Differential effects of experimental increases in sociality on ectoparasites of free-ranging raccoons

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Summary

1. Parasite transmission depends on the rate at which hosts come into contact with one another or the infectious stages of parasites. However, host contact rates and their influence on parasite transmission are difficult to quantify in natural settings and can fluctuate with host behaviour and the ecological constraints of parasites.

2. We investigated how experimental increases in rates of contact and social aggregation affected ectoparasite prevalence and intensity of free-ranging raccoons (Procyon lotor). Twelve independent raccoon populations were subjected to differential resource provisions for 2 years: a clumped food distribution to aggregate hosts (n = 5 aggregated populations), a dispersed food distribution to control for the effects of food without aggregating hosts (n = 3) and a no food treatment (n = 4).

3. Remote cameras indicated that aggregation sizes and rates of contact were three to four times greater in aggregated compared with that in non-aggregated populations. The number of ticks (adult Dermacentor variabilis) on raccoons in aggregated populations was 1.5–2.5 times greater from May to July, the primary time of tick seasonal occurrence. Conversely, louse (Trichodectes octomaculatus) populations were c. 40% sparser on male raccoons in aggregated (compared with that in non-aggregated) populations because of greater overdispersion of lice and a larger number of male hosts harbouring fewer parasites. No treatment-related differences were found among fleas (Orchopeas howardi).

4. These results were not consistent with our current understanding of parasite transmission; greater rates of host sociality led to increases in a parasite that does not rely on host contact for transmission (ticks) and declines in a parasite that depends on host contact for transmission (lice). We concluded that D. variabilis increased in aggregated sites 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 these locations. Several factors may have contributed to sparser louse populations on male hosts, including a dilution effect that lowered per capita infestation levels.

5. These results indicate that ectoparasites can interact in unique ways with their hosts that are not consistent with other types of parasite species or models of their transmission.

Key-words: host, infestation, mammal, parasite, wildlife

Introduction

Parasite transmission depends on the rate at which hosts come into contact with one another or with the infectious stages of parasites. This contact rate is generally viewed as influenced by habitat quality and population density (Anderson et al. 1981). Problematically, contact rates are difficult to quantify in natural settings and can fluctuate with host behaviour (Anderson & May 1991; Caley & Ramsey 2001). As a result, those interested in the general relationships between host characteristics, such as sociality and the probability of being parasitized, have used intra- and interspecific correlational analyses. For instance, cross-species studies suggest that parasites can exert selective pressures on host social structures (Davies et al. 1991; Hochberg 1991) and intraspecific studies generally show positive correlations between group size or density and the number of parasite species per host or parasite intensity (Keymer & Read 1991; Moller, Dufva & Allander 1993; Krasnov, Khokhlova & Shenbrot 2002). The general cause of these relationships may

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be increased contact within groups and, thus, increased opportunities for parasite transmission (Freeland 1979; Hoogland 1979; Moore, Simberloff & Freehling 1988; Poulin 1991; Côté & Poulin 1995; Porteous & Pankhurst 1998; Tella 1979; Moore, Simberloff & Freehling 1988; Poulin 1991). Sociality can result in decreased parasitism if group living allows more efficient vector-avoidance behaviours such as grooming, or if living with other potential hosts creates a dilution effect which decreases the chance of a particular individual being singled out by a vector or parasite (Duncan & Vigne 1979; Rubenstein & Hohmann 1989; Mooring & Hart 1992; Côté & Gross 1993; Gompper 2004; Fauchald et al. 2007; Vicente et al. 2007). In addition, some species may show density-dependent disease resistance or acquired immune resistance to particular parasites (Craig et al. 1996; Wilson et al. 2002). Furthermore, the evidence used to assess the relationship between social contact and parasitism is mainly correlational and the causal direction of this relationship is typically unknown. As some researchers suggest that some group size is limited by parasite abundance and impact on host fitness (Alexander 1974; Freeland 1976, 1979), the associated question of whether the shift from an asocial, low-contact lifestyle to a more social or high-contact lifestyle carries with it an increased parasite burden has not been examined intraspecifically (Møller et al. 1993).

