pm 0.53$, $n = 10$; control with food $= 2.30 \pm 0.83$, $n = 10$; control without food $= 2.07 \pm 0.67$, $n = 13$). These differences were not apparent in the second year of the experiment (2007), as species richness of endoparasites with direct life cycles increased across all age classes compared to 2006 (Fig. 1a).

The best fit models of indirectly transmitted parasite species ($\Delta$AIC$_c$, of 0–2) included all four factors (age, sex, food, aggregation) from the a priori model set (Table 2). The top model was age + food, with a model weight of 0.438 and overdispersion parameter of 1.018. Model averaged estimates and odds ratios indicated age class I and sites with food had 30–40% fewer indirectly transmitted parasite species (Table 3).

The role of age and food additions on indirectly transmitted species richness is best understood when considered together. In control sites with no food additions, age classes I and II had the lowest number of parasites and their 95% CI overlapped little with the larger number of parasites supported by age classes III and IV (Fig. 1c). Conversely, the number of indirectly transmitted parasite species was similar among all age classes of animals that inhabited sites with food, while the age classes III and IV exhibited divergent patterns in sites with versus without food (Fig. 1c). The lower species richness among older age classes in sites with food was primarily due to aggregated sites (mean $\pm 95\%$ CI of ages III and IV combined: aggregated $= 2.18 \pm 0.34$, $n = 44$; control with food $= 2.57 \pm 0.36$, $n = 47$; control without food $= 3.17 \pm 0.39$, $n = 48$).

### Discussion

Parasite species richness of raccoons was relatively high and consistent across the 12 sites in this study. Photo analyses indicated that the permanent food piles effectively increased the co-occurrence and group size of raccoons in the aggregated sites, and that this effect did not occur in the control sites with and without food. Yet despite increases in rates of contact and localized use of the permanent food piles by hosts, aggregated populations did not exhibit any increase in endoparasite species richness. Conversely, food supplementation decreased the richness of indirectly transmitted endoparasites, particularly among the oldest age classes of hosts that harbored the most parasites.

Alterations in resource availability led to a decline in the number of indirectly transmitted parasite species per raccoon. Assessments of mean parasite species richness indicated that animals from the aggregated category were the primary
Table 3. Model averaged estimates and odds ratios of parameters included in the 90% confidence set of models used to estimate the number of directly and indirectly transmitted endoparasite species among raccoons in control, control with food, and aggregated sites (2006–2007).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Model averaged estimate</th>
<th>Unconditional SE</th>
<th>Odds ratio</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Directly transmitted parasites</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year (2006)</td>
<td>–0.521</td>
<td>0.115</td>
<td>0.570</td>
<td>0.454</td>
<td>0.716</td>
</tr>
<tr>
<td>Age II (15–38 months)</td>
<td>–0.228</td>
<td>0.165</td>
<td>0.781</td>
<td>0.551</td>
<td>1.088</td>
</tr>
<tr>
<td>Age III (39–57 months)</td>
<td>0.293</td>
<td>0.156</td>
<td>1.392</td>
<td>1.003</td>
<td>1.932</td>
</tr>
<tr>
<td>No food</td>
<td>–0.113</td>
<td>0.085</td>
<td>0.807</td>
<td>0.633</td>
<td>1.031</td>
</tr>
<tr>
<td>Sex (female)</td>
<td>0.011</td>
<td>0.035</td>
<td>1.046</td>
<td>0.831</td>
<td>1.317</td>
</tr>
<tr>
<td>No aggregation</td>
<td>0.002</td>
<td>0.023</td>
<td>0.968</td>
<td>0.763</td>
<td>1.228</td>
</tr>
<tr>
<td>Indirectly transmitted parasites</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Age I (5–14 months)</td>
<td>–0.3627</td>
<td>0.236</td>
<td>0.639</td>
<td>0.408</td>
<td>1.002</td>
</tr>
<tr>
<td>Age II (15–38 months)</td>
<td>–0.1676</td>
<td>0.186</td>
<td>0.811</td>
<td>0.548</td>
<td>1.204</td>
</tr>
<tr>
<td>Age III (39–57 months)</td>
<td>0.1990</td>
<td>0.204</td>
<td>1.272</td>
<td>0.833</td>
<td>1.942</td>
</tr>
<tr>
<td>No food</td>
<td>0.2803</td>
<td>0.193</td>
<td>1.456</td>
<td>1.063</td>
<td>1.994</td>
</tr>
<tr>
<td>Sex (female)</td>
<td>0.0004</td>
<td>0.041</td>
<td>0.999</td>
<td>0.742</td>
<td>1.344</td>
</tr>
<tr>
<td>No aggregation</td>
<td>0.0170</td>
<td>0.041</td>
<td>1.236</td>
<td>0.909</td>
<td>1.681</td>
</tr>
</tbody>
</table>

1The parameters year (2007), age (IV), sex (male), food and aggregation were redundant and set to 0 in model averaged estimates and 1 in odds ratios.