Here we examined the relationship between ectoparasite intensity and rates of host contact in a natural setting. Specifically, we manipulated the contact rate and social aggregation among hosts that is intermediate between the predicted responses of ticks and lice.

Materials and methods

STUDY SYSTEM

Study sites (n = 12) were located on state or federal public lands within 60 km of Columbia, MO, USA. Sites consisted of second-growth oak (Quercus spp.) and hickory (Carya spp.) forest with a maple (Acer spp.) and cedar (Juniperus virginiana) understory. We considered all sites to be independent of one another, as we captured > 700 individuals with > 500 recapture events from 2005 to 2007, and no animals were observed to move between sites (Monello 2009).

Each site was assigned to one of three treatments in January 2006: a permanent feeding station receiving 35 kg/week of dog food at a single location to aggregate raccoons (n = 5 populations), highly dispersed distribution of the same quantity of dog food to control for the effects of food addition but not aggregate hosts (control with food, n = 3 populations) and a no food treatment (control without food, n = 4 populations). Treatments were assigned randomly within geographically defined subsets that were used to assure that treatments were interspersed and to control for unidentified regional effects. The control sites with food were provisioned by placing food in 0.25-kg piles (c.140 per week) that were randomly moved each week throughout a 4-km² portion of each study site. All provisions were maintained from January to September in 2006 and 2007.

HOST SAMPLING

Trampines of 15 pairs of Tomohawk box traps (30 in total) were established at each site. A single trap was placed c.50 m on each side of a 1-km transect, with adjacent traps spaced 75–100 m apart. Raccoons were trapped for ≥10 days at each site two to three times per year between March and November. Traps were baited with mackerel and checked daily. Raccoons were immobilized with ketamine hydrochloride and xylazine (Evans 2002), tagged, weighed, sexed and aged by body size, genital morphology and tooth eruption and wear (Grau, Sanderson & Rogers 1970). This resulted in five age classes: cub < 5 months; I: 5–14 months; II: 15–38 months; III: 39–57 months and IV+: > 57 months. Data from cubs, which were generally free of ectoparasites (Monello & Gompper 2007, 2009), and recaptured animals were not included in analyses.

Remote infrared film cameras (DeerCam DC-300; Non-Typical Inc., Green Bay, WI, USA) were used to monitor feeding station use, rates of contact and raccoon aggregation sizes in experimental (hereafter referred to as aggregated sites) and control sites. 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 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 5 days. All cameras were placed at c.0.5-m height on a tree near the food or bait. Aggregation size was recorded as the maximum number of raccoons, excluding cubs, observed per night in a single photograph at each site. Instantaneous contact rates (%) were assessed for each site by dividing the number of camera days with photographs that had ≥2 raccoons (excluding cubs) by the total number of camera days. We assigned a categorical variable for short-term contact while at the feeding station of 0 (no contact within the c.16-m² camera range) or
1 (contact with conspecifics within the range) (Gompper & Wright 2005).

As food additions may influence population density and body condition, and thus ectoparasites, we quantified population density and relative body condition. We calculated population density of each site by estimating adult population size in 2007 using closed population models in Popan-5 (Arnason & 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 tranpeline by a buffer of three fourths of the median summer home range of raccoons (Kenward 1985) from rural sites in Illinois (Prange et al. 2004), which were comparable to preliminary home range estimates from sites in this study (M. Wehtje, unpublished data). 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.

PARASITE QUANTIFICATION

Adults D. variabilis are relatively large (≥3 mm in length), occur seasonally in our study sites and are readily found on animals in the field without magnification (Monello & Gompper 2007). We quantified adult D. variabilis by a thorough search of the entire body. Analyses included only those tick counts that were conducted between April and August, which corresponds to the time period when adult ticks are present at all of our study sites and able to obtain a complete blood meal (Monello & Gompper 2007).

We quantified the relative abundance of lice and fleas via 10 strokes with a flea comb from the base of the neck to the base of the tail on the dorsal region of raccoons (Monello & Gompper 2009). Animals that were wet or muddy could not be combed and were excluded. Hair and ectoparasites were immediately placed in a plastic bag, sealed and frozen within 8 hours. In the laboratory, lice and fleas were identified to species and quantified under a dissecting scope.

Measures of parasitism follow Bush et al. (1997); prevalence was the percentage of hosts infested and intensity represents the population size of a parasite species among infested animals (i.e. animals without parasites are not included in measures of intensity). We used generalized linear models with a binomial distribution and logit transformation to determine whether the presence or absence (i.e. parasites) are not included in measures of intensity). We used generalized linear models with a binomial distribution and logit transformation to determine whether the presence or absence (i.e. parasites)

MODEL SELECTION – PARASITE INTENSITY

We used information-theoretic model selection to evaluate the ability of treatments, host characteristics and month to explain the intensity of each ectoparasite species. Model factors included aggregation, food supplementation, host age and sex and month of capture. *A priori* hypothesis and model formulation was based in part on the best-fit models from previous research that was conducted at these sites in the absence of experimental manipulations (Monello & Gompper 2007, 2009). We included aggregation and food supplementation as separate factors with the previously identified variables from the best-fit models and conducted separate analyses for each ectoparasite species (Table S1; available online). Intercept-only and global models were also included in model selection procedures for each ectoparasite. Year was not included as a factor because no significant model effects of year were found for any of the ectoparasite species (P ≥ 0.086 in all cases).

We used generalized linear models with a negative binomial distribution and log link for model selection (Wilson & Grenfell 1997; Hardin & Hilbe 2007). Ectoparasite intensity of individual raccoons was the sample unit. We conducted a goodness-of-fit test to assess the ability of model factors to explain ectoparasite intensity by comparing the global model against the intercept-only model (Franklin et al. 2000). For each ectoparasite species, we proceeded with model selection procedures only if global models provided a better fit than intercept-only models (P = 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 (AAICc) in the candidate set. Models with a AAICc value ≤2 of the best-fitting model were considered to have substantial empirical support as a best-fitting model. To better assess model structure, 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 & Anderson 2002).

Results

RACCOON AGGREGATION, BODY CONDITION AND DENSITY

Aggregation size of adult raccoons was the greatest in sites with the permanent feeding stations (Kruskal–Wallis H' = 230.948, d.f. = 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% 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 photos), 15% in control with food sites (n = 149) and 0% in control without food sites (n = 43). Photograph capture effort in the control with and without food sites (215–330 photograph nights per year per site) exceeded the aggregated sites (70–105 photograph nights per year per site) because cameras in the aggregated sites always ran out of film (but not food) within 3 days.

Raccoon density did not differ among treatments (Kruskal–Wallis H' = 0.50, d.f. = 2, P = 0.778), averaging 29 ± 7.3 (SE) in control without food sites (range 22–33.6, n = 4), 34.8 ± 7.6 in control with food sites (range 29–35.2, n = 3) and 32.3 ± 8.50 in aggregated sites (range 12.9–46.4, 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).
ECTOPARASITE PREVALENCE