Driver of such effects. However, odds ratios from model selection procedures indicated that the addition of food was more important. This apparent discrepancy is due to the moderate declines in the number of indirectly transmitted parasite species in control with food sites (vs aggregated food sites) and can be resolved by considering the implications of food dispersal; aggregated food piles were large and predictable in location, whereas dispersed food piles were small and unpredictable. Raccoons in aggregated treatments were able to travel directly to the same spot to obtain food, while those in control with food sites still had to search for food. Thus, the likelihood of coming into contact with and consuming intermediate hosts that harbor infectious parasites was lower for raccoons in aggregated versus control with food sites. Two alternative explanations are also plausible. First, increased nutrition can decrease susceptibility to parasitism (Ezenwa 2004, Hines et al. 2007). We consider this unlikely to underlie the patterns observed in this study because similar declines in species richness were not observed among directly transmitted parasites. Further, only female body condition improved in sites with food additions (Monello and Gompper 2010). Second, food or social aggregations could alter the distribution of intermediate hosts. This is also unlikely because such effects would be localized in aggregated sites (where the primary decline of indirectly transmitted parasite species occurred); food plots were less than 5 m in diameter and visibly altered areas were less than 20 m in diameter (Monello unpubl.). Thus, a decline in the diversity of diet is the most plausible reason for the observed decline in species richness of parasites with indirect life cycles.

Species richness of parasites with a direct life cycle was generally not altered by treatments. The only notable difference was that animals in age class III displayed greater species richness of directly transmitted parasites in aggregated sites during the first year of the experiment (based on 95% CI). It is unclear why this would occur only in age class III animals, and these results may be due to a type II error associated with a large number of comparisons. Overall, the lack of differences among the treatments do not concur with other research that has found increases in parasite burdens in fed or aggregated populations (Wright and Gompper 2005, Hines et al. 2007). However, the interaction between aggregation and population density has not been well studied. Monello and Gompper (2010) found a directly transmitted louse species responded to host aggregation by becoming less abundant due to a dilution effect that lowered per capita infestation levels among males. In contrast, a tick species that does not rely on host contact for transmission became more abundant on hosts because they can detect and seek out hosts and were more likely to drop off after obtaining a blood meal and re-attach to raccoons in the areas near the feeding stations. Such counterintuitive results suggest that many parasitic species can interact in unique ways with their hosts that are inconsistent with generally accepted expectations derived from an understanding of transmission mechanisms. Alternatively, animals in this study may be exposed to infectious parasites at a relatively high rate and aggregation cannot further increase many of the parasites that are transmitted fecal-oral. Such a conclusion is consistent with Prange et al. (2004), who found that raccoons in high density populations do not temporally segregate themselves from each other and suggested that, even in the absence of social aggregation, such populations are at risk for greater parasite transmission.

The fluke Eurytrema procyonis declined due to the addition of food and was the only parasite that exhibited statistically significant differences between treatments. This suggests the intake of intermediate hosts for this parasite, which include grasshoppers and snails, declined to a greater degree or made up a larger part of the raccoon diet than other intermediate hosts in this study (Carney et al. 1970). It is also noteworthy that the prevalence of B. procyonis was twice as great in aggregated versus control populations. Although this difference was not statistically significant when a Bonferroni correction was conducted, the findings here are consistent with previous research that found greater rates of contact or localized concentrations of raccoons may facilitate transmission of this parasite (Gompper and Wright 2005).
Figure 1. Average number (± 95% CI) of parasite species detected per raccoon (n = 289). (a) Directly transmitted parasite species in 2006 (filled circles) and 2007 (open circles). (b) Directly transmitted parasite species at sites with food (open circles; note this includes aggregated and control with food sites) and without food (control; filled circles). (c) Indirectly transmitted parasite species in sites with food (open circles; note this includes aggregated and control with food sites) and without food (control; filled circles).

These results further emphasize the need to consider parasite life cycles when infra- and component community processes are examined. Distinct differences were apparent in this study when parasites with direct and indirect life cycles were considered separately. Further research is needed to determine the effects of experimentally increased rates of contact or social aggregation among a variety of species and populations. The results of this study suggest the outcome among infracommunities may largely depend on ecosystem properties that determine animal contact, such as host spacing patterns and host feeding diet ecology.

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