We captured and assessed parasites for 414 raccoons during 2006 and 2007 (mean number of individuals per site type ± SE: control without food: 25.8 ± 3.3, n = 103; control with food: 40.3 ± 3.3, n = 121; experimental: 38.0 ± 7.6, n = 190). The male : female capture ratio was similar in each treatment category during both years of the experiment (mean of both years ± SE: control without food: 1.1 ± 0.3, control with food: 1.2 ± 0.2, aggregated: 1.2 ± 0.1; contingency table Chi-squared test, \( P > 0.0521 \) across both years or within individual years). Prevalence of *D. variabilis* averaged 93 ± 2% (mean ± 95% CI; all estimates of data dispersion hereafter represent 95% CI) across all sites and did not differ between treatments (\( P > 0.0450 \) for all comparisons). The prevalence of lice did not differ because of treatment or treatment × month (\( P > 0.196 \) in both cases), but did exhibit a sex × treatment interaction (\( \chi^2 = 71.886, \text{ d.f.} = 3, \ P < 0.0001 \)). Pairwise comparisons of the sex × treatment interaction term indicated that male raccoons had a greater prevalence of lice than females regardless of treatment category (\( P < 0.0001 \) for all comparisons). Overall, almost 3× more male raccoons (71 ± 6%, \( n = 217 \)) harboured lice than females (28 ± 7%; \( n = 197 \)). However, even though prevalence of lice was lower among males in aggregated sites, there were no within-sex treatment differences detected for males or females (\( P > 0.185 \) for all within sex treatment comparisons). Prevalence of the flea *O. howardi* was 14 ± 3% overall and did not differ between treatments (\( P > 0.079 \) for all comparisons).

ECTOPARASITE INTENSITY

Infested animals in aggregated populations harboured more adult *D. variabilis* ticks (mean intensity: 36.4 ± 5.8, range 1–137, \( n = 127 \) animals) than those in control without food (22.6 ± 4.4, range 1–103, \( n = 81 \)) and control with food populations (24.1 ± 4.8, range 1–122, \( n = 87 \)). Maximum tick intensities were maintained from May to July in aggregated populations, whereas intensity in control populations with and without food increased through summer, peaked in July and consistently displayed a lower intensity than aggregated populations (Fig. 1).

Intensity of lice was lower in aggregated populations (control without food = 67 ± 21, \( n = 55 \); control with food = 70 ± 23, \( n = 56 \); aggregated = 50 ± 8, \( n = 94 \)). However, there were sex-specific treatment differences; female raccoons exhibited little difference in louse intensity among treatments, whereas males in aggregated populations had a lower intensity of lice than those in control with and without food populations (Fig. 2). The intensity of lice on male raccoons in aggregated treatments exhibited greater overdispersion (variance : mean = 12.999) than the intensity in control with food (variance : mean = 9.611) and control without food (variance : mean = 9.30) categories, with a greater number of male hosts in aggregated treatments harbouring fewer lice (Fig. 3). The intensity and distribution of lice on females were similar among treatments (Fig. 3).

Intensity of fleas did not exhibit any patterns among treatments (control without food: 1.8 ± 0.5, \( n = 16 \); control with food: 1.7 ± 1.2, \( n = 17 \); aggregated: 2.0 ± 0.6, \( n = 25 \)) or host sex (males = 2.0 ± 0.7, \( n = 37 \); females = 1.7 ± 0.6, \( n = 21 \)).

MODEL SELECTION

Goodness-of-fit tests that compared the global and intercept-only models found a significant difference for *D. variabilis* ticks (likelihood ratio Chi-square = 52.090, d.f. = 10, \( P < 0.0001 \)) and lice (Likelihood ratio \( \chi^2 = 32.188 \), d.f. = 14, \( P = 0.0004 \)). There were no differences between the global and intercept-only models for fleas (Likelihood ratio \( \chi^2 = 6.635 \), d.f. = 13, \( P = 0.920 \)) and so model selection analyses were not conducted for this species. The best-fit models for *D. variabilis* tick intensity were aggregation + month and aggregation + month + sex (Table 1; overdispersion parameter of best-fit model = 0.732). The combined weight of evidence for these two mod-
Ticks (intensity in non-aggregated populations was 0 indicated that aggregation increased tick intensity, as tick incidence of 0 documentmentation was the global model, which had a weight of evidence >0 these best-fit models, and all models with a weight of evidence underperformed compared with models with aggregation (Tables 1 and 2). Model-averaged estimates indicated that sex was the most important variable, with the intensity of lice on females being 0.32-0.64 times that of males when included in the model. Aggregation had the opposite relationship to that found with ticks, with non-aggregated populations having louse populations that were denser than that on aggregated populations (Table 2).

Discussion
We observed large shifts in ectoparasite intensity because of increased host contact and aggregation. The direction and magnitude of these effects were parasite specific and inconsistent with our original predictions. Tick intensity increased to maximum levels earlier in the season and was 1.5-2.5 times higher throughout their seasonal occurrence on animals in aggregated sites. Conversely, louse intensity was lower in aggregated sites and fleas exhibited no differences among treatments. Such findings suggest that the outcome of increases in host contact or aggregation is highly variable and depends on the host-parasite association in question. Other studies on ecto- and endoparasites have also attributed increases (Arneberg et al. 1998; Morand & Poulin 1998; Krasnov et al. 2002; Wright & Gompper 2005) and declines (Mooring & Hart 1992; Fauchald et al. 2007; Vicente et al. 2007) in macroparasite abundance or intensity to population density and group size, but to our knowledge this is the first study to examine such questions in an experimental manner across ectoparasite taxa within the same system and host.

Table 1. Ranking of models estimating intensity of ticks (adult Dermacentor variabilis) and lice (Trichodectes octomaculatus) on raccoons from sites subjected to aggregation and resource treatments

<table>
<thead>
<tr>
<th>Model</th>
<th>Log-likelihood</th>
<th>No. parameters</th>
<th>ΔAICc</th>
<th>AICc weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ticks (n = 295 raccoons)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(I_{\text{aggregation + month}})</td>
<td>-1270.31</td>
<td>6</td>
<td>0.00</td>
<td>0.46</td>
</tr>
<tr>
<td>(I_{\text{aggregation + month + sex}})</td>
<td>-1269.87</td>
<td>7</td>
<td>1.21</td>
<td>0.25</td>
</tr>
<tr>
<td>(I_{\text{aggregation + month + age}})</td>
<td>-1268.87</td>
<td>9</td>
<td>3.46</td>
<td>0.08</td>
</tr>
<tr>
<td>(I_{\text{aggregation + food + month + age + sex}})</td>
<td>-1266.82</td>
<td>11</td>
<td>3.65</td>
<td>0.08</td>
</tr>
<tr>
<td>(I_{\text{food + month + sex}})</td>
<td>-1271.23</td>
<td>7</td>
<td>3.93</td>
<td>0.07</td>
</tr>
<tr>
<td>Lice (n = 205 raccoons)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(I_{\text{aggregation + sex}})</td>
<td>-577.50</td>
<td>3</td>
<td>0.00</td>
<td>0.54</td>
</tr>
<tr>
<td>(I_{\text{sex}})</td>
<td>-579.33</td>
<td>2</td>
<td>1.61</td>
<td>0.24</td>
</tr>
<tr>
<td>(I_{\text{food + sex}})</td>
<td>-578.87</td>
<td>3</td>
<td>2.75</td>
<td>0.14</td>
</tr>
</tbody>
</table>

Rankings are based on generalized linear models with a negative binomial distribution and log identity, and only models in the 90% confidence interval are shown.

attracted to CO2 plumes from the large, consistent host (Brunner & Ostfeld 2008). The intensity of lice was lower on males in aggregated sites, but no treatment differences were observed among females. Fewer lice on males in aggregated sites was because of greater overdispersion, which resulted in a larger proportion of hosts with sparser louse populations in comparison with non-aggregated sites (Figs 2 and 3). Smaller per capita parasitism in denser social groups (i.e. parasite dilution) has been observed in other studies, but these observations are primarily from ungulates and mobile ectoparasites that have a negligible population response, to greater host numbers (Côté & Poulin 1995; Fauchald & Hart 1992). Indeed, higher contact and aggregation are predicted to increase the prevalence and intensity of lice, which complete their life cycle within 30–40 days (Durden 2001) and should benefit from increased transmission opportunities. However, dilution could be responsible for the patterns observed in this study if it results in a greater number of smaller louse populations (because of increased transmission) that are less likely to persist or be detected with the methods used here.

These findings indicate that even in the absence of density alterations, host social behaviour, contact and resource distribution can alter the infestation levels of directly transmitted ectoparasites. Thus, the interaction between host contact and ectoparasites appears to be considerably more complex than the current understanding, which is primarily based on models of endoparasite abundance (Anderson & May 1978; Dobson 1990).

There are several possible reasons for the increase in tick intensity in aggregated sites: ticks may seek out the established feeding areas; stationary raccoons may be more likely to be found and infested by questing ticks; and raccoons may be transporting ticks to the site where nymphs have a greater probability of dropping off, moulting and later re-infesting raccoons at the food plots. These hypotheses are non-exclusive and supported by other studies. Adult D. variabilis concentrate and focus questing behaviour in areas that exhibit greater wildlife and human activity (Burg 2001), and can move up to 100 m to reach such areas (Carroll & Nichols 1986). Dermacentor spp. are capable of detecting and seeking out sources of CO2 (e.g. Garcia 1965) and are probably attracted to CO2 plumes from the large, consistent host. Adult D. variabilis can over-winter or complete their entire life cycle in one summer in Missouri (Kollars et al. 2000), which probably contributes to the extended period of high infestation levels observed in aggregated sites. The importance of aggregation relative to other variables in this experiment suggests that changes in host social behaviour or space use can overshadow other factors that typically influence tick intensity, such as host age or sex (Monello & Gompper 2007). Higher tick intensities that are maintained at their maximum level for a longer period of time could also alter pathogen transmission between ticks and hosts, with the direction and magnitude of effect dependent on whether the host is an efficient reservoir for the pathogen (Brunner & Ostfeld 2008).
found no sex-related differences in the use of food plots (M. Wehtje, unpublished data).

No relationships were observed between fleas and treatment categories. One likely reason for this is that Sciurus spp. are the primary hosts of *O. howardi* (Durden 1980) and alterations to raccoon ecology may have little or no impact on the relatively low levels of prevalence and intensity observed in this study. This is consistent with previous work from these sites in the absence of experimental manipulations that found peak flea abundance during the spring but no other abiotic or biotic correlates of flea infestation (Monello & Gompper 2009; see also Durden 1980). It is also possible that fleas primarily reside and infest hosts in dens and resting sites, and thus increased social contact outside these settings has little influence on flea burden.

Results from this study suggest that parasite life-history characteristics — including route of transmission, ability to survive and travel off-host, and host specificity — are critical in predicting how ectoparasite populations will respond to alterations in host demographics or behavioural ecology. Models of directly transmitted endoparasites that predict a positive relationship between parasite abundance and host demographics or behavioural ecology. Models of directly transmitted endoparasites that predict a positive relationship between parasite abundance and host contact (Anderson & May 1978; Dobson 1990) have been found to fit some host-flea interactions (Krasnov et al. 2002). However, our results suggest that additional host-ectoparasite relationships need to be investigated prior to assuming such relationships for other ectoparasites. Ectoparasites are subjected to both environmental and host influences and exhibit vastly different constraints between taxa in terms of movement abilities, survival off-host, behaviour and routes of reproduction. Yet, even when such characteristics are taken into account, it is difficult to accurately predict the general response to host aggregation or contact rates. Ticks are not reliant on host contact or aggregation for successful infestation, yet in this study they displayed the greatest treatment-related differences, perhaps by their ability to seek out hosts and a life cycle that includes bouts of host detachment and attachment that probably moved them closer to aggregation sites. To elucidate such patterns among diverse host and parasite types, we emphasize the need for more empirical research on this topic in a manner that directly compares the responses of multiple parasite species.

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References


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**Supporting Information**

Additional Supporting Information may be found in the online version of this article.

**Table S1.** *A priori* hypotheses and corresponding models of ectoparasite intensity of raccoons subjected to aggregation and resource treatments (*β₀* is the intercept and *β_i*(*X*) are the parameters of independent variables). Model selection was conducted for each ectoparasite species and included global and intercept models. As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